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Twelve new species of *Cyrtodactylus* Gray (Squamata: Gekkonidae) from isolated limestone habitats in east-central and southern Myanmar demonstrate high localized diversity and unprecedented microendemism

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Twelve new karst-adapted species of the gekkonid genus *Cyrtodactylus* Gray are described from the Shan Hills and Salween River Basin of Myanmar. Three species occur in rocky habitats along karst ridges and nine species are micro-endemics restricted to isolated karst caves and towers. This high, localized diversity underscores the archipelago-like nature and microendemism associated with karst habitat-islands. Eleven of the 12 new species are not related to other Indo-Burmese species and form four monophyletic species groups nested within a larger Indo-Chinese clade of Southeast Asian species. Phylogenetic relationships and distributions indicate *Cyrtodactylus* originated in the Himalayan uplands and dispersed westward through Myanmar with subsequent invasions back into eastern and southern Myanmar. These new species highlight the understudied nature of karst biodiversity in general and karst herpetology in particular. Extensive karst ecosystems throughout the massive Shan Plateau of eastern Myanmar remain largely unexplored and are likely to harbour tens—if not hundreds—of undiscovered species. The unique and complex structure of understudied limestone ecosystems throughout Southeast Asia are habitats in which amphibians and reptiles have specialized, speciated and become endemic. In an age of biodiversity crisis, managing and conserving these ecosystems throughout Southeast Asia should be given greater priority. A key to the species of *Cyrtodactylus* of Myanmar is provided.

ADDITIONAL KEYWORDS: biogeography – conservation – *Cyrtodactylus* – Indo-China – karst ecosystems – key – Myanmar – new species – Shan Hills – systematics.

INTRODUCTION

The gekkonid genus *Cyrtodactylus* Gray is by far the most diverse gekkotan lineage and, as has been repeatedly noted elsewhere, the rate at which new species are being described shows no sign of abating. Most species of *Cyrtodactylus* occupy habitats with an abundance of rocky substrates and many species have independently evolved varying combinations of suites of characteristics that are adaptive for living exclusively on rocks—either granite or limestone—and locomoting in all planes of orientation (Grismer *et al.*, 2015b, 2016a; Grismer & Grismer, 2017). Although *Cyrtodactylus* ranges from Pakistan to the

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western Pacific, the bulk of the newly discovered species come from limestone (karst) habitats in Laos, Vietnam, Thailand and Peninsular Malaysia (37 species from 2010 to 2016; see Uetz, Freed & Hosek, 2016). Throughout the Thai-Malay Peninsula in particular, surveys have demonstrated that the ecological and physical complexity of limestone ecosystems can harbour a suite of syntopic, microendemic amphibians and reptiles that are often restricted to a single limestone cave, ridge or karst tower (Grismer et al., 2016a, b and references therein). These distinctive, insular micro-ecosystems provide unique combinations of ecological features—vertical to inverted substrates, climatic stability, low illumination, relaxed predation, reduced prey base—not found in the surrounding forested areas and can promote and drive ecological speciation (Schluter, 2001; Rundle & Nosil, 2005; Nosil, 2012). Thus, the potential for the discovery of new species in these understudied ecosystems cannot be overstated. In Peninsular Malaysia alone, 16 new species of reptiles from only 13 different limestone formations have been described in the last eight years (see Grismer *et al.*, 2016b and references therein), leaving 558 formations in that region (Price, 2014) yet to be surveyed. Therefore, by extension, this would suggest that the vast, unexplored limestone regions of other Southeast Asian nations should harbour untold numbers of new endemic species.

Despite the increasing annual rates at which new species of *Cyrtodactylus* are being described from Southeast Asia, only two new species (Connette *et al.*, 2017) from Myanmar have been added since the nine species described by Bauer (2002, 2003) and the single species described by Mahony (2009)—which is particularly ironic given the extensive nature of limestone habitats throughout the eastern and southern sections of this country. Of the nine species described by Bauer (2002, 2003), it is difficult to say if any (with the exception of perhaps *C. chrysopylos* Bauer from the Pyadalin Cave) are confined to limestone habitats as no natural history information accompanied their descriptions. Wood *et al.* (2012) demonstrated that seven of these nine Burmese species and two others from western Myanmar formed a monophyletic group.

At the invitation of the Forestry Department of Myanmar and Fauna and Flora International, we were given reasonably unrestricted access into some of the limestone regions in the lowland areas of the Salween River Basin in the southern states of Mon and Kayin and upland areas along the western edge of the Shan Hills in Mandalay Region and Shan State in east-central Myanmar (Figs 1, 2). During this short survey period from 3 to 18 October 2016, we visited 19 different limestone habitats (caves, karst towers, hills) and discovered 12 new species of *Cyrtodactylus*, three new species of *Hemiphyllodactylus* Bleeker (Grismer *et al.*, 2017) and two new species of *Hemidactylus* Oken (L. L. Grismer *et al.*, in prep). Inferences using molecular data from 1505 base pairs (bp) of the mitochondrial gene NADH dehydrogenase subunit 2 (*ND2*) and its flanking tRNA regions indicate that 11 of the 12 new species of *Cyrtodactylus* are not closely related to any of the Indo-Burmese species of Agarwal *et al.* (2014) that range west of the Shan Hills nor do they form an exclusive, monophyletic group with each other. They do however form a clade with other Indo-Chinese species from Thailand, Cambodia and Vietnam exclusive

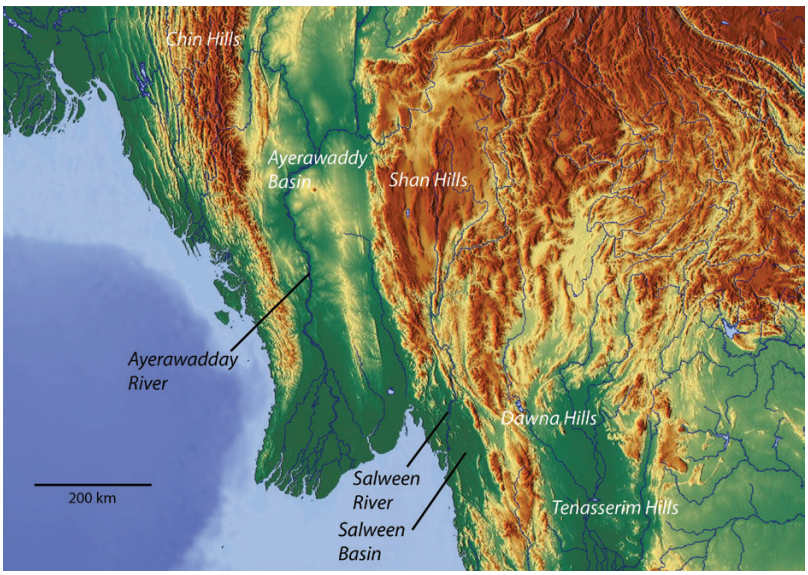

Figure 1. Major geographic features of Myanmar referred to herein.

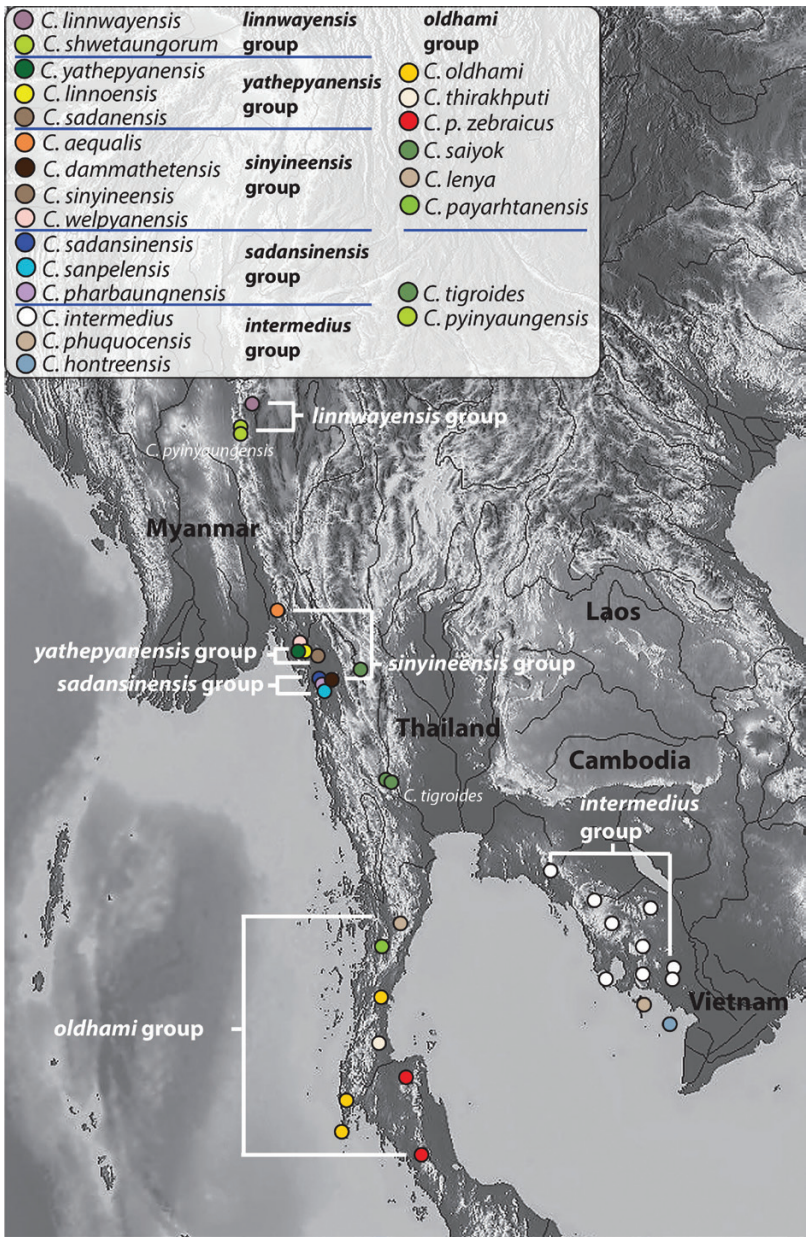

Figure 2. Distribution of the species in the species groups of the Indo-Chinese clade.

of other Southeast Asian taxa. The single remaining new species from near Pyinyaung Village, Mandalay Region forms a monophyletic group with *C. annandalei* Bauer and another new species from Popa Mountain, Mandalay Region that was misidentified in Wood *et al.* (2012) and Agarwal *et al.* (2014) as *C. feae* Boulenger (G. R. Zug, unpubl. data). In this paper, we describe the 12 new species of *Cyrtodactylus*, outline their phylogenetic relationships to each other and other Southeast Asian species, provide a preliminary scenario of their origin and biogeographic history, and provide a key to the species of *Cyrtodactylus* of Myanmar.

MATERIAL AND METHODS

TAXON SAMPLING AND OUTGROUP SELECTION

The primary aim of this study was to investigate the taxonomy and phylogenetic relationships of the newly discovered species of *Cyrtodactylus* from the Shan Hills and Salween River Basin based on 1548 bp of *ND2* and its flanking tRNAs (WANCY). The data set of Agarwal *et al.* (2014), which included exemplars of all the major *Cyrtodactylus* clades in Wood *et al.* (2012), was augmented with 90 samples from Myanmar and ten samples from western and Peninsular Thailand, totalling

169 samples. *Hemidactylus angulatus* Hallowell, *H. frenatus* Duméril & Bibron, *H. garnotii* Duméril & Bibron, *H. mabouia* (Moreau de Jonnes) and *H. turcicus* (Linneaus) served as outgroups based on the phylogeny of Wood *et al.* (2012). All new sequences were deposited in GenBank (Table 1).

Molecular data

Genomic DNA was isolated from liver or skeletal muscle specimens stored in 95% ethanol using the Qiagen DNeasy tissue kit (Valencia, CA, USA). *ND2* 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 (concentration 10 µM), 1.0 µL heavy strand primer (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 (5 U/µL) and 6.4 µL ultra-pure H_2O. PCR reactions were executed on an Eppendorf Mastercycler 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 48–50 °C for 35 s, followed by a cycle extension at 72 °C for 35 s, for 31 cycles. All PCR products were visualized on a 1.0% agarose gel electrophoresis. Successful PCR products were vacuum purified using MANU 30 PCR plates (Millipore) and purified products were resuspended in ultra-pure water. Purified PCR products were sequenced using the ABI Big-Dye Terminator v3.1 Cycle Sequencing Kit in an ABI GeneAmp PCR 9700 thermal cycler. Cycle sequencing reactions were purified with Sephadex G-50 Fine (GE Healthcare) and sequenced on an ABI 3730xl DNA Analyzer at the BYU (Brigham Young University) DNA Sequencing Centre (DNASC). Primers used for amplification and sequencing are presented in Table 2. Sequences were analysed from both the 3′ and the 5′ ends separately to confirm congruence between the reads. Both the forward, reverse and the two internal sequences were uploaded and edited in Geneious version v6.1.8 (Kearse *et al.*, 2012) and were edited therein. The protein-coding region of the *ND2* sequence was aligned by eye. Mesquite v3.04 (Maddison & Maddison, 2015) was used to calculate the correct amino acid reading frame and to confirm the lack of premature stop codons. Uncorrected pairwise sequence divergences were calculated in MEGA7.0 (Kumar, Stecher & Tamura, 2016).

Three different phylogenetic analyses were employed. A maximum likelihood (ML) analysis was implemented in IQ-TREE (Nguyen *et al.*, 2015) and using Bayesian Information Criterion (BIC), calculated K3P+I+G4 to be the best-fit model of evolution for the tRNA and TVM+I+G4 for the first codon position and TIM3+G4 for the second and third codon positions. One thousand bootstrap pseudoreplicates via the ultra-fast bootstrap approximation algorithm were employed and nodes having ML UFboot values (UF) of 95 and above were considered significantly supported (Minh, Nguyen & von Haeseler, 2013). A Bayesian analysis was carried out in MrBayes 3.2.3. on XSEDE (Ronquist *et al.*, 2012) using CIPRES (Cyberinfrastructure for Phylogenetic Research; Miller, Pfeiffer & Schwartz, 2010) employing default priors and the partitioning scheme and models of evolution most closely approximating those used in the ML analysis. Two simultaneous runs were performed with four chains, three hot and one cold. The simulation ran for 70 000 000 generations, was sampled every 70 000 generations using the Markov Chain Monte Carlo (MCMC) and the first 25% of each run was discarded as burn-in. Stationarity and .p files from each run were checked in Tracer v1.6 to ensure effective sample sizes (ESS) were above 200 for all parameters (Rambaut *et al.*, 2014). Nodes with Bayesian posterior probabilities (BPP) of 0.95 and above were considered well-supported (Huelsenbeck *et al.*, 2001; Wilcox *et al.*, 2002). A time-calibrated Bayesian inference analysis was implemented in BEAUti version 1.8.0 (Bayesian Evolutionary Analysis Utility) and run on BEAST version 1.8.0 (Bayesian Evolutionary Analysis Sampling Trees; Drummond *et al.*, 2012) employing an uncorrelated lognormal relaxed clock with unlinked substitution and clock models and monophyly unchecked for taxon sets. A GTR+Gamma substitution model was selected for each codon position. MCMC chains were run using Coalescent tree priors for 200 million generations and logged every 20 000 generations. It has been demonstrated that the third codon position is susceptible to substitution saturation (Zamudio, Jones & Ward, 1997; Carranza *et al.*, 2000; Brandley *et al.*, 2011; Grismer *et al.*, 2015a) and could contribute to overestimating node ages. However, Grismer *et al.* (2015a) noted that although third codon position saturation was evident in their study of the gekkonid *Hemiphyllodactylus*, it was not a significant factor in estimating node ages across various codon and gene partition schemes and was consistent with similar node age estimates using nuclear genes on the same taxa (Heinicke *et al.*, 2011). Fossil calibrations from Agarwal *et al.* (2014) on essentially the same data set used herein, placed a mean date of 31.4 millions of years (95% HPD 36.2–27.2 Myr; Agarwal *et al.*, 2017) on the node between the *Cyrtodactylus pulchellus* complex and the remaining Southeast Asian taxa containing the *intermedius* group and this was used herein as a constraint prior to date the same node with a standard deviation (SD) of 1.5%. Maximum clade credibility trees using mean heights at the nodes were generated using TreeAnnotator v.1.8.0 (Rambaut & Drummond, 2013) with a burn-in of 1000 trees. The BEAST log files

Table 1. GenBank accession numbers for the newly recorded specimens used for the molecular phylogenetic analyses

Taxon	Catalogue no.	Locality	GenBank no.
Cyrtodactylus aequalis	LSUHC 12895	Kyaiktiyo Hill, Mon State, Myanmar (N17°28.819, E97°05.974)	MF872275
***C. dammathetensis* sp. nov.**	LSUHC 12862	Dammathet Cave 19.8 km east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°30.380, E97°48.629)	MF872276
***C. dammathetensis* sp. nov.**	LSUHC 12863	Dammathet Cave 19.8 km east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°30.380, E97°48.629)	MF872277
***C. dammathetensis* sp. nov.**	LSUHC 12864	Dammathet Cave 19.8 km east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°30.380, E97°48.629)	MF872278
***C. linnwayensis* sp. nov.**	BYU 52213	Lay Htuck Cave, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°12.964, E96°33.288)	MF872279
***C. linnwayensis* sp. nov.**	BYU 52214	Yum Twing Gyi Cave, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°12.964, E96°33.288)	MF872280
***C. linnwayensis* sp. nov.**	LSUHC 12970	Yae Htuck Cave, Linn-Way Village, 13.3 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°13.675, E96°33.403)	MF872281
***C. linnwayensis* sp. nov.**	LSUHC 12971	Yae Htuck Cave, Linn-Way Village, 13.3 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°13.675, E96°33.403)	MF872282
C. linnwayensis sp. nov.	LSUHC 12972	Yae Htuck Cave, Linn-Way Village, 13.3 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°13.675, E96°33.403)	MF872283
***C. linnwayensis* sp. nov.**	LSUHC 12973	Yae Htuck Cave, Linn-Way Village, 13.3 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°13.675, E96°33.403)	MF872284
***C. linnwayensis* sp. nov.**	LSUHC 12980	Lay Htuck Cave, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°12.964, E96°33.288)	MF872285
***C. linnwayensis* sp. nov.**	LSUHC 12981	Lay Htuck Cave, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°12.964, E96°33.288)	MF872286
***C. linnwayensis* sp. nov.**	LSUHC 12983	Yum Twing Gyi Cave, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°12.964, E96°33.288)	MF872287
***C. linnwayensis* sp. nov.**	LSUHC 12984	Yum Twing Gyi Cave, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°12.964, E96°33.288)	MF872288
***C. linnwayensis* sp. nov.**	LSUHC 12986	Yum Twing Gyi Cave, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°12.964, E96°33.288)	MF872289
***C. linnoensis* sp. nov.**	BYU 52230	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872290
***C. linnoensis* sp. nov.**	BYU 52231	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872291
***C. linnoensis* sp. nov.**	BYU 52232	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872292
***C. linnoensis* sp. nov.**	BYU 52233	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872293
***C. linnoensis* sp. nov.**	LSUHC 12824	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872294

Table 1. *Continued*

Taxon	Catalogue no.	Locality	GenBank no.
***C. linnoensis* sp. nov.**	LSUHC 12825	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872295
***C. linnoensis* sp. nov.**	LSUHC 12826	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872296
***C. linnoensis* sp. nov.**	LSUHC 12829	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872297
***C. linnoensis* sp. nov.**	LSUHC 12832	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872298
***C. linnoensis* sp. nov.**	LSUHC 12833	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872299
***C. linnoensis* sp. nov.**	LSUHC 12834	Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402)	MF872300
C. oldhami	MS 460	Kraburi District, Phang-nga Province, Thailand	MF872301
C. oldhami	MS 585	Muang District, Ranong Province, Thailand	MF872302
C. cf. *peguensis zebraicus*	CUMZ THA R2005 073054	Tham Khao Lang, Petchaburi Province, Thailand	GU550727.1
***C. pharbaungensis* sp. nov.**	BYU 52215	Pharpoun Cave 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°17.118, E97°54.056)	MF872303
***C. pharbaungensis* sp. nov.**	LSUHC 12870	Pharpoun Cave 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°17.118, E97°54.056)	MF872304
***C. pharbaungensis* sp. nov.**	LSUHC 12871	Pharpoun Cave 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°17.118, E97°54.056)	MF872305
***C. pharbaungensis* sp. nov.**	LSUHC 12873	Pharpoun Cave 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°17.118, E97°54.056)	MF872306
***C. pyinyaungensis* sp. nov.**	BYU 52234	5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.191, E96°24.296)	MF872307
C. saiyok	MS 484	Sai Yok National Park, Kanchanaburi Province, Thailand	MF872308
C. saiyok	MS 480	Suang Phung, Ratchaburi Province, Thailand	MF872309
***C. sadanensis* sp. nov.**	BYU 52216	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872310
***C. sadanensis* sp. nov.**	BYU 52217	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872311
***C. sadanensis* sp. nov.**	BYU 52218	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872312
***C. sadanensis* sp. nov.**	BYU 52219	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872313
***C. sadanensis* sp. nov.**	LSUHC 12841	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872314
***C. sadanensis* sp. nov.**	LSUHC 12841	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872315
***C. sadanensis* sp. nov.**	LSUHC 12842	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872316
***C. sadanensis* sp. nov.**	LSUHC 12843	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872317
***C. sadanensis* sp. nov.**	LSUHC 12844	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872318
***C. sadanensis* sp. nov.**	LSUHC 12845	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872319

Table 1. *Continued*

Taxon	Catalogue no.	Locality	GenBank no.
***C. sadanensis* sp. nov.**	LSUHC 12846	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872320
***C. sadanensis* sp. nov.**	LSUHC 12847	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872321
***C. sadanensis* sp. nov.**	LSUHC 12848	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872322
***C. sadanensis* sp. nov.**	LSUHC 12849	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872323
***C. sadanensis* sp. nov.**	LSUHC 12853	Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872324
***C. sadansinensis* sp. nov.**	BYU 52220	Sadan Sin Cave 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°31.729, E97°43.056)	MF872325
***C. sadansinensis* sp. nov.**	LSUHC 12855	Sadan Sin Cave 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°31.729, E97°43.056)	MF872326
***C. sadansinensis* sp. nov.**	LSUHC 12856	Sadan Sin Cave 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°31.729, E97°43.056)	MF872327
***C. sadansinensis* sp. nov.**	LSUHC 12857	Sadan Sin Cave 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°31.729, E97°43.056)	MF872328
***C. sadansinensis* sp. nov.**	LSUHC 12858	Sadan Sin Cave 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°31.729, E97°43.056)	MF872329
***C. sadansinensis* sp. nov.**	LSUHC 12859	Sadan Sin Cave 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°31.729, E97°43.056)	MF872330
***C. sanpelensis* sp. nov.**	BYU 52221	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872331
***C. sanpelensis* sp. nov.**	BYU 52222	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872332
***C. sanpelensis* sp. nov.**	BYU 52223	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872333
***C. sanpelensis* sp. nov.**	BYU 52224	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872334
***C. sanpelensis* sp. nov.**	LSUHC 12875	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872336
***C. sanpelensis* sp. nov.**	LSUHC 12877	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872337
***C. sanpelensis* sp. nov.**	LSUHC 12877	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872335
***C. sanpelensis* sp. nov.**	LSUHC 12878	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872338
***C. sanpelensis* sp. nov.**	LSUHC 12879	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872339

Table 1. *Continued*

Taxon	Catalogue no.	Locality	GenBank no.
***C. sanpelensis* sp. nov.**	LSUHC 12880	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872340
***C. sanpelensis* sp. nov.**	LSUHC 12881	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872341
***C. sanpelensis* sp. nov.**	LSUHC 12883	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872342
***C. sanpelensis* sp. nov.**	LSUHC 12886	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872343
***C. sanpelensis* sp. nov.**	LSUHC 12887	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872344
***C. sanpelensis* sp. nov.**	LSUHC 12889	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	MF872345
***C. sanpelensis* sp. nov.**	LSUHC 12890	Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388)	xxxxxxxxx
***C. shwetaungorum* sp. nov.**	BYU 52225	5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.191, E96°24.296)	MF872346
***C. shwetaungorum* sp. nov.**	BYU 52226	5.0 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.499, E96°24.582)	MF872347
***C. shwetaungorum* sp. nov.**	BYU 52227	5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.191, E96°24.296)	MF872348
***C. shwetaungorum* sp. nov.**	LSUHC 12935	5.0 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.499, E96°24.582)	MF872349
***C. shwetaungorum* sp. nov.**	LSUHC 12937	5.0 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.499, E96°24.582)	MF872350
***C. shwetaungorum* sp. nov.**	LSUHC 12896	5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.191, E96°24.296)	MF872351
***C. shwetaungorum* sp. nov.**	LSUHC 12897	5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.191, E96°24.296)	MF872352
***C. shwetaungorum* sp. nov.**	LSUHC 12898	5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.191, E96°24.296)	MF872353
***C. sinyineensis* sp. nov.**	LSUHC 12835	Sin Yine Cave 18.5 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872354
***C. sinyineensis* sp. nov.**	LSUHC 12836	Sin Yine Cave 18.5 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872355
***C. sinyineensis* sp. nov.**	LSUHC 12837	Sin Yine Cave 18.5 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493)	MF872356
C. thirakhupti	ZMKU_R_00732, LSUHC 12467	Tham Khao Sonk Hill, Surat Thani Province, Thailand	MF872357
C. thirakhupti	ZMKU_R_00733, LSUHC 12468	Tham Khao Sonk Hill, Surat Thani Province, Thailand	MF872358

Table 1. *Continued*

Taxon	Catalogue no.	Locality	GenBank no.
***C. welpyanensis* sp. nov.**	LSUHC 12784	Wel Pyan Cave 35 km north of Hpa-an, Hpa-an District, Kayin State, Myanmar (N17°12.188, E97°37.066)	MF872359
***C. welpyanensis* sp. nov.**	LSUHC 12785	Wel Pyan Cave 35 km north of Hpa-an, Hpa-an District, Kayin State, Myanmar (N17°12.188, E97°37.066)	MF872360
***C. welpyanensis* sp. nov.**	LSUHC 12786	Wel Pyan Cave 35 km north of Hpa-an, Hpa-an District, Kayin State, Myanmar (N17°12.188, E97°37.066)	MF872361
***C. welpyanensis* sp. nov.**	LSUHC 12792	Wel Pyan Cave 35 km north of Hpa-an, Hpa-an District, Kayin State, Myanmar (N17°12.188, E97°37.066)	MF872362
***C. yathepyanensis* sp. nov.**	BYU 52228	Yathe Pyan Cave 9 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.114, E97°34.243)	MF872363
***C. yathepyanensis* sp. nov.**	BYU 52229	Yathe Pyan Cave 9 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.114, E97°34.243)	MF872364
***C. yathepyanensis* sp. nov.**	LSUHC 12821	Yathe Pyan Cave 9 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.114, E97°34.243)	MF872365
***C. yathepyanensis* sp. nov.**	LSUHC 12822	Yathe Pyan Cave 9 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.114, E97°34.243)	MF872366
***C. yathepyanensis* sp. nov.**	LSUHC 12823	Yathe Pyan Cave 9 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.114, E97°34.243)	MF872367

Accession numbers for the other specimens used are in Agarwal *et al.* (2014).

Table 2. Primer sequences used in this study for amplification and sequencing the *ND2* gene and the flanking tRNAs

Primer name	Primer reference		Sequence
L4437b	Macey *et al.* (1997)	External	5′-AAGCAGTTGGGCCCATACC-3′
CyrtintF1	Siler *et al.* (2010)	Internal	5′-TAGCCYTCTCYTCYATYGCCC-3′
CyrtintR1	Siler *et al.* (2010)	Internal	5′-ATTGTKAGDGTRGCYAGGSTKGG-3′
H5934	Macey *et al.* (1997)	External	5′-AGRGTGCCAATGTCTTTGTGRTT-3′

were visualized and checked in Tracer 1.6.0 (Rambaut *et al.*, 2014) to ensure ESS values were above 200 for all parameters.

Morphological analysis

Colour notes were taken from living specimens and digital images of living specimens of all possible age classes prior to preservation. Measurements were taken on the left side of the body when possible to the nearest 0.1 mm by M.S.G. using Mitutoyo dial callipers under a Nikon SMZ 1500 dissecting microscope. Measurements taken were: snout-vent length (SVL), taken from the tip of snout to the vent; tail length (TL), taken from the vent to the tip of the tail, original or regenerated; tail width (TW), taken at the base of the tail immediately posterior to the postcloacal swelling; forearm length (FL), taken on the dorsal surface from the posterior margin of the elbow while flexed 90° to the inflection of the flexed wrist; tibia length (TBL), taken on the ventral surface from the posterior surface of the knee while flexed 90° to the base of the heel; axilla to groin length (AG), taken from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hindlimb at its insertion point on the body; head length (HL), the distance from the posterior margin of the retroarticular process of the lower jaw to the tip of the snout; head width (HW), measured at the angle of the jaws; head depth (HD), the maximum height of head measured from the occiput to the throat; eye diameter (ED), the greatest horizontal diameter of the eyeball; eye to ear distance (EE), measured from the anterior edge of the ear opening to the posterior edge of the eyeball; eye to snout distance (ES), measured from anteriormost margin of the eyeball to the tip of snout; eye to nostril distance (EN), measured from the anterior margin of the eye ball to the posterior margin of the external nares; inter orbital distance (IO), measured between the anterior edges of the orbit; ear diameter (EL), the greatest vertical distance of the ear opening; and internarial distance (IN), measured between the nares across the rostrum.

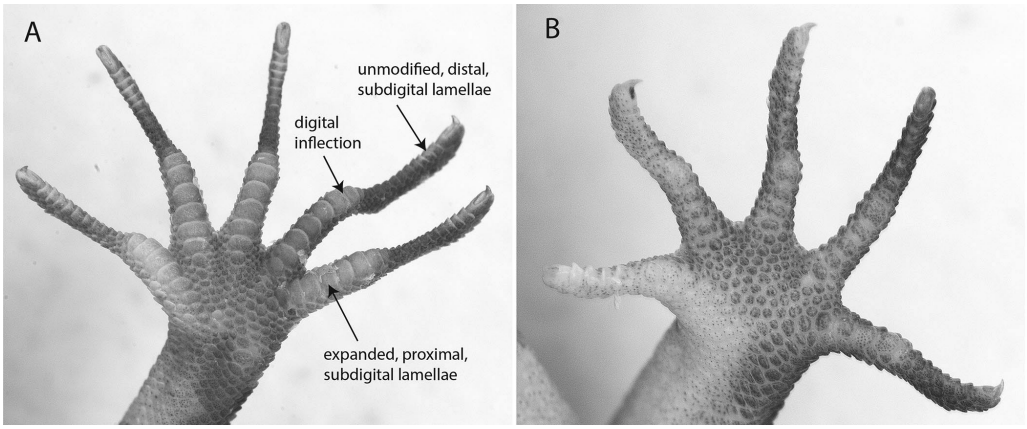

Figure 3. Underside of the right hand of (A) ***Cyrtodactylus linnoensis* sp. nov.** (BYU 52231) and (B) ***C. pyinyaungensis* sp. nov.** (BYU 52234) illustrating gross differences in digit and subdigital lamellae morphology.

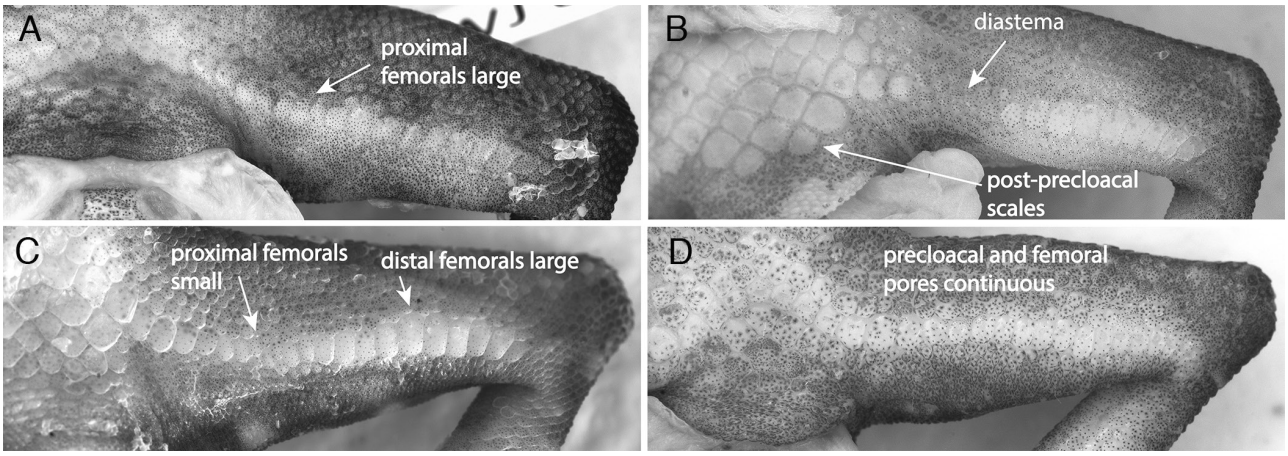

Figure 4. Differences in, and arrangement of femoral, precloacal and post-precloacal scale morphology. A, *Cyrtodactylus aequalis* (LSUHC 12895). B, ***Cyrtodactylus sanpelensis* sp. nov.** (LSUHC 12883). C, ***Cyrtodactylus linnoensis* sp. nov.** (BYU 52231). D, ***Cyrtodactylus dammathetensis* sp. nov.** (LSUHC 12862).

Meristic characters taken by M.S.G. were the numbers of supralabial (SL) and infralabial (IL) scales counted from the largest scale immediately below the posterior margin of the eyeball to the rostral and mental scales, respectively; the number of paravertebral tubercles (PVT) between limb insertions counted in a straight line immediately left of the vertebral column; the number of longitudinal rows of body tubercles (LRT) counted transversely across the centre of the dorsum from one ventrolateral fold to the other; the number of longitudinal rows of ventral scales (VS) counted transversely across the centre of the abdomen from one ventrolateral fold to the other; the number of expanded subdigital lamellae proximal to the digital inflection on the fourth toe (4TLE) counted from the base of the first phalanx where it contacts the body of the foot to the largest scale on the digital inflection (Fig. 3), large continuous scales on the palmar and plantar surfaces were not counted; the number of small, unmodified subdigital lamellae distal to the digital inflection on the fourth toe (4TLU) counted from the digital inflection to the claw (Fig. 3); and the total number of subdigital lamellae (4TL) beneath the fourth toe (i.e. 4TLE + 4TLU = 4TL). The total number of enlarged femoral scales (FS) from each thigh combined as a single metric. In some species, only the distalmost scales are greatly enlarged and the proximal scales are smaller, whereas in others the greatly enlarged scales are continuous with the enlarged precloacal scales and the separation of the two scales rows was determined to be at a point even with the lateral body margin (Fig. 4). The total number of femoral pores (FP) in males (i.e. the sum of the number of enlarged pore-bearing femoral scales from each leg combined as a single metric—not all enlarged femoral scales have pores). The number of enlarged precloacal scales (PS); the number of precloacal pores in (PP)

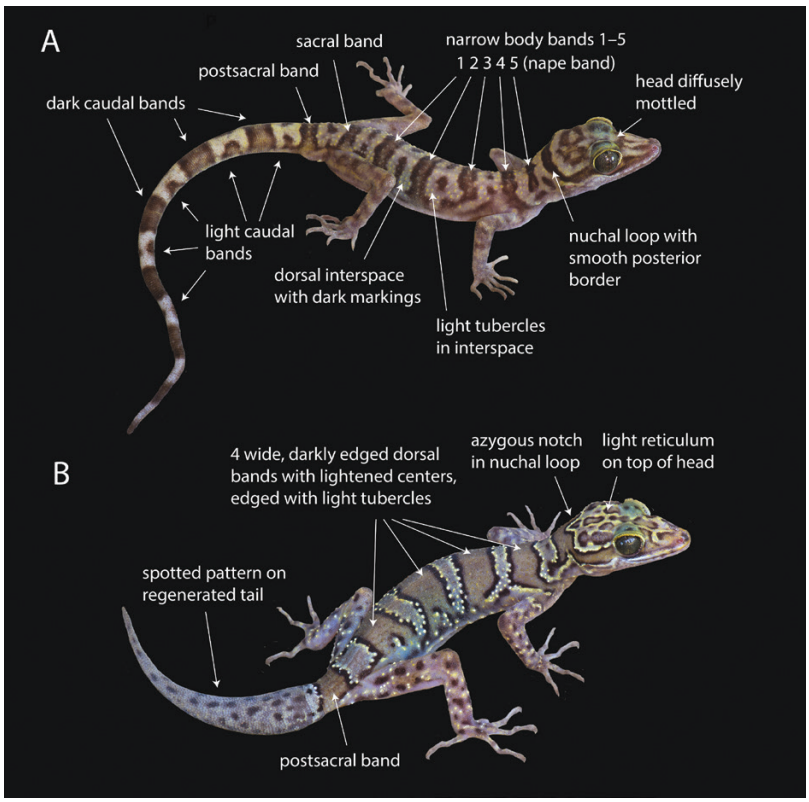

Figure 5. Some of the colour pattern characteristics used to differentiate species in the Indo-Chinese clade. A, ***Cyrtodactylus pharbaungensis* sp. nov.** (LSUHC 12871). B, ***Cyrtodactylus linnwayensis* sp. nov.** (BYU 52215).

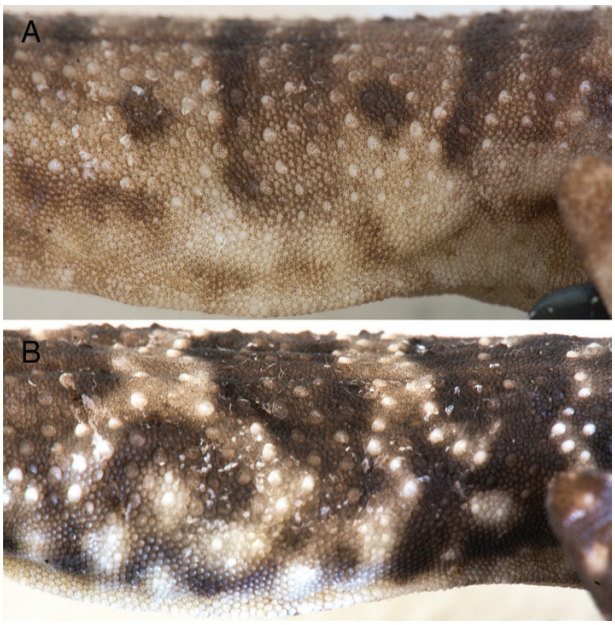

Figure 6. A, weak, less densely packed tuberculation in ***Cyrtodactylus pharbaungensis* sp. nov.** (LSUHC 12871). B, strong tuberculation in ***C. linnoensis* sp. nov.** (BYU 52231).

in males; the number of continuous femoroprecloacal pores (FPP) in males (Fig. 4); and the number of rows of post-precloacal scales (PPS) on the midline between the enlarged precloacal scales and the vent (Fig. 4); number of body bands (BB) between the nuchal loop (dark band running from eye to eye) and the hindlimb insertions not including the sacral or postsacral bands, although the dark band on the nape—which is variably present—is considered as part of this count (Fig. 5); the number of light caudal bands (LCB) on an original tail; and the number of dark caudal bands (DCB) on an original tail.

Non-meristic morphological characters evaluated were the degree of body tuberculation—weak tuberculation referring to dorsal body tubercles that are relatively low, small, less densely packed and weakly keeled, whereas prominent tuberculation refers to tubercles that are larger, higher (raised) and prominently keeled (Fig. 6); body tubercles extending past the base of the tail or not (Fig. 7); enlarged femoral scales and precloacal scales contiguous or separated by a diastema at the base of the femora (Fig. 4); and the relative length to width ratio of the transversely expanded, median subcaudal scales and whether or not they extend onto the lateral surface of the tail (Fig. 8).

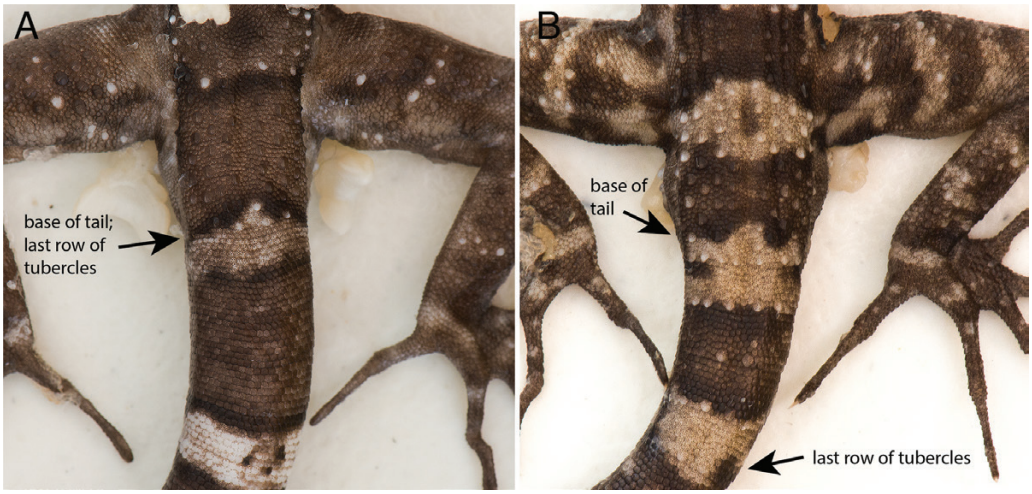

Figure 7. A, body tubercles not extending past the base of the tail in ***Cyrtodactylus shwetaungorum* sp. nov.** (LSUHC 12937). B, body tubercles extending past the base of the tail in ***C. dammathetensis* sp. nov.** (LSUHC 12862).

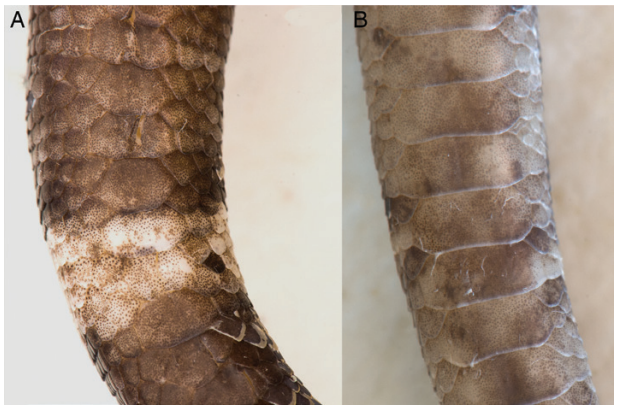

Figure 8. A, median subcaudal scales approximately twice as wide as long not extending onto the lateral surface of the tail in ***Cyrtodactylus shwetaungorum* sp. nov.** (LSUHC 12937). B, median subcaudal scales approximately three times as wide as long, extending onto the lateral surface of the tail in ***C. dammathetensis* sp. nov.** (LSUHC 12862).

Colour pattern characters (Fig. 5) evaluated were the nuchal loop being continuous from eye to eye, separated medially into paravertebral elements, bearing an anterior azygous notch or not, and the posterior border being straight (smooth), sinuous or jagged; the first dorsal body band bearing an anterior, azygous notch or not; dorsal body bands bearing paired, paravertebral elements or not; dark dorsal body bands wider than light interspaces, with or without lightened centres, edged with light tubercles or not, zigzag-shaped or more regular (straight or even); dark markings present or absent in the dorsal interspaces; light tubercles dispersed throughout the dorsal interspaces or not; ventrolateral body fold white, appearing as a wide or narrow stripe; top of head bearing combinations of dark diffuse mottling or dark, distinct blotches overlain with a light-coloured reticulating network or not; anterodorsal margin of thighs and brachia whitish due to a lack of dark pigment; light caudal bands bearing dark markings or immaculate; light caudal bands encircle tail or not; dark caudal bands wider than light caudal bands; and regenerated tail bearing a pattern of distinct, dark spots or not.

An analysis of variance (ANOVA) was performed to ascertain if statistically significant mean differences among meristic characters ($P < 0.05$) existed. ANOVAs having a P-value less than 0.05 indicating that statistical differences existed were subjected to a Tukey HSD test to ascertain which population pairs differed significantly from each other. Principal component analysis (PCA) and discriminant analysis of principal components (DAPC) were used to determine if species of each species group occupied a unique position in morphospace and the degree to which their variation in morphospace coincided with their species boundaries delimited by the molecular phylogenetic and univariate analyses. PCA, implemented by the prcomp command in R v 3.2.1 (R Core Team, 2015), searches for the best overall low-dimensional representation of significant morphological variation in the data. Femoral and precloacal pore counts were excluded from the PCA due to their presence in only males. All PCA data were log-transformed prior to analysis and scaled to their SD in order to normalize their distribution so as to ensure characters with very large and very low values did not over-leverage the results owing to intervariable non-linearity. To characterize clustering and separation in morphospace, a DAPC was performed to search for linear combinations of morphological variables having the greatest between-group variance and the smallest within-group variance (Jombart, Devillard & Balloux,

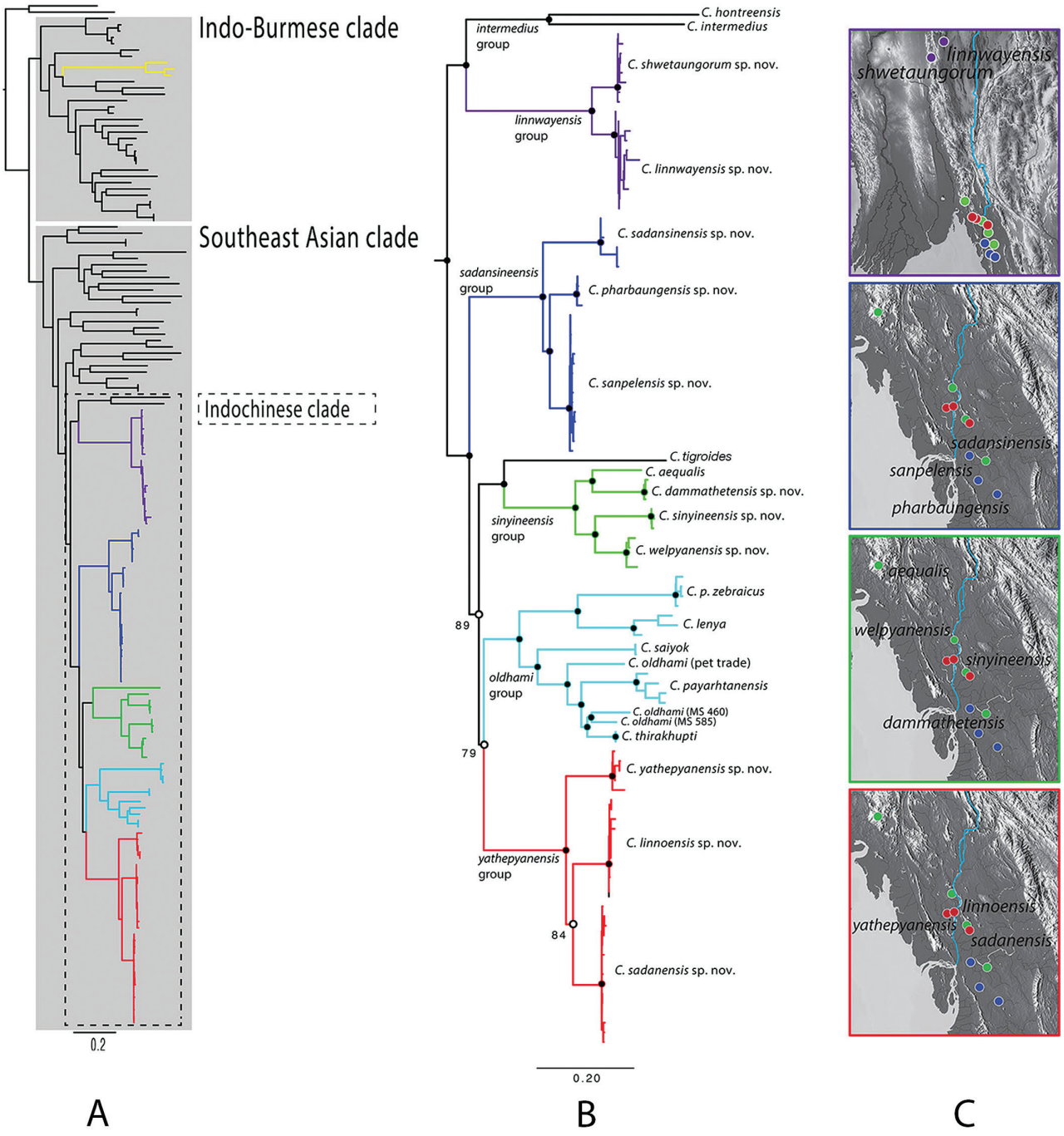

Figure 9. A, maximum likelihood topology illustrating the relationships of the Indo-Burmese, Southeast Asian and Indo-Chinese clades. Yellow branches represent *Cyrtodactylus annadalei* and the sister species ***C. pyinyaungensis* sp. nov.** and *Cyrtodactylus* sp. Popa. B, maximum likelihood topology of the Indo-Chinese clade showing the relationships of the species groups to one another and the interspecies relationships within each species group. Solid circles represent nodes supported by BPP and UF values of greater than 95% and 95, respectively. Open circles denote weakly supported nodes of UF values < 95. C, distribution of the species within the colour-coded Burmese species groups in relation to the Salween River denoted in blue.

2010). DAPC relies on log-transformed data from the PCA as a prior step to ensure that variables analysed are not correlated and number fewer than the sample size. Principal components with eigenvalues greater than one were retained for the DAPC analysis according to the criterion of Kaiser (1960). All statistical

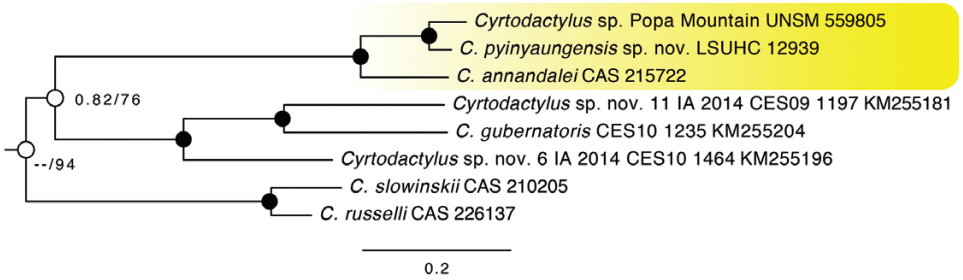

Figure 10. Maximum likelihood topology showing the relationships of *Cyrtodactylus annandalei*, ***C. pyinyaungensis* sp. nov.** and *Cyrtodactylus* sp. Popa Mountain to each other and other closely related species of within the Indo-Burmese clade. Solid circles represent nodes supported by BPP and UF values of greater than 95% and 95, respectively. Open circles denote weakly supported nodes.

analyses were performed using the platform R v 3.2.1 (R Core Team, 2015).

Museum abbreviations follow Frost (2016) except for LSUHC referring to the La Sierra University Herpetological Collection, La Sierra University, Riverside, CA, USA; MS referring to Montri Sumontha, Ranong Marine Fisheries Station, Ranong 85000, Thailand; and PLWJ referring to Perry L. Wood, Jr. field series, Department of Biology, Brigham Young University, Provo, UT 84602, USA).

RESULTS

All three molecular analyses showed complete topological congruence with well-supported nodes throughout most of the tree and all analyses indicate that the 12 new species described below from east-central and southern Myanmar do not form a monophyletic group but are embedded within two different major clades of Indo-Malayan *Cyrtodactylus* (Fig. 9). The population from just north of Pyinyaung village in the Shan Hills from Mandalay Region is nested with a larger well-supported (BPP 1.00/UF 99) clade of Indo-Burmese species (Figs 9, 10) first identified by Wood *et al.* (2012) and augmented by Agarwal *et al.* (2014). The analyses further indicate that the individuals from the 11 other newly discovered populations from Mandalay Region, Shan, Kayin and Mon states collectively comprise four of six well-supported (1.00/100) monophyletic species groups referred to here as the *intermedius* (*sensu* Grismer *et al.*, 2015b), *linnwayensis*, *sadansinensis*, *sinyineensis*, *oldhami* and *yathepyanensis* groups. All these groups belong to a larger, well-supported (1.00/100) clade of Southeast Asian species within which they comprise a well-supported (0.98/100) Indo-Chinese clade (Fig. 9). The Indo-Chinese clade contains two major lineages, each with multiple subclades. One of these well-supported (0.99/96) major lineages is composed of the *linnwayensis* group from the Shan Mountains and its sister lineage the *intermedius* group from the hilly Cardamom regions of eastern Thailand, southern Cambodia and southern Vietnam (Figs 2, 9). The other well-supported (0.99/100) major lineage contains the remaining three species groups from Myanmar and a predominately Thai species group of which the *sadansinensis* group is the weakly supported (--/89) basal species group lineage (Figs 2, 9). The remaining two Burmese species groups are related to multiple lineages of taxa from western Thailand and the Thai-Malay Peninsula. *Cyrtodactylus tigroides* Bauer from western Thailand is the sister species to the *sinyineensis* group, whereas the well-supported (1.00/100) *oldhami* group containing *C.* cf. *peguensis zebraicus* Taylor, *C. saiyok* Panitvong, Sumontha, Tunprasert, & Pauwels, *C. oldhami* (Theobold), *C. thirakhupti* Pauwels, Bauer, Sumontha, & Chanhome from western and Peninsular Thailand and *C. lenya* Connette, *et al.* and *C. payarhtensis* Connette, *et al.* from Peninsular Myanmar is the weakly supported (--/79) sister lineage to the well-supported (1.00/100) *yathepyanensis* group (Figs 2, 9). The molecular analyses further indicate that the new Burmese species are strongly supported (1.00/100) as being exclusive lineages—comprised only of individuals from their respective populations (Figs 9, 11).

The tree recovered here (Fig. 9) differs from that of Wood *et al.* (2012) and Agarwal *et al.* (2014) in that the *oldhami* group and *C. tigroides* in their trees are not part of a well-supported clade containing the *intermedius* group but are related to species from Papua New Guinea. Wood *et al.* (2012) recovered the *intermedius* group in an unsupported polytomy containing the *pulchellus* group (*sensu* Grismer *et al.*, 2012) plus the sister species *C. elok* Dring and *C. interdigitalis* Ulber and placed the *oldhami* group and *C. tigroides* in another unsupported polytomy containing a Papua New

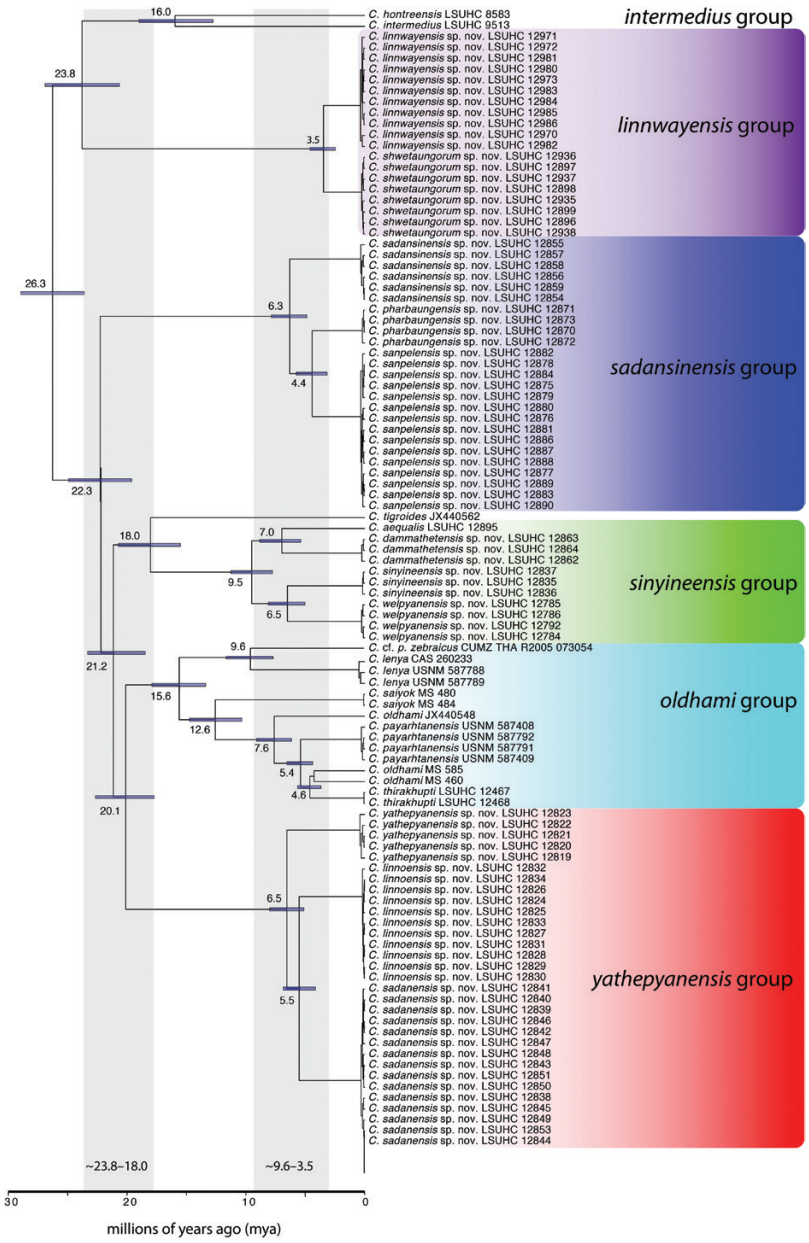

Figure 11. BEAST chronogram of the species and species groups of the Indo-Chinese clade. Numbers at the nodes are mean ages in millions of years. Bars at the nodes represent the 95% highest posterior density (HPD) about the means.

Guinean group. Agarwal *et al.* (2014) recovered the *intermedius* group as part of an unsupported polytomy containing the *pulchellus* group, the *oldhami* group, *C. tigroides* and a Paupa New Guinean group. Owing to the addition of the new Burmese species and additional species from the *oldhami* group, the polytomous nodes of Wood *et al.* (2012) and Agarwal *et al.* (2014) are resolved and all three well-supported analyses recover the *intermedius* group as the well-supported (0.99/96) sister lineage to the *linnwayensis* group and the *oldhami* group is placed with Indo-Chinese species—as opposed to New Guinean species—and may be the sister lineage to the *yathepyanensis* group (Fig. 9).

The univariate and multivariate morphological analyses support the molecular analyses by indicating that the new species within each group are well-separated from each other in morphospace with no overlap (Fig. 12; Fig. S1) and bear a number of statistically significant mean differences in varying combinations of meristic characters (Tables 3–5). Additionally, notable consistent differences in scale morphology and aspects

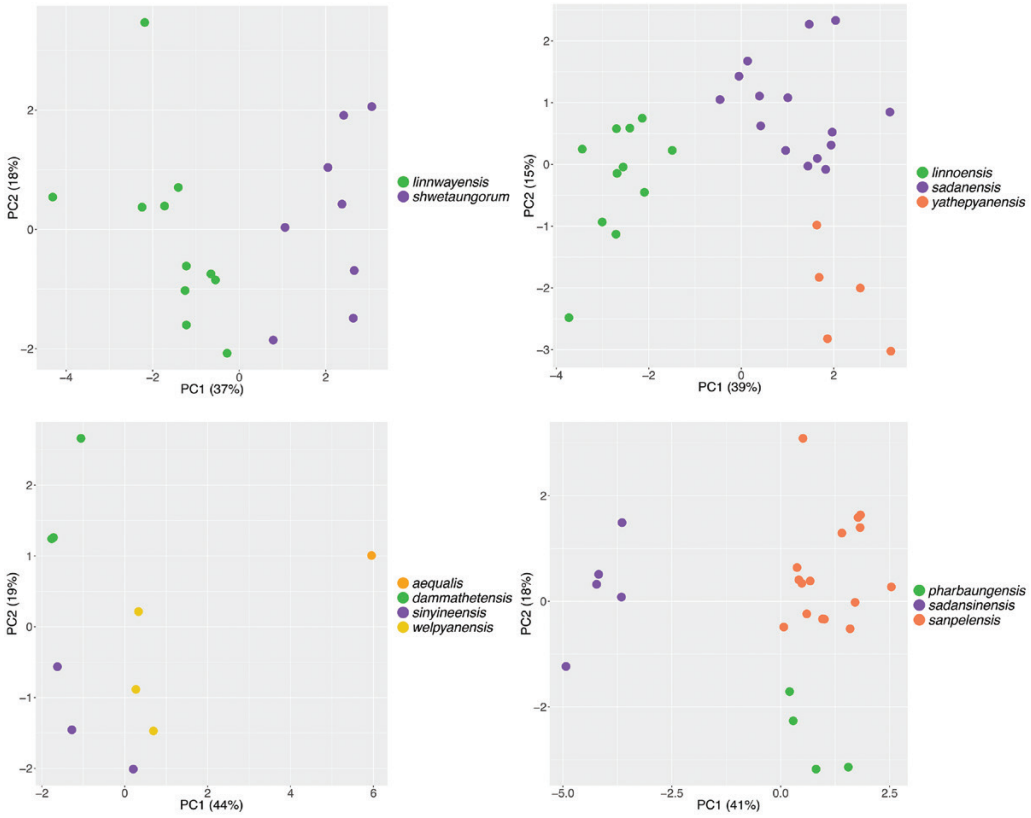

Figure 12. Principal component analysis (PCA) of the species of the *linnwayensis* species group, *sadansinensis* species group, *yathepyanensis* species group and *sinyineensis* species group showing complete separation of all species within each group along the first two principal components.

of coloration and pattern also provide reliable diagnostic character differences among the species (Table 7). The content of each new species group, the group's definition, and the diagnoses and descriptions of the new species within each group follows.

SYSTEMATICS AND TAXONOMY

ORDER SQUAMATA OPPEL, 1811
FAMILY GEKKONIDAE GRAY, 1825
GENUS *CYRTODACTYLUS* GRAY, 1827

CYRTODACTYLUS PYINYAUNGENSIS SP. NOV.

PYINYAUNG BENT-TOED GECKO
(FIG. 13; TABLE 6)

Holotype: Adult male LSUHC 13149 collected on 30 March 2017 at 1030 h by Myint Kyaw Thura, Htet Kyaw, Myint Kyaw Lin, Mathhew L. Murdoch, Marta S. Grismer and L. Lee Grismer from 5.7 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region, Myanmar (N20°52.191, E96°24.296; 472 m in elevation).

Paratypes: Adult female BYU 52234 collected on 12 October 2016 at 1030 h by Evan S. H. Quah, Perry L. Wood, Jr., Matthew L. Murdoch, Myint Kyaw Thura, Thaw Zin, Aung Lin, Htet Kyaw and L. Lee Grismer from 5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region, Myanmar (N20°52.191, E96°24.296; 642 m in elevation). Adult female LSUHC 13150 and adult male LSUHC 13149 bear the same collection data as the holotype. Adult female 13147 bears the same collection as the holotype except that it was collected on 29 March 2017.

Diagnosis: Cyrtodactylus pyinyaungensis sp. nov. differs from all congeners by having the unique combination of 25–30 paravertebral tubercles; 15–18 longitudinal rows of body tubercles; 30–36 ventral scales; relatively short digits (Fig. 3) with 16–19 subdigital lamellae beneath the fourth toe; raised to moderately keeled body tubercles; no caudal tubercles; enlarged femoral scales; femoral pores in males; relatively narrow subcaudal scales; top of head bearing large, irregularly shaped, dark markings

Table 3. Matrix of statistically significant mean differences of characters between species pairs of the *sinyineensis* group

	***dammathetensis* sp. nov.**	***aequalis* sp. nov.**	***sinyineensis* sp. nov.**
***dammathetensis* sp. nov.**	*	*	*
***aequalis* sp. nov.**	IL, VS, FS, PPS	*	*
***sinyineensis* sp. nov.**	LRT, FS, PS	IL, LRT, VS, PPS	*
***welpyanensis* sp. nov.**	PS, BB	LRT, VS, PS, PPS	SL, IL

Abbreviations are listed in the Material and Methods.

Table 4. Matrix of statistically significant mean differences of characters between species pairs of the *yathepyanensis* group

	***linnoensis* sp. nov.**	***sadanensis* sp. nov.**
***linnoensis* sp. nov.**	*	*
***sadanensis* sp. nov.**	SL, IL, PVT, LRT, VS, FS, 4TLE, 4TL, PP	*
***yathepyanensis* sp. nov.**	IL, PVT, LRT, VS, FS, 4TL, U4TL, BB, PP	SL, LRT, BB, FS

Abbreviations are listed in the Material and Methods.

Table 5. Matrix of statistically significant mean differences of characters between species pairs of the *sadansisnensis* group

	***pharbaungensis* sp. nov.**	***sanpelensis* sp. nov.**
***pharbaungensis* sp. nov.**	*	*
***sanpelensis* sp. nov.**	FS, FP	*
***sadansinensis* sp. nov.**	PVT, LRT, FS, PS, 4TLU, 4TL, PPS, PP	PVT, LRT, VS, FS, PS, 4TLU, 4TL, PPS, FP, PP

Abbreviations are listed in the Material and Methods.

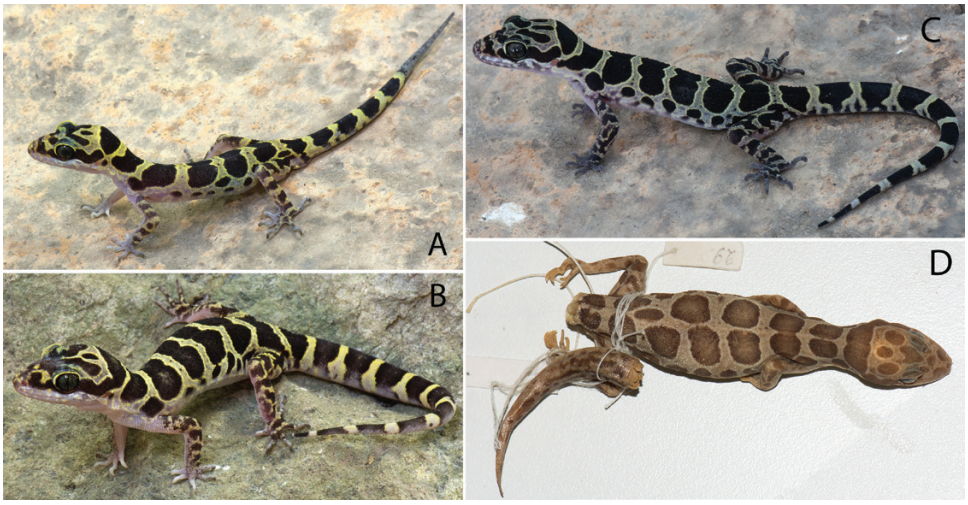

Figure 13. A, adult male holotype of ***Cyrtodactylus pyinyaungensis* sp. nov.** (LSUHC 13149) from 5.7 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region, Myanmar. B, adult female paratype (LSUHC 13150) from the type locality. C, adult female paratype (LSUHC 13147) from the type locality. D, syntype of *C. peguensis* (BMNH 1946.8.23.10) from Palon, Pegu State, Myanmar.

Table 6. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus pyinyaungensis* sp. nov.**

	BYU 52234 paratype	LSUHC 13150 paratype	LSUHC 13148 paratype	LSUHC 13147 paratype	LSUHC 13149 holotype
Sex	F	F	M	F	M
Supralabials	8	8	8	8	8
Infralabials	6	6	6	6	6
Body tubercles low and rounded (dome-shaped)	No	No	No	No	No
Body tubercles pointed and keeled (triangular)	Yes	Yes	Yes	Yes	Yes
Paravertebral tubercles	26	25	30	30	30
Longitudinal rows of tubercles	15	16	17	18	16
Tubercles extend beyond base of tail	No	No	No	No	No
Ventral scales	32	36	30	30	31
Proximal subdigital lamellae on fourth toe	5(R,L)	5(R,L)	5(R,L)	5(R,L)	6R,6L
Distal subdigital lamellae on fourth toe	11(R,L)	11(R)12(L)	12(R,L)	12(R,L)	13(R,L)
Total subdigital lamellae on fourth toe	16	16(R)17(L)	17	17	19(R,L)
Enlarged femoral scales (R/L)	10R,12L	10(R,L)	10(R,L)	12R,11L	9R,11L
Femoral pores (R/L)	/	/	9(R,L)	/	8R,9L
Enlarged femoral and precloacal scales continuous	No	No	No	No	No
Precloacal pores	/	/	8	/	8
Post-precloacal scales rows	2	2	2	2	2
Medial subcaudals two or three times wider than long	Yes	Yes	Yes	Yes	Yes
Medial subcaudals extend onto lateral surface of tail	No	No	No	No	No
Nuchal loop divided medially	No	No	No	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No
Posterior border of nuchal loop	Smooth	Smooth	Smooth	Smooth	Smooth
Dorsal banding with paravertebral elements	Yes	Yes	Yes	Yes	Yes
Number of body bands	6	6	6	6	5
Dorsal bands wider than interspaces	Yes	Yes	Yes	Yes	Yes
Dorsal bands with lightened centres	No	No	No	No	No
Dorsal bands edged with white tubercles	Yes	Yes	Yes	Yes	Yes
Dark markings in dorsal interspaces	No	No	No	No	No
Ventrolateral fold whitish	No	No	No	No	No
Top of head diffusely mottled, blotched or patternless	Blotched	Blotched	Blotched	Blotched	Blotched
Light reticulum on top of head	No	No	No	No	No
Anterodorsal margin of thighs lacking pigment	No	No	No	No	No
Anterodorsal margin of brachia lacking pigment	No	No	No	No	No
White caudal bands bearing dark markings	Yes	No	No	Yes	No
White caudal bands encircle tail	No	No	No	No	No
Number of light caudal bands	9	11	13	10	/

Table 6. *Continued*

	BYU 52234 paratype	LSUHC 13150 paratype	LSUHC 13148 paratype	LSUHC 13147 paratype	LSUHC 13149 holotype
Number of dark caudal bands	9	11	13	11	/
Dark caudal bands wider than light caudal bands	Yes	Yes	Yes	Yes	Yes
Mature regenerated tail spotted	/	/	/	/	No
SVL	67.7	71.7	55.5	64.3	58.6
TL	70	74	59	66	62
TW	6.1	6.9	6.0	5.8	5.5
FL	10.7	10.4	8.4	10.3	9.2
TBL	12.5	12.4	10.3	11.2	10.0
AG	28.5	33.0	22.5	28.5	25.7
HL	18.4	18.8	14.4	18.4	17.0
HW	12.6	13.2	10.2	11.8	10.5
HD	7.8	8.7	6.4	7.1	6.3
ED Boulenger, 1893	5.3	5.3	3.5	4.3	4.2
EE	5.3	5.7	3.6	5.2	4.6
ES	7.3	7.3	6.5	7.5	6.4
EN	5.3	5.7	4.7	5.1	4.8
IO	5.1	5.7	5.1	5.8	5.6
EL	1.9	1.8	1.8	1.7	1.9
IN	3.0	3.1	1.9	2.5	2.6

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable.

and lacking a light-coloured reticulum; nuchal loop not divided medially, lacking an anterior azygous notch, posterior border straight; five or six dark dorsal bands arranged as medially confluent, large, hourglass-shaped, paravertebral markings, wider than interspaces, lacking lightened centres and edged with white tubercles; no dark markings or white tubercles in dorsal interspaces; weak ventrolateral fold and anterodorsal margin of thighs and brachia pigmented; 9–13 dark and light caudal bands; white caudal bands immaculate, not encircling tail; and dark caudal bands wider than white caudal bands.

Description of holotype: Adult male SVL 58.6 mm; head moderate in length (HL/SVL 0.29), wide (HW/HL 0.62), flat (HD/HL 0.37), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region concave, canthus rostralis rounded; snout moderate (ES/HL 0.37), rounded in dorsal profile; eye large (ED/HL 0.25); ear opening elliptical, obliquely oriented, moderate in size (EL/HL 0.11); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided by dorsal furrow, bordered posteriorly by large left and right supranasals, smaller postrostral, laterally by first supralabials; external nares bordered anteriorly by rostral, anterodorsally by large supranasal, posteriorly by three small postnasals, ventrally by first supralabial in point contact; 8(R,L) square to rectangular supralabials extending to below midpoint of eye, fourth supralabial largest; 6(R,L) infralabials tapering smoothly posteriorly; scales of rostrum and lores flat, larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with slightly enlarged tubercles; dorsal superciliaries rectangular, smooth; mental triangular, bordered laterally by first infralabials and posteriorly by large, left and right trapezoidal postmentals that contact medially for 60% of their length posterior to mental; one row of slightly enlarged chinshields extending posteriorly to fourth infralabial; and gular and throat scales small, granular to subimbricate, grading posteriorly into larger, flatter, smooth, imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.44) with weak ventrolateral folds in life; dorsal scales small, interspersed with small, raised, subconical, semi-regularly arranged weakly keeled tubercles; tubercles extend from occiput onto base of tail but no farther; tubercles on occiput and nape very small, those on posterior portion of body larger, more strongly keeled; approximately 16 longitudinal rows of dorsal tubercles; 30 paravertebral tubercles; approximately 31 flat, imbricate, ventral scales larger than dorsal scales; eight pore-bearing precloacal scales; two rows of large postprecloacal scales; and no deep precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.16); flat scales of forearm larger than those on body, not interspersed with tubercles; palmar scales rounded, slightly raised; digits well-developed, relatively short, inflected at basal, interphalangeal joints; digits slightly narrower distal to inflections; claws well-developed, sheathed by a dorsal and ventral scale; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.17), covered dorsally by granular scales interspersed with large, conical, keeled tubercles and anteriorly by flat, slightly larger scales; ventral scales of femora flat, imbricate, larger than dorsals, 8(R)9(L) pore-bearing femoral scales; 9(R)11(L) enlarged femoral scales not continuous with enlarged precloacal scales; small postfemoral scales form an abrupt union with large, flat ventral scales of posteroventral margin of thigh; subtibial scales flat, imbricate; plantar scales low, flat; digits relatively short, well-developed, inflected at basal, interphalangeal joints; 6(R)7(L) small, unmodified, subdigital lamellae proximal to joint inflection on fourth toe; 13(R,L) slightly larger subdigital lamellae distal to inflection including the large subinflection scale and the ventral claw sheath; and claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail moderate in proportions, 5.9 mm in width at base, tapering to a point, first 35 mm of tail original, last 27 mm regenerated; dorsal scales of base of tail granular rapidly becoming flatter posteriorly; median row of transversely enlarged subcaudal scales twice as wide as long, not extending onto lateral margin of tail; two enlarged postcloacal tubercles on both sides of base of tail; and postcloacal scales flat.

Coloration in life (Fig. 13)*:* Dorsal ground colour of head body, limbs and tail yellow; dark, transverse bar present on rostrum; top of head bearing a large, dark-brown, irregularly shaped, smoothly edged chevron followed by a large medial spot; labial regions white, forming a distinct line of demarcation between them and a darkly coloured rostrum; wide, dark-brown, nuchal loop extending discontinuously from posterior border of one eye to the other, bearing a straight posterior border, no anterior, azygous notch; wide, dark-brown, band on neck beginning and ending just posterior to ear openings followed by four, wide, dorsal hourglass-shaped bands arranged as medially confluent, large, paravertebral ellipses; bands wider than interspaces, lacking lightened centres, edged with bright-yellow tubercles; one hourglass-shaped post-sacral band; generally no dark markings or white tubercles in interspaces; lower flanks bearing a row of large, dark-brown, circular markings edged in yellow; weak ventrolateral fold, anterodorsal margins of thigh and brachia pigmented not whitish; limbs bearing dark, irregularly shaped bands; four dark and five light caudal bands on original position of tail; light caudal bands immaculate not encircling tail; dark caudal bands wider than light caudal bands; regenerated portion of tail gray bearing darker, irregular markings; and all ventral surfaces generally immaculate.

Figure 14. Microhabitat structure of ***Cyrtodactylus pyinyaungensis* sp. nov.** 5.3 km north of Pyinyaung Village in the Sai Taung Range at the Apache Cement factory mining site, Mandalay Region, Myanmar.

Variation (Fig. S2): The paratypes closely approximate the holotype in all aspects of coloration and pattern. BYU 52234 and 13147 tend to have a more white than yellow ground colour. The posterior body bands of LSUHC 13150 are more obliquely oriented. The interspaces and light areas on the top of the head in LSUHC 13147 are less immaculate. Meristic differences are listed in Table 6.

Distribution: Cyrtodactylus pyinyaungensis sp. nov. is known only from the type locality 5.3 km north of Pyinyaung Village, Mandalay Region (Fig. 2) and the adjacent hills in the Sai Taung Range 2.5 km directly east. It is presumed *C. pyinyaungensis* sp. nov. ranges much farther in all directions through the hilly lowlands of this region.

Etymology: The specific epithet, *pyinyaungensis* (pronounced *pin-yong-ensis*), is a noun in apposition in reference to the type locality.

Natural history: The holotype and the paratypes (LSUHC 13147–48, 13150) were collected in highly disturbed habitats in a low range of mudstone hills (Fig. 14). The area was being burned at the time of collection and the small fires throughout these hills and the surrounding hills will burn for months until the onset of the monsoon season in early to mid-June.

Table 7. Summary statistics and diagnostic characters separating ***Cyrtodactylus pyinaungensis* sp. nov.,** *C. peguensis* and *C. annandalei*

	***pyinyaungensis* sp. nov.**	*peguensis*	*annandalei**
Summary statistics			
Supralabial scales (SL)			
Mean	8.0	9	/
SD	0	0	/
Range	8	9	7 or 8
N	5	2	3
Infralabial scales (IL)			
Mean	6.0	7	/
SD	0	0	/
Range	6	7	10
N	5	2	3
Paravertebral tubercles (PVT)			
Mean	28.2	25	/
SD	2.49	0	/
Range	25–30	25	/
N	5	2	/
Longitudinal rows of body tubercles (LRT)			
Mean	16.4	14	/
SD	1.14	0	/
Range	15–18	14	16–18
N	5	2	3
Ventral scales (VS)			
Mean	31.8	44.0	/
SD	2.49	1.0	/
Range	30–36	43–45	43
N	5	2	3
Expanded fourth toe lamellae (4TLE)			
Mean	5.2	7	/
SD	±0.45	0	/
Range	5 or 6	7	/
N	5	2	/
Unmodified fourth toe lamellae (4TLU)			
Mean	11.8	12	/
SD	±0.84	0	/
Range	11–13	12	/
N	5	2	/
Total fourth toe lamellae (4TL)			
Mean	17.0	19	/
SD	±1.22	0	/
Range	16–19	19	10
N	5	2	3
Enlarged femoral scales (FS)			
Mean	21.0	/	/
SD	1.41	/	/
Range	20–23	0	0
N	5	2	3
Enlarged femoral pores (FS)			
Mean	17.5	0	/
SD	1.0	0	/
Range	17 or 18	0	10 or 11
N	2	0	1
Enlarged precloacal scales (PS)			

Table 7. *Continued*

	***pyinyaungensis* sp. nov.**	*peguensis*	*annandalei**
Mean	8.0	7.5	/
SD	0	0.50	/
Range	8	7 or 8	8–12
N	5	2	3
Precloacal pores (PP)			
Mean	8	7.5	/
SD	0	0.50	/
Range	8	7 or 8	11 or 12
N	2	2	3
Post-precloacal scale rows (PPS)			
Mean	2	3	/
SD	0	0	/
Range	2	3	/
N	3	3	/
Body bands (BB)			
Mean	5.8	6	/
SD	0.45	0	/
Range	5 or 6	6	5
N	5	2	3
Light caudal bands (LCB)			
Mean	10.8	12	/
SD	1.71	0	/
Range	9–13	12	11
N	4	1	3
Dark caudal bands (DCB)			
Mean	11.0	12	/
SD	1.63	0	/
Range	9–13	12	11 or 12
N	4	1	3
Morphology			
Body tubercles low, weakly keeled	No	Yes	No
Body tubercles raised, moderately to strongly keeked	Yes	No	Yes
Tubercles extend beyond base of tail	No	No	No
Enlarged femoral scales present	Yes	No	No
Enlarged femoral and precloacal scales continuous	No	/	/
Pore-bearing femoral and precloacal scales continuous	/	/	/
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	/	/
Medial subcaudal scales two or three times wider than long	Yes	Yes	Yes
Medial subcaudal extend onto lateral surface of tail	No	No	No
Colour pattern			
Nuchal loop divided medially	No	No	No
Nuchal loop with anterior azygous notch	No	No	No
Posterior border of nuchal loop	Straight	Straight	Straight
Band on nape	Yes	Yes	Yes
Dorsal banding with paravertebral elements	Yes	Yes	No
Paravertebral elements of dorsal bands confluent	Yes	No	/
Dorsal bands wider than interspaces	Yes	Yes	No
Dorsal bands bearing lightened centres	No	Yes	No
Dorsal bands edged with light-coloured tubercles	Yes	Yes	No
Shape of dorsal bands	Hourglass	Paired blotches	Diagonal
Dark markings in dorsal interspaces	No	No	No

Table 7. *Continued*

	***pyinyaungensis* sp. nov.**	*peguensis*	*annandalei**
Ventrolateral body fold whitish	No	No	/
Top of head diffusely mottled, blotched or unicolour	Blotched	Blotched	Unicolour
Light reticulum on top of head	No	No	No
Anterodorsal margin of thighs darkly pigmented	No	No	No
Anterodorsal margin of brachia darkly pigmented	No	No	No
Light caudal bands bearing dark markings	Variable	Yes	Variable
Light caudal bands encircle tail	No	No	/
Dark caudal bands wider than light caudal bands	Yes	Yes	No
Mature regenerated tail spotted	No	No	/
Maximum SVL (mm)	71.7	70.2	55.3

/, data were unobtainable or not applicable.
*Data from Bauer (2003).

Nonetheless, five specimens were observed in two nights. BYU 52234 was collected during October of the previous year (2016) approximately 0.3 m above the ground on the side of a karst boulder. The collection site is situated at the lower end of a steeply sloping valley composed of disturbed secondary forest, scattered outcroppings of karst boulders and shallow lateral drainages feeding into the valley floor at 642 m elevation. Only one specimen was seen in this habitat in four nights of searching. These observations suggest that *C. pyinyaungensis* sp. nov. is a habitat generalist in hilly areas bearing rocky substrates. One hatchling was observed on 29 March 2017 but no gravid females were found.

Comparisons: Cyrtodactylus pyinyaungensis sp. nov. is part of a large clade of Indo-Burmese species within which it is closely related to *C. annandalei* from which it differs in having six vs. ten infralabial scales; 16–19 vs. ten total subdigital lamellae on the fourth toe; 30–36 vs. 43 ventral scales; 17 or 18 vs. ten or 11 femoral pores; eight vs. 11 or 12 precloacal pores; the presence vs. the absence of enlarged femoral scales; the dorsal bands being wider as opposed to narrower than the interspaces and edged with light-coloured tubercles; the dark caudal bands being wider than the light caudal bands; and the top of the head being blotched as opposed to patternless (Table 7). The sister population of *C. pyinyanugensis* sp. nov. from Popa Mountain approximately 120 km to the west was misidentified as *C. feae* (USNM 559805; Wood *et al.*, 2012 and Agarwal *et al.*, 2014) and was reported to L.L.G. to be *C. peguensis* (G. R. Zug, unpubl. data). Although we do not have access to this specimen, a comparison of its sister species, *C. pyinyaungensis* sp. nov., to one of the syntypes of *C. peguensis* (BMNH 1946.8.23.10) shows that although they are similar in overall colour pattern (Fig. 13), they differ in that the former has fewer rows of longitudinal tubercles (11 vs. 14); fewer ventral scales (30–36 vs. 43–45); enlarged femoral scales; and femoral pores (Table 7); and dorsal pattern composted of confluent paravertebral markings as opposed to large, separate, paravertebral spots (Fig. 13). Genetic distances among the species of this group range from 11.3 to 15.1%.

The intermedius *group*

The monophyletic *intermedius* group is the sister lineage to the *linnwayensis* group (Fig. 9) and ranges from Hon Tre and Phu Quoc islands and isolated mountainous regions in the Mekong Delta of southern Vietnam west through the Cardamom Mountains of southern Cambodia and south-eastern Thailand (Grismer *et al.*, 2015b; Fig. 2) and is composed of *Cyrotdactylus intermedius* (Smith), *C. phuquocensis* Ngo, Grismer & Grismer, and *C. hontreensis* Ngo, Grismer & Grismer. The *intermedius* group is defined by the following characters (Ngo, Grismer & Grismer, 2008, 2010): 9–13 supralabials; 9–12 infralabials; 14–22 longitudinal rows of dorsal tubercles; 38–50 ventral scales; 15–19 subdigital lamellae on the fourth toe; no enlarged femoral not contiguous with enlarged precloacal scales; 7–10 precloacal pores in males; post-preclocal scales large; wide, transverse caudal scales; top of head unicolour to sparsely blotched; no anterior azygous notch in nuchal loop or first body band; no band on nape; 3–5 regularly shaped body bands with lightened centres and edged with light tubercles or markings; anterodorsal margins of thighs, brachia and ventrolateral fold not pigmented; and maximum SVL 72.3–78.0 mm.

The linnwayensis *group*

The *linnwayensis* group is a monophyletic group composed of the sister species *Cyrtodactylus linnwayensis* sp. nov.

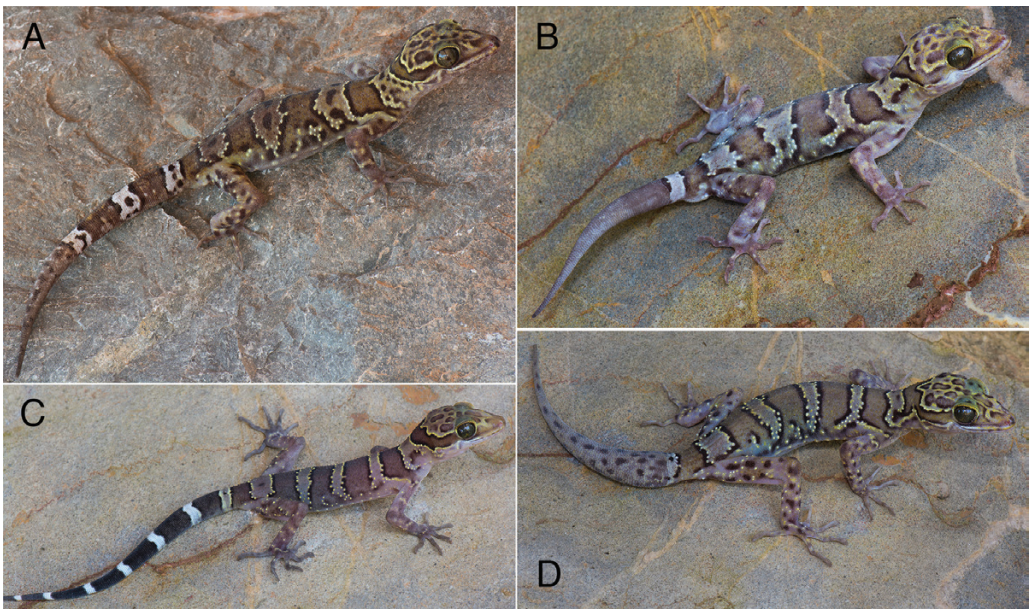

Figure 15. Colour pattern variation in ***Cyrtodactylus linnwayensis* sp. nov.** from the type locality of Yum Twing Gyi and Yae Htwat caves, Linn-Way Village, 12.7 km north-east of Ywarngan, Taunggyi District, Shan State, Myanmar. A, adult male holotype (LSUHC 12983) from Yum Twing Gyi Cave. B, C and D are adult male paratype (LSUHC 12971), subadult male paratype (LSUHC 12973) and adult female paratype (LSUHC 12972), respectively, from Yae Htwat Cave.

and *C. shwetaungorum* sp. nov. (Fig. 9) and range through the western regions of the Shan Hills of the Mandalay Region and Shan State (Fig. 2). This group is defined by the following range of characters 7–9 supralabials; 6–8 infralabials; dorsal body tubercles low, weakly keeled, not extending beyond base of tail; 25–35 paravertebral tubercles; 13–21 longitudinal rows of tubercles; 33–42 ventral scales; 20–23 subdigital lamellae on the fourth toe; enlarged femoral and precloacal scales continuous; 24–32 enlarged femoral scales nearly the same size throughout; 15–22 femoral pores in males; 8–12 enlarged precloacal scales; 6–11 precloacal pores in males; three or four post-precloacal scale rows; transverse caudal scales twice as wide as long, not extending onto lateral subcaudal regions; top of head mottled and bearing light-coloured, reticulated pattern; no band on nape; three or four regular (vs. zigzagged) body bands with lightened centres and edged with light tubercles; anterodorsal margins of thighs, brachia and ventrolateral fold pigmented; eight or nine light caudal bands; 7–9 dark caudal bands; and maximum SVL 101.7–102.2 mm (Table 7). The description and diagnosis of each species follows.

CYRTODACTYLUS LINNWAYENSIS SP. NOV.

LINN-WAY BENT-TOED GECKO

(FIG. 15; TABLE 9)

Holotype: Adult male LSUHC 12983 collected on 15 October 2016 at 1500 h by Evan S. H. Quah, L. Lee Grismer, Perry L. Wood, Jr., Myint Kyaw Thura, Thaw Zin, Matthew L. Murdoch and Htet Kyaw from the Yum Twing Gyi Cave, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°12.964, E96°33.288; 1130 m in elevation).

Paratypes: Adult males LSUHC 12984 and BYU 52214 and adult female LUSHC 12986 bear the same collection data as the holotype. Adult male LSUHC 12980, subadult male BYU 52213 and juvenile male LSUHC 12981 bear the same collection data as the holotype except they were collected from an adjacent cave (Lay Htwat Cave) 20 m away between 1800 and 2000 h. Adult male and female LSUHC 12971–72, respectively, and juvenile males LSUHC 12970 and 19273 were collected on 14 October 2016 between 1500 and 2000 h by Myint Kyaw Thura, Evan S. H. Quah, L. Lee Grismer, Perry L. Wood, Jr., Thaw Zin, Matthew L. Murdoch, Marta S. Grismer and Htet Kyaw from the Yae Htwat Cave, Linn-Way Village, 13.3 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (N21°13.675, E96°33.403; 1132 m in elevation) and 1 km north of Yum Twing Gyi Cave.

Diagnosis: Cyrtodactylus linnwayensis sp. nov. differs from all congeners by having the unique combination of 7–9 supralabials; 6–8 infralabials; 25–33 paravertebral tubercles; 13–18 longitudinal rows of body tubercles; 34–42 ventral scales; relatively long digits with 8–10 expanded fourth toe subdigital lamellae proximal to the

Table 8. Summary statistics and diagnostic characters of the new species from the Burmese species groups

	linnwayensis group		*sadansineensis* group		
	***shwetaungorum* sp. nov.**	***linnwayensis* sp. nov.**	***pharpbaungensis* sp. nov.**	***sanpelensis* sp. nov.**	***sadansinensis* sp. nov.**
Summary statistics					
Supralabial scales (SL)					
Mean	8.3	8	9	9.6	9
SD	±0.71	±0.89	0	±0.62	±0.71
Range	7–9	7–9	9	9–11	8–10
N	8	11	4	16	5
Infralabial scales (IL)					
Mean	6.9	7	7	7.4	7.4
SD	±0.64	±0.63	0	±0.50	±0.55
Range	6–8	6–8	7	7 or 8	7 or 8
N	8	11	4	16	5
Paravertebral tubercles (PVT)					
Mean	33.1*	29.4*	29	28.9	26.8
SD	±1.36	±1.86	±0.82	±1.34	±1.30
Range	31–35	25–33	28–30	27–31	25–28
N	8	11	4	16	5
Longitudunal rows of body tubercles (LRT)					
Mean	18.9*	16.4*	13.5	13.3	10
SD	±0.99	±1.36	±1.00	±0.58	±0.71
Range	18–21	13–18	12–14	12–14	9–11
N	8	11	4	16	5
Ventral scales (VS)					
Mean	37.3	39.7	35.5	37.3	33.2
SD	±2.71	±2.37	±1.91	±2.05	±1.30
Range	33–40	34–42	34–38	35–41	31–34
N	8	11	4	16	5
Expanded fourth toe lamellae (4TLE)					
Mean	8.3	8.8	8.25	8.3	8.4
SD	±0.46	±0.6	±0.96	±0.45	±0.55
Range	8 or 9	8–10	7–9	8 or 9	8 or 9
N	8	11	4	16	5
Unmodified fourth toe lamellae (4TLU)					
Mean	12.4	13.1	12.8	12.7	14.4
SD	±0.92	±0.54	±0.96	±0.48	±0.89
Range	11–14	12–14	12–14	12 or 13	14–16
N	8	11	4	16	5

Table 8. *Continued*

	linnwayensis group		*sadansineensis* group		
	***shwetaungorum* sp. nov.**	***linnwayensis* sp. nov.**	***pharpbaungensis* sp. nov.**	***sanpelensis* sp. nov.**	***sadansinensis* sp. nov.**
Total fourth toe lamellae (4TL)					
Mean	20.6	21.9	21	20.9	22.8
SD	±0.92	±0.7	0	±0.68	±0.84
Range	20–22	21–23	21	20–22	22–24
N	8	11	4	16	5
Enlarged femoral scales (FS)					
Mean	28.1	27.9	31	16.6	21.4
SD	±2.59	±2.26	±2.60	±1.67	±1.67
Range	24–32	24–32	28–34	14–20	19–23
N	8	11	4	16	5
Femoral pores (FP)					
Mean	15.7	17.6	17.3	12.4	20.5
SD	±1.15	±4.28	±2.50	±2.82	±0.50
Range	15–17	10–22	14–20	8–16	20 or 21
N	3	7	4	8	2
Enlarged precloacal scales (PS)					
Mean	9.8	10.5	9.8	10.6	13.6
SD	±0.89	±1.13	±1.00	±0.89	±1.14
Range	8–11	9–12	9–11	9–12	12–15
N	8	11	4	16	5
Precloacal pores (PP)					
Mean	10	8	7	7.25	13.0
SD	±1.73	±2.12	±1.41	±0.46	±1.00
Range	8–10	6–10	5–8	7 or 8	12–14
N	3	9	4	8	2
Post-precloacal scale rows (PPS)					
Mean	3	4	2	2	3
SD	0	0	0	0	0
Range	3	4	2	2	3
N	3	11	4	16	5
Body bands (BB)					
Mean	4	3.5	5.8	5	5
SD	0	±0.52	±0.5	±0.37	0
Range	4	3 or 4	5 or 6	4 or 5	5
N	8	11	4	16	5

Table 8. *Continued*

	linnwayensis group		*sadansineensis* group		
	***shwetaungorum* sp. nov.**	***linnwayensis* sp. nov.**	***pharpbaungensis* sp. nov.**	***sanpelensis* sp. nov.**	***sadansinensis* sp. nov.**
Light caudal bands (LCB)					
Mean	8.3	8.2	7.3	8.3	10
SD	±0.58	±0.45	±1.15	±1.11	±1.00
Range	8 or 9	8 or 9	6–8	7–10	9–11
N	3	9	3	6	2
Dark caudal bands (DCB)					
Mean	8.3	8.4	8.3	8.1	9
SD	±1.15	±0.55	±1.15	±1.35	±1.00
Range	7–9	8 or 9	7–9	7–10	8–10
N	3	9	3	6	2
Morphology					
Body tubercles low, weakly keeled	Yes	Yes	Variable	Yes	Yes
Body tubercles raised, moderately to strongly keeked	No	No	Variable	No	No
Tubercles extend beyond base of tail	No	No	No	No	No
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes	No	No
Pore-bearing femoral and precloacal scales continuous	No	No	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No	No	No
Medial subcaudal scales two or three times wider than long	2	2	3	3	3
Medial subcaudal extend onto lateral surface of tail	No	No	Yes	Yes	Yes
Colour pattern					
Nuchal loop divided medially	No	1(Yes),10(No)	No	No	No
Nuchal loop with anterior azygous notch	No	Yes	No	No	No
Posterior border of nuchal loop	Straight	Usually straight	Straight	Straight/sinuous	Sinuous

Table 8. *Continued*

	linnwayensis group		*sadansineensis* group		
	***shwetaungorum* sp. nov.**	***linnwayensis* sp. nov.**	***pharpbaungensis* sp. nov.**	***sanpelensis* sp. nov.**	***sadansinensis* sp. nov.**
Band on nape	No	No	Yes	Yes	Yes
Dorsal banding with paravertebrtal elements	No	No	No	No	No
Dorsal bands wider than interspaces	Yes	Variable	Same or no	Same or no	Same or no
Dorsal bands bearing lightened centres	Yes	Yes	Yes	Yes	Yes
Dorsal bands edged with light-coloured tubercles	Yes	Yes	No	No	No
Shape of dorsal bands	Regular	Variable	Regular	Regular	Regular
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	No	No	Variable	Yes	No
Top of head diffusely mottled, blotched or patternless	Blotched	Blotched	Mottled	Mottled	Mottled
Light reticulum on top of head	Yes	Yes	No	No	No
Anterodorsal margin of thighs darkly pigmented	Yes	Yes	No	No	Yes
Anterodorsal margin of brachia darkly pigmented	Yes	Yes	Variable	No	Yes
Light caudal bands bearing dark markings	No	5(Yes)1(No)	Yes	Yes	Yes
Light caudal bands encircle tail	Yes	Variable	No	No	No
Dark caudal bands wider than light caudal bands	Yes	Yes	Variable	Yes	Same or no
Mature regenerated tail spotted	No	Yes	/	No	No
Maximum SVL (mm)	102.2	101.7	70.4	73.9	69.6

Table 8. *Continued*

	sinyineensis group				*yathepyanensis* group		
	***dammathetensis* sp. nov.**	*aequalis*	***sinyineensis* sp. nov.**	***welpyanensis* sp. nov.**	***linnoensis* sp. nov.**	***sadanensis* sp. nov.**	***yathepyanensis* sp. nov.**
Summary statistics							
Supralabial scales (SL)							
Mean	9	8	9.7	8.3	9.5	10.4	9.6
SD	0	0	±0.58	±0.6	±0.52	±0.51	±0.55
Range	9	8	9 or 10	8 or 9	9 or 10	10 or 11	9 or 10
N	3	1	3	3	11	15	5
Infralabial scales (IL)							
Mean	7.7	6	8	7	7.3	8	8.4
SD	±0.58	0	0	0	±0.47	±0.53	±0.55
Range	7 or 8	6	8	7	7 or 8	7–9	8 or 9
N	3	1	3	3	11	15	5
Paravertebral tubercles (PVT)							
Mean	31.7	36	33.7	31.7	26.3	31.5	31.6
SD	±1.15	0	±1.2	±1.5	±0.47	±1.13	±0.55
Range	31–33	36	33–35	30–33	26 or 27	30–33	31 or 32
N	3	1	3	3	11	15	5
Longitudunal rows of body tubercles (LRT)							
Mean	14.3	19	15	16	13.5	14.3	18.4
SD	±1.15	0	0	0	±0.82	±0.70	±0.55
Range	13–15	19	15	16	13–15	13–15	18 or 19
N	3	1	3	3	11	15	5
Ventral scales (VS)							
Mean	26.7	19	28	29.3	36.9	32.0	30.6
SD	±1.53	0	±1.0	±1.2	±1.04	±1.73	±0.89
Range	25–28	19	27–29	28–30	35–38	30–35	30–32
N	3	1	3	3	11	15	5
Expanded fourth toe lamellae (4TLE)							
Mean	8.7	9	9	8	9.3	8.5	8.8
SD	±0.58	0	±1.0	0	±0.47	±0.74	±0.45
Range	8 or 9	9	8–10	8	9 or 10	7–9	8 or 9
N	3	1	3	3	11	15	5
Unmodified fourth toe lamellae (4TLU)							
Mean	12.3	13	11.3	12	13.9	13.7	13.2
SD	±0.58	0	±0.58	±1.0	±0.3	±0.49	±0.84
Range	12 or 13	13	11 or 12	11–13	13 or 14	13 or 14	12–14
N	3	1	3	3	11	15	5

Table 8. *Continued*

	sinyineensis group				*yathepyanensis* group		
	***dammathetensis* sp. nov.**	*aequalis*	***sinyineensis* sp. nov.**	***welpyanensis* sp. nov.**	***linnoensis* sp. nov.**	***sadanensis* sp. nov.**	***yathepyanensis* sp. nov.**
Total fourth toe lamellae (4TL)							
Mean	21.0	22	20.3	20	23.2	22.1	22
SD	0	0	±1.6	±1.0	±0.6	±0.74	±1.22
Range	21	22	19–21	19–21	22–24	21–23	20–23
N	3	1	3	3	11	15	5
Enlarged femoral scales (FS)							
Mean	33.0	25	26.3	30.3	24.1	37.9	30.6
SD	±2.65	0	±0.58	±0.58	±9.33	±2.22	±3.71
Range	31–36	25	26 or 27	30–31	12–37	34–41	25–34
N	3	1	3	3	11	15	5
Femoral pores (FP)							
Mean	36.0	13	16	20	12.8	12.0	14
SD	0	0	0	0	±1.04	0	0
Range	36	13	16	20	12–14	12	14
N	1	1	1	2	8	3	1
Enlarged precloacal scales (PS)							
Mean	8.3	5	11	12	11.5	11.9	10.8
SD	±0.58	0	±1.0	±1.0	±1.44	±0.80	±1.3
Range	8 or 9	5	10–12	11–13	9–13	10–13	10–13
N	3	1	3	3	11	15	5
Precloacal pores (PP)							
Mean	9	5	5	7.5	5.1	2.3	6
SD	0	0	0	±0.5	±0.39	±1.15	0
Range	9	5	5	7 or 8	4–6	2 or 3	6
N	1	1	1	2	8	3	1
Post-precloacal scale rows (PPS)							
Mean	3.0	3	3	3	3.2	3.0	3
SD	0	0	0	0	±0.4	0	0
Range	3	3	3	3	3 or 4	3	3
N	3	1	3	3	11	15	5
Body bands (BB)							
Mean	5.0	5.5	5.5	6	5.9	5.5	5
SD	0	0	±0.71	0	±0.3	±0.52	±0.45
Range	5	5.5	5 or 6	6	5 or 6	5 or 6	4–6
N	3	1	2	3	11	15	11

Table 8. *Continued*

	sinyineensis group				*yathepyanensis* group		
	***dammathetensis* sp. nov.**	*aequalis*	***sinyineensis* sp. nov.**	***welpyanensis* sp. nov.**	***linnoensis* sp. nov.**	***sadanensis* sp. nov.**	***yathepyanensis* sp. nov.**
Light caudal bands (LCB)							
Mean	10.3	9	9	9	15	16	13
SD	±0.71	0	0	0	0	0	0
Range	10 or 11	9	9	9	15	16	13
N	3	1	1	1	1	2	1
Dark caudal bands (DCB)							
Mean	10.7	9	9	10	14	17	13
SD	±0.71	0	0	0	0	0	0
Range	10 or 11	9	9	10	14	17	13
N	3	1	1	1	1	2	1
Morphology							
Body tubercles low, weakly keeled	No	No	No	No	No	No	No
Body tubercles raised, moderately to strongly keeked	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Tubercles extend beyond base of tail	Yes	Yes	Yes	No	Yes	Yes	Yes
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes	Yes	Variable	No	Yes
Pore-bearing femoral and precloacal scales continuous	Yes	No	No	No	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	Yes	No	No	No	Yes	Yes	Yes
Medial subcaudal scales two or three times wider than long	3	2	2	2	2	3	3
Medial subcaudal extend onto lateral surface of tail	Yes	No	No	No	Yes	Yes	Yes
Colour pattern							
Nuchal loop divided medially	Variable	Yes	No	No	Variable	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No	No	No
Posterior border of nuchal loop	Jagged	Straight	Jagged	Jagged	Variable	Variable	Variable
Band on nape	Yes	Yes	Yes	Yes	Yes	Yes	Yes

Table 8. *Continued*

	sinyineensis group				*yathepyanensis* group		
	***dammathetensis* sp. nov.**	*aequalis*	***sinyineensis* sp. nov.**	***welpyanensis* sp. nov.**	***linnoensis* sp. nov.**	***sadanensis* sp. nov.**	***yathepyanensis* sp. nov.**
Dorsal banding with paravertebrtal elements	Yes	Yes	No	No	No	No	No
Dorsal bands wider than interspaces	Yes	Yes	Yes	Yes	Yes	No	Same
Dorsal bands bearing lightened centres	No	No	Weak	No	Faint	Faint	No
Dorsal bands edged with light-coloured tubercles	No	Yes	Yes	No	Yes	Partly	Yes
Shape of dorsal bands	Jagged	/	Jagged	Jagged	Jagged	Weakly jagged	Regular
Dark markings in dorsal interspaces	Yes	No	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	Faintly	No	No	Yes	Yes	Faint	Yes
Top of head diffusely mottled, blotched or patternless	Mottled	No	Mottled	Mottled	Mottled	Mottled	Mottled
Light reticulum on top of head	No	Mottled	No	No	No	No	No
Anterodorsal margin of thighs darkly pigmented	Yes	Yes	Yes	Yes	No	No to faint	Yes
Anterodorsal margin of brachia darkly pigmented	Yes	Yes	Yes	Yes	Faint to yes	Variable	Yes
Light caudal bands bearing dark markings	No	No	Yes	Yes	Yes	Yes	Yes
Light caudal bands encircle tail	No	Yes	No	No	No	No	No
Dark caudal bands wider than light caudal bands	Yes	No	Yes	Yes	Yes	Same or yes	Yes
Mature regenerated tail spotted	/	Yes	No	No	No	No	No
Maximum SVL (mm)	69.3	87.0	91.6	70.6	78.0	73.8	72.7

SD, standard deviation; *N*, sample size.
*Significant statistical differences between means.

Table 9. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus linnwayeneis*** **sp. nov.**

Locality	LSUHC 12983 holotype	LSUHC 12984 paratype	BYU 52214 paratype	LSUHC 12986 paratype	LSUHC 12980 paratype	LSUHC 12981 paratype	BYU 52213 paratype	LSUHC 12970 paratype	LSUHC 12971 paratype	LSUHC 12972 paratype	LSUHC 12973 paratype
	Yum Twing Gyi	Yum Twing Gyi	Yum Twing Gyi	Yum Twing Gyi	Lay Htwat	Lay Htwat	Lay Htwat	Yae Htwat	Yae Htwat	Yae Htwat	Yae Htwat
Sex	M	M	M	F	M	M	M	M	M	F	M
Supralabials	7	9	7	9	8	8	8	7	7	9	9
Infralabials	7	7	7	6	7	7	8	7	6	8	7
Body tubercles low, weakly keeled	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Body tubercles raised, moderately to strongly keeked	No	No	No	No	No	No	No	No	No	No	No
Paravertebral tubercles	29	29	29	29	30	30	30	30	25	33	29
Longitudinal rows of body tubercles	13	16	16	17	17	17	17	15	17	18	17
Tubercles extend beyond base of tail	No	No	No	No	No	No	No	No	No	No	No
Ventral scales	42	39	38	40	42	39	39	42	34	41	41
Expanded subdigital lamellae on fourth toe	10	9	9	9	9	9	8	8	9	9	8
Unmodified subdigital lamellae on fourth toe	13	12	13	14	13	13	13	13	13	13	14
Total subdigital lamellae on fourth toe	23	21	22	23	22	22	21	21	22	22	22
Enlarged femoral scales (R/L)	14RL	13RL	14RL	14R/13	15RL	11R13L	13RL	15R12L	16R14L	17R15L	14RL
Femoral pores (R/L)	11R10L	9R8L	5RL	/	10R9L	/	7RL	/	11R11L	/	10R10L
Enlarged precolacal scales	12	11	10	9	10	11	9	12	10	10	12
Precloacal pores	10	8	6	/	8	7	8	9	10	/	9
Post-precloacal scales rows	4	4	4	4	4	4	4	4	4	4	4
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Pore-bearing femoral and precloacal scales continuous	No	No	No	No	No	No	No	No	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No	No	No	No	No	No	No	No	No
Medial subcaudals two or three times wider than long	2	2	2	2	2	2	2	2	/	2	2

Table 9. *Continued*

Locality	LSUHC 12983 holotype	LSUHC 12984 paratype	BYU 52214 paratype	LSUHC 12986 paratype	LSUHC 12980 paratype	LSUHC 12981 paratype	BYU 52213 paratype	LSUHC 12970 paratype	LSUHC 12971 paratype	LSUHC 12972 paratype	LSUHC 12973 paratype
	Yum Twing Gyi	Yum Twing Gyi	Yum Twing Gyi	Yum Twing Gyi	Lay Htwat	Lay Htwat	Lay Htwat	Yae Htwat	Yae Htwat	Yae Htwat	Yae Htwat
Medial subcaudals extend onto lateral surface of tail	No	No	No	No	No	No	No	No	No	No	No
Nuchal loop divided medially	No	Yes	No	No	No	No	No	No	No	No	No
Nuchal loop with anterior azygous notch	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Posterior border of nuchal loop	Straight	Straight	Straight	Straight	Straight	Straight	Straight	Straight	Sinuous	Straight	Straight
Band on nape	No	No	No	No	No	No	No	No	No	No	No
Dorsal banding with paravertebral elements	No	No	No	No	No	No	No	No	No	No	No
Number of body bands	3	4	4	3	3	4	3	4	3	4	4
Dorsal bands wider than interspaces	Yes	Same	Yes	No	No	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal bands bearing lightened centres	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal bands edged with light tubercles	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal band borders	Variable	Smooth	Smooth	Variable	Variable	Smooth	Smooth	Smooth	Variable	Smooth	Smooth
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	No	No	No	No	No	No	No	No	No	No	No
Top of head diffusely mottled, blotched or patternless	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched
Light reticulum on top of head	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Anterodorsal margin of thighs darkly pigmented	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Anterodorsal margin of brachia darkly pigmented	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Light caudal bands bearing dark markings	Yes	Yes	/	/	/	No	Yes	Yes	/	/	Yes

Table 9. *Continued*

Locality	LSUHC 12983 holotype	LSUHC 12984 paratype	BYU 52214 paratype	LSUHC 12986 paratype	LSUHC 12980 paratype	LSUHC 12981 paratype	BYU 52213 paratype	LSUHC 12970 paratype	LSUHC 12971 paratype	LSUHC 12972 paratype	LSUHC 12973 paratype
	Yum Twing Gyi	Yum Twing Gyi	Yum Twing Gyi	Yum Twing Gyi	Lay Htwat	Lay Htwat	Lay Htwat	Yae Htwat	Yae Htwat	Yae Htwat	Yae Htwat
Light caudal bands encircle tail	No	No	/	/	/	No	No	Yes	/	/	Yes
Number of light caudal bands	/	8	/	/	/	9	8	8	/	/	8
Number of dark caudal bands	/	9	/	/	/	9	8	8	/	/	8
Dark caudal bands wider than light caudal bands	Yes	Yes	/	/	/	Yes	Yes	Yes	/	/	Yes
Mature regenerated tail spotted	Yes	/	Yes	/	Yes	/	/	/	/	Yes	/
SVL	101.5	92.3	100.2	99.7	101.3	62.5	81.5	61.2	101.7	98.1	68.5
TL	97r	108.0	100r	12b	74r	72r	97.0	/	69r	86r	80.0
TW	9.7	9.5	9.5	9.5	11.6	6.1	7.9	5.7	11.5	9.4	6.6
FL	16.7	15.0	16.7	15.7	15.8	10.6	13.4	10.2	17.2	16.5	12.1
TBL	19.0	17.6	17.1	18.6	19.9	11.5	15.1	11.7	20.3	19.0	12.8
AG	44.0	39.7	43.6	45.1	42.0	26.9	33.8	25.1	42.3	42.1	28.5
HL	28.2	25.7	27.8	28.1	29.9	19.2	23.5	18.6	27.9	28.3	21.8
HW	20.4	18.3	20.3	20.1	21.8	12.8	16.0	13.1	20.3	19.7	13.9
HD	11.5	11.0	11.6	12.0	13.7	7.2	9.1	7.5	11.8	11.3	8.0
ED	6.1	5.9	6.1	6.8	6.6	4.8	5.1	4.3	6.8	6.7	4.5
EE	8.1	7.3	8.3	8.2	8.0	5.6	6.2	5.1	8.1	8.0	6.4
ES	12.3	10.4	12.2	11.9	11.6	8.0	9.8	7.2	12.3	11.0	8.3
EN	9.6	8.0	9.1	9.0	9.3	6.2	7.6	5.5	8.6	9.3	6.4
IO	7.8	6.3	7.3	8.2	6.7	5.2	6.4	4.5	7.3	7.8	5.3
EL	2.7	2.1	2.0	2.0	8.4	2.1	2.4	0.8	3.0	2.7	1.6
IN	3.3	3.1	3.1	3.2	3.1	2.1	3.2	2.4	3.3	3.1	2.7

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable; r, regenerated; b, broken.

digital inflection, 12–14 unmodified distal subdigital lamellae and 21–23 total subdigital lamellae; low, weakly keeled, dorsal body tubercles; tubercles not extending beyond base of tail; enlarged femoral and precloacal scales not continuous; 24–32 enlarged femoral scales; enlarged femoral scales nearly equal in size; 10–22 femoral pores in males not continuous with pore-bearing precloacal scales; 9–12 enlarged, precloacal scales; 6–10 precloacal pores in males; four rows of enlarged post-precloacal scales; transverse subcaudal scales twice as wide as long midway down the tail and not extending onto the lateral margins of the tail; top of head bearing dark blotches and light-coloured, reticulum; nuchal loop rarely paired, bearing an anterior, azygous notch, and nearly always having a smooth posterior border; first body band bearing an anterior, azygous notch; no band on nape; three or four dark, variably shaped dorsal bands with no paravertebral elements, bands usually as wide or wider than interspaces bearing lightened centres, edged with light tubercles; dark markings in dorsal interspaces but no light-coloured tubercles; anterodorsal margins of thighs, brachia and ventrolateral fold pigmented; eight or nine light caudal bands bearing dark markings in adults and usually encircling tail; nine dark caudal bands wider than light caudal bands; and mature regenerated tail spotted.

Description of holotype: Adult male SVL 101.5 mm; head moderate in length (HL/SVL 0.28), wide (HW/HL 0.72), flat (HD/HL 0.41), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region concave, canthus rostralis rounded; snout elongate (ES/HL 0.44), rounded in dorsal profile, broad in lateral profile; eye large (ED/HL 0.22); ear opening oval, small (EL/HL 0.10); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally, bordered posteriorly by left and right supranasals contacting on midline, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals and ventrally by first supralabial; 7(R,L) rectangular supralabials extending to below midpoint of eye; 7(R,L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, much larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with small tubercles; dorsal superciliaries weakly pointed and directed posteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals which contact medially for 70% of their length posterior to mental; two rows of variably enlarged chinshields border all infralabials; gular and throat scales granular, grading posteriorly into larger, subimbricate pectoral and ventral scales.

Body relatively short (AG/SVL 0.43) with well-defined ventrolateral folds; dorsal scales small, raised and interspersed with large, low, semi-regularly arranged, weakly keeled tubercles; tubercles extend from nape to base of tail but no farther; tubercles on nape smaller but sharper than those on posterior portion of body and less strongly keeled; 29 paravertebral tubercles; approximately 13 longitudinal rows of dorsal tubercles; 42 flat, subimbricate, ventral scales larger than dorsal scales; enlarged femoral and precloacal scales continuous; 28 enlarged, femoral scales; 21 femoral pores; 12 enlarged precloacal scales; ten precloacal pores; four rows of large, post-precloacal scales; and no deep precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.16); slightly raised, juxtaposed scales of forearm larger than those on body, intermixed with tubercles; palmar scales flat; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; widened proximal subdigital lamellae do not extend onto palm; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.19), covered dorsally by small, raised, juxtaposed scales intermixed with large tubercles and bearing flat, slightly larger scales anteriorly; ventral femoral scales imbricate, larger than dorsals; one row of 14(R,L) enlarged femoral scales in contact with enlarged precloacal scales; enlarged femoral scales nearly equal in size; 11(R)10(L) femoral pores; small, postfemoral scales form an abrupt union with larger, flat ventral scales of posteroventral margin of thigh; subtibial scales flat, imbricate; plantar scales flat; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 10(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection that do not extend onto sole, 13(R,L) unmodified subdigital lamellae distal to inflection; and claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail moderate in proportions, 97 mm in length, last 45 mm regenerated, 9.7 mm in width at base, tapering to a point; dorsal scales of tail flat; median row of transversely expanded subcaudal scales twice as wide as long, not extending onto lateral subcaudal region; two enlarged postcloacal tubercles at base of tail on left hemipenal swelling only; and postcloacal scales flat.

Coloration in life (*Fig. 15*)*:* Dorsal ground colour of head body, limbs and tail yellowish tan; top of head and rostrum bearing, diffuse, irregularly shaped, dark blotches outlined by a yellow reticulum; superciliary scales yellowish; dark nuchal loop outlined in yellow bearing an anterior, azygous

notch and straight, posterior margin; three wide body bands wider than interspaces, bearing lightened centres, lacking paravertebral elements, edged with yellowish tubercles; first dorsal band bearing an anterior, azygous notch; no band on nape; one postsacral band; anterior interspaces yellowish, posterior interspaces brown, all bearing large, dark markings; limbs mottled with yellowish markings and diffuse dark spots; dark caudal bands bearing lightened centres, wider than light caudal bands; light caudal bands bearing dark markings, not encircling tail; regenerated portion of tail bearing dark and light spots; all ventral surfaces beige, generally unpigmented; and subcaudal region darker.

Variation (*Fig. S2*)*:* There is a subtle colour pattern polymorphism in the banding pattern in the type series. The paratypes LSUHC 12971, 12980 and 12986 closely approximate the holotype in aspects of colour pattern by having three wide, light-brown, variably shaped, dorsal bands and mottled interspaces, whereas paratypes LSUHC 12972–73, 12984 and BYU 52214 have four darker, more regularly shaped dorsal bands and immaculate interspaces. LSUHC 12970 and 12981 are juveniles with incomplete posterior bands. The azygous nuchal notch is so deep in LSUHC 12984 the nuchal loop is completely bifurcated. In the holotype LSUHC 12983, the notch is closed anteriorly. LSUHC 12971 has a unicolour tan, newly regenerated tail, whereas the mature regenerated tails of LSUHC

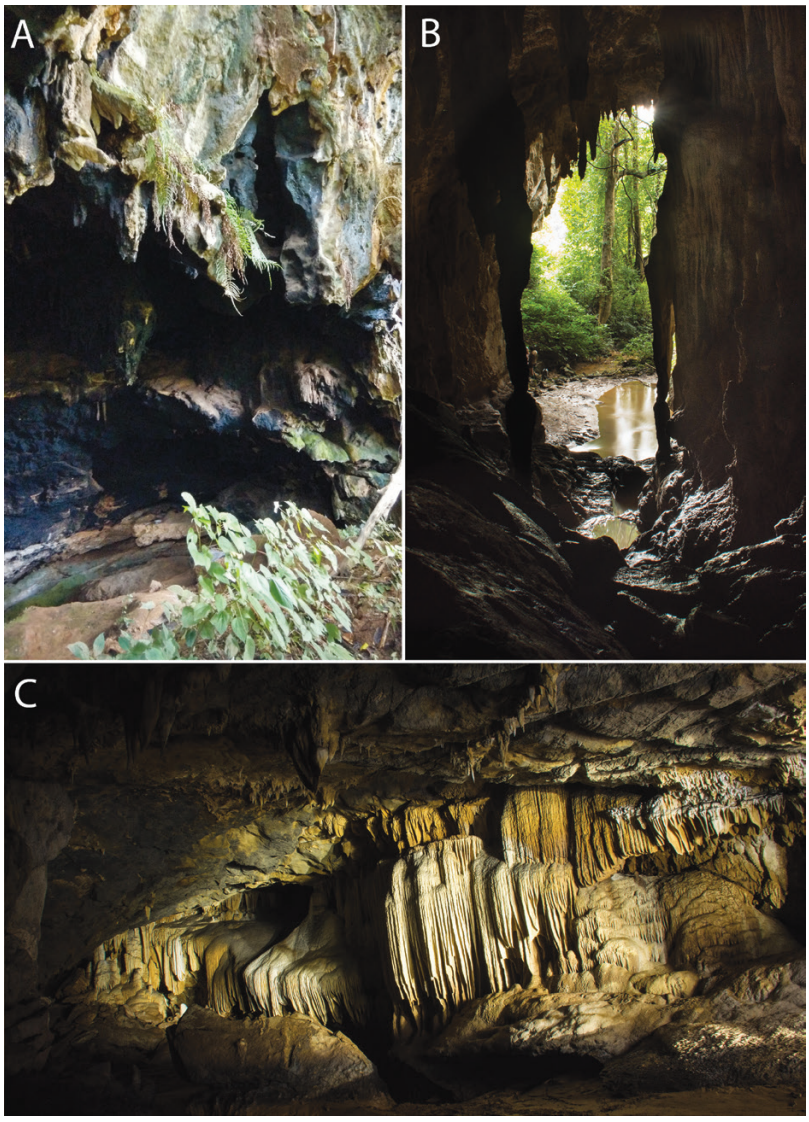

Figure 16. Cave mouths of Yae Htwat (A) and Lay Htwat Caves (B) and the interior of Yum Twing Gyu Cave (C), Shan State, Myanmar.

12972, 12980 and BYU 52214 have dark spots. The subcaudal scales of the regenerated scales in LSUHC 12970–72, 12980 and BYU 52214 are transversely elongate and irregularly arranged. Meristic and mensural differences are presented in Table 9.

Distribution: Cyrtodactylus linnwayensis sp. nov. is known only from Lay Htwat, Yae Htwat and Yum Twing Gyi caves near Linn-Way Village, 12.7–13.3 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar (Figs 2, 9).

Etymology: The specific epithet, *linnwayensis*, is a noun in apposition in reference to Linn-Way Village near the type locality.

Natural history: Lay Htwat, Yae Htwat and Yum Twing Gyi caves are situated along the same karst ridge that arcs around a low, flat depression that fills with water during the monsoon season. The northernmost cave, Yae Htwat, has a wide (~10 m), high (~40 m) opening formed by an underground river flowing out of the cave. The cave floor is approximately 10 m above the cave entrance and requires climbing to access it. Approximately 100 m back from the entrance, the cave opens up to 50–60 m in width. The centre of the cave has a small stream running though it and the cave floor is strewn with small, stream-worn stones. There are several cracks, holes and narrow side passages along the cave walls as well as several small to large stalactites and stalagmites and deep fissures (~15 m) bearing running water in the centre of the cave that provide the necessary microhabitat for geckos (Fig. 16). Between 1300 and 1500 h, one specimen was found approximately 100 m in from the cave entrance running across the cave floor near the wall in near total darkness and another was found 2 m up on the cave wall only 20 m in from the cave entrance where light was still plentiful. After dark, between 1900 and 2100 h, two additional specimens were found on the sides of boulders along the karst ridge outside the cave entrance.

Lay Htwat and Yum Twing Gyi caves are approximately 1 km south of Yae Htwat Cave and the openings of the former are no more than 30 m apart. Lay Htwat Cave has a 2 m by 2 m opening and the interior of the cave is congested with numerous, narrow passages, cracks, holes, cave formations of all sizes and shapes, and a deep underground stream. At 1800 h we collected one *C. linnwayensis* sp. nov. 2 m up on the cave wall along a side passage just inside the entrance. Yum Twing Gyi Cave has an approximately 60 m wide and 15 m high opening. This cave too has water but is much more open and the centre of the cave has several boulder formations that looked as though they had fallen from the roof. Stalactites, stalagmites and side passages occur throughout the cave and specimens were collected and observed on all these structures. During the evening between 1900 and 2200 h, we collected and observed additional specimens on the sides of karst boulders along the hilly ridge outside the caves. One juvenile (LSUHC 12981) was found on the trunk of a tree growing across a karst boulder.

Comparisons: Cyrtodactylus linnwayensis sp. nov. is part of the *linnwayensis* group. Student's *t*-tests indicate that *C. linnwayensis* sp. nov. and its sister species *C. shwetaungorum* are statistically different in their mean values of paravertebral tubercles and longitudinal rows of tubercles, generally indicating that *C. shwetaungorum* is more tuberculate than *C. linnwayensis* sp. nov. (Table 8). It differs further from *C. shwetaungorum* sp. nov. by having four vs. three rows of enlarged post-precloacal scale rows, a much lighter ground colour, light caudal bands that do not encircle the tail and a mature regenerated tail that is spotted (Table 8). The PCA analysis which loads most heavily for the total number of fourth toe lamellae and the number of post-precloacal scales—accounting for 54% of the total variation along the first two components (Table S1)— shows they occupy non-overlapping regions in morphospace (Fig. 12). The genetic distance between the species of this group is 10.2% (Table 10) and morphological and colour pattern differences from other species in the Indo-Chinese clade are listed in Table 8.

CYRTODACTYLUS SHWETAUNGORUM SP. NOV.

SHWETAUNG BENT-TOED GECKO

(FIG. 17; TABLE 11)

Holotype: Adult male LSUHC 12937 collected on 12 October 2016 at 1930 h by Thaw Zin, Evan S. H. Quah, L. Lee Grismer, Perry L. Wood, Jr., Myint Kyaw Thura, Matthew L. Murdoch and Htet Kyaw from 5.0 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.191, E96°24.296; 624 m in elevation).

Paratypes: Adult males LSUHC 12935 and BYU 52226 and subadult female BYU 52227 bear the same collection data as the holotype. Adult females LSUHC 12897 and BYU 52225 and juvenile female LSUHC 12896 were collected on 11 October 2016 between 1800 and 2200 h by L. Lee Grismer, Perry L. Wood, Jr., Myint Kyaw Thura, Evan S. H. Quah, Thaw Zin, Matthew L. Murdoch and Htet Kyaw from 5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region (N20°52.273, E96°24.319; 731 m in elevation).

Table 10. Percent uncorrected pairwise sequence divergence for species of the Burmese species groups calculated from 1548 base pairs of the mitochondrial gene *ND2*

	1	2	3	4	5	6	7	8	9	10	11	12
1. *C. aequalis*	*	*	*	*	*	*	*	*	*	*	*	*
2. ***C. dammathetensis* sp. nov.**	0.110	**0.005**	*	*	*	*	*	*	*	*	*	*
3. ***C. sadansineensis* sp. nov.**	0.210	0.244	**0.003**	*	*	*	*	*	*	*	*	*
4. ***C. linnoensis* sp. nov.**	0.236	0.239	0.181	**0.000**	*	*	*	*	*	*	*	*
5. ***C. linnwayensis* sp. nov.**	0.236	0.252	0.241	0.228	**0.000**		*	*	*	*	*	*
6. ***C. pharbaungensis* sp. nov.**	0.213	0.207	0.117	0.181	0.236	**0.000**	*	*	*	*	*	*
7. ***C. sadanensis* sp. nov.**	0.238	0.224	0.169	0.112	0.214	0.151	**0.007**	*	*	*	*	*
8. ***C. sanpelensis* sp. nov.**	0.172	0.191	0.131	0.181	0.220	0.087	0.135	**0.001**	*	*	*	*
9. ***C. shwetaungorum* sp. nov.**	0.268	0.252	0.249	0.244	0.102	0.244	0.230	0.228	**0.000**	*	*	*
10. ***C. sinyineensis* sp. nov**.	0.152	0.165	0.197	0.252	0.260	0.215	0.218	0.204	0.252	**0.010**	*	*
11. ***C. welpyanensis* sp. nov.**	0.134	0.148	0.184	0.228	0.236	0.203	0.194	0.176	0.250	0.118	**0.004**	*
12. ***C. yathepyanensis* sp. nov.**	0.277	0.278	0.197	0.110	0.225	0.213	0.127	0.184	0.233	0.246	0.242	**0.009**

Bolded percentages along the diagonal are intraspecific divergences.

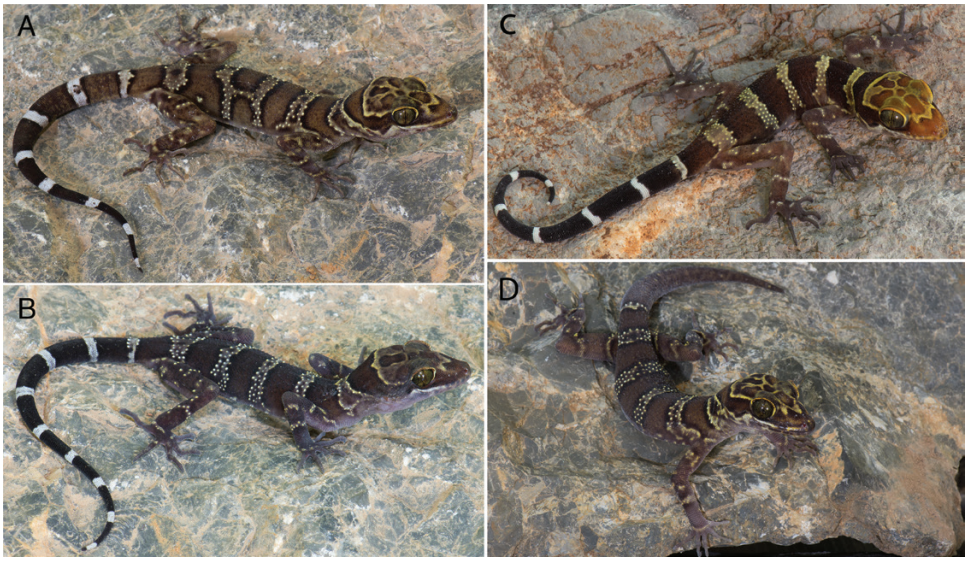

Figure 17. A, adult male holotype of ***Cyrtodactylus shwetaungorum* sp. nov.** (LSUHC 12937) from the type locality, 5.0 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region. B, subadult male paratype (BYU 52227) from the type locality. C, hatchling (LSUHC 13043) from the type locality. D, adult female (LSUHC 13097) from Pyinyaung River, 5 km south of the type locality.

Additional specimens observed: Hatchlings (LSUHC 13043–45) collected on 19 March 2017 from the type locality and adult female (LSUHC 13097) collected on 23 March 2017 from Pyinyuang River, 5 km south of the type locality.

Diagnosis: Cyrtodactylus shwetaungorum sp. nov. differs from all congeners by having the unique combination of 7–9 supralabials; 6–8 infralabials; 31–35 paravertebral tubercles; 18–21 longitudinal rows of body tubercles; 33–40 ventral scales; relatively long digits with eight or nine expanded subdigital lamellae on the fourth toe proximal to the digital inflection, 11–14 unmodified distal subdigital lamellae and 20–22 total subdigital lamellae; low, weakly keeled, dorsal body tubercles; tubercles not extending beyond base of tail; enlarged femoral and precloacal scales continuous; 24–32 enlarged femoral scales; enlarged femoral scales nearly equal in size; 15–17 femoral pores in males; 8–10 enlarged precloacal scales; 8–10 precloacal pores in males; three rows of enlarged post-precloacal scales; transverse subcaudal scales twice as wide as long midway down the tail not extending onto the lateral subcaudal region; top of head blotched, bearing a yellow reticulum; nuchal loop not divided medially, not bearing an anterior,

Table 11. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus shwetaungor um* sp. nov.**

	LSUHC 12937 holotype	LSUHC 12935 paratype	BYU 52226 paratype	BYU 52227 paratype	LSUHC 12896 paratype	LSUHC 12897 paratype	LSUHC 12898 paratype	BYU 52225 paratype
Locality	Lower site	Lower site	Lower site	Lower site	Upper site	Upper site	Upper site	Upper site
Sex	m	m	m	f	f	f	f	f
Supralabials	7	8	8	8	9	9	9	8
Infralabials	6	6	7	7	7	8	7	7
Body tubercles low, weakly keeled	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Body tubercles raised, moderately to strongly keeked	No	No	No	No	No	No	No	No
Paravertebral tubercles	33	32	33	33	33	35	31	35
Longitudinal rows of body tubercles	21	19	19	18	19	18	19	18
Tubercles extend beyond base of tail	No	No	No	No	No	No	No	No
Ventral scales	40	35	33	38	37	40	40	35
Expanded subdigital lamellae on fourth toe	8	9	8	8	8	8	8	9
Unmodified subdigital lamellae on fourth toe	12	11	13	12	12	12	14	13
Total subdigital lamellae on fourth toe	20	20	21	20	20	20	22	22
Enlarged femoral scales (R/L)	15RL	13R/14	15R17L	15RL	13R13L	15R/14L	12RL	14R13L
Femoral pores (R/L)	8R7L	8R7L	8R9L	/	/	6R/9L	/	/
Enlarged precolacal scales	8	10	11	10	10	10	9	10
Precloacal pores	8	10	9	8	10	10	9	9
Post-precloacal scales rows	3	3	3	3	3	3	3	3
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Pore-bearing femoral and precloacal scales continuous	No	No	No	No	No	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No	No	No	No	No	No

Table 11. *Continued*

	LSUHC 12937 holotype	LSUHC 12935 paratype	BYU 52226 paratype	BYU 52227 paratype	LSUHC 12896 paratype	LSUHC 12897 paratype	LSUHC 12898 paratype	BYU 52225 paratype
Locality	Lower site	Lower site	Lower site	Lower site	Upper site	Upper site	Upper site	Upper site
Medial subcaudals two or three times wider than long	2	/	2	2	2	2	2	2
Medial subcaudals extend onto lateral surface of tail	No	/	No	No	No	No	No	No
Nuchal loop divided medially	No	No	No	No	No	No	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No	No	No	No
Posterior border of nuchal loop	Straight	Straight	Straight	Straight	Straight	Straight	Straight	Straight
Band on nape	No	No	No	No	No	No	No	No
Dorsal banding with paravertebral elements	No	No	No	No	No	No	No	No
Number of body bands	4	4	4	4	4	4	4	4
Dorsal bands wider than interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal bands bearing lightened centres	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal bands edged with light-coloured tubercles	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal band borders	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	No	No	No	No	No	No	No	No
Top of head diffusely mottled, blotched or patternless	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched	Blotched
Light reticulum on top of head	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Anterodorsal margin of thighs darkly pigmented	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Anterodorsal margin of brachia darkly pigmented	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Light caudal bands with dark markings	No	/	/	No	No	/	/	/

Table 11. *Continued*

	LSUHC 12937 holotype	LSUHC 12935 paratype	BYU 52226 paratype	BYU 52227 paratype	LSUHC 12896 paratype	LSUHC 12897 paratype	LSUHC 12898 paratype	BYU 52225 paratype
Locality	Lower site	Lower site	Lower site	Lower site	Upper site	Upper site	Upper site	Upper site
Light caudal bands encircle tail	Yes	/	/	Yes	Yes	/	/	/
Number of light caudal bands	8	/	/	9	8	/	/	/
Number of dark caudal bands	9	/	/	9	7	/	/	/
Dark caudal bands wider than light caudal bands	Yes	/	/	Yes	Yes	/	/	/
Mature regenerated tail spotted	No	No	No	No	No	No	No	No
SVL	94.9	93.0	90.3	74.1	62.5	101.7	100.4	102.2
TL	114.0	12b	90r	92.0	85.0	66r	76r	88r
TW	10.5	10.4	9.6	7.4	5.9	9.8	10.6	9.0
FL	16.0	15.0	15.1	13.1	11.4	16.3	15.6	16.9
TBL	19.1	18.0	18.5	15.3	12.6	19.4	20.1	18.7
AG	39.7	39.0	35.8	30.4	28.4	43.0	42.4	45.3
HL	27.5	25.2	27.0	22.8	19.4	29.3	27.1	27.8
HW	19.7	19.4	18.8	15.5	13.5	20.0	19.6	19.8
HD	11.2	11.0	10.6	8.5	8.3	11.9	11.7	12.1
ED	5.8	5.7	5.4	4.9	4.5	6.3	6.2	6.8
EE	8.8	7.5	8.1	6.5	5.1	7.8	8.0	7.5
ES	11.4	11.1	11.3	9.8	8.2	11.7	11.3	11.9
EN	8.6	8.5	8.9	8.0	5.8	9.1	9.0	9.7
IO	8.5	7.0	7.5	6.2	5.8	7.3	7.9	7.9
EL	3.0	1.9	2.2	2.0	2.0	3.1	2.3	2.3
IN	3.1	3.0	3.3	2.7	2.4	2.9	3.3	3.5

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable; r, regenerated; b, broken.

azygous notch, and having a straight posterior border; no band on nape; four dark, regularly shaped, dorsal bands with no paravertebral elements, much wider than interspaces, centres lightened, edged with light tubercles; no azygous notch in first dorsal band; dark markings in dorsal interspaces; anterodorsal margins of thighs, brachia and ventrolateral fold not whitish; eight or nine light caudal bands encircling tail, lacking dark markings; 7–9 dark caudal bands wider than light caudal bands; and fully regenerated tail not spotted.

Description of holotype: Adult male SVL 94.9 mm; head moderate in length (HL/SVL 0.29), wide (HW/HL 0.72), flat (HD/HL 0.41), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region concave, canthus rostralis rounded; snout elongate (ES/HL 0.42), rounded in dorsal profile, broad in lateral profile; eye large (ED/HL 0.21); ear opening oval (EL/HL 0.11); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally, bordered posteriorly by left and right supranasals and one azygous scale, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals and ventrally by first supralabial; 7(R)8(L) rectangular supralabials extending to below midpoint of eye; 6(R,L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, much larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with small tubercles; dorsal superciliaries weakly pointed and directed posteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by large, left and right, trapezoidal postmentals contacting medially for 50% of their length posterior to mental; two rows of variably enlarged chinshields bordering all infralabials; and gular and throat scales granular, grading posteriorly into larger, subimbricate pectoral and ventral scales.

Body relatively short (AG/SVL 0.42) with well-defined, ventrolateral folds; dorsal scales small, raised and interspersed with large, low, semi-regularly arranged, weakly keeled tubercles; tubercles extend from nape to base of tail but no farther; tubercles on nape smaller but sharper than those on posterior portion of body and less strongly keeled; 33 paravertebral body tubercles; approximately 21 longitudinal rows of body tubercles; 40 flat, subimbricate, ventral scales larger than dorsal scales; enlarged femoral and precloacal scales continuous; 15 femoral pores; eight enlarged precloacal scales; eight precloacal pores; three rows of large, postprecloacal scales; and no deep precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.17); raised, juxtaposed scales of forearm larger than those on body, intermixed with tubercles; palmar scales flat; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; widened, proximal subdigital lamellae do not extend onto palm; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.20), covered dorsally by small, raised, juxtaposed scales intermixed with large tubercles and bearing flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsals, one row of 15(R,L) enlarged femoral scales in contact with enlarged precloacal scales; 8(R)7(L) femoral pores; small, postfemoral scales form an abrupt union with larger, flat, ventral scales of posteroventral margin of thigh; subtibial scales flat, imbricate; plantar scales flat; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 8(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection that do not extend onto sole, 12(R,L) unmodified lamellae distal to inflection; and claws well-developed, sheathed by a dorsal and ventral scale at base.

Tail original, moderate in proportions, 114.0 mm in length, 10.5 mm in width at base, tapering to a point; dorsal scales of tail flat; median row of transversely expanded subcaudal scales twice as wide as long, not extending to lateral caudal region; two enlarged, postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

Coloration in life (*Fig. 17*)*:* Dorsal ground colour of head body, limbs and tail brown; top of head and rostrum bearing, irregularly shaped, dark blotches outlined by a yellow reticulum; dark, occipital, hourglass marking; superciliary scales yellowish; dark nuchal loop outlined in yellow bearing a straight posterior margin and no azygous notch; four wide, regularly shaped, dark, body bands much wider than interspaces, bearing lightened centres, lacking paravertebral elements, edged with yellowish tubercles; first dorsal band lacking azygous notch; third body band divided on right side; no band on nape; one postsacral band; interspaces thin, bearing large, dark, diffuse markings; limbs mottled with yellowish markings and diffuse, dark spots and bands; dark caudal bands, wider than light caudal bands; anterior two bands bearing slightly lightened centres; anterior light caudal bands bearing dark markings, encircling tail; all ventral surfaces dusky, weakly pigmented; and subcaudal region darker.

Variation (*Fig. S3*)*:* The paratypes generally approximate the holotype in aspects of colour pattern, the difference being that they have no body bands that are completely divided laterally and they are all

Figure 18. Habitat of ***Cyrtodactylus shwetaungorum* sp. nov.** at the type locality, 5.0 km north of Pyinyaung Village in the Sai Taung Range at the Apache Cement factory mining site, Mandalay Region.

darker and more uniform in colour. In BYU 52225, the third body band bifurcates on the left flank. LSUHC 12935 lacks a tail and LSUHC 12897–99 and BYU 52226 have regenerated tails. Hatchlings LSUHC 13043–45 have solid dark-brown dorsal ground colour and five regularly shaped, yellow dorsal bands. The top of the head id dull-orange and overlain with a yellow reticulum. The tail is black with seven or eight thin white bands (Fig. 17). LSUHC 12896 and BYU 52227 are a juvenile and subadult, respectively, and show no difference in colour pattern, suggesting that the ontogenetic changes occur coloration and pattern happen early on in life. Meristic and mensural differences are presented in Table 11.

Distribution: *Cyrtodactylus shwetaungorum* sp. nov. is known from the type locality 5.0 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region, Myanmar and along the Pyinyaung River 5 km south of the type locality (Figs 2, 9). It likely occurs further to the north and south of these localities along the karstic Sai Taung Range.

Etymology: The specific epithet, *shwetaungorum* (pronounced *shway-tong-orum*), is a patronym honouring the Shwe Taung Cement Company Limited for their genuine, proactive efforts to protect the biodiversity encompassed in their mining operations in Myanmar by setting aside areas to be reserved and not quarried. The company is particularly interested in setting aside specific areas to protect *C. pyinyaungensis* sp. nov. and *C. shwetaungorum* sp. nov.

Natural history: The upper and lower (735 and 642 m in elevation, respectively) collection sites are contiguous along the same valley. These sites occur in disturbed, secondary, bamboo forest with varying sizes of limestone outcroppings along a drainage with several smaller ravines leading into the main drainage area. Each ravine is lined with limestone outcroppings and limestone boulders are scattered throughout the ravine bottom. The boulders themselves are perforated with several cracks and holes that provide ideal microhabitat structure for gekkonids (Fig. 18). These structures provided retreat sites during the day in which geckos remain inactive but are used as escape sites into which they would flee at night upon our approach. Eight specimens of *C. shwetaungorum* sp. nov. were seen over the course of two nights during October of 2016 of which seven were captured. All were on the base of large limestone rocks, fallen logs or on the ground and would flee towards rocks when illuminated with light. Three hatchlings were observed during additional observations on 19 and 23 March but no gravid females were observed. Other gekkonids observed in the area were *C. pyinyaungensis* sp. nov., *Gekko gecko* and *Hemidactylus* sp. nov.

Comparisons: See *Cyrtodactylus linnwayensis* sp. nov.

Remarks: The close morphological similarity between *C. linnwayensis* sp. nov. and *C. shewtaungorum* sp. nov. leaves open the hypothesis that these two species may be conspecific and their sister species relationship may be a result of sampling error despite their minimum sequence divergence of 10.2%. Although they are separated from one another by approximately 40 km straight-line distance across an intermontane valley and occur at different elevations in different climates and different types of forests—a cool, wet, upland forest at 1130 m in elevation for *C. linnwayensis* sp. nov. and a hot, dry, lowland forest at 642–735 m for *C. shwetaungorm* sp. nov.—they occupy a fairly continuous, mountainous terrain bearing sporadic karst habitats and caves that arc around the northern end of an intermontane valley. Plans have been made to collect from additional karst areas between their localities (if they exist) and to test the 'different species and sampling error' hypotheses. At this juncture, we believe the ecological, morphological and genetic data favour a separate species hypothesis.

The sadansinensis *group*

The monophyletic *sadansinensis* group occurs within the lowland flood plain of the Salween River Basin in Mon State and is composed of *Cyrtodactylus sadansinensis* sp. nov. and the sister species *C. pharbaungensis* sp. nov. and *C. sanpelensis* sp. nov. (Fig. 9). The *sadansinensis* group is defined by the flowing range

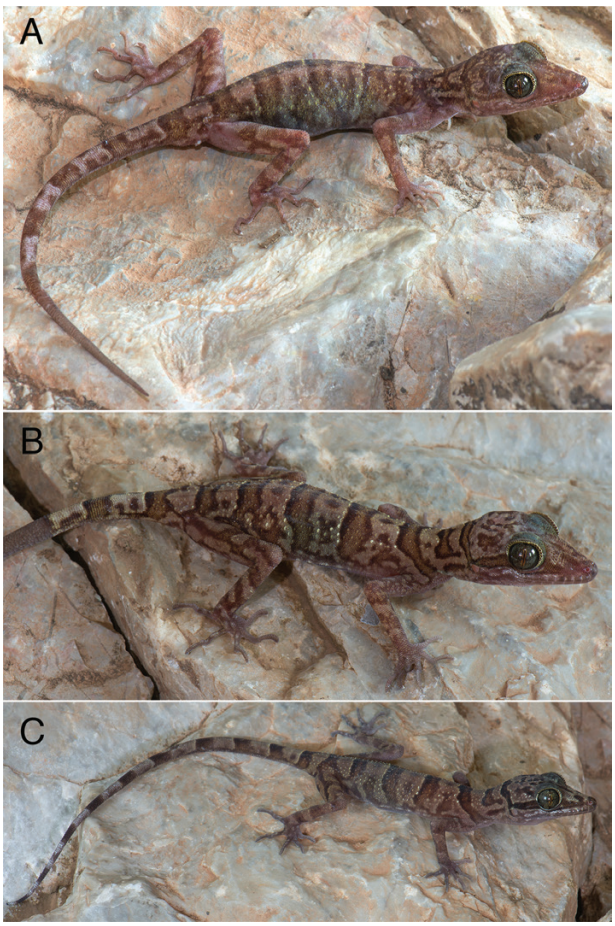

Figure 19. A, adult male holotype of ***Cyrtodactylus sadansinensis* sp. nov.** (LSUHC 12857) from the type locality of Sadan Sin Cave, 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar. B, adult female paratype (LSUHC 12859) from the type locality. C, juvenile male paratype (LSUHC 12856) from the type locality.

of characters: 8–11 supralabial scales; seven or eight infralabial scales; dorsal body tubercles low, weekly keeled, not extending beyond base of tail; 25–31 paravertebral tubercles; 9–14 longitudinal rows of body tubercles; 31–41 ventral scales; 20–24 subdigital lamellae on the fourth toe; 14–34 enlarged femoral scales; femoral scales usually equal in size; 8–21 femoral pores in males; 9–15 enlarged precloacal scales; 5–14 precloacal pores in males; two or three post-precloacal scale rows; medial subcaudal scales three times wider than long, extending onto lateral subcaudal region; top of head bearing dark, mottled pattern with no yellow reticulum; no anterior, azygous notch in nuchal loop; dark band on nape; 4–6 regularly shaped body bands with lightened centres, not edged with light tubercles; anterodorsal margins of thighs and brachia pigmented; ventrolateral fold not whitish; 6–11 light caudal bands not encircling tail; 7–10 dark caudal bands; and maximum SVL 69.6–73.9 mm (Table 8). The description and diagnosis of each new species of this group follows.

CYRTODACTYLUS SADANSINENSIS SP. NOV.

SADAN SIN CAVE BENT-TOED GECKO

(FIG. 19; TABLE 12)

Holotype: Adult male LSUHC 12857 collected on 6 October 2016 at 1600 h by Evan S. H. Quah, Perry L. Wood, Jr., Matthew L. Murdoch, Thaw Zin, Myint Kyaw Thura, Htet Kyaw and L. Lee Grismer from Sadan Sin Cave 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°31.729, E97°43.056; 26 m in elevation).

Paratypes: Adult females BYU 52220, 12858–59 and juvenile male LSUHC 12856 bear the same collection data as the holotype.

Diagnosis: Cyrtodactylus sadansinensis sp. nov. differs from all congeners by having the unique combination of 8–10 supralabials; seven or eight infralabials; 25–28 paravertebral tubercles; 9–11 longitudinal rows of body tubercles; 31–34 ventral scales; relatively long digits with eight or nine expanded subdigital lamellae on the fourth toe proximal to the digital inflection, 14–16 unmodified distal subdigital lamellae, 22–24 total subdigital lamellae; low and rounded, weakly keeled, dorsal, body tubercles not extending onto tail; enlarged femoral and precloacal scales not continuous; 19–23 enlarged femoral scales; 20 or 21 femoral pores in males; 12–15 enlarged precloacal scales; 12–14 precloacal pores in males; three rows of enlarged post-precloacal scales; subcaudal scales three times as wide as long, extending onto sides of tail; top of head bearing a dark mottled pattern, no yellow reticulum; nuchal loop not divided medially, lacking an azygous notch, and usually having a sinuous posterior border; five dark, regularly shaped, dorsal bands never wider than interspaces, bearing lightened centres, not edged with white tubercles; first dorsal band lacking azygous notch; dark markings in dorsal interspaces; ventrolateral fold not whitish; anterodorsal margin of thighs and brachia pigmented; 9–11 light caudal bands bearing dark markings, not encircling tail; 8–10 dark caudal bands never wider than light caudal bands; and regenerated tails immaculate, uniform brown.

Description of holotype: Adult male SVL 69.6 mm; head moderate in length (HL/SVL 0.30), wide (HW/HL 0.66), flat (HD/HL 0.37), distinct from neck,

Table 12. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus sadansinensis* sp. nov.**

	LSUHC 12857 holotype	BYU 12854 52220	LSUHC 12856 paratype	LSUHC 12858 paratype	LSUHC 12859 paratype
Sex	M	F	M	F	F
Supralabials	9	8	10	9	9
Infralabials	7	7	8	8	7
Body tubercles low, weakly keeled	Yes	Yes	Yes	Yes	Yes
Body tubercles raised, moderately to strongly keeked	No	No	No	No	No
Paravertebral tubercles	28	28	25	27	26
Longitudinal rows of body tubercles	10	11	9	10	10
Tubercles extend beyond base of tail	No	No	No	No	No
Ventral scales	33	34	34	31	34
Expanded subdigital lamellae on fourth toe	8	8	8	9	9
Unmodified subdigital lamellae on fourth toe	14	16	14	14	14
Total subdigital lamellae on fourth toe	22	24	22	23	23
Enlarged femoral scales (R/L)	11R10L	11R12L	11R12L	11R10L	9R10L
Femoral pores (R/L)	11R10L	/	10RL	/	/
Enlarged precolacal scales	15	14	12	13	14
Precloacal pores	14	/	12	/	/
Post-precloacal scales rows	3	3	3	3	3
Enlarged femoral and precloacal scales continuous	No	No	No	No	No
Pore-bearing femoral and precloacal scales continuous	No	No	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No	No	No
Medial subcaudals two or three times wider than long	3	3	3	3	3
Medial subcaudals extend onto lateral surface of tail	Yes	Yes	Yes	Yes	Yes
Nuchal loop divided medially	No	No	No	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No
Posterior border of nuchal loop	Sinuous	Sinuous	Sinuous	Sinuous	Sinuous
Band on nape	Yes	Yes	Yes	Yes	Yes
Dorsal banding with paravertebral elements	No	No	No	No	No
Number of body bands	5	5	5	5	5
Dorsal bands wider than interspaces	No	No	No	Same	No
Dorsal bands with lightened centres	Yes	Yes	Yes	Yes	Yes
Dorsal bands edged with white tubercles	No	No	No	No	No
Dorsal band borders	Smooth	Smooth	Smooth	Smooth	Smooth
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes
Ventrolateral fold whitish	No	No	No	No	No
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No	No	No

Table 12. *Continued*

	LSUHC 12857 holotype	BYU 12854 52220	LSUHC 12856 paratype	LSUHC 12858 paratype	LSUHC 12859 paratype
Anterodorsal margin of thighs darkly pigmented	Yes	Yes	Yes	Yes	Yes
Anterodorsal margin of brachia darkly pigmented	Yes	Yes	Yes	Yes	Yes
White caudal bands with dark markings	Yes	Yes	Yes	Yes	Yes
White caudal bands encircle tail	No	No	No	No	No
Number of light caudal bands	/	/	11	9	/
Number of dark caudal bands	/	/	10	8	/
Dark caudal bands wider than light caudal bands	Same	Same	No	Same	No
Mature regenerated tail spotted	No	No	No	No	No
SVL	69.6	68.1	48.7	67.6	66.7
TL	87.0r	82.0r	72.0	101.0	93.0r
TW	7.9	7.0	4.1	7.2	5.9
FL	11.8	11.1	8.5	12.2	11.4
TBL	13.4	12.7	10.5	14.3	112.9
AG	30.7	29.0	20.5	27.1	29.2
HL	20.8	20.7	15.7	21.0	20.3
HW	13.6	13.3	9.8	12.7	13.0
HD	7.7	7.6	5.5	7.2	6.8
ED	5.3	4.9	4.1	5.7	4.7
EE	5.4	5.0	3.4	5.5	5.1
ES	8.8	8.9	7.0	8.9	8.9
EN	6.6	6.6	4.7	7.0	6.9
IO	4.8	4.5	4.0	5.9	5.8
EL	2.2	1.7	1.8	2.2	2.6
IN	2.2	2.0	1.6	2.2	2.3

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable; r, regenerated.

triangular in dorsal profile; lores inflated, prefrontal region weakly concave, canthus rostralis flattened; snout elongate (ES/HL 0.42), rounded in dorsal profile, flat in lateral profile; eye large (ED/HL 0.25); ear opening elliptical, vertically oriented, moderate in size (EL/HL 0.10); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by an inverted Y-shaped furrow, bordered posteriorly by large left and right supranasals and one small azygous internasal, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by large supranasal, posteriorly by two postnasals, ventrally by first supralabial; 9(R,L) square supralabials extending to below midpoint of eye; 7(R,L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with slightly enlarged tubercles; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals contacting medially for 45% of their length posterior to mental; one row of slightly enlarged chinshields bordering all infralabials; gular and throat scales small, flat, grading posteriorly into larger, subimbricate pectoral and ventral scales.

Body relatively short (AG/SVL 0.44) with well-defined ventrolateral folds; dorsal scales small, raised, interspersed with small, low, subconical, semi-regularly arranged, weakly keeled tubercles; tubercles extend from occiput onto base of tail but no farther; tubercles on occiput and nape very small, those on posterior portion of body larger and keeled; approximately ten longitudinal rows of body tubercles; 28 paravertebral tubercles; 33 flat, subimbricate, ventral scales larger than dorsal scales; enlarged femoral and precloacal scales discontinuous; 21 enlarged femoral scales; 21 femoral pores; 15 large precloacal scales; 14 precloacal pores; three rows of large, post-precloacal scales; and no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.17); flat scales of forearm larger than those on body, not interspersed with tubercles; palmar scales flat; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.19), covered dorsally by granular scales and anteriorly by flat, slightly larger scales, and generally atuberculate; ventral scales of thigh flat, imbricate, larger than dorsal scales, one row of 11(R)10(L) enlarged femoral scales on distal one-half not in contact with enlarged precloacal

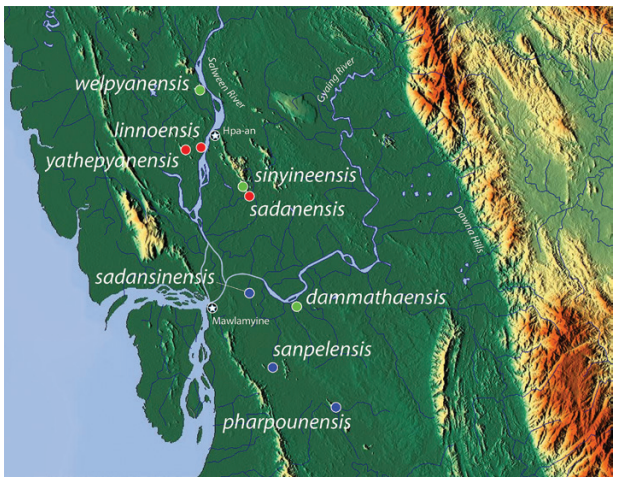

Figure 20. Distribution of the karst-adapted species of *Cyrtodactylus* in the Salween River Basin of Kayin and Mon states, Myanmar. Blue, red and green circles represent species of the *sadansinensis*, *yathepyanensis* and *sinyineensis* species groups, respectively.

scales; 11(R)10(L) femoral pores; subtibial scales flat, imbricate; small postfemoral scales form an abrupt union with larger, flat ventral scales of posteroventral margin of thigh; plantar scales low, flat; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 8(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection, 14(R,L) unmodified subdigital lamellae distal to inflection; 22 total subdigital lamellae; claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Proximal two-thirds of tail original, moderate in proportions, 87.0 mm in length, 7.9 mm in width at base, tapering to a point; dorsal scales of base of tail granular rapidly becoming flatter and larger posteriorly; median row of wide, transversely expanded subcaudal scales three times as wide as long extending onto lateral surface of tail; two enlarged postcloacal tubercles at base of tail on hemipenal swelling; and postcloacal scales flat.

Coloration in life (*Fig. 19*): Dorsal ground colour of head body, limbs and tail tan to faintly magenta; top of head and rostrum covered with faint, irregular mottlings, no yellow reticulum; superciliary scales yellowish; nuchal band faint, unnotched anteromedially and bearing a sinuous posterior margin; cruciform pattern on nape; five regularly shaped body bands with lightened centres, not wider than interspaces, and one sacral band; limbs irregularly banded; dorsal interspaces bearing dark markings; proximal, dorsal portion of thighs lacking pigment; brachia and ventrolateral

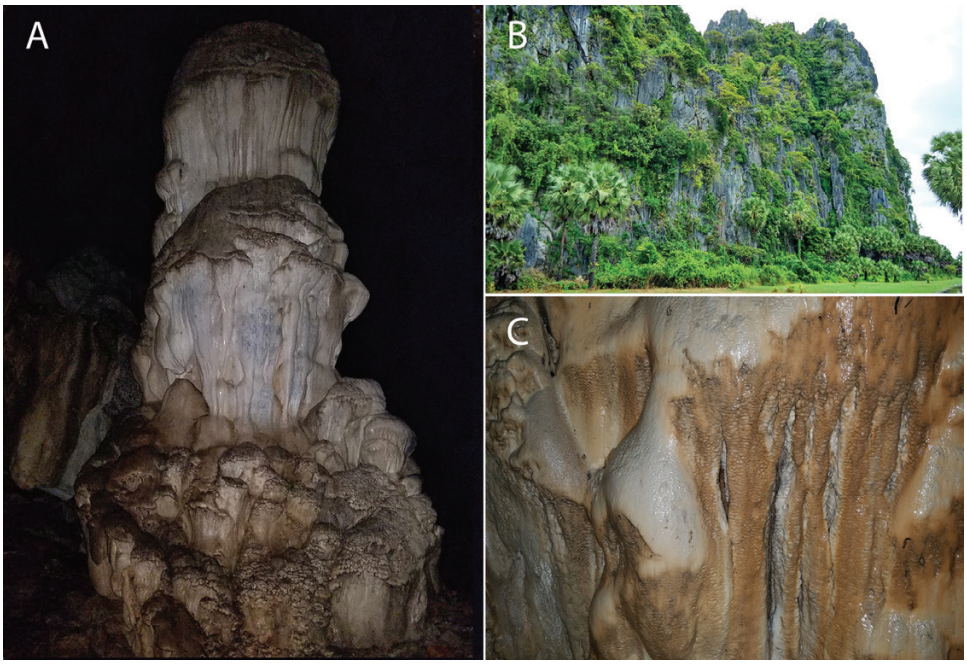

Figure 21. A and C, microhabitat structure inside Sadan Sin Cave, Mon State, Myanmar. B, limestone structure of the hillside outside of Sadan Cave.

folds dark; dark caudal bands bearing lightened centres; light caudal bands bear dark markings, do not encircle tail; ventral surfaces of head body and limbs beige with stippled lateral edges; and subcaudal region brown.

Variation (Fig. S4): The paratypes differ most notably from the holotype in having bolder, better-defined, dorsal markings. BYU 52220 is generally darker overall and the juvenile LSUHC 12856 (SVL = 48.7 mm) generally lacks dark pigment in the dorsal body interspaces. Meristic and mensural differences are presented in Table 12.

Distribution: Cyrtodactylus sadansinensis sp. nov. is known only from Sadan Sin Cave 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar (Fig. 20).

Etymology: The specific epithet, *sadansinensis*, is a noun in apposition in reference to the type locality of Sadan Sin Cave.

Natural history: Sadan Sin Cave is situated on the eastern side of a small, isolated karst hill approximately 520 m wide, 1650 m long and 74 m high that is surrounded by paddy fields. The opening of the cave is approximately 60 m above the base of the hill. The interior of the cave

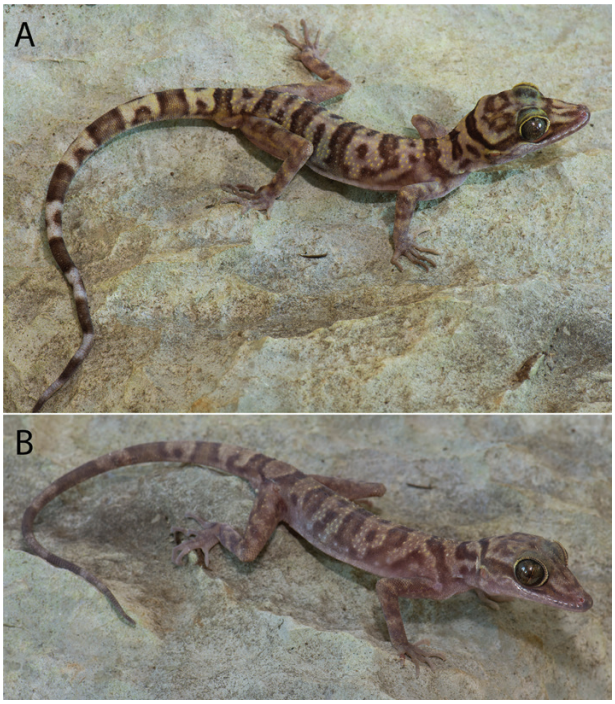

Figure 22. A, adult male holotype of ***Cyrtodactylus pharbaungensis* sp. nov.** (LSUHC 12871) from the type locality of Pharbaung Cave, 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar. B, adult male paratype (LSUHC 12873) from the type locality.

Table 13. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus pharbaungensis* sp. nov.**

	LSUHC 12871 holotype	LSUHC 12870 paratype	BYU 52215 paratype
Sex	M	M	M
Supralabials	9	9	9
Infralabials	7	7	7
Body tubercles low, weakly keeled	No	No	Yes
Body tubercles raised, moderately to strongly keeked	Yes	Yes	No
Paravertebral tubercles	29	28	30
Longitudinal rows of body tubercles	14	14	14
Tubercles extend beyond base of tail	No	No	No
Ventral scales	34	38	36
Expanded subdigital lamellae on fourth toe	9	7	9
Unmodified subdigital lamellae on fourth toe	12	14	12
Total subdigital lamellae on fourth toe	21	21	21
Enlarged femoral scales (R/L)	17R17L	12R16L	16RL
Femoral pores (R/L)	9R9L	9R11L	9R9L
Enlarged precolacal scales	10	11	9
Precloacal pores	8	8	5
Post-precloacal scales rows	2	2	2
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes
Pore-bearing femoral and precloacal scales continuous	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No
Medial subcaudals two or three times wider than long	3	3	3
Median subcaudals extend onto lateral subcaudal region	Yes	Yes	Yes
Nuchal loop divided medially	No	No	No
Nuchal loop with anterior azygous notch	No	No	No
Posterior border of nuchal loop	Straight	Straight	Straight
Band on nape	Yes	Yes	Yes
Dorsal banding with paravertebral elements	No	No	No
Number of body bands	6	6	6
Dorsal bands wider than interspaces	No	Same	No
Dorsal bands bearing lightened centres	Yes	Yes	Yes
Dorsal bands edged with light tubercles	No	No	No
Dorsal band borders	Smooth	Smooth	Smooth
Dark markings in dorsal interspaces	Yes	Yes	Yes
Ventrolateral body fold whitish	Yes	Yes	No
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No
Anterodorsal margin of thighs darkly pigmented	No	No	No
Anterodorsal margin of brachia darkly pigmented	Weakly	No	Yes
Light caudal bands with dark markings	Yes	Yes	Yes
Light caudal bands encircle tail	No	No	No
Number of light caudal bands	8	/	8
Number of dark caudal bands	9	/	9
Dark caudal bands wider than light caudal bands	Variable	Yes	Same
Mature regenerated tail spotted	/	/	no
SVL	70.4	64.2	68.1
TL	104.0	80.0	35.0
TW	7.1	5.6	6.2
FL	11.8	11.4	11.0
TBL	13.5	12.5	13.6
AG	26.8	29.0	29.6
HL	21.6	18.5	19.8

Table 13. *Continued*

	LSUHC 12871 holotype	LSUHC 12870 paratype	BYU 52215 paratype
HW	14.6	12.3	14.0
HD	8.2	7.5	8.3
ED	5.0	4.6	5.4
EE	5.2	4.7	4.7
ES	8.9	8.7	8.2
EN	7.5	6.6	7.0
IO	5.6	4.2	5.6
EL	1.8	1.9	2.3
IN	1.9	2.2	2.2

Abbreviations are listed in Material and Methods. R, right; L, left; /, data unobtainable or not applicable.

Figure 23. A, cave entrance and outside microhabitat structure of the limestone walls of Pharbaung Cave, Mon State. B, microhabitat structure of the interior cave wall of Pharbaung Cave.

is extensive, very dark and airy with several alcoves, cracks and passageways, providing adequate retreat for geckos. The more open interior is crowded by fluted stalactites and stalagmites that are bathed in a thin sheet of running water (Fig. 21). During both day and night, *C. sadansinensis* sp. nov. was found on these cave structures. Amazingly, three of the five specimens collected were found in the flutes of stalagmites of the cave wall with water flowing over their bodies. To our knowledge, this has never been reported for geckos and is an indication that not only do these caves generate and harbour endemic species they also select for novel life styles. The forest habitat outside the cave is highly disturbed and the vegetation had been cleared, leaving the face vulnerable to direct sunlight during the day (Fig. 21). As such, only one specimen was seen at night on the outside of the cave. *Gekko gecko* was observed on the outside of the cave as well.

Comparisons: Cyrtodactylus sadansinensis sp. nov. is part of the *sadansinensis* group that includes *C. sadansinensis* and the sister species *C. pharbaungensis* sp. nov. and *C. sanpelensis* sp. nov. (Fig. 9). The PCA and DAPC analyses indicate that

the species of this group are completely separate in morphospace (Fig. 12) where the first two principal components account for 59% of the total variation and load most heavily for longitudinal rows of tubercles, enlarged precloacal scales, and number of unmodified and total number of fourth toe subdigital lamellae (Table S2). These species are even further separated in the DAPC analysis where only the first four components are retained (Fig. S5). Additionally, all three species have statistically significant different mean values for their number of paravertebral tubercles, longitudinal rows of dorsal body tubercles, enlarged femoral scales, enlarged precloacal scales, unmodified subdigital lamellae on the fourth toe, post-precloacal scales rows and precloacal pores, and not lacking pigment in the anterodorsal margins of the thighs and brachia (Table 5). It differs further from *C. pharbaungensis* by not having continuous, enlarged femoral and precolacal scales (Table 8). Varying combinations of other differences between *C. pharbaungensis* sp. nov. and *C. sanpelensis* sp. nov. as well as the other newly described species in the Indo-Chinese clade are presented in Table 8. Genetic distances among the species of this group range from 8.7 to 13.1% (Table 10).

CYRTODACTYLUS PHARBAUNGENSIS SP. NOV.

PHARBAUNG CAVE BENT-TOED GECKO

(FIG. 22; TABLE 13)

Holotype: Adult male LSUHC 12871 collected on 7 October 2016 between 1600 and 1500 h by L. Lee Grismer, Marta S. Grismer, Myint Kyaw Thura, Evan S. H. Quah, Perry L. Wood, Jr., Matthew L. Murdoch, Thaw Zin and Htet Kyaw from Pharbaung Cave 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°17.118, E97°54.056; 47 m in elevation).

Paratypes: Adult males BYU 52215, LSUHC 12870 and 12873 bear the same collection data as the holotype.

Diagnosis: Cyrtodactylus pharbaungensis sp. nov. differs from all congeners by having the unique combination of nine supralabials; seven infralabials; 12–14 longitudinal rows of body tubercles; 28–30 paravertebral tubercles; 34–38 ventral scales; relatively long digits with 7–9 expanded subdigital lamellae on the fourth toe proximal to the digital inflection, 12–14 unmodified distal subdigital lamellae, 21 total subdigital lamellae; body tuberculation variable; body tubercles not extending beyond base of tail; enlarged femoral and precloacal scales continuous; 28–34 enlarged femoral scales; enlarged femoral scales generally equal in size; 14–20 femoral pores in males; 9–11 enlarged precloacal scales; 5–8 precloacal pores in males; two rows of enlarged post-precloacal scales; subcaudal scales three times as wide as long, extending onto lateral surface of tail; top of head bearing a dark mottled pattern, no yellow reticulum; nuchal loop divided medially, lacking an anterior, azygous notch, posterior border straight; five or six dark, regularly shaped, dorsal bands narrower than interspaces with lightened centres, not edged with white tubercles; first dorsal band lacking azygous notch; dark markings in dorsal interspaces; ventrolateral folds whitish; anterodorsal margin of thighs and brachia lacking pigment; 6–8 light caudal bands bearing dark markings and not encircling tail; and 7–9 dark caudal bands of varying width relative to light caudal bands.

Description of holotype: Adult male SVL 70.4 mm; head moderate in length (HL/SVL 0.31), wide (HW/HL 0.67), flat (HD/HL 0.38), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region moderately concave, canthus rostralis flattened; snout elongate (ES/HL 0.41), rounded in dorsal profile, flat in lateral profile; eye large (ED/HL 0.23); ear opening round, moderate in size (EL/HL 0.08); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by inverted Y-shaped furrow, bordered posteriorly by left and right supranasals and one azygous internasal, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial; 9(R,L) square supralabials extending to below midpoint of eye; 7(R,L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput not intermixed with tubercles; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right, trapezoidal postmentals contacting medially for 55% of their length posterior to mental; one row of slightly enlarged chinshields bordering all infralabials; and gular and throat scales small, flat, grading posteriorly into larger subimbricate pectoral and ventral scales.

Body relatively short (AG/SVL 0.38) with well-defined ventrolateral folds; dorsal scales small, raised, interspersed with moderately sized, low, subconical, semi-regularly arranged, weekly keeled tubercles; tubercles extend from nape onto base of tail but no farther; tubercles on nape very small, those on posterior portion of body larger, more heavily keeled; approximately 14 longitudinal rows of dorsal body tubercles; 29 paravertebral tubercles; 34 flat, subimbricate, ventral scales larger than dorsal scales; ten enlarged

precloacal scales; eight precloacal pores; two rows of large post-precloacal scales; and no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.17); flat scales of forearm larger than those on body, not interspersed with tubercles; palmar scales flat; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; claws well-developed, base sheathed by a dorsal and ventral scale; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.19), covered dorsally by granular scales intermixed with larger tubercles and bearing flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsal scales, one row of 17(R,L) enlarged femoral scales in contact with enlarged precloacal scales; 9(R,L) femoral pores; subtibial scales flat, imbricate; small postfemoral scales form an abrupt union with larger, flat ventral scales of posteroventral margin of thigh; plantar scales low, slightly raised; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 9(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection, 12(R,L) unmodified subdigital lamellae distal to inflection, 21 total subdigital lamellae; and claws well-developed, base sheathed by a dorsal and ventral scale.

Tail original, moderate in proportions, 104.0 mm in length, 7.1 mm in width at base, tapering to a point; dorsal scales of base of tail flat, rapidly becoming larger posteriorly; median row of wide, transversely expanded subcaudal scales three times as wide as long extending onto lateral surface of tail; two enlarged postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

Coloration in life (*Fig. 22*)*:* Dorsal ground colour of head body, and limbs tan, that of anterior portion of tail dull-yellow; top of head and rostrum bearing dark, diffuse, oval and lineate somewhat mottled pattern, no yellow reticulum; superciliary scales yellow; dark-brown nuchal band distinct, unnotched anteromedially, posterior margin smooth; short band on nape bordered laterally and anterolaterally by large, dark markings; six generally regularly shaped body bands (including nape band) with lightened centres, narrower than interspaces, not edged with light-coloured tubercles; one sacral band; interspaces bearing distinct, dark markings; limbs faintly and irregularly banded; brachia weakly pigmented; dorsal margin of thighs unpigmented; and ventrolateral body folds whitish; nine dark caudal bands bearing lightened centres, of varying width relative to eight light caudal bands; white caudal bands not encircling tail, bearing dark markings; ventral surfaces of head body and limbs beige with stippled lateral edges; and anterior subcaudal region beige, posterior region brown.

Variation (Fig. S6): The paratypes differ most notably from the holotype in the distinction of the dorsal markings. BYU 52215 and LSUHC 12873 are generally darker overall and the yellowish tubercles in the interspaces are more visible. The posterior one-half of the tail of LSUHC 12870 is regenerated. Meristic and mensural differences are presented in Table 13.

Distribution: Cyrtodactylus pharbaungensis sp. nov. is known only from Pharbaung Cave 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (Fig. 20).

Etymology: The specific epithet, *pharbaungensis* (pronounced *far-bong-ensis*), is a noun in apposition in reference to the type locality of Pharbaung Cave.

Natural history: Pharbaung Cave is situated on the north-east side of a small karst hill approximately 70 m wide, 480 m long and 271 m high and is surrounded by paddy fields. The opening of the cave is wide (~50 m)

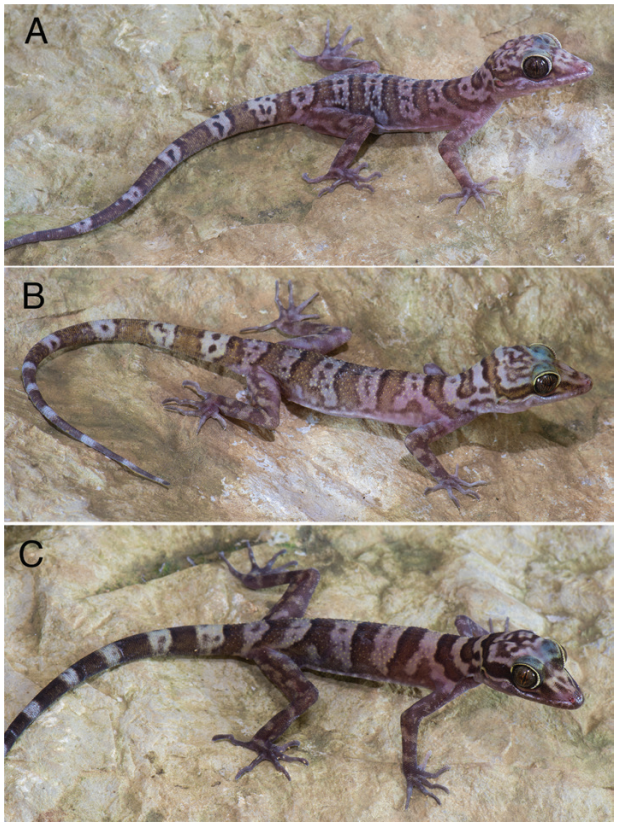

Figure 24. Paratypes of ***Cyrtodactylus sanpelensis* sp. nov.** from the type locality of Sanpel Cave, 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar illustrating the range of variation in coloration and pattern. A, adult male LSUHC 12878. B, adult male LSUHC 12887. C, adult female LSUHC 12886.

Table 14. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus sanpelensis* sp. nov.**

	LSUHC 12877 holotype	LSUHC 12875 paratype	BYU 52221 paratype	LSUHC 12878 paratype	LSUHC 12879 paratype	LSUHC 12880 paratype	LSUHC 12881 paratype	BYU 52222 paratype
Sex	M	M	F	F	F	F	M	F
Supralabials	10	9	9	10	10	10	9	9
Infralabials	7	7	7	7	8	8	7	7
Body tubercles low, weakly keeled	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Body tubercles raised, moderately to strongly keeked	No	No	No	No	No	No	No	No
Paravertebral tubercles	28	27	28	28	29	30	29	31
Longitudinal rows of body tubercles	14	14	13	13	13	13	14	13
Tubercles extend beyond base of tail	No	No	No	No	No	No	No	No
Ventral scales	37	41	35	40	39	40	35	38
Expanded subdigital lamellae on fourth toe	8	9	8	8	8	9	8	8
Unmodified subdigital lamellae on fourth toe	13	13	13	12	13	12	13	13
Total subdigital lamellae on fourth toe	21	22	21	20	21	21	21	21
Enlarged femoral scales	12R8L	8RL	9R11L	8R6L	8RL	8RL	9R7L	8R9L
Femoral pores	8R8L	5R4L	/	/	/	/	7R6L	/
Enlarged precolacal scales	11	11	11	12	10	11	11	9
Precloacal pores	8	7	/	/	/	/	7	/
Post-precloacal scales rows	2	2	2	2	2	2	2	2
Enlarged femoral and precloacal scales continuous	No	No	No	No	No	No	No	No
Pore-bearing femoral and precloacal scales continuous	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No	No	No	No	No	No
Medial subcaudals two or three times wider than long	3	3	3	3	3	3	3	3
Medial subcaudals extend onto lateral subcaudal region	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Nuchal loop divided medially	No	No	No	No	No	No	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No	No	No	No
Posterior border of nuchal loop	Sinuous	Straight	Straight	Straight	Straight	Straight	Sinuous	Sinuous
Band on nape	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal banding with paravertebral elements	No	No	No	No	No	No	No	No
Number of body bands	5	5	5	5	5	5	5	5
Dorsal bands wider than interspaces	No	No	Same	Same	No	No	No	No
Dorsal bands bearing lightened centres	Yes	No	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal bands edged with light tubercles	No	No	No	No	No	No	No	No

Table 14. *Continued*

	LSUHC 12877 holotype	LSUHC 12875 paratype	BYU 52221 paratype	LSUHC 12878 paratype	LSUHC 12879 paratype	LSUHC 12880 paratype	LSUHC 12881 paratype	BYU 52222 paratype
Dorsal band borders	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No	No	No	No	No	No
Anterodorsal margin of thighs darkly pigmented	No	No	No	No	No	No	No	No
Anterodorsal margin of brachia darkly pigmented	No	No	No	No	No	No	No	No
Light caudal bands with dark markings	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Light caudal bands encircle tail	No	No	No	No	No	No	No	No
Number of light caudal bands	/	/	/	/	7	9	/	8
Number of dark caudal bands	/	/	/	/	7	10	/	8
Dark caudal bands wider than light caudal bands	Yes	Yes	/	Yes	Yes	Yes	/	Yes
Mature regenerated tail spotted	No	No	No	No	No	No	No	No
SVL	70.7	73.9	67.5	68.9	68.1	69.4	69.6	67.9
TL	110.0	107.0	59.0r	98.0	89.0	99.0	85.0	95.0
TW	7.2	7.5	6.5	7.1	6.3	5.9	6.0	6.3
FL	12.4	12.4	12.0	11.6	11.8	11.9	11.4	10.7
TBL	14.7	14.7	14.3	13.6	14.5	14.5	12.4	14.2
AG	30.7	25.8	28.4	28.0	28.9	30.6	30.6	29.0
HL	22.6	21.8	20.3	21.5	20.8	20.9	20.7	21.0
HW	14.6	15.3	13.0	14.6	13.2	13.6	13.5	13.2
HD	9.2	8.5	7.8	8.8	7.4	8.2	8.4	7.7
ED	5.7	5.8	5.1	6.2	5.1	5.5	5.1	5.6
EE	5.4	6.1	4.5	5.6	4.9	4.7	5.1	4.8
ES	10.0	9.7	8.7	9.7	9.6	8.7	8.9	9.0
EN	6.7	6.8	7.1	6.9	7.0	6.1	6.6	7.2
IO	5.6	6.1	5.3	6.1	4.9	5.4	5.9	6.0
EL	2.4	2.5	2.3	2.2	2.6	2.2	2.1	2.6
IN	2.1	2.2	2.3	2.1	2.3	2.1	2.1	2.1
	LSUHC 12883 paratype	BYU 52223 paratype	LSUHC 12886 paratype	LSUHC 12885 paratype	LSUHC 12887 paratype	BYU 52224 paratype	LSUHC 12889 paratype	LSUHC 12890 paratype
Sex	M	M	F	/	M	F	M	M
Supralabials	10	9	9	11	9	10	10	10
Infralabials	7	7	8	7	8	7	7	8

Table 14. *Continued*

	LSUHC 12883 paratype	BYU 52223 paratype	LSUHC 12886 paratype	LSUHC 12885 paratype	LSUHC 12887 paratype	BYU 52224 paratype	LSUHC 12889 paratype	LSUHC 12890 paratype
Body tubercles low, weakly keeled	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Body tubercles raised, moderate to strongly keeked	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Paravertebral tubercles	30	31	29	28	29	31	27	28
Longitudinal rows of tubercles	13	14	13	12	13	13	14	13
Tubercles extend beyond base of tail	No	No	No	No	No	No	No	No
Ventral scales	38	35	36	36	35	36	36	39
Expanded subdigital lamellae on fourth toe	9	8	8	8	8	8	9	8
Unmodified subdigital lamellae on fourth toe	13	13	13	13	12	12	13	12
Total subdigital lamellae on fourth toe	22	21	21	21	20	20	22	20
Enlarged femoral scales (R/L)	9RL	7R8L	9R8L	7R8L	10R8L	8RL	9R7L	8RL
Femoral pores (R/L)	6R8L	7R6L	/	/	6R7L	/	6R4L	7R6L
Enlarged precolacal scales	11	11	11	11	9	9	10	11
Precloacal pores	8	7	/	/	7	/	7	8
Post-precloacal scales rows	2	2	2	2	2	2	2	2
Enlarged femoral and precloacal scales continuous	No	No	No	No	No	No	No	No
Pore-bearing femoral and precloacal scales continuous	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No	No	No	No	No	No
Medial subcaudal scales two or three times wider than long	3	3	3	3	3	3	3	3
Transverse subcaudal extend onto lateral subcaudal region	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Nuchal loop divided medially	No	No	No	No	No	No	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No	No	No	No
Posterior border of nuchal loop	Sinuous	Straight	Sinuous	Sinuous	Straight	Sinuous	Straight	Straight
Band on nape	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal banding with paravertebrtal elements	No	No	No	No	No	No	No	No
Number of body bands	5	5	5	4	5	5	5	5
Dorsal bands wider than interspaces	No	No	Same	Same	Same	No	Same	Same
Dorsal bands bearing lightened centres	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal bands edged with light tubercles	No	No	No	No	No	No	No	No
Dorsal band borders	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Light tubercles in interspaces	No	No	No	No	No	No	No	No
Ventrolateral body fold whitish	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes

Table 14. *Continued*

	LSUHC 12883 paratype	BYU 52223 paratype	LSUHC 12886 paratype	LSUHC 12885 paratype	LSUHC 12887 paratype	BYU 52224 paratype	LSUHC 12889 paratype	LSUHC 12890 paratype
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No	No	No	No	No	No
Anterodorsal margin of thighs pigmented	No	No	No	No	No	No	No	No
Anterodorsal margin of brachia pigmented	No	No	No	No	No	No	No	No
Light caudal bands with dark markings	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Light caudal bands encircle tail	No	No	No	No	No	No	No	No
Number of light bands on tail	/	/	/	8	9	/	7	10
Number of dark bands on tail	/	/	/	7	7	/	8	10
Dark caudal bands wider than light caudal bands	/	/	Yes	Yes	Yes	Yes	Same	Yes
Mature regenerated tail spotted	No	No	No	No	No	No	No	No
SVL	73.7	73.0	60.1	39.2	70.5	68.3	68.8	67.5
TL	81.0r	95.0r	54.0b	49.0	107.0	102.0r	100.0	98.0
TW	6.8	5.9	5.6	2.7	6.2	6.0	6.0	6.2
FL	12.1	12.8	10.3	6.7	11.4	11.3	11.8	11.7
TBL	14.6	14.6	12.9	7.6	14.6	13.7	13.9	13.4
AG	29.6	29.5	26.1	16.7	30.4	31.1	24.3	28.1
HL	22.1	23.3	18.7	12.2	21.5	20.4	21.7	20.2
HW	15.0	14.0	11.8	7.8	14.1	13.6	13.8	14.4
HD	8.2	8.4	6.8	4.6	7.6	8.0	7.9	7.7
ED	5.8	5.0	4.2	3.1	5.3	5.2	5.3	5.0
EE	5.3	5.0	4.8	3.3	5.7	4.7	5.5	5.4
ES	9.8	8.8	8.4	5.6	8.9	9.1	9.3	8.8
EN	7.7	7.1	5.2	4.1	7.5	6.8	7.0	6.6
IO	6.4	5.2	4.4	3.1	5.5	5.9	5.8	5.0
EL	2.4	2.0	2.2	1.1	1.7	2.1	2.2	1.9
IN	2.2	2.0	1.5	1.5	2.1	2.2	1.9	2.1

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable; r, regenerated; b, broken.

and high (~20 m) and approximately 60 m above the base of the hill. The interior of the cave is also wide and high with small outcroppings in the centre and alcoves, deep cracks and stalagmites along the walls (Fig. 23). Lizards were observed only along the edges of the walls and not in the middle structures. Some were observed in narrow cracks 1–5 m above the cave floor and others were found crawling across the ground near cracks and small outcroppings into which they could retreat. One specimen was collected on the wall at the cave entrance 1 m above the cave floor. A juvenile was observed in a crack 4–5 m above the cave floor but could not be caught. It is likely that at night, when the cave is darker, lizards utilize all the microhabitat structures. *Hemidactylus garnotii* was observed on the hillside outside the cave.

Comparisons: Cyrtodactylus pharbaungensis sp. nov. is part of the *sadansinensis* group. The PCA and DAPC analyses indicate that the species of this group are completely separate in morphospace where the first two principal components account for 59% of the total variation (Fig. 12) and load most heavily for longitudinal rows of dorsal body tubercles, enlarged precloacal scales, and number of unmodified and total number of fourth toe lamellae (Table S2). *Cyrtodactylus pharbaungensis* sp. nov. is well-differentiated from *C. sadansinensis* sp. nov. by having statistically significant differences in its mean number of paravertebral tubercles, longitudinal rows of dorsal body tubercles, enlarged femoral scales, enlarged precloacal scales, unmodified subdigital lamellae on the fourth toe, post-precloacal scales rows and precloacal pores and by having continuous, femoral and precloacal scales (Table 8). It less well-separated from its sister species *C. sanpelensis* sp. nov. by only showing statistically significant differences in its mean number of enlarged femoral scales and femoral pores. However, the enlarged femoral and precloacal scales in *C. pharbaungesis* sp. nov. are continuous and are discontinuous in *C. sanpelensis* sp. nov.; and in *C. pharbaungesis* sp. nov. the dorsal bands are not wider than the interspaces, whereas they are in *C. sanpelensis* sp. nov. (Table 8). Varying combinations of other differences between *C. sadansisnensis* sp. nov. and *C. sanpelensis* sp. nov. as well as the other newly described species are presented in Table 7. Genetic distances among the species of this group range from 8.7 to 13.1% (Table 10).

CYRTODACTYLUS SANPELENSIS SP. NOV.

SANPEL CAVE BENT-TOED GECKO

(FIG. 24; TABLE 14)

Holotype: Adult male LSUHC 12877 collected on 8 October 2016 between 1600 and 2000 h by Myint Kyaw Thura, L. Lee Grismer, Marta S. Grismer, Evan S. H. Quah, Perry L. Wood, Jr., Matthew L. Murdoch, Thaw Zin and Htet Kyaw from Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°22.427, E97°46.388; 44 m in elevation).

Paratypes: Adult males BYU 52223, LSUHC 12875, 12881, 12883, 12887, 12889–90, adult females BYU 52221–22, 52224, LSUHC 12878–80, 12886 and juvenile LSUHC 12885 bear the same collection data as the holotype.

Diagnosis: Cyrtodactylus sanpelensis sp. nov. differs from all congeners by having the unique combination of 9–11 supralabials; seven or eight infralabials; 12–14 rows of longitudinal body tubercles; 27–31 paravertebral tubercles; 35–41 ventral scales; relatively long digits with eight or nine expanded subdigital lamellae proximal to the digital inflection on the fourth toe, 12 or 13 unmodified distal subdigital lamellae, 20–22 total subdigital lamellae; low, weakly keeled, dorsal body tubercles; body tubercles not extending beyond base of tail; enlarged femoral and precloacal scales not continuous; 14–20 enlarged femoral scales; 8–16 femoral pores in males; 9–12 enlarged precloacal scales; seven or eight precloacal pores in males; two rows of enlarged post-precloacal scales; median subcaudal scales three times as wide as long, extending onto lateral surface of tail; top of head diffusely mottled, no yellow reticulum; nuchal loop not divided medially, lacking an anterior, azygous notch, posterior border straight or sinuous; five (rarely four), dark, regularly shaped, dorsal bands not wider than interspaces, nearly always with lightened centres, not edged with white tubercles; band on nape present; dark markings in dorsal interspaces; ventrolateral fold not whitish; anterodorsal margin of thighs and brachia unpigmented; 7–10 light caudal bands bearing dark markings, not encircling tail; 7–10 dark caudal bands wider than light caudal bands; and regenerated tail not spotted.

Description of holotype: Adult male SVL 70.7 mm; head moderate in length (HL/SVL 0.32), wide (HW/HL 0.65), flat (HD/HL 0.41), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region moderately concave, canthus rostralis flattened; snout elongate (ES/HL 0.44), rounded in dorsal profile, flat in lateral profile; eye large (ED/HL 0.25); ear opening round, moderate in size (EL/HL 0.11); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by inverted Y-shaped furrow, bordered posteriorly by left and right supranasals, one azygous internasal, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial; 10(R,L) square supralabials extending to below midpoint

of eye; 8(R)7(L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput not intermixed with tubercles; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals contacting medially for 50% of their length posterior to mental; one row of slightly enlarged chinshields bordering all infralabials; and gular and throat scales small, flat, grading posteriorly into larger, subimbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.43) with well-defined ventrolateral folds; dorsal scales small, raised and interspersed with moderately sized, subconical, low, semi-regularly arranged, weakly keeled tubercles; tubercles extend from nape to base of tail but no farther; tubercles absent on nape, tubercles on posterior portion of body largest and more heavily keeled; approximately 14 longitudinal rows of body tubercles; 28 paravertebral tubercles; 37 flat, subimbricate, ventral scales larger than dorsal scales; 11 enlarged, precloacal scales; eight precloacal pores; two rows of large post-precloacal scales; and no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.18); slightly raised scales of forearm larger than those on body, not interspersed with tubercles; palmar scales slightly raised flat; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.21), covered dorsally by raised scales intermixed with larger tubercles, bearing flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsal scales, one row of 12(R)8(L) enlarged femoral scales not in contact with enlarged precloacal scales; 8(R,L) femoral pores; subtibial scales flat, imbricate; small postfemoral scales form abrupt union with larger, flat ventral scales of posteroventral margin of thigh; plantar scales low, slightly raised; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 8(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection, 13(R,L) unmodified subdigital lamellae distal to inflection, 21 total subdigital lamellae; and claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail original, moderate in proportions, 110.0 mm in length, 7.2 mm in width at base, tapering to a point; dorsal caudal scales flat; transversely expanded, median subcaudal scales three times as wide as long, extending onto lateral surface of tail; two enlarged postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

Coloration in life (Fig. 24): Dorsal ground colour of head body, limbs and tail magenta; top of head and rostrum diffusely mottled, no yellow reticulum; superciliary scales dull-yellow; dark-brown nuchal band unnotched anteromedially, bearing a sinuous posterior margin; short, hourglass-shaped, band on nape bordered laterally and anterolaterally by diffuse, dark markings; four generally evenly bordered bands on body bearing lightened centres, not wider than interspaces; one sacral band; interspaces bearing distinct dark markings; limbs diffusely and irregularly banded; anterodorsal margins of thighs and brachia not darkly pigmented; ventrolateral body folds whitish; dark caudal bands with lightened centres, wider than light caudal bands; light caudal bands bear dark markings, do not encircle tail; ventral surfaces of head body and limbs beige with stippled lateral edges; and subcaudal region darker, variegated.

Variation (Fig. S7): The colour pattern of the paratypes varies little from that of the holotype. LSUHC 12885

Figure 25. A, interior of the entrance of Sanpel Cave, Mawlamyine District, Mon State, Myanmar showing some of the religious statues and cave wall microhabitat on which ***Cyrtodactylus sanpelensis* sp. nov.** was collected. B, microhabitat structure of the limestone wall outside the entrance to Sanpel Cave.

is a juvenile and has bolder body bands, lacks a nuchal band and has immaculate dorsal interspaces indicating some ontogenetic change in colour pattern is present. LSUHC 12875 is much darker and the interspaces more heavily mottled. The posterior border of the nuchal loop in BYU 52223–24, LSUHC 12875–80, 12887 and 12890 is straight as opposed to sinuous. The lateral sections of the dorsal bands in LSUHC 12886 are quite faded on the flanks. BYU 52221, 5223, LSUHC 12881 and 12883 have partially regenerated tails. Meristic and mensural differences are presented in Table 14.

Distribution: Cyrtodactylus sanpelensis sp. nov. is known only from Sanpel Cave 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (Fig. 20).

Etymology: The specific epithet, *sanpelensis*, is a noun in apposition in reference to the type locality of Sanpel Cave.

Natural history: Sanpel Cave is situated at the north end of a small karst ridge approximately 53 m wide, 189 m long and 194 m high. The ridge is surrounded by paddy fields and is adjacent to a small, ephemeral river to the east. The opening of the cave is small (~8 m high and ~6 m) and approximately 20 m above the base of the hill. The interior of the cave is complex with many side passages that extend to great depths below the entrance. There are several stalactites, cracks in the walls and side passages that lizards utilize as retreats. Just inside the entrance of the cave are several religious statues on which a number of lizards were collected. Lizards were abundant inside the cave both day and night. After dark, lizards were extremely common on the outside karst hillside that also had an abundance of cracks and holes (Fig. 25). Lizards were even found in well-illuminated areas near the monastery. In essence, there was no rocky habitat that lizards did not utilize. No lizards were seen on vegetation. The juvenile LSUHC 12885 was found on a brick wall. *Gekko gecko* was observed on the outside of the cave.

Comparisons: Cyrtodactylus sanpelensis sp. nov. is part of the *sadanensis* group. See Comparisons section for *C. sadansinensis* sp. nov. and *C. pharbaungensis* sp. nov.

The sinyineensis *group*

The monophyletic *sinyineensis* group is composed of the sister species *Cyrtodactylus sinyineensis* sp. nov. and *C. welpyanensis* sp. nov., and the sister species *C.*

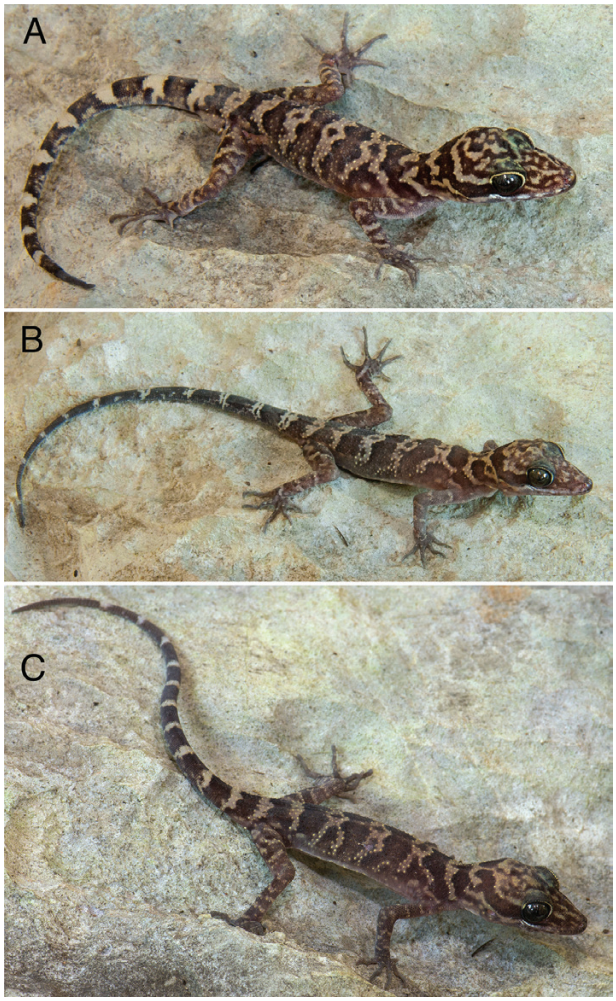

Figure 26. Type specimens of ***Cyrtodactylus dammathetensis* sp. nov.** from the type locality of Dammathet Cave, 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar showing the range of variation in coloration and pattern. A, adult male holotype (LSUHC 12862). B and C, adult female paratypes LSUHC 12863 and 12864, respectively.

dammathetensis sp. nov. and *C. aequalis* Bauer (Fig. 9). This group ranges from the uplands of the southern section of the Shan Hills in Kayin State to the lowland flood plain of the Salween River Basin in Kayin and Mon and states (Fig. 20). It could be argued that *C. tigroides* belongs in this group given it is the sister lineage. However, the deep genetic divergence between *C. tigroides* and the *sinyinensis* group is commensurate with that between the Thai sister lineages of the other Burmese species groups and it is likely that when the phylogenetic relationships of additional Thai species are known, *C. tigroides* will likely align with them in a separate species group as is the case for the *intermedius* group and the *zebraicus* group (Fig. 9). The *sinyineensis*

Table 15. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus dammathetensis* sp. nov.**

	LSUHC 12862 holotype	LSUHC 12863 paratype	LSUHC 12864 paratype
Sex	M	F	F
Supralabials	9	9	9
Infralabials	8	7	8
Body tubercles low, weakly keeled	No	No	No
Body tubercles raised, moderately to strongly keeked	Yes	Yes	Yes
Paravertebral tubercles	33	31	31
Longitudinal rows of body tubercles	15	13	15
Tubercles extend beyond base of tail	Yes	Yes	Yes
Ventral scales	27	25	28
Expanded subdigital lamellae on fourth toe	9	8	9
Unmodified subdigital lamellae on fourth toe	12	13	12
Total subdigital lamellae on fourth toe	21	21	21
Enlarged femoral scales	18RL	15R16L	16RL
Femoral pores	18RL	/	/
Enlarged precolacal scales	9	8	8
Precloacal pores	9	/	/
Post-precloacal scales rows	3	3	3
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes
Pore-bearing femoral and precloacal scales continuous	Yes	Yes	Yes
Enlarged proximal femoral scales ~1/2 size of distal femorals	Yes	Yes	Yes
Medial subcaudals two or three times wider than long	3	3	3
Medial subcaudals extend onto lateral subcaudal region	Yes	Yes	Yes
Nuchal loop divided medially	No	No	Yes
Nuchal loop with anterior azygous notch	No	No	No
Posterior border of nuchal loop	Jagged	Jagged	Jagged
Band on nape	Yes	Yes	Yes
Dorsal banding with paravertebral elements	Yes	Yes	Yes
Number of body bands	5	5	5
Dorsal bands wider than interspaces	Yes	Yes	Yes
Dorsal bands bearing lightened centres	No	No	No
Dorsal bands edged with light tubercles	No	No	No
Dorsal band borders	Jagged	Jagged	Jagged
Dark markings in dorsal interspaces	Yes	Yes	Yes
Ventrolateral body fold whitish	Faintly	Faintly	Faintly
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No
Anterodorsal margin of thighs darkly pigmented	Yes	Yes	Yes
Anterodorsal margin of brachia darkly pigmented	Yes	Yes	Yes
Light caudal bands with dark markings	No	Yes	No
Light caudal bands encircle tail	No	No	No
Number of light caudal bands	10	10	11
Number of dark caudal bands	10	11	11
Dark caudal bands wider than light caudal bands	Yes	Yes	Yes
Mature regenerated tail spotted	/	/	/
SVL	69.3	59.8	53.0
TL	80.0r	83.0	76.0
TW	7.9	6.0	5.1
FL	10.9	9.4	9.3
TBL	13.1	11.4	11.4
AG	29.6	24.4	20.6

Table 15. *Continued*

	LSUHC 12862 holotype	LSUHC 12863 paratype	LSUHC 12864 paratype
HL	20.5	17.1	17.4
HW	13.3	11.8	10.8
HD	7.8	7.0	6.0
ED	5.6	4.4	4.1
EE	5.0	4.4	4.2
ES	8.5	7.8	7.4
EN	6.9	5.6	6.6
IO	5.2	4.4	4.7
EL	2.2	2.2	1.6
IN	2.2	1.9	1.9

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable; r, regenerated.

group is defined by the flowing range of characters: 8–10 supralabials; 6–8 infralabials; dorsal body tubercles raised, moderately to strongly keeled, usually extending beyond base of tail; 30–36 paravertebral tubercles; 13–19 longitudinal rows of body tubercles; 19–30 ventral scales; 19–22 total subdigital lamellae; enlarged femoral and precloacal scales continuous; 25–36 enlarged femoral scales nearly the same size throughout; 13–36 femoral pores in males; 5–13 enlarged precloacal scales; 4–9 precloacal pores in males; three post-precloacal scale rows; transverse, median subcaudal scales usually twice as wide as long, not extending onto lateral surface of tail; top of head bearing a dark mottled pattern; no anterior, azygous notch in nuchal loop; dark band on nape; five or six variably shaped body bands generally lacking lightened centres; anterodorsal margins of thighs and brachia darkly pigmented; 9–11 light caudal bands encircling tail; 9–11 dark caudal bands; and maximum SVL 69.3–91.6 mm (Table 8). The description and diagnosis of each new species follows.

CYRTODACTYLUS DAMMATHETENSIS SP. NOV.

DAMMATHET CAVE BENT-TOED GECKO

(FIG. 26; TABLE 15)

Holotype: Adult male LSUHC 12862 collected on 7 October 2016 at 2000 h by Matthew L. Murdoch, L. Lee Grismer, Marta S. Grismer, Myint Kyaw Thura, Evan S. H. Quah, Perry L. Wood, Jr., Thaw Zin and Htet Kyaw from Dammathet Cave 19.8 km east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (N16°30.380, E97°48.629; 25 m in elevation).

Paratypes: Adult females LSUHC 12863–64 bear the same collection data as the holotype.

Diagnosis: Cyrtodactylus dammathetensis sp. nov. differs from all congeners by having the unique combination of nine supralabials; seven or eight infralabials; 13–15 longitudinal rows of body tubercles; 31–33 paravertebral tubercles; 25–28 ventral scales; relatively long digits with eight or nine expanded subdigital lamellae proximal to the digital inflection on the fourth toe, 12 or 13 unmodified distal subdigital lamellae, 21 total subdigital lamellae; raised, moderately keeled, dorsal body tubercles; tubercles extend beyond base of tail; enlarged femoral and precloacal scales continuous; enlarged proximal femoral scales less than one-half the size of enlarged distal femoral scales; 31–36 enlarged femoral scales; 36 femoral pores in males; eight or nine enlarged precloacal scales; nine precloacal pores in males; three rows of enlarged post-precloacal scales; median subcaudal scales three times as wide as long, extending to lateral surface of tail; top of head darkly mottled, no yellow reticulum; nuchal loop variably paired, no pronounced, anterior, azygous notch, posterior border jagged; five jagged, dark, dorsal bands with paravertebral elements, wider than interspaces, lacking lightened centres, not edged with white tubercles; nape band present; dark markings in dorsal interspaces; ventrolateral folds faintly whitish; anterodorsal margins of thighs and brachia darkly pigmented; ten or 11 light caudal bands variably bearing dark markings, not encircling tail; and ten or 11 dark caudal bands wider than light caudal bands.

Description of holotype: Adult male SVL 69.3 mm; head moderate in length (HL/SVL 0.30), wide (HW/HL 0.65), flat (HD/HL 0.38), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region shallowly concave, canthus rostralis rounded; snout elongate (ES/HL 0.41), rounded in dorsal profile, not flat in lateral profile; eye large (ED/HL 0.27); ear opening round, moderate in size (EL/HL 0.11); eye

to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by inverted Y-shaped furrow, bordered posteriorly by left and right supranasals and one azygous internasal, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by three postnasals, ventrally by first supralabial; 9(R,L) square supralabials extending to below midpoint of eye; 8(R)7(L) infralabials tapering posteriorly to below midpoint of eye; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with small tubercles laterally; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals contacting medially for 65% of their length posterior to mental; one row of slightly enlarged chinshields bordering all infralabials; and gular and throat scales small, flat, grading posteriorly into larger, subimbricate pectoral and ventral scales.

Body relatively short (AG/SVL 0.42) with well-defined ventrolateral folds; dorsal scales small, raised and interspersed with large, subconical, semi-regularly arranged, moderate to strongly keeled tubercles; tubercles extend from nape to beyond base of tail; tubercles on nape smaller than those on posterior portion of body, less sharply keeled; approximately 15 longitudinal rows of body tubercles; 33 paravertebral tubercles; 27 flat, subimbricate, ventral scales larger than dorsal scales; nine enlarged precloacal scales; nine precloacal pores; three rows of large post-precloacal scales; and no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.16); raised scales of forearm larger than those on body, interspersed with small tubercles; palmar scales raised; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; widened proximal subdigital lamellae do not extend onto palm; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.19), covered dorsally by granular scales intermixed with large tubercles and bearing flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsals, one row of 18(R,L) enlarged femoral scales in contact with enlarged precloacal scales; enlarged femoral scales generally equal in size; 18(R,L) femoral pores; subtibial scales flat, imbricate; small postfemoral scales form abrupt union with larger, flat ventral scales of posteroventral margin of thigh; plantar scales raised; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 9(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection, 12(R,L) unmodified subdigital lamellae distal to inflection, 21 total subdigital lamellae; claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail moderate in proportions, 80.0 mm in length, last 10.0 mm regenerated, 7.9 mm in width at base, tapering to a point; dorsal scales of tail flat; median subcaudal scales three as wide as long, extending onto lateral surface of tail; 3(R)4(L) enlarged postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

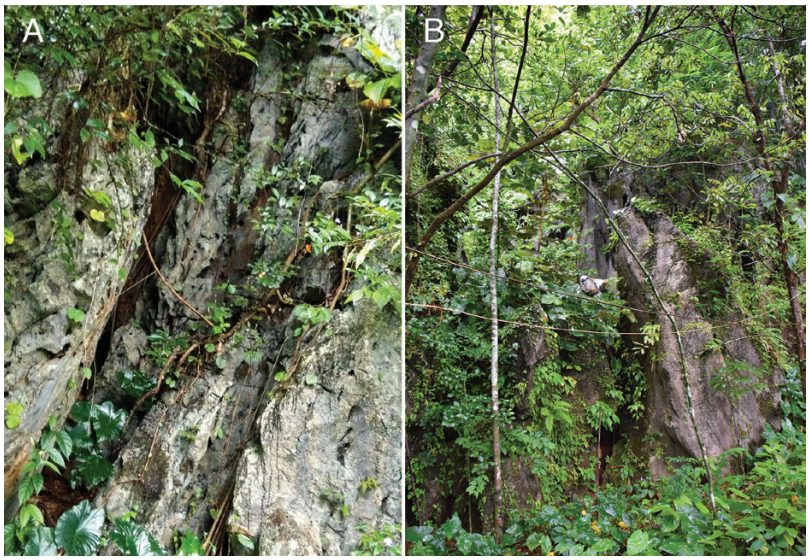

Figure 27. A and B, microhabitat structure of the limestone hillside outside Dammathet Cave, Mawlamyine District, Mon State, Myanmar.

Coloration in life (Fig. 26): Dorsal ground colour of head body, and limbs tan, that of anterior portion of tail dull-yellow; top of head and rostrum bearing a network of dark-brown, diffuse mottlings, no yellow reticulum; superciliary scales yellow; dark-brown, nuchal band distinct, unnotched anteromedially, and bearing a jagged posterior margin; short, jagged band on nape; five jagged body bands not bearing light centres, wider than interspaces, bearing paravertebral elements; one sacral band; interspaces bearing distinct, dark, medial spot; banding on limbs distinct, irregular; thighs and brachia; ventrolateral body folds faintly whitish; dark caudal bands bear lightened centres, wider than white caudal bands; light caudal bands usually immaculate, not encircling tail; ventral surfaces deeply pigmented, dusky in appearance; subcaudal region dark-brown with lighter mottling.

Variation (Fig. S8): The female paratypes differ to varying extents from the holotype in aspects of the dorsal colour pattern. LSUHC 12864 has a paired nuchal loop and dark markings in the lateral regions of the dorsal interspaces. The paravertebral aspects of the dorsal bands are more prominent in the paratypes and in LSUHC 12863 the anteromedial margin of the nuchal loop is nearly notched. Meristic and mensural differences are presented in Table 15.

Distribution: Cyrtodactylus dammathetensis sp. nov. is known only from Dammathet Cave 19.8 km east of Mawlamyine, Mawlamyine District, Mon State, Myanmar (Fig. 20).

Figure 28. Paratypes of ***Cyrtodactylus sinyineensis* sp. nov.** from the type locality of Sin Yine Cave, 18.5 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar showing the range of variation in coloration and pattern. A and B, adult females LSUHC 12837 and 12836, respectively.

Etymology: The specific epithet, *dammathetensis*, is a noun in apposition in reference to the type locality of Dammathet Cave.

Natural history: Dammathet Cave is located immediately south of Dammathet Village and situated on the north end of a thin, westward projecting ridge of a larger karst hill approximately 274 m wide, 1250 m long and 170 m high that is surrounded by paddy fields. The opening of the cave is narrow and behind a locked door controlled by a nearby monastery. The interior of the cave is high (~20 m), open and filled with religious statues and murals along the walls, leaving little in the way of microhabitat for *Cyrtodactylus*. We searched the cave during the afternoon but saw only *Hemidactylus frenatus*. The exterior of the cave along the base of the hill is shaded by vegetation and the limestone is very porous, deeply incised in places, and has several cracks and holes (Fig. 27). We returned here 2 days later after dark and observed four specimens and caught three. All were found on dry surfaces on the karst hillside sheltering from light rain. They were syntopic with *Hemidactylus brookii*.

Comparisons: Cyrtodactylus dammathetensis sp. nov. is part of the *sinyineensis* group. The PCA and DAPC analyses indicate that the species of this group are completely separate in morphospace where the first two principal components account for 63% of the total variation (Fig. 12) and load most heavily for numbers of infralabials, longitudinal rows of tubercles, expanded subdigital lamellae on the fourth toe and post-precloacal scale rows (Table S3). *Cyrtodactylus dammathetensis* sp. nov. is well-differentiated from *C. aequalis*, *C. sinyineensis* sp. nov. and *C. welpyanensis* sp. nov. by having varying combinations of statistically different mean values of infralabial scales, ventral scales, enlarged femoral scales, post-preprecloacal scale rows, longitudinal rows of body tubercles, precloacal scales and body bands (Table 3). It differs further from *C. sinyineensis* sp. nov. and *C. welpyanensis* sp. nov. in having paravertebral elements in the dorsal banding pattern (Table 8). Morphological and colour pattern differences from other species in the Indo-Chinese clade are listed in Table 8. Genetic distances among the species of this group range from 11.0 to 16.5% (Table 10).

CYRTODACTYLUS SINYINEENSIS SP. NOV.

SIN YINE CAVE BENT-TOED GECKO

(FIG. 28; TABLE 16)

Holotype: Adult male LSUHC 12835 collected on 5 October 2016 at 1600 h by L. Lee Grismer, Perry

Table 16. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus sinyineensis* sp. nov.**

	LSUHC 12835 holotype	LSUHC 12837 paratype	LSUHC 12836 paratype
Sex	M	F	F
Supralabials	10	9	10
Infralabials	8	8	8
Body tubercles low, weakly keeled	No	No	No
Body tubercles raised, moderately to strongly keeked	Yes	Yes	Yes
Paravertebral tubercles	33	35	33
Longitudinal rows of body tubercles	15	15	15
Tubercles extend beyond base of tail	Yes	Yes	Yes
Ventral scales	27	29	28
Expanded subdigital lamellae on fourth toe	8	10	9
Unmodified subdigital lamellae on fourth toe	11	11	12
Total subdigital lamellae on fourth toe	19	21	21
Enlarged femoral scales (R/L)	13RL	14R13L	13RL
Femoral pores (R/L)	9RL	/	/
Enlarged precolacal scales	10	11	12
Precloacal pores	5	/	/
Post-precloacal scales rows	3	3	3
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes
Pore-bearing femoral and precloacal scales continuous	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No
Medial subcaudals two or three times wider than long	/	2	2
Medial subcaudals extend onto lateral subcaudal region	No	No	No
Nuchal loop divided medially	No	No	No
Nuchal loop with anterior azygous notch	No	No	No
Posterior border of nuchal loop	Jagged	Jagged	Jagged
Band on nape	Yes	Yes	Yes
Dorsal banding with paravertebral elements	No	No	No
Number of body bands	6	/	5
Dorsal bands wider than interspaces	Yes	Yes	Yes
Dorsal bands bearing lightened centres	Weak	Weak	Weak
Dorsal bands edged with light tubercles	Weak	Yes	Yes
Dorsal band borders	Jagged	Jagged	Jagged
Dark markings in dorsal interspaces	Yes	Yes	Yes
Ventrolateral body fold whitish	No	No	No
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No
Anterodorsal margin of thighs darkly pigmented	Yes	Yes	Yes
Anterodorsal margin of brachia darkly pigmented	Yes	Yes	Yes
Light caudal bands with dark markings	/	Yes	Yes
Light caudal bands encircle tail	/	No	No
Number of light caudal bands	/	/	9
Number of dark caudal bands	/	/	9
Dark caudal bands wider than light caudal bands	/	Yes	Yes
Mature regenerated tail spotted	/	No	/
SVL	88.3	91.6	86.2
TL	58.9	93.0	126.0
TW	9.8	8.2	8.2
FL	14.4	14.3	13.6
TBL	17.2	17.6	15.4
AG	39.0	44.2	40.4

Table 16. *Continued*

	LSUHC 12835 holotype	LSUHC 12837 paratype	LSUHC 12836 paratype
HL	26.4	26.7	24.2
HW	17.3	18.2	17.3
HD	10.3	11.1	10.1
ED	6.5	6.7	6.0
EE	6.2	6.8	6.4
ES	10.4	11.0	10.4
EN	8.8	8.1	8.7
IO	7.3	8.4	9.0
EL	3.3	3.9	2.9
IN	2.9	2.8	2.8

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable.

L. Wood, Jr., Matthew L. Murdoch, Myint Kyaw Thura, Evan S. H. Quah, Thaw Zin, Htet Kyaw and Marta S. Grismer from Sin Yine Cave 18.5 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493; 26 m in elevation).

Paratypes: Adult females LSUHC 12836–37 bear the same collection data as the holotype.

Diagnosis: Cyrtodactylus sinyineensis sp. nov. differs from all congeners by having the unique combination of nine or ten supralabials; eight infralabials; 15 longitudinal rows of body tubercles; 33–35 paravertebral tubercles; 27–29 ventral scales; relatively long digits with 8–10 expanded subdigital lamellae proximal to the digital inflection on the fourth toe, 11 or 12 unmodified, distal, subdigital lamellae; 19–21 total subdigital lamellae; raised, moderate to strongly keeled, dorsal body tubercles extending beyond base of tail; enlarged femoral and precloacal scales continuous; 26 or 27 enlarged femoral scales nearly equal in size; 18 femoral pores in males; 10–12 enlarged precloacal scales; five precloacal pores in males; three rows of enlarged, post-precloacal scales; median subcaudal scales twice as wide as long, not extending onto lateral surface of tail; top of head bearing diffuse dark mottling, no yellow reticulum; nuchal loop not divided medially, lacking an anterior, azygous notch, posterior border jagged; five or six dark, jagged dorsal bands wider than interspaces bearing weakly lightened centres, edged with yellow tubercles; nape band present; dark markings in dorsal interspaces variable; ventrolateral folds not whitish; anterodorsal margins of thighs and brachia darkly pigmented; nine light-coloured, caudal bands bearing dark markings, not encircling tail; and nine dark caudal bands wider than light caudal bands.

Description of holotype: Adult male SVL 88.3 mm; head moderate in length (HL/SVL 0.30), wide (HW/HL 0.65), flat (HD/HL 0.39), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region shallowly concave, canthus rostralis rounded; snout elongate (ES/HL 0.39), rounded in dorsal profile, not flat in lateral profile; eye large (ED/HL 0.25); ear opening round, moderate in size (EL/HL 0.12); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by inverted Y-shaped furrow, bordered posteriorly by left and right large supranasals meeting on midline, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial; 10(R)9(L) square supralabials extending to below midpoint of eye; 8(R,L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with small tubercles; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals contacting for 65% of their length posterior to mental; one row of slightly enlarged chinshields bordering all infralabials; and gular and throat scales small, flat, grading posteriorly into larger, subimbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.44) with well-defined ventrolateral folds; dorsal scales small, raised and interspersed with large, conical, semi-regularly arranged, moderate to strongly keeled tubercles; tubercles extend from nape to beyond base of tail; tubercles on nape smaller than those on posterior portion of body; approximately 15 longitudinal rows of body tubercles; 33 paravertebral tubercles; 27 flat, subimbricate, ventral scales larger than dorsal scales;

ten enlarged precloacal scales; five precloacal pores; three rows of large, post-precloacal scales; and no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.16); flat scales of forearm larger than those on body, not interspersed with small tubercles; palmar scales flat; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; expanded, proximal, subdigital lamellae do not extend onto palm; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.19), covered dorsally by granular scales intermixed with large tubercles and bearing flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsals, one row of 13(R,L) nearly equally sized, enlarged femoral scales in contact with enlarged precloacal scales; 9(R,L) femoral pores; subtibial scales flat, imbricate; small postfemoral scales form abrupt union with larger, flat ventral scales of posteroventral margin of thigh; plantar scales slightly raised; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 8(R,L) transversely expanded subdigital lamellae on fourth toe, 11(R,L) unmodified subdigital lamellae distal to inflection, 19 total subdigital lamellae; and claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail regenerated, 58.9 mm in length, 9.8 mm in width at base, tapering to a point; dorsal scales of tail flat; 3(R,L) enlarged postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

Coloration in life: Dorsal ground colour of head body, and limbs dark-brown, that of posterior portion of tail whitish; top of head and rostrum darkly mottled bearing a network of diffuse, yellow markings but no reticulum; superciliary scales yellow; dark-brown, nuchal band distinct, unnotched anteromedially, bearing a jagged posterior margin; large, dark, paravertebral markings on nape; six jagged body bands bearing weakly lightened centres, wider than interspaces; one incomplete sacral band; interspaces bearing diffuse, dark markings; limbs darkly mottled not banded; thighs and brachia, darkly pigmented; ventrolateral body folds not whitish; and ventral surfaces pigmented, dusky in appearance.

Variation (Fig. 28; Fig. S9): The female paratypes differ to varying extents from the holotype in aspects of the dorsal colour pattern. LSUHC 12836 has a complete tail with a median row of wide, transversely expanded subcaudal scales twice as wide as long; nine dark caudal bands bearing lightened centres, wider than light caudal bands; nine light caudal bands with dark

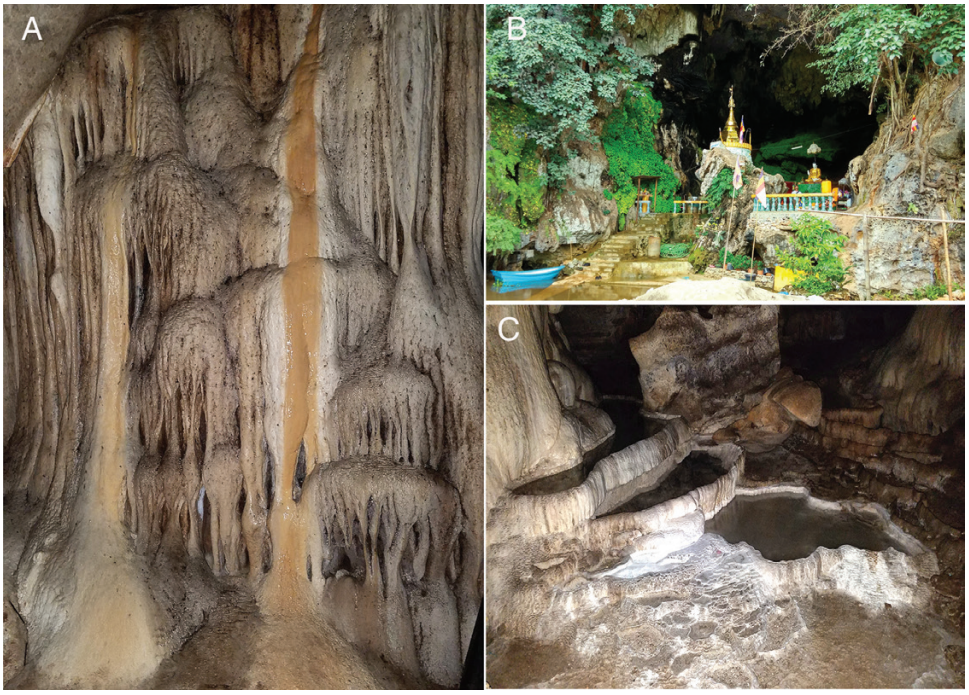

Figure 29. A, microhabitat structure of stalactites along the cave wall inside Sin Yine Cave, 18.5 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar. B, entrance to Sin Yine Cave. C, microhabitat structure on the floor of Sin Yine Cave.

spots, not encircling tail; and a dark-brown subcaudal region. LSUHC 12837 has lineate components to its dorsal pattern with a generally yellow hue and a regenerated tail with dark, irregularly shaped markings. Meristic differences are listed in Table 16.

Distribution: *Cyrtodactylus sinyineensis* sp. nov. is known only from Sin Yine Cave 18.5 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (Fig. 20).

Etymology: The specific epithet, *sinyineensis*, is a noun in apposition in reference to the type locality of Sin Yine Cave.

Natural history: Sin Yine Cave is situated on the south end of a large, isolated, karst hill approximately 3.6 km wide, 16.4 km long and 338 m high that is surrounded by paddy fields and located immediately south-east of Hpa-an. Sin Yine Cave is connected to Sadan Cave as they occur along the same, semicircular karst ridge. The mouth of Sin Yine Cave is approximately 700 m away from the southern opening of Sadan Cave across an ephemerally flooded paddy field. The interior of the Sin Yine Cave is wide (~25 m) and it has the appropriate microhabitat (fluted stalactites and stalagmites, alcoves, cracks, small side caves, etc.) necessary for *Cyrtodactylus* (Fig. 29). A total of three specimens were collected: LSUHC 12837 was 1 m above the cave floor on a stalagmite with water flowing down its face; LSUHC 12835 was seen running across the ground through water at the base of a stalagmite; and LSUHC 12836 was found 2 m above the cave floor on the cave wall. All lizards were found in close proximity (~15 m) to one another in near total darkness, approximately 100 m from the cave entrance.

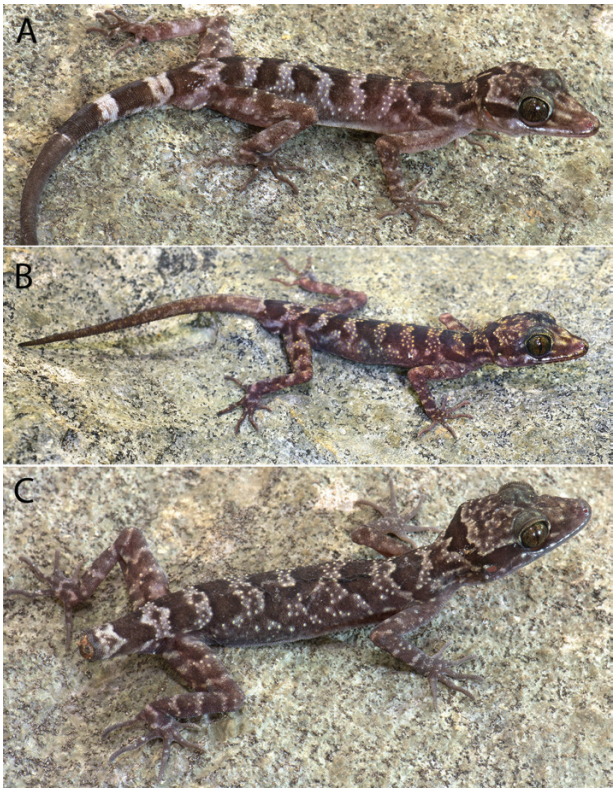

Figure 30. Type specimens of ***Cyrtodactylus welpyanensis* sp. nov.** from the type locality of Welpyan Cave 35, km north of Hpa-an, Hpa-an District, Kayin State, Myanmar. A, adult male holotype (LSUHC 12784). B and C, adult female paratypes LSUHC 12886 and 12785, respectively.

Comparisons: *Cyrtodactylus sinyineensis* sp. nov. is part of the *sinyineensis* group. The PCA and DAPC analyses indicate that the species of this group are completely separate in morphospace where the first two principal components account for 63% of the total variation (Fig. 12) and load most heavily for numbers of infralabials, longitudinal rows of body tubercles, expanded subdigital fourth toe lamellae and post-precloacal scale rows (Table S3). *Cyrtodactylus sinyineensis* sp. nov. is well-differentiated from *C. aequalis*, *C. dammanthaensis* sp. nov. and *C. welpyanensis* sp. nov. by having varying combinations of statistically different mean values of infralabials, supralabials, ventral scales, enlarged femoral scales, precloacal scales; and longitudinal rows of body tubercles (Table 3). It differs further from its sister species, *C. welpyanensis* sp. nov., by having dorsal bands edged with light tubercles and having a maximum SVL of 91.6 mm vs. 70.6 mm. It differs further from *C. dammathetensis*, and *C. aequalis* by lacking paravertebral elements in the dorsal banding pattern (Table 8). Morphological and colour pattern differences from other species in the Indo-Chinese clade are listed in Table 8. Genetic distances among the species of this group range from 11.0 to 16.5% (Table 10).

CYRTODACTYLUS WELPYANENSIS SP. NOV.
WEL PYAN CAVE BENT-TOED GECKO
(FIG. 30; TABLE 17)

Holotype: Adult male LSUHC 12874 collected on 3 October 2016 at 1500 h by Myint Kyaw Thura, L. Lee Grismer, Perry L. Wood, Jr., Matthew L. Murdoch, Evan S. H. Quah, Thaw Zin, Htet Kyaw and Marta S. Grismer from Wel Pyan Cave 35 km north of Hpa-an, Hpa-an District, Kayin State, Myanmar (N17°12.188, E97°37.066; 21 m in elevation).

Paratypes: Adult female LSUHC 12785 and adult male 12786 bear the same collection data as the holotype.

Table 17. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus welpyanensis* sp. nov.**

	LSUHC 12784 holotype	LSUHC 12785 paratype	LSUHC 12786 paratype
Sex	M	F	M
Supralabials	8	8	9
Infralabials	7	7	7
Body tubercles low, weakly keeled	No	No	No
Body tubercles raised, moderately to strongly keeked	Yes	Yes	Yes
Paravertebral tubercles	30	33	32
Longitudinal rows of body tubercles	16	16	16
Tubercles extend beyond base of tail	No	/	/
Ventral scales	30	30	28
Expanded subdigital lamellae on fourth toe	8	8	8
Unmodified subdigital lamellae on fourth toe	11	13	12
Total subdigital lamellae on fourth toe	19	21	20
Enlarged femoral scales (R/L)	14R16L	14R16L	17R14L
Femoral pores (R/L)	7R9L	/	8RL
Enlarged precolacal scales	11	12	13
Precloacal pores	7	/	8
Post-precloacal scales rows	3	3	3
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes
Pore-bearing femoral and precloacal scales continuous	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	No	No	No
Medial subcaudals two or three times wider than long	2	/	2
Medial subcaudals extend onto lateral subcaudal region	No	No	No
Nuchal loop divided medially	No	No	No
Nuchal loop with anterior azygous notch	No	No	No
Posterior border of nuchal loop	Jagged	Jagged	Jagged
Band on nape	Yes	Yes	Yes
Dorsal banding with paravertebral elements	No	No	No
Number of body bands	6	6	6
Dorsal bands wider than interspaces	Yes	Yes	Yes
Dorsal bands bearing lightened centres	No	No	No
Dorsal bands edged with light tubercles	No	No	No
Dorsal band borders	Jagged	Jagged	Jagged
Dark markings in dorsal interspaces	Yes	Yes	Yes
Ventrolateral body fold whitish	Yes	Yes	Yes
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No
Anterodorsal margin of thighs darkly pigment	Yes	Yes	Yes
Anterodorsal margin of brachia darkly pigment	Yes	Yes	Yes
Light caudal bands with dark markings	Yes	Yes	/
Light caudal bands encircle tail	No	No	/
Number of light caudal bands	/	9	/
Number of dark caudal bands	/	10	/
Dark caudal bands wider than light caudal bands	Yes	Yes	/
Mature regenerated tail spotted	No	No	No
SVL	69.2	70.6	68.9
TL	86.0r	73.0b	72.0
TW	6.8	6.7	7.0
FL	11.9	11.9	12.1
TBL	13.9	12.9	13.8
AG	31.5	29.4	27.9

Table 17. *Continued*

	LSUHC 12784 holotype	LSUHC 12785 paratype	LSUHC 12786 paratype
HL	20.8	21.1	19.5
HW	13.0	13.4	13.4
HD	7.8	7.4	7.7
ED	5.7	5.2	5.2
EE	4.9	5.3	4.5
ES	8.7	8.4	9.3
EN	6.7	6.5	6.5
IO	5.2	5.6	5.2
EL	1.7	2.5	1.9
IN	2.1	2.5	2.5

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable; r, regenerated; b, broken.

Diagnosis: Cyrtodactylus welpyanensis sp. nov. differs from all congeners by having the unique combination of eight or nine supralabials; seven infralabials; 16 longitudinal rows of body tubercles; 30–33 paravertebral tubercles; 28–30 ventral scales; relatively long digits with eight expanded subdigital lamellae proximal to the digital inflection on the fourth toe, 11–13 unmodified, distal, subdigital lamellae, 19–21 total subdigital lamellae; raised, moderate to strongly keeled, dorsal body tubercles not extending beyond base of tail; enlarged femoral and precloacal scales continuous; 30–31 nearly equally sized, enlarged, femoral scales; 16 femoral pores in males; 11–13 enlarged precloacal scales; 7–8 precloacal pores in males; three rows of enlarged post-precloacal scales; subcaudal scales twice as wide as long, not extending onto lateral surface of tail; top of head darkly mottled, no yellow reticulum; nuchal loop not divided medially, lacking an anterior, azygous notch, posterior border jagged; six dark dorsal bands lacking paravertebral elements, wider than interspaces, lacking lightened centres, not edged with white tubercles; nape band present; dark markings in dorsal interspaces; ventrolateral folds whitish; anterodorsal margins of thighs and brachia darkly pigmented; nine light caudal bands bearing dark markings, not encircling tail; ten dark caudal bands wider than light caudal bands; and mature regenerated tail unicolour.

Description of holotype: Adult male SVL 69.2 mm; head moderate in length (HL/SVL 0.30), wide (HW/HL 0.62), flat (HD/HL 0.37), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region shallowly concave, canthus rostralis rounded; snout elongate (ES/HL 0.42), rounded in dorsal profile, not flat in lateral profile; eye large (ED/HL 0.28); ear opening round, moderate in size (EL/HL 0.08); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by inverted Y-shaped furrow, bordered posteriorly by left and right supranasals and one azygous internasal, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals and ventrally by first supralabial; 8(R)10(L) square supralabials extending to below midpoint of eye; 7(R,L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with small tubercles laterally; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals contacting for 45% of their length posterior to mental; one row of slightly enlarged, chinshields bordering all infralabials; and gular and throat scales small, flat, grading posteriorly into larger, subimbricate pectoral and ventral scales.

Body relatively short (AG/SVL 0.46) with well-defined, ventrolateral folds; dorsal scales small, raised and interspersed with large, subconical, semi-regularly arranged, moderate to strongly keeled tubercles; tubercles extend from nape to base of tail but no farther; tubercles on nape smaller than those on posterior portion of body and less sharply keeled; approximately 16 longitudinal rows of body tubercles; 30 paravertebral tubercles; 30 flat, subimbricate, ventral scales larger than dorsal scales; 11 enlarged precloacal scales; seven precloacal pores; three rows of large post-precloacal scales; and no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.17); flat scales of forearm larger than those on body, not interspersed with small tubercles; palmar scales flat; digits well-developed, relatively long,

inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; widened, proximal, subdigital lamellae do not extend onto palm; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.20), covered dorsally by raised scales intermixed with large tubercles; flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsal scales, one row of 14(R)16(L) nearly equally sized, enlarged, femoral scales in contact with enlarged precloacal scales; 7(R)9(L) femoral pores; subtibial scales flat, imbricate; small, postfemoral scales form abrupt union with larger, flat ventral scales of posteroventral margin of thigh; plantar scales raised; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 8(R,L) expanded subdigital lamellae on fourth toe proximal to joint inflection, 11(R,L) unmodified subdigital lamellae distal to inflection, 19 total subdigital lamellae; and claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail moderate in proportions, 86.0 mm in length, last 50.0 mm regenerated, 6.8 mm in width at base, tapering to a point; dorsal scales of tail flat; medial subcaudal scales twice as wide as long, not extending onto lateral surface of tail; 4(R,L) enlarged postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

Figure 31. A, entrance to Welpyan Cave, Kayin State, Myanmar. B, microhabitat structure of the cave walls inside Welpyan Cave.

Coloration in life (*Fig. 30*)*:* Dorsal ground colour of head body, and limbs faintly magenta, that of anterior portion of tail dull-white; top of head and rostrum bearing a network of dark, diffuse mottling, no yellow reticulum; superciliary scales whitish; dark-brown, jagged, nuchal loop, unnotched anteromedially, deeply incised posteromedially; short, jagged incomplete band on nape; six jagged, dark, body bands not bearing lightened centres, wider than interspaces, not bearing paravertebral elements; one sacral band; interspaces bearing faint, dark markings, most extensive on flanks; irregularly shaped, faint bands on thighs; thighs and brachia darkly pigmented; ventrolateral body folds whitish; dark caudal bands not bearing lightened centres, wider than light caudal bands; light caudal bands with dark markings, not encircling tail; and ventral surfaces pigmented, dusky in appearance, more so beneath limbs and tail, less so in gular region.

Variation (Fig. S10): The paratypes closely approximate holotype in aspects of dorsal colour pattern. The dorsal band in the shoulder region in LSUHC 12786 is not bifurcated and it has a completely, nearly unicolour tan, regenerated tail. LSUHC 12785 is much darker overall. Meristic and mensural differences are presented in Table 17.

Distribution: Cyrtodactylus welpyanensis sp. nov. is known only from Wel Pyan Cave 35 km north of Hpa-an, Hpa-an District, Kayin State, Myanmar (Fig. 29).

Etymology: The specific epithet, *welpyanensis* (pronounced *way-pee-an-ensis*), is a noun in apposition in reference to the type locality of Wel Pyan Cave.

Natural history: Wel Pyan Cave is located along the west side of the Salween River and situated on the eastern flank of a small karst hill approximately 0.5 km wide, 1.3 km long and 256 m high that is surrounded by paddy fields. The opening of the cave is narrow (~10 × 10 m) and situated approximately 25 m above the base of the hill. The interior of the cave is complex and filled with blind caverns, stalactites and a maze of small, underground passageways through which water courses and through which a flatulent monk guided us (Fig. 31). We found three specimens of *C. welpyanensis* sp. nov. at approximately 1500 h 2–6 m up on clean, dry, smooth surfaces of the cave walls all within 10 m of each other and all within 50 m of the cave entrance where light still penetrated. Outside the cave, the base of the karst hill was jagged, deeply incised with

small, steep ravines and riddled with boulders that had broken away from the hillside. We do not believe that *C. welpyanensis* sp. nov. is restricted to the interior of the cave and if we had not been unexpectedly rushed away due to safety concerns, we believe many more specimens would have been found outside the cave after dark. The only other gekkonid seen was *H. frenatus*.

Comparisons: Cyrtodactylus welpyanensis sp. nov. is part of the *sinyineensis* group. The PCA and DAPC analyses indicate that the species of this group are completely separated in morphospace where the first two principal components account for 63% of the total variation (Fig. 12; Fig. S5) and load most heavily for numbers of infralabials, longitudinal rows of body tubercles, expanded subdigital lamellae on the fourth toe and post-precloacal scale rows (Table S3). *Cyrtodactylus wlepyanensis* sp. nov. is well-differentiated from *C. aequalis*, *C. sinyineensis* sp. nov. and *C. dammathetensis* sp. nov. by having varying combinations of statistically different mean values of supralabial scales, infralabial scales, ventral scales, longitudinal rows of body tubercles, precloacal scales and body bands (Table 3). It differs further from the other species in the *sinyineensis* group in that the body tubercles do not extend past the base of the tail and from *C. aequalis* and *C. sinyineensis* sp. nov. in that the dark body bands are not edged with light tubercles (Table 8). Morphological and colour pattern differences from other species in the Indo-Chinese clade are listed in Table 8. Genetic distances among the species of this group range from 11.0 to 16.5% (Table 10).

The oldhami *group*

The monophyletic *oldhami* group is composed of *Cyrtodactylus* cf. *peguensis zebraicus*, a polyphyletic *C. oldhami*, *C. thirakhupti*, *C. payarhtanensis* and *C. lenya* from the Thai-Malay Peninsula just north of the Isthmus of Kra and *C. saiyok* from southwestern Thailand (Figs 2, 9). This group undoubtedly contains more Thai species but until researchers describing new species from this region realize that taking tissue samples in an age of integrative taxonomy is imperative, we will never know. The *oldhami* group is highly variable and defined by the following characters from Smith (1935), Taylor (1963), Pauwels *et al.* (2004), Grismer & Norhayati (2008), Panitvong *et al.* (2014) and in part by Connette *et al.* (2017): 9–13 supralabials; 9–12 infralabials; 14–20 longitudinal rows of body tubercles; 23–40 ventral scales; 7–20 subdigital lamellae; femoral pores absent; 0–8 precloacal pores in males; post-preclocal scales large; wide, transverse, medial, subcaudal scales; no anterior azygous notch in nuchal loop; no band on nape; 4–7 variably shaped body bands with lightened centres or dorsal pattern composed of light lines or pairs of dark paravertebral blotches; anterodorsal margins of thighs and brachia and ventrolateral folds pigmented; and maximum SVL 61.0–83.0 mm. Connette *et al.* (2017) recovered *C. payarhtanensis* as the sister species of a genetic sample of *C. oldhami* from the pet trade that has no voucher or locality. We sequenced two vouchered southern Thai specimens (MS 460, 585) from Ranong and Phang-nga Provinces, respectively, that form a monophyletic group but exclude the pet trade specimen, indicating *C. oldhami* may be polyphyletic. Our data further indicate that *C. thirakhupti* is the sister species of *C. oldhami* (MS 460, 585) and that *C. payarhtanensis* is sister to that group (Fig. 9).

Figure 32. Type series of ***Cyrtodactylus yathepyanensis* sp. nov.** from the type locality of Yathe Pyan Cave, 9 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar showing the range of variation in coloration and pattern. A, adult female paratype LSUHC 12821. B, adult male holotype LSUHC 12823. C, adult female paratype BYU 52229.

The yathepyanensis *group*

The monophyletic *yathepyanensis* group is composed of *Cyrtodactylus yathepyanensis* sp. nov. and the sister

Table 18. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus yathepyanensis* sp. nov.**

	LSUHC 12823 holotype	LSUHC 12822 paratype	BYU 52228 paratype	BYU 52229 paratype	LSUHC 12821 paratype
Sex	M	F	F	F	F
Supralabials	10	10	10	9	9
Infralabials	9	8	9	8	8
Body tubercles low, weakly keeled	No	No	No	No	No
Body tubercles raised, moderately to strongly keeked	Yes	Yes	Yes	Yes	Yes
Paravertebral tubercles	32	31	32	31	32
Longitudinal rows of body tubercles	19	18	18	19	18
Tubercles extend beyond base of tail	Yes	Yes	Yes	Yes	Yes
Ventral scales	30	32	30	30	31
Expanded subdigital lamellae on fourth toe	9	9	9	9	8
Unmodified subdigital lamellae on fourth toe	14	13	14	13	12
Total subdigital lamellae on fourth toe	23	22	23	22	20
Enlarged femoral scales (R/L)	16R17L	15RL	13R12L	17R16L	16R14L
Femoral pores (R/L)	9R8L	/	/	/	/
Enlarged precolacal scales	11	13	10	10	10
Precloacal pores	6	/	/	/	/
Post-precloacal scales rows	3	3	3	3	3
Enlarged femoral and precloacal scales continuous	Yes	Yes	Yes	Yes	Yes
Pore-bearing femoral and precloacal scales continuous	No	No	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	Yes	Yes	Yes	Yes	Yes
Medial subcaudals two or three times wider than long	3	3	3	3	3
Medial subcaudals extend onto lateral subcaudal region	Yes	Yes	Yes	Yes	Yes
Nuchal loop divided medially	No	No	No	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No
Posterior border of nuchal loop	Sinuous	Jagged	Jagged	Jagged	Sinous
Band on nape	No	Yes	No	Yes	Yes
Dorsal banding with paravertebral elements	No	No	No	No	No
Number of body bands	4	6	5	5	5
Dorsal bands wider than interspaces	Same	Same	Same	Same	Same
Dorsal bands bearing lightened centres	No	No	No	No	No
Dorsal bands edged with light tubercles	Yes	Yes	Yes	Yes	Yes
Dorsal band borders	Smooth	Jagged	Jagged	Jagged	Smooth
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	Yes	Yes	Yes	Yes	Yes
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No	No	No
Anterodorsal margin of thighs darkly pigment	Yes	Yes	Yes	Yes	Yes
Anterodorsal margin of brachia darkly pigment	Yes	Yes	Yes	Yes	Yes
Light caudal bands with dark markings	Yes	Yes	Yes	Yes	Yes
Light caudal bands encircle tail	No	No	No	No	No
Number of light caudal bands	/	/	/	/	13
Number of dark caudal bands	/	/	/	/	13
Dark caudal bands wider than light caudal bands	Yes	Yes	Yes	Yes	Yes
Mature regenerated tail spotted	No	No	No	/	/
SVL	68.0	71.3	71.3	71.4	72.7
TL	71.0	73.0	73.0	71.0	75.0
TW	8.1	7.0	6.4	6.9	6.9

Table 18. *Continued*

	LSUHC 12823 holotype	LSUHC 12822 paratype	BYU 52228 paratype	BYU 52229 paratype	LSUHC 12821 paratype
FL	11.6	11.1	10.2	11.3	12.0
TBL	14.7	13.4	12.6	13.1	13.3
AG	28.0	32.2	31.7	30.6	32.3
HL	19.7	21.4	20.4	21.9	20.4
HW	14.1	14.2	13.2	13.8	14.2
HD	8.1	8.4	7.8	8.6	7.9
ED	5.0	5.4	4.9	5.5	5.2
EE	5.4	5.7	5.6	6.0	5.2
ES	9.1	9.4	9.2	9.8	9.3
EN	7.1	7.2	7.1	6.6	7.1
IO	6.6	5.8	5.6	6.0	6.1
EL	3.6	3.2	2.7	3.0	3.8
IN	2.4	2.1	2.4	2.2	2.2

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable.

species *C. linnoensis* sp. nov. and *C. sadanensis* sp. nov. from the lowland flood plain of the Salween River Basin of Kayin and Mon and states (Figs 9, 20). The *yathepyanensis* group is defined by the flowing range of characters: 9–11 supralabials; 7–9 infralabials; dorsal body tubercles raised, moderately to strongly keeled, extending beyond base of tail; 13–19 longitudinal rows of body tubercles; 26–33 paravertebral tubercles; 30–38 ventral scales; 21–24 subdigital lamellae; 12–37 enlarged femoral scales, proximal scales one-half to one-third the size of distal scales; 12–14 femoral pores in males; 9–13 enlarged precloacal scales; 2–6 precloacal pores in males; three or four post-precloacal scale rows; transverse caudal scales two or three times as wide as long, extending onto lateral surface of tail; top of head bearing dark, mottled pattern; no anterior, azygous notch in nuchal loop; band on nape; 4–6 regularly shaped body bands lacking or with only faint, lightened centres, edged with light tubercles; anterodorsal margins of thighs darkly pigment; ventrolateral folds not whitish; 13–16 light caudal bands not encircling tail; 13–17 dark caudal bands; and maximum SVL 72.3–78.0 mm (Table 8). The description and diagnosis of each species follows.

CYRTODACTYLUS YATHEPYANENSIS SP. NOV.

YATHE PYAN CAVE BENT-TOED GECKO

(FIG. 32; TABLE 18)

Holotype: Adult male LSUHC 12823 collected on 4 October 2016 at 1800 h by Evan S. H. Quah, Matthew L. Murdoch, L. Lee Grismer, Marta S. Grismer, Myint Kyaw Thura, Perry L. Wood, Jr., Thaw Zin and Htet Kyaw from Yathe Pyan Cave 9 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.114, E97°34.243; 22 m in elevation).

Paratypes: Adult females BYU 52228–29 and LSUHC 12822 bear the same collection data as the holotype.

Diagnosis: Cyrtodactylus yathepyanensis sp. nov. differs from all congeners by having the unique combination of nine or ten supralabials; eight or nine infralabials; 18 or 19 longitudinal rows of body tubercles; 31 or 32 paravertebral tubercles; 30–32 ventral scales; relatively long digits with eight or nine expanded subdigital lamellae proximal to the digital inflection on the fourth toe, 12–14 unmodified, distal, subdigital lamellae, 20–23 total subdigital lamellae; raised, moderately to strongly keeled, dorsal body tubercles extending beyond base of tail; enlarged femoral and precloacal scales continuous; 25–34 enlarged femoral scales, proximal scales one-half to one-third the size of distal scales; 17 femoral pores in males; 10–13 enlarged precloacal scales; six precloacal pores in males; three rows of enlarged post-precloacal scales; medial subcaudal scales three times as wide as long extending onto lateral surface of tail; top of head bearing diffuse dark mottling, no yellow reticulum; nuchal loop not divided medially, lacking an anterior, azygous notch, posterior border sinuous to jagged; 4–6 dark, jagged, dorsal bands lacking paravertebral elements, same width as interspaces, lacking lightened centres, edged with light tubercles; dark markings and lacking light tubercles in dorsal interspaces; ventrolateral folds whitish; anterodorsal margins of

thighs and brachia darkly pigmented; 13 light caudal bands bearing dark markings, not encircling tail; 13 dark caudal bands wider than light caudal bands; and mature, regenerated tail not spotted.

Description of holotype: Adult male SVL 68.0 mm; head moderate in length (HL/SVL 0.29), wide (HW/HL 0.72), flat (HD/HL 0.41), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region concave, canthus rostralis rounded; snout elongate (ES/HL 0.46), rounded in dorsal profile, not flat in lateral profile; eye large (ED/HL 0.25); ear opening round, moderate in size (EL/HL 0.19); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by an inverted Y-shaped furrow, bordered posteriorly by left and right supranasals contacting on midline, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by three postnasals and ventrally by first supralabial; 10(R,L) square supralabials extending to below midpoint of eye; 9(R,L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with tubercles; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals contacting for 60% of their length posterior to mental; one row of slightly enlarged, chinshields bordering all infralabials; and gular and throat scales small, flat, grading posteriorly into larger, subimbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.41) with well-defined ventrolateral folds; dorsal scales small, raised and interspersed with large, conical, semi-regularly arranged, moderately to strongly keeled tubercles extending from nape to beyond base of tail; tubercles on nape smaller than those on posterior portion of body, less sharply keeled; approximately 19 longitudinal rows of body tubercles; 32 paravertebral tubercles; 30 flat, subimbricate, ventral scales larger than dorsal scales; 11 enlarged precloacal scales; six precloacal pores; three rows of large, post-precloacal scales; and no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.17); slightly raised scales of forearm larger than those on body, interspersed with small tubercles; palmar scales flat; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; widened, proximal, subdigital lamellae do not extend onto palm; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.22), covered dorsally by granular scales intermixed with large tubercles and bearing flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsal scales, one row of 16(R)17(L) enlarged, femoral scales in contact with enlarged precloacal scales; proximal femoral scales one-half to one-third the size of distal femoral scales; 9(R)8(L) femoral pores; subtibial scales flat, imbricate; small, postfemoral scales form abrupt union with larger, flat, ventral scales of posteroventral margin of thigh; plantar scales raised; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 9(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection not extending onto sole, 14(R,L) unmodified subdigital lamellae distal to inflection, 23 total subdigital lamellae; and claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail moderate in proportions, 71.0 mm in length, last 35.0 mm regenerated, 8.1 mm in width at base, tapering to a point; dorsal scales of tail flat; medial subcaudal scales three times as wide as long extending onto lateral surface of tail; 2(R,L) enlarged, postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

Coloration in life (*Fig. 32*)*:* Dorsal ground colour of head body, and limbs tan, that of anterior portion of tail dull-yellow; top of head bearing, medial, diffuse dark mottling, no yellow reticulum; rostrum bearing diffuse, dark, lineate markings; superciliary scales tan; distinct, dark-brown nuchal loop, notched posteromedially not anteromedially, and bearing a sinuous posterior margin; no band on nape; four regularly shaped body bands not bearing light centres, same width as interspaces, lacking paravertebral elements; one sacral band; interspaces bearing dark markings, especially on flanks; banding on limbs indistinct, mottled with yellowish markings; anterodorsal margins of thighs and brachia pigmented; ventrolateral body folds whitish; dark caudal bands lacking lightened centres, wider than light caudal bands; light caudal bands bearing dark markings, not encircling tail; ventral surfaces pigmented, dusky in appearance; and subcaudal region gray with light mottling.

Variation (*Fig. 32; Fig. S11*)*:* The female paratypes generally approximate the holotype in aspects of colour pattern. LSUHC 12819 is somewhat darker overall and BYU 52228–29 and LSUHC 12822 have weakly pigmented, ventrolateral body folds. The nape band is present in BYU 52229 and LSUHC 12821–22. BYU 52228 and LSUHC 128221 have original tails. Meristic and mensural differences are presented in Table 18.

Distribution: Cyrtodactylus yathepyanensis sp. nov. is known only from Yathe Pyan Cave 9 km south-west

Figure 33. Microhabitat structure of the limestone hillside outside Yathe Pyan Cave, Kayin State, Myanmar.

of Hpa-an, Hpa-an District, Kayin State, Myanmar (Fig. 20).

Etymology: The specific epithet, *yathepyanensis* (pronounced *ya-thay-pee-an-ensis*), is a noun in apposition in reference to the type locality of Yathe Pyan Cave.

Natural history: Yathe Pyan Cave is located at the south end of a karst hill approximately 1.2 km wide, 3.7 km long and 241 m high that is surrounded by paddy fields and situated just west of the Salween River. The opening of the cave is very wide and high (~45 m by ~20 m) and the cave is filled with religious structures. It extends for nearly 0.5 km and opens up again on the western side of the hill. No *C. yathepyanensis* sp. nov. were seen inside the cave during the afternoon at 1600 h but two were observed deep within cracks outside the cave at the base of the karst hill. This portion of the hill has several boulders, cracks and holes that serve as retreats (Fig. 33). During the evening, only one specimen was observed at the entrance of the cave although they were quite common outside the cave. One hatchling was observed. Lizards were extremely wary and difficult to catch and when observed, all were in close proximity to retreat sites. This was quite different from other species (i.e. *C. sadanensis* sp. nov., *C. pharbaungensis* sp. nov., *C. sanpelensis* sp. nov. and *C. linnoensis* sp. nov.) we had collected in similar habitats on the hillsides outside of caves and we suspect the presence of numerous *Gecko gecko*, which could easily be a potential predator, could have been the reason. Other gekkonids observed were *Gehyra mutilata* and *H. frenatus*.

Comparisons: Cyrtodactylus yathepyanensis sp. nov. is part of the *yathepyanensis* group. The PCA and DAPC analyses indicate that the species of this group are completely separate in morphospace and that the first two principal components account for 54% of the

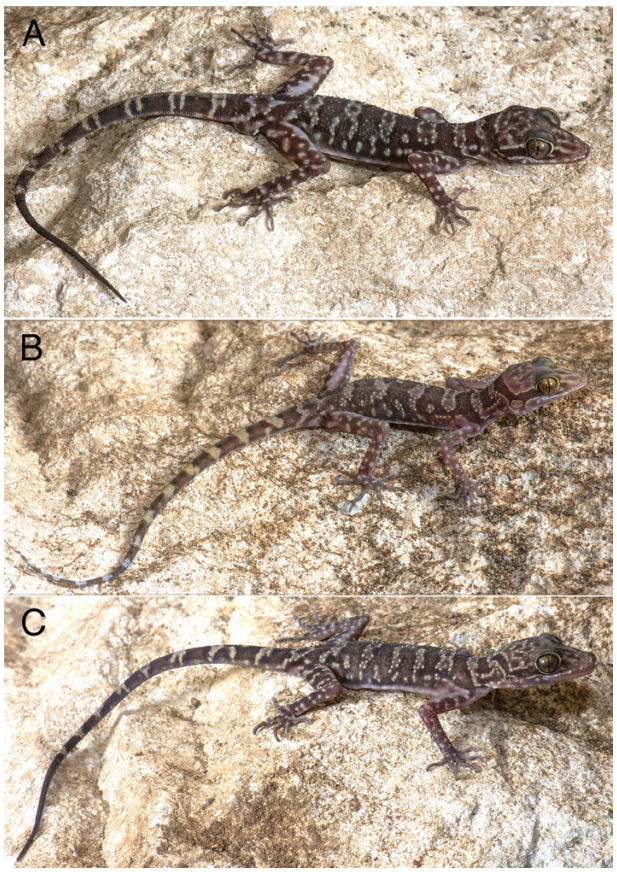

Figure 34. Type specimens of ***Cyrtodactylus linnoensis* sp. nov.** from the Linno Cave region, 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar showing the range of variation in coloration and pattern. A, adult male holotype (LSUHC 12826). B, juvenile male paratype (BYU 52233). C, adult female paratype (LSUHC 12824).

total variation (Fig. 12; Fig. S5) and load most heavily for numbers of paravertebral tubercles and ventral scales (Table S4). *Cyrtodactylus yathepyanensis* sp. nov. is well-differentiated from *C. linnoensis* sp. nov. and *C. sadanensis* sp. nov. by having varying combinations of statistically different mean values of supralabial and infralabial scales, paravertebral tubercles, unmodified and total fourth toe lamellae, ventral scales, enlarged femoral scales, and longitudinal rows of body tubercles and precloacal pores (Table 4). It differs further from *C. sadanensis* sp. nov. and some *C. linnoensis* sp. nov. in having continuous vs. discontinuous enlarged femoral and precloacal scales and pigmented vs. unpigmented thighs and brachia, and from *C. sadanensis* sp. nov. in having a smaller maximum SVL (72.8 mm vs. 78.0 mm; Table 8). Morphological and colour pattern differences from other species in the Indo-Chinese clade are listed in Table 8. Genetic distances among the species of this group range from 11.0 to 12.7% (Table 10).

CYRTODACTYLUS LINNOENSIS SP. NOV.

LINNO CAVE BENT-TOED GECKO

(FIG. 34; TABLE 19)

Holotype: Adult male LSUHC 12826 collected on 4 October 2016 at 2000 h by L. Lee Grismer, Perry L. Wood, Jr., Evan S. H. Quah, Matthew L. Murdoch, Marta S. Grismer, Myint Kyaw Thura, Thaw Zin and Htet Kyaw from the Linno Cave region 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°50.551, E97°36.402; 25 m in elevation).

Paratypes: Adult males BYU 52230–31, 52323, LSUHC 12829, 12832–34, juvenile male BYU 52223 and adult females LSUHC 12824–25 bear the same collection data as the holotype.

Diagnosis: Cyrtodactylus linnoensis sp. nov. differs from all congeners by having the unique combination of nine or ten supralabials; seven or eight infralabials; 13–15 rows of longitudinal body tubercles; 26 or 27 paravertebral tubercles; 35–38 ventral scales; relatively long digits with nine or ten expanded subdigital lamellae proximal to the digital inflection on the fourth toe, 13 or 14 unmodified, distal, subdigital lamellae, 22–24 total subdigital lamellae; raised, moderately to strongly keeled, dorsal, body tubercles extending beyond base of tail; 12–37 enlarged femoral scales, proximal scales one-half to one-third the size of distal scales; 12–14 femoral pores in males; 9–13 enlarged precloacal scales; 4–6 precloacal pores in males; three or four rows of enlarged post-precloacal scales; medial subcaudal scales three times as wide as long, extending onto lateral surface of tail; top of head bearing diffuse, dark mottling, no yellow reticulum; nuchal loop lacking an anterior, azygous notch, posterior border usually sinuous; five or six dark, jagged, dorsal bands lacking paravertebral elements, wider than interspaces, faintly lightened centres, edged with light-coloured tubercles; band on nape; dark markings but no light-coloured tubercles in dorsal interspaces; ventrolateral folds whitish; anterodorsal margins of thighs lack pigment; brachia at least faintly pigmented; 15 light-coloured caudal bands bearing dark markings, not encircling tail; 14 dark caudal bands wider than light caudal bands; and mature, regenerated tail not spotted.

Description of holotype: Adult male SVL 74.9 mm; head moderate in length (HL/SVL 0.29), wide (HW/HL

Table 19. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus linnoensis* sp. nov.**

	LSUHC 12826 holotype	LSUHC 12824 paratype	LSUHC 12825 paratype	BYU 52230 paratype	BYU 52231 paratype	LSUHC 12829 paratype	BYU 52232 paratype	BYU 52233 paratype	LSUHC 12832 paratype	LSUHC 12833 paratype	LSUHC 12834 paratype
Sex	M	F	F	M	M	M	M	M	M	M	M
Supralabials	9	9	10	10	9	9	9	10	9	10	10
Infralabials	8	7	8	7	7	7	8	7	7	7	7
Body tubercles low, weakly keeled	No	No	No	No	No	No	No	No	No	No	No
Body tubercles raised, moderately to strongly keeked	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Paravertebral tubercles	26	27	26	26	27	26	26	26	26	27	26
Longitudinal rows of body tubercles	13	13	13	13	14	15	13	13	14	13	15
Tubercles extend beyond base of tail	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventral scales	38	36	36	37	38	36	38	35	37	37	38
Expanded subdigital lamellae on fourth toe	9	10	9	9	9	9	9	9	9	10	10
Unmodified subdigital lamellae on fourth toe	14	14	14	14	14	14	14	13	14	14	14
Total subdigital lamellae on fourth toe	23	24	23	23	23	23	23	22	23	24	24
Enlarged femoral scales (R/L)	17RL	9RL	8RL	7R11L	10R12L	6RL	8R7L	12R10L	16R17L	19R18L	20R17L
Femoral pores (R/L)	6R6L	/	/	5R7L	6R7L	6R6L	6R7L	/	8R8L	7R7L	8RL
Enlarged precolacal scales	13	12	10	12	12	10	10	12	13	9	13
Precloacal pores	5	/	/	4	4	5	5	5	5	4	6
Post-precloacal scales rows	3	3	3	3	3	4	3	3	3	3	4
Enlarged femoral and precloacal scales continuous	Yes	No	No	No	No	No	No	No	Yes	Yes	Yes
Pore-bearing femoral and precloacal scales continuous	No	No	No	No	No	No	No	No	No	No	No

Table 19. *Continued*

	LSUHC 12826 holotype	LSUHC 12824 paratype	LSUHC 12825 paratype	BYU 52230 paratype	BYU 52231 paratype	LSUHC 12829 paratype	BYU 52232 paratype	BYU 52233 paratype	LSUHC 12832 paratype	LSUHC 12833 paratype	LSUHC 12834 paratype
Enlarged proximal femoral scales ~1/2 size of distal femorals	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Medial subcaudals two or three times wider than long	3	3	3	3	3	3	3	3	3	3	3
Medial subcaudals extend onto lateral subcaudal region	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Nuchal loop divided medially	No	Yes	No	Yes	No	Yes	No	No	Yes	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No	No	No	No	No	No	No
Posterior border of nuchal loop	Sinuous	Sinuous	Jagged	Sinuous	Sinuous	Sinuous	Sinuous	Sinuous	Sinuous	Sinuous	Sinuous
Band on nape	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal banding with paravertebral elements	No	No	No	No	No	No	No	No	No	No	No
Number of body bands	5	6	5	5	5	5	5	5	5	5	5
Dorsal bands wider than interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal bands bearing lightened centres	Faint	Faint	Faint	Faint	Faint	Faint	Faint	Faint	Faint	Faint	Faint
Dorsal bands edged with light tubercles	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal band borders	Jagged	Jagged	Jagged	Jagged	Jagged	Jagged	Jagged	Jagged	Jagged	Jagged	Jagged
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled

Table 19. *Continued*

	LSUHC 12826 holotype	LSUHC 12824 paratype	LSUHC 12825 paratype	BYU 52230 paratype	BYU 52231 paratype	LSUHC 12829 paratype	BYU 52232 paratype	BYU 52233 paratype	LSUHC 12832 paratype	LSUHC 12833 paratype	LSUHC 12834 paratype
Light reticulum on top of head	No	No	No	No	No	No	No	No	No	No	No
Anterodorsal margin of thighs darkly pigmented	No	No	No	No	No	No	No	No	No	No	No
Anterodorsal margin of brachia darkly pigmented	Faint	Faint	Yes	Yes	Yes	Faint	Faint	Faint	Faint	Faint	Faint
Light caudal bands with dark markings	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Light caudal bands encircle tail	No	No	No	No	No	No	No	No	No	No	No
Number of light caudal bands	/	/	/	/	/	/	/	15	/	/	/
Number of dark caudal bands	/	/	/	/	/	/	/	14	/	/	/
Dark caudal bands wider than light caudal bands	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Mature regenerated tail spotted	No	No	No	No	No	No	No	No	No	No	No
SVL	74.9	76.0	77.5	73.4	74.8	75.8	76.1	55.7	76.9	78.0	76.6
TL	79.0	116.0r	96.0r	92.0r	89.0r	109.0r	45.0b	87	99.0r	99.0r	105.0r
TW	7.6	6.5	7.0	7.6	8.6	8.1	8.8	4.6	8.4	8.2	8.5
FL	13.2	14.5	12.6	13.5	13.6	14.3	14.9	9.5	13.8	13.1	14.2
TBL	16.3	15.4	17.4	15.0	16.7	15.3	16.4	12.3	17.1	16.0	16.7
AG	34.5	33.7	34.5	31.4	32.3	32.7	34.3	23.2	32.5	31.7	32.7
HL	21.7	21.6	22.4	21.9	22.8	21.5	21.3	15.8	20.8	21.2	22.0
HW	13.5	13.5	14.1	13.0	13.9	14.3	14.1	9.7	14.6	14.6	14.0
HD	8.8	8.0	9.2	8.0	9.3	8.9	8.0	6.0	8.4	8.7	9.0
ED	5.0	5.6	6.4	4.9	5.8	6.1	5.4	4.5	5.8	5.9	5.8
EE	5.7	5.2	5.0	5.4	5.3	5.8	5.3	3.9	5.3	5.7	5.4
ES	10.2	9.5	10.3	9.3	10.0	9.3	9.7	6.8	9.7	9.7	9.7
EN	8.0	7.9	7.4	7.8	7.9	7.7	7.2	5.4	7.5	7.5	7.6

Table 19. *Continued*

	LSUHC 12826 holotype	LSUHC 12824 paratype	LSUHC 12825 paratype	BYU 52230 paratype	BYU 52231 paratype	LSUHC 12829 paratype	BYU 52232 paratype	BYU 52233 paratype	LSUHC 12832 paratype	LSUHC 12833 paratype	LSUHC 12834 paratype
IO	6.6	6.5	6.6	6.4	6.6	6.3	6.4	4.4	6.9	5.9	6.7
EL	2.9	3.7	3.1	3.1	3.1	3.0	2.9	2.5	2.7	3.0	2.9
IN	2.5	2.0	2.5	2.2	2.3	2.2	2.2	1.9	2.3	2.1	2.3

Abbreviations are listed in Material and Methods. R, right; L, left; /, data unobtainable or not applicable; r, regenerated; b, broken.

0.62), flat (HD/HL 0.41), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region concave, canthus rostralis rounded; snout elongate (ES/HL 0.47), rounded in dorsal profile, moderately flat in lateral profile; eye large (ED/HL 0.23); ear opening round, moderate in size (EL/HL 0.13); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by inverted Y-shaped furrow, bordered posteriorly by left and right supranasals contacting on midline and minute azygous scale, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial; 9(R,L) square supralabials extending to below midpoint of eye; 8(R,L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with small tubercles laterally; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large left and right trapezoidal postmentals contacting for 70% of their length posterior to mental; one row of slightly enlarged chinshields bordering all infralabials; and gular and throat scales small, flat, grading posteriorly into larger, subimbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.46) with well-defined ventrolateral folds; dorsal scales small, raised and interspersed with large, conical, semi-regularly arranged, moderately to strongly keeled tubercles extending from nape to beyond base of tail; tubercles on nape smaller than those on posterior portion of body, less sharply keeled; approximately 13 longitudinal rows of body tubercles; 26 paravertebral tubercles; 38 flat, subimbricate, ventral scales larger than dorsal scales; 13 enlarged precloacal scales; five precloacal pores; three rows of large, post-precloacal scales; no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.18); slightly raised scales of forearm larger than those on body, lacking tubercles; palmar scales low, rounded; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; widened, proximal, subdigital lamellae do not extend onto palm; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.22), covered dorsally by raised scales intermixed with large tubercles and bearing flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsal scales, one row 17(R,L) of enlarged femoral scales in contact with enlarged precloacal scales, proximal femoral scales one-half to one-third the size of distal femoral scales; 6(R,L) femoral

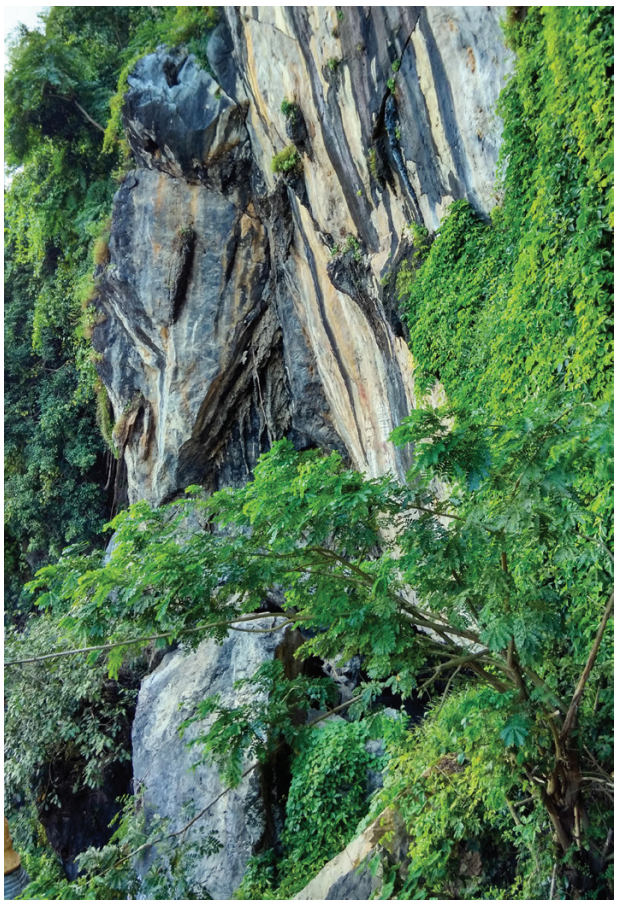

Figure 35. Microhabitat structure of the limestone hillside outside of Linno Cave, Kayin State, Myanmar.

pores; small, postfemoral scales form an abrupt union with larger, flat ventral scales of posteroventral margin of thigh; subtibial scales flat, imbricate; plantar scales raised; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 9(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection that do not extend onto sole, 14(R,L) unmodified subdigital lamellae distal to inflection, 23 total subdigital lamellae; and claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail original, moderate in proportions, 79.0 mm in length, 7.6 mm in width at base, tapering to a point; dorsal scales of tail flat; medial subcaudal scales three times as wide as long, extending onto lateral surface of tail; 2(R,L) enlarged, postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

Coloration in life: Dorsal ground colour of head body, and limbs grey, that of anterior portion of tail very dull-yellow; top of head bearing, diffuse, dark mottlings, yellow reticulum absent; rostrum bearing diffuse, dark, lineate markings; superciliary scales yellowish; dark-brown, nuchal loop bearing a sinuous posterior border connects with dark, nape band laterally; five jagged, body bands wider than interspaces, bearing faintly lightened centres, lacking paravertebral elements, edged with light tubercles; one nape band; one chevron-shaped postsacral band; interspaces bearing large dark markings, especially on flanks; line of yellowish spots on lower flanks; banding on limbs indistinct, mottled with yellowish markings; anterodorsal margins of thighs unpigmented; anterodorsal margins of brachia faintly to heavily pigmented; ventrolateral folds whitish; dark caudal bands not bearing lightened centres, wider than light caudal bands; light caudal bands bearing dark markings, not encircling tail; ventral surfaces pigmented, dusky in appearance; and subcaudal region dark with lighter mottling.

Variation (*Fig. S12*)*:* The paratypes reasonably approximate the holotype in aspects of colour pattern. The nuchal loop is divided in BYU 52230, LSUHC 12824, 12829 and 12832. In LSUHC 12825, the dorsal bands are so wide and dark, they are difficult to discern. Although BYU 52233 is a juvenile, its colour pattern is not notably more contrasted or different from the range of variation observed in the adults, indicating that an ontogenetic change is absent. Meristic and mensural differences are presented in Table 19.

Distribution: Cyrtodactylus linnoensis sp. nov. is known only from the Linno Cave region 5 km southwest of Hpa-an, Hpa-an District, Kayin State, Myanmar (Fig. 20).

Etymology: The specific epithet, *linnoensis*, is a noun in apposition in reference to the type locality.

Natural history: The Linno Cave region is situated at the north-east end of a small karst hill approximately 340 m wide, 430 m long and 57 m high located on the west bank of Salween River. It is actually the northwest section of a much larger karst hill that has been bisected by the Salween River. The collecting area is a vertical karst wall approximately 250 m in length and 20 m tall that parallels the river and leads to the Linno Cave at its north-eastern terminus (Fig. 35). The habitat along the wall has several deep cracks, holes, side chambers and deep incisions that serve as refuge sites for geckos during the day. Additionally, the wall is sheltered by vegetation. The last 50 m of the wall near the cave lack vegetation and here we saw only *Hemidactylus brookii* and *Gekko gecko* both day and night. At night, *Cyrtodactylus linnoensis* sp. nov. were abundant and occurred along the entire wall

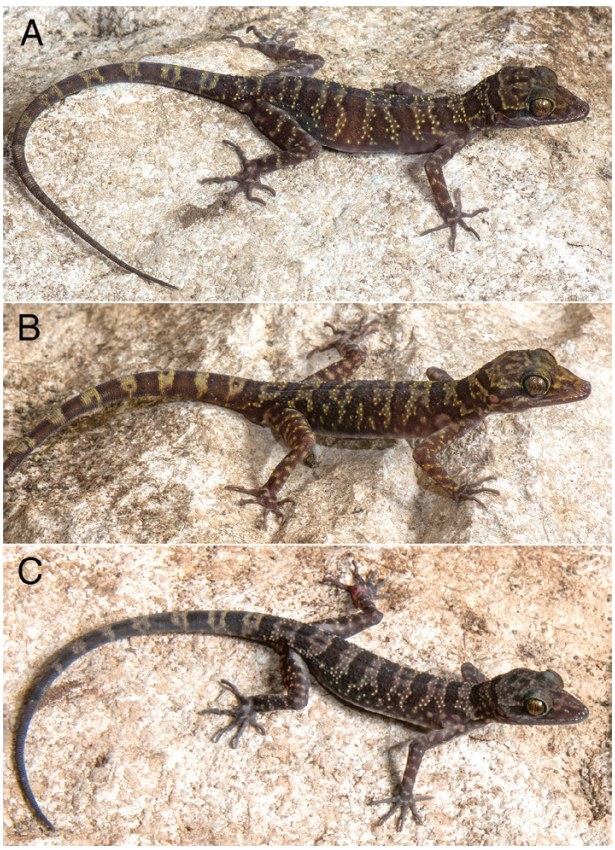

Figure 36. Paratypes of ***Cyrtodactylus sadanensis* sp. nov.** from the type locality of Sadan Cave, 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar showing the range of variation in coloration and pattern. A, adult female paratype (LSUHC 12849). B, adult male holotype (LSUHC 12839). C, subadult female paratype (BYU 52219).

except where the vegetation was lacking and where *H. brookii* was abundant. We found no geckos inside Linno Cave. We believe the abundance of bats, rats, cockroaches and a near-toxic atmosphere made the cave uninhabitable for *Cyrtodactylus*. Much of the cave surfaces were covered with a dark gelatinous ooze through which geckos would likely be unable to locomote.

Comparisons: Cyrtodactylus linnoensis is part of the *yathepyanensis* group. The PCA and DAPC analyses indicate that the species of this group are completely separate in morphospace and that the first two principal components account for 54% of the total variation (Fig. 12; Fig. S5) and load most heavily for numbers of paravertebral tubercles and ventral scales (Table S4). *Cyrtodactylus linnoensis* sp. nov. is well-differentiated from *C. yathepyanensis* sp. nov. and *C. sadanensis* sp. nov. by having varying combinations of statistically different mean values of supralabial and infralabial scales, paravertebral tubercles, expanded, unmodified and total fourth toe lamellae, ventral scales, enlarged femoral scales, longitudinal rows of body tubercles and precloacal pores (Table 8). It differs further from *C. sadanensis* sp. nov. in having a larger maximum SVL (78.0 mm vs. 73.8 mm). Morphological differences from other species in the Indo-Chinese clade are listed in Table 8. Genetic distances among the species of this group range from 11.0 to 12.7% (Table 10).

CYRTODACTYLUS SADANENSIS SP. NOV.

SADAN CAVE BENT-TOED GECKO

(FIG. 36; TABLE 20)

Holotype: Adult male LSUHC 12839 collected on 5 October 2016 at 1700 h by L. Lee Grismer, Evan S. H. Quah, Perry L. Wood, Jr., Myint Kyaw Thura, Thaw Zin, Matthew L. Murdoch, Marta S. Grismer and Htet Kyaw from the Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (N16°44.605, E97°29.493; 26 m in elevation).

Paratypes: Adult males BYU 52218 and LSUHC 12848, adult females BYU 52216–17, 52219, LSUHC 12841–47, 12849 and 12853 bear the same collection data as the holotype.

Diagnosis: Cyrtodactylus sadanensis sp. nov. differs from all congeners by having the unique combination of ten or 11 supralabials; 7–9 infralabials; 13–15 longitudinal rows of body tubercles; 30–33 paravertebral tubercles; 30–35 ventral scales; relatively long digits with 7–9 expanded, subdigital lamellae on fourth toe proximal to digital inflection, 13 or 14 unmodified, distal, subdigital lamellae and 21–23 total subdigital lamellae; raised, moderately to strongly keeled, dorsal body tubercles extending beyond base of tail; enlarged femoral and precloacal scales not continuous; 34–41 enlarged femoral scales; 12 or 13 femoral pores in males; 10–13 enlarged precloacal scales; two or three precloacal pores in males; three rows of enlarged post-precloacal scales; medial subcaudal scales three times as wide as long, extending onto lateral surface of tail; top of head bearing diffuse, dark mottling, lacking yellow reticulum; nuchal loop not divided medially, lacking an anterior azygous notch; five rarely six dark, weakly jagged, dorsal bands generally lacking paravertebral elements, same width or narrower than interspaces, faintly lightened centres, edged with yellowish tubercles; dark markings in dorsal interspaces; ventrolateral folds whitish; anterodorsal margins of thighs generally lack pigment; 16 light caudal bands bearing dark markings, not encircling tail;

Table 20. Meristic, mensural and colour pattern data from the type series of ***Cyrtodactylus sadanensis* sp. nov.**

	LSUHC 12839 holotype	BYU 52218 paratype	LSUHC 12848 paratype	LSUHC 12853 paratype	BYU 52219 paratype	LSUHC 12843 paratype	LSUHC 12846 paratype	LSUHC 12842 paratype
Sex	M	M	M	F	F	F	F	F
Supralabials	11	11	10	10	10	11	10	10
Infralabials	9	8	8	7	8	7	8	8
Body tubercles low, weakly keeled	No	No	No	No	No	No	No	No
Body tubercles raised, moderately to strongly keeked	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Paravertebral tubercles	32	30	32	30	31	31	30	32
Longitudinal rows of body tubercles	14	14	14	13	15	15	14	14
Tubercles extend beyond base of tail	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventral scales	31	31	35	32	32	32	35	30
Expanded subdigital lamellae on fourth toe	7	7	8	8	8	9	9	9
Unmodified subdigital lamellae on fourth toe	14	14	13	14	14	14	14	13
Total subdigital lamellae on fourth toe	21	21	21	22	22	23	23	22
Enlarged femoral scales (R/L)	19RL	21R20L	17R22L	17R19L	22R17L	22R21L	20R19L	17RL
Femoral pores (R/L)	6R7L	6R6L	6R6L	/	/	/	/	/
Enlarged precolacal scales	10	12	11	12	12	12	12	13
Precloacal pores	3	2	2	/	/	/	/	/
Post-precloacal scales rows	3	3	3	3	3	3	3	3
Enlarged femoral and precloacal scales continuous	No	No	No	No	No	No	No	No
Pore-bearing femoral and precloacal scales continuous	No	No	No	No	No	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Medial subcaudals two or three times wider than long	3	3	3	3	3	3	3	3
Medial subcaudals extend onto lateral surface of tail	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Nuchal loop divided medially	No	No	No	No	No	No	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No	No	No	No
Posterior border of nuchal loop	Sinuous	Straight	Straight	Sinuous	Straight	Sinuous	Sinuous	Straight
Band on nape	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal banding with paravertebral elements	No	No	No	No	No	No	No	No
Number of body bands	5	5	5	5	6	5	5	5
Dorsal bands wider than interspaces	No	Same	No	Same	Same	Same	Same	Same
Dorsal bands bearing lightened centres	Faint	Faint	Faint	Faint	Faint	Faint	Faint	Faint
Dorsal bands edged with light tubercles	Partly	Partly	Partly	Partly	Partly	Partly	Partly	Partly
Dorsal band borders	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	Faint	Faint	Faint	Faint	Faint	Faint	Faint	Faint

Table 20. *Continued*

Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No	No	No	No	No	No
Anterodorsal margin of thighs pigmented	No	No	No	No	No	Faint	No	No
Anterodorsal margin of brachia pigmented	No	No	No	No	Yes	Faint	No	Faint
Light caudal bands with dark markings	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Light caudal bands encircle tail	No	No	No	No	No	No	No	No
Number of light caudal bands	/	/	/	16	/	/	/	16
Number of dark caudal bands	/	/	/	17	/	/	/	17
Dark caudal bands wider than light caudal bands	Yes	Same	Same	Yes	Same	Yes	Same	Yes
Mature regenerated tail spotted	No	No	No	/	No	No	No	/
SVL	73.8	69.3	71.7	68.8	61.7	64.0	58.5	64.3
TL	112.0r	43.0	111.0r	104.0	83.0	90.0r	73.0r	95.0
TW	8.7	6.2	7.5	6.5	6.1	6.0	5.9	6.8
FL	13.0	11.9	12.1	12.4	11.3	11.3	9.9	10.4
TBL	16.2	14.0	14.1	13.8	13.4	13.8	12.1	13.5
AG	29.9	28.0	31.0	31.0	29.0	26.3	26.2	29.8
HL	21.5	19.1	19.7	17.8	16.7	19.6	17.0	18.0
HW	14.8	12.5	13.7	12.9	11.2	12.2	10.8	11.7
HD	7.9	7.0	8.0	7.5	7.6	7.2	7.2	7.6
ED	5.6	4.5	5.1	4.4	4.3	4.7	4.4	4.4
EE	5.4	4.8	5.1	4.3	4.3	4.9	3.8	4.7
ES	8.6	8.5	9.1	8.2	7.7	8.5	7.5	7.8
EN	7.4	6.2	6.7	6.7	6.1	6.9	5.7	5.9
IO	5.4	4.3	6.1	4.9	4.5	5.3	4.3	4.9
EL	3.4	2.7	2.8	3.0	2.7	2.2	3.2	2.5
IN	2.3	2.0	2.1	2.3	1.9	1.9	1.7	1.8
		LSUHC 12847 paratype	LSUHC 12844 paratype	LSUHC 12849 paratype	BYU 52217 paratype	LSUHC 12841 paratype	BYU 52216 paratype	LSUHC 12845 paratype
Sex		F	F	F	F	F	F	F
Supralabials		10	10	10	10	11	11	11
Infralabials		8	8	9	8	8	8	8
Body tubercles low, weakly keeled		No	No	No	No	No	No	No
Body tubercles raised, moderately to strongly keeked		Yes	Yes	Yes	Yes	Yes	Yes	Yes

Table 20. *Continued*

	LSUHC 12847 paratype	LSUHC 12844 paratype	LSUHC 12849 paratype	BYU 52217 paratype	LSUHC 12841 paratype	BYU 52216 paratype	LSUHC 12845 paratype
Paravertebral tubercles	32	33	30	33	32	31	33
Longitudinal rows of body tubercles	13	14	15	15	15	14	15
Tubercles extend beyond base of tail	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventral scales	32	35	31	32	32	30	30
Expanded subdigital lamellae on fourth toe	9	9	9	9	9	8	9
Unmodified subdigital lamellae on fourth toe	14	14	13	14	13	14	13
Total subdigital lamellae on fourth toe	23	23	22	23	22	22	22
Enlarged femoral scales (R/L)	16R18L	19R20L	19R17L	18RL	18R21L	20R19L	17R22L
Femoral pores (R/L)	/	/	/	/	/	/	/
Enlarged precolacal scales	12	13	12	12	12	13	11
Precloacal pores	/	/	/	/	/	/	/
Post-precloacal scales rows	3	3	3	3	3	3	3
Enlarged femoral and precloacal scales continuous	No	No	No	No	No	No	No
Pore-bearing femoral and precloacal scales continuous	No	No	No	No	No	No	No
Enlarged proximal femoral scales ~1/2 size of distal femorals	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Medial subcaudals two or three times wider than long	3	3	3	3	3	3	3
Medial subcaudals extend onto lateral surface of tail	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Nuchal loop divided medially	No	No	No	No	No	No	No
Nuchal loop with anterior azygous notch	No	No	No	No	No	No	No
Posterior border of nuchal loop	Sinuous	Straight	Sinuous	Sinuous	Sinuous	Sinuous	Sinuous
Band on nape	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Dorsal banding with paravertebrtal elements	No	No	No	No	No	No	No
Number of body bands	5	5	5	5	5	5	5
Dorsal bands wider than interspaces	Same	Same	Same	Same	Same	No	Same
Dorsal bands bearing lightened centres	Faint	Faint	Faint	Faint	Faint	Faint	Faint
Dorsal bands edged with light tubercles	Partly	Partly	Partly	Partly	Partly	Yes	Yes
Shape of dorsal bands	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged	Weakly jagged
Dark markings in dorsal interspaces	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Ventrolateral body fold whitish	Faint	Faint	Faint	Faint	Faint	Faint	Faint
Top of head diffusely mottled, blotched or patternless	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled	Mottled
Light reticulum on top of head	No	No	No	No	No	No	No
Anterodorsal margin of thighs pigmented	No	Faint	Faint	No	Faint	Faint	No
Anterodorsal margin of brachia pigmented	Yes	Faint	Faint	Faint	Yes	No	No
Light caudal bands with dark markings	Yes	Yes	Yes	Yes	Yes	Yes	Yes

Table 20. *Continued*

	LSUHC 12847 paratype	LSUHC 12844 paratype	LSUHC 12849 paratype	BYU 52217 paratype	LSUHC 12841 paratype	BYU 52216 paratype	LSUHC 12845 paratype
Light caudal bands encircle tail	No	No	No	No	No	No	No
Number of light caudal bands	/	/	/	/	/	/	/
Number of dark caudal bands	/	/	/	/	/	/	/
Dark caudal bands wider than light caudal bands	Yes	/	Same	Same	Yes	/	Same
Mature regenerated tail spotted	No	No	No	No	No	No	No
SVL	59.2	59.5	73.7	67.6	63.1	70.9	69.0
TL	84.0	/	110.0	22.0b	66.0r	85.0	113r
TW	5.5	6.1	7.5	5.3	6.2	7.6	6.7
FL	9.9	9.7	13.1	11.1	11.1	12.3	11.4
TBL	12.1	11.8	15.9	14.0	13.3	15.6	13.6
AG	26.3	25.7	32.4	30.2	27.6	30.5	30.5
HL	18.0	15.7	21.7	19.3	18.3	19.7	19.6
HW	10.9	11.1	13.8	12.2	12.2	13.8	13.3
HD	6.5	7.1	8.2	8.0	7.2	8.1	7.6
ED	4.1	4.2	5.2	5.0	4.7	4.9	5.3
EE	4.3	4.0	5.5	4.9	4.9	4.5	4.7
IN	2.0	1.8	2.3	1.9	2.1	2.1	2.0

Abbreviations are listed in the Material and Methods. R, right; L, left; /, data unobtainable or not applicable; r, regenerated; b, broken.

17 dark caudal bands same width or wider than light caudal bands; and mature, regenerated tail not spotted.

Description of holotype: Adult male SVL 73.8 mm; head moderate in length (HL/SVL 0.29), wide (HW/HL 0.69), flat (HD/HL 0.37), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region concave, canthus rostralis rounded; snout elongate (ES/HL 0.40), rounded in dorsal profile, not flattened in lateral profile; eye large (ED/HL 0.26); ear opening pare-shaped, moderate in size (EL/HL 0.16); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally by inverted Y-shaped furrow, bordered posteriorly by left and right supranasals and small azygous scale, laterally by first supralabials; supranasal separated by two small, azygous scales; external nares bordered anteriorly by rostral, dorsally by supranasal, posteriorly by two postnasals, ventrally by first supralabial; 11(R,L) square supralabials extending to below midpoint of eye; 9(R)8(L) infralabials tapering posteriorly to below orbit; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput; scales on top of head and occiput intermixed with small tubercles; dorsal superciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large, left and right trapezoidal postmentals contacting for 50% of their length posterior to mental; one row of slightly enlarged chinshields bordering all infralabials; and gular and throat scales small, flat, grading posteriorly into larger, subimbricate pectoral and ventral scales.

Body relatively short (AG/SVL 0.41) with well-defined ventrolateral folds; dorsal scales small, raised and interspersed with large, conical, semi-regularly arranged, moderately to strongly keeled tubercles; tubercles extend from nape to beyond base of tail; tubercles on nape smaller than those on posterior portion of body, less sharply keeled; approximately 14 longitudinal rows of body tubercles; 32 paravertebral tubercles; 31 flat, subimbricate, ventral scales larger than dorsal scales; ten enlarged precloacal scales; three precloacal pores; three rows of large, post-precloacal scales; and no deep, precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.18); slightly raised, subimbricate scales of forearm larger than those on body, lacking tubercles; palmar scales low, rounded; digits well-developed, relatively long, inflected at basal, interphalangeal joints; digits much more narrow distal to inflections; widened, proximal, subdigital lamellae do not extend onto palm; claws well-developed, sheathed by a dorsal and ventral scale at base; hindlimbs more robust than forelimbs, moderate in length (TBL/SVL 0.22), covered dorsally by raised scales intermixed with larger tubercles and bearing flat, slightly larger scales anteriorly; ventral scales of thigh flat, imbricate, larger than dorsal scales, one row of 19(R,L) enlarged femoral scales in contact with enlarged precloacal scales, proximal femoral scales one-half to one-third distal femoral scales; 6(R)7(L) femoral pores; small postfemoral scales form abrupt union with larger, flat ventral scales of posteroventral margin of thigh; subtibial scales flat, imbricate; plantar scales raised; digits relatively long, well-developed, inflected at basal, interphalangeal joints; 7(R,L) transversely expanded subdigital lamellae on fourth toe proximal to joint inflection not extending onto sole, 14(R,L) unmodified subdigital lamellae distal to inflection, 21 total subdigital lamellae; distal one-half of digit 1 of left hand missing; and claws well-developed, base of claw sheathed by a dorsal and ventral scale.

Tail moderate in proportions, 112.0 mm in length, last 40.0 mm regenerated, 8.7 mm in width at base, tapering to a point; dorsal scales of tail flat; medial subcaudal scales three times as wide as long, extending onto lateral surface of tail; 2(R,L) enlarged postcloacal tubercles at base of tail on hemipenal swellings; and postcloacal scales flat.

Coloration in life: Dorsal ground colour of head body, limbs and yellowish tan; top of head bearing, diffuse, irregularly shaped, dark mottling, yellow reticulum absent; rostrum bearing diffuse, dark, speckling; superciliary scales yellowish; dark, nuchal loop bearing a sinuous posterior margin; five weakly jagged, body bands narrower than interspaces, bearing faintly lightened centres, lacking paravertebral elements, partly edged with light tubercles, posterior two bands broken and irregularly shaped; one sacral band; interspaces bearing large, dark, diffuse, medial spots; dark markings on flanks; dark banding on limbs indistinct, mottled with yellowish markings; anterodorsal margins of thighs and brachia not pigmented; ventrolateral folds faintly whitish; dark caudal bands bearing slightly lightened centres, wider than light caudal bands; light caudal bands bearing dark markings, not encircling tail; venter beige, generally unpigmented; and subcaudal region darker.

Variation (*Fig. 36; Fig. S13*): The paratypes closely approximate the holotype in aspects of colour pattern. LSUHC 12851 has six instead of five body bands. BYU 52217, LSUHC 12844 and 12948 have broken tails and LSUHC 12846 is missing its right arm. The nape band on BYU 52218, LSUHC 12845 and 12847 is divided medially. Meristic and mensural differences are presented in Table 20.

Distribution: Cyrtodactylus sadanensis sp. nov. is known only from the Sadan Cave 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar (Fig. 20).

Figure 37. A, microstructure of the limestone at the entrance of Sadan Cave, Kayin State, Myanmar. B, limestone hillside in which Sadan Cave and Sin Yine Cave are located. C, cave entrance of Sadan Cave. D, opening in the top of Sadan Cave.

Etymology: The specific epithet, *sadanensis*, is a noun in apposition in reference to the type locality of Sadan Cave.

Natural history: Sadan Cave is located immediately south-east of Hpa-an and situated on the south end of a large, isolated, karst hill approximately 3.6 km wide, 16.4 km long and 338 m high that is surrounded by paddy fields. Sadan Cave is connected to Sin Yine Cave as they occur along the same, semicircular, karst ridge. The mouth of Sadan Cave is approximately 700 m from the opening of Sin Yine Cave across an ephemerally flooded paddy field. The interior of Sadan Cave is wide, airy and high-roofed and approximately 0.25 km in length from the southern entrance to the northern exit. Most of the interior of the cave is smooth-walled and there is not an abundance of the appropriate microhabitat structure necessary for *Cyrtodactylus* similar to what we had observed in other caves. Outside the cave along the base of the karst hill, has an abundance of cracks, holes, and broken boulders and associated rubble that had been shed from the hillside (Fig. 37). *Cyrtodactylus* were common and ubiquitous in this habitat after dark and absent only from the nearby vegetation. Only one lizard was seen in the cave.

Comparisons: Cyrtodactylus sadanensis sp. nov. is part of the *yathepyanensis* group. The PCA and DAPC analyses indicate that the species of this group are completely separate in morphospace and that the first two principal components account for 55% of the total variation (Fig. 12; Fig. S5) and load most heavily for numbers of paravertebral tubercles and ventral scales (Table 8). See Comparisons for *C. yathepyanensis* sp. nov. and *C. linnoensis* sp. nov. for additional differences among them. Morphological differences from other species in the Indo-Chinese clade are listed in Table 8.

Remarks: The fact that *Cyrtodactylus sadanensis* sp. nov. is sympatric but not syntopic with *C. sinyineensis* from Sin Yine Cave is an indication of the degree of niche partitioning that may occur in many of the karst habitats we explored. The hillside walls outside Sadan Cave are continuous with those of Sin Yine Cave and would enable these two species to share the same microhabitat. Yet the larger *C. sinyineensis*

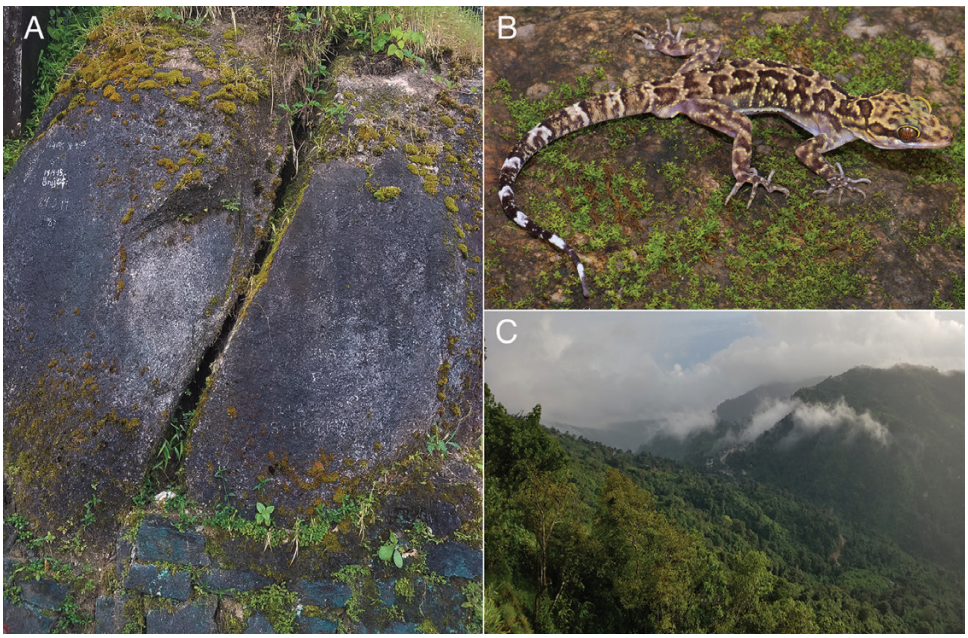

Figure 38. A, granite boulder microhabitat of *Cyrtodactylus aequalis* at the Golden Rock Pagoda on Mount Kyaiktiyo located on the Paung-laung ridge of the eastern Yoma Mountains, Mon State, Myanmar. B, adult male *C. aequalis* (LSUHC 12895) from Mount Kyaiktiyo. C, upland habitat of *C. aequalis* in the Yoma Mountains.

sp. nov. (maximum SVL = 91.6 mm) was only found inside the cave at least 100 m from the opening and the smaller *C. sadanensis* sp. nov. (maximum SVL = 73.8 mm) was abundant on the karst walls outside the cave. Additionally, these two species do not occur in the same species group, indicating that this karst system has been invaded multiple times.

TAXONOMIC COMMENTS ON *CYRTODACTYLUS AEQUALIS, C. FEAE, C. PEGUENSIS* AND *C. VARIEGATUS*

CYRTODACTYLUS AEQUALIS BAUER, 2003

Type locality: 'Kyaik-Hti-Yo Wildlife Sanctuary, Kyaik Hto Township, Mon State, Myanmar (17°26'38.1"N, 97°05'56.8"E)'. Holotype: CAS 222185.

Remarks: The description of *Cyrtodactylus aequalis* was based on a single specimen that was purported to be an adult male in the 'Holotype' section of the description but in the 'Description' section it is referred to as an adult female (Bauer, 2003). Bauer (2003) noted that the femoral and precloacal pores were 'minute' which is characteristic of most females of *Cyrtodactylus*, whereas the 13 femoral and five precloacal pores in the adult male examined here (LSUHC 12895) are large and well-developed (Fig. 4A).

Natural history: Although not reported in the original description, the holotype was collected at 436 m in elevation alongside a mountain road that terminates at the Golden Rock pilgrimage site. The habitat at the collection site is degraded, secondary forest with outcroppings of large granite boulders. LSUHC 12895 was taken at the end of this road on Kyaiktiyo Hill in the Paung-laung ridge of the Eastern Yoma Mountains (N17°28.819, E97°05.974) at 1101 m at 1600 h. The specimen was found within a crack between two large granite boulders (Fig. 38). Although *C. aequalis* is part of the sinyineensis group that contains lowland, karst-adapted species, it is a granite dwelling species ranging from at least 436–1101 m above sea level. This would indicate that granite rock and not elevation is the limiting factor of its distribution. Being a relatively large species (maximum SVL = 90 mm; Bauer, 2003) nested within a species group composed of smaller (maximum SVL = 69.3–91.6 mm), karst-adapted species suggests that its use of granitic substrate is a microhabitat shift from karst to granite.

CYRTODACTYLUS FEAE (BOULENGER, 1893)

Type locality: 'Puepoli, Karin Bia-po, elevation: 3200–3400 feet' Kayah State, Myanmar. Holotype: in the Museo Civico di Storia Naturale di Genova, Genova, Italy. Catalogue number unknown.

Remarks: The specimen of '*Cyrtodactylus feae*' (USNM 559805) from Popa Mountain, Mandalay Region in the phylogeny of Wood *et al.* (2012) and Agarwal *et al.* (2014) forms a monophyletic group with *C. annandalei* and *C. pyinyaungensis* sp. nov. (Fig. 10). However, USNM 559805 was misidentified (G. R. Zug, unpubl. data). *Cyrtodactylus feae* is known only from the type locality of Bia-po Keba, Karen-ni District, Kayah State (19°15N, 97°30E; Hallermann, 2006: 139) at 900–1000 m in elevation that is approximately 280 km to the south-east of Popa Mountain across the Ayerawaddy River Basin in a different mountain range. USNM 559805 was re-identified as *C. peguensis* (G. R. Zug, unpubl. data) although this identification too is questionable (see *C. peguensis* below).

The coloration and pattern of *C. shwetaungorum* sp. nov. is quite similar to the illustration of the holotype and only known specimen of *C. feae* (Boulenger 1893: Plate 7). However, *C. feae* has 32 continuous, femoroprecloacal pores, whereas *C. shwetaungorum* sp. nov. has 23–28 and the SVL of *C. feae* is 47 mm (although it may be a juvenile) and that of *C. shwetaungorum* sp. nov. ranges up to 102.2 mm. The type locality of *C. feae* is 214 km south-west of that of *C. shwetaungorum* sp. nov. although their habitats may be continuous through a U-shape range of mountainous terrain. We hypothesize that the holotype of *C. feae* is a juvenile and that molecular data will place it within the *linnwayensis* group.

Cyrtodactylus peguensis (Boulenger, 1893)

Type locality: "Palon", Bago Region, Myanmar. Syntypes: BM 1946.8.23.10 and 1893.10.9.2.

Remarks: A disjunct, southern population of *Cyrtodactylus peguensis* has long been known to occur from various localities in Peninsular Thailand from immediately south of the Isthmus of Kra southward to central Trang Province (Laidlaw, 1901; Annandale, 1913; Smith, 1935; Taylor, 1963; Chan-ard, Parr & Nabhitabhata, 2015) and the specimens of *C. peguensis* in Wood *et al.* (2012), Agarwal *et al.* (2014) and here come from these southern regions. As first noted by Smith (1935), however, the southern populations differ markedly in squamation and colour pattern from the holotype from Palon, Pegu, Myanmar minimally 1000 km to the north-west and he questioned the validity of considering these disjunct populations as conspecific. We share Smith's (1935) concern but until genetic data from the type locality of *C. peguensis* are available (which we just collected in May 2017), we consider the southern populations as *Cyrtodactylus* cf. *peguensis zebraicus* Taylor.

Based on the similarity of colour pattern and squamation of one of the syntypes of *C. peguensis* (see BM 1946.8.23.10; Fig. 13) we examined and compared to *C. pyinyaungensis* sp. nov, we hypothesize that *C. peguensis* from the type locality will be part of the Indo-Burmese clade and closely related to *C. pyinyaungensis* sp. nov., *C. annandalei* and the Popa Mountain population and not related to *C.* cf. *p. zebraicus* from Peninsular Thailand of the Indo-Chinese clade. Given the phylogenetic relationships and distribution of the former three species and the microendemism common in karst-adapted species, it is unlikely that the Popa Mountain population is not conspecific with *C. peguensis* from the type locality 300 km to the south from the Bago Yoma Range. We also hypothesize that *C.* cf. *p. zebraicus* of the Indo-Chinese clade is not conspecific with the widely allopatric *C. peguensis*.

Cyrtodactylus variegatus (Blyth, 1859)

Type locality: 'Moulmein [=Mawlamyine, Mon State]'. Holotype: ZSI 6188.

Remarks: Blyth (1859) ambiguously reported the type locality of *Cyrtodactylus variegatus* to be Moulmein (=Mawlamyine, Mon State). In reporting on a second specimen, Annandale (1913) noted that the type locality was probably inland from Mawlamyine in the Dawna Hills, approximately 75 km to the east in the Amherst District (=Mawlamyine District). Blyth's (1859) description of the colour pattern of the holotype and the illustration of the second specimen in Annandale (1913: Plate 16)—which according to Smith (1935) 'agrees well with Blyth's description'—generally matches the colour pattern of *C. dammathetensis* sp. nov., *C. welpyanensis* sp. nov., *C. linnoensis* sp. nov., *C. sadanensis* sp. nov. and *C. yathepyanensis* sp. nov. although it is most similar to the former from Dammathet Cave, approximately 50 km to the west of the Dawna Hills. Like *C. variegatus*, the dorsal bands in *C. dammathetensis* sp. nov. are jagged and the nuchal loop has a tendency to be divided medially. It is clear from Blyth's (1859) description of the holotype and more importantly from Smith's (1935) more detailed redescription that the specimen is an adult male (SVL = 71 mm) with a 'continuous series of 32 preanal and femoral [= femoroprecloacal] pores' (the key of Bauer [2003] erroneously reports *C. variegatus* as having only precloacal pores). Of the species in the Indo-Chinese clade, only *C. dammathetensis* sp. nov. has continuous femoroprecloacal pores that number 45 in the holotype (LSUHC 12862)—much higher than that reported by Smith (1935). We hypothesize that molecular and additional morphological data will place *C. variegatus*

in the *sinyineensis* group. Preparations to survey the Dawna Hills are being made.

Cox *et al.* (1998) stated that *C. variegatus* inhabited caves in mountainous regions in northern and western Thailand but could give no specific locality as he did not work on these sections of the pocket guide in which these data are reported (M. J. Cox, unpubl. data). The data from this report were simply followed by Chanard *et al.* (2015). The photograph in Cox *et al.* (1998: 87) purported to be *C. variegatus* is actually *C. dumnuii* Bauer, Kunya, Sumontha, Niyomwan, Pauwels, Chanhome, & Kunya, likely from its only known locality in Chang Mai Province. Thus, to date, *C. variegatus* is possibly known only from the Dawna Hills.

DISCUSSION

Agarwal *et al.* (2014) demonstrated that *Cyrtodactylus* ranging from regions west of the Shan Hills at the eastern edge of the Ayerawaddy River Basin to as far west as northern India, formed a clade of Indo-Burmese species that was the sister lineage to a clade of Southeast Asian species from east of the Salween River in eastern Myanmar. Results herein indicate the Southeast Asian clade contains a more exclusive Indo-Chinese clade that ranges from the newly sampled regions of east-central and southern Myanmar west of the Salween River through Peninsular Thailand to southern Vietnam. The Indo-Burmese and the Indo-Chinese clades are not sister lineages and are almost completely allopatric. This would indicate that the presence of these clades in Myanmar is the result of independent events. Agarwal *et al.* (2014) and Wood *et al.* (2012) posit that *Cyrtodactylus* radiated westward from upland regions north of the eastern Himalayas of India and Myanmar with one lineage crossing the Ayerawaddy and Salween River Basins in the Middle Eocene (~46–36 Myr) giving rise to the Southeast Asian clade. Given that the Indo-Chinese clade is one of the most recently derived lineages within the Southeast Asian clade (Fig. 9) and that Burmese taxa within this clade only occur east of the Ayerawaddy River Basin (Fig. 2), indicate that there were dispersal events back into eastern Myanmar beginning approximately 29 Myr as suggested by the BEAST analysis (Fig. 11). Given that the three, non-Burmese lineages of the Indo-Chinese clade all occur east of the Tenasserim Mountains and are the sister lineages to three different Burmese species groups would indicate at least three independent reinvasions into Myanmar occurred. The evolution of the *sinyineensis*, *yathepyanensis* and *sadanensis* groups happened within a relatively short period of time between approximately 10.5 and 6.5 Myr, whereas the formation of the *linnwayensis* group is more recent at approximately 3.9 Myr (Fig. 11). Agarwal *et al.* (2014) inferred that their data indicated the Salween River and its associated alluvial plains lacking rocky habitats acted as a barrier to gene flow and that it was crossed only once in the Eocene. Our data are in general agreement but indicate that there are numerous isolated karst habitats throughout the Salween River Basin that are occupied by species of the *sinyineensis* and *yathepyanensis* groups that notably occur on both sides of the Salween River (Fig. 20), indicating that geckos could very well have occurred on both sides of the Salween River in the past, and that these habitat-islands could have facilitated dispersal in both directions across this basin.

The Indo-Chinese clade contains strong nodal support throughout much of the tree except for three nodes with very short branch lengths (Fig. 9). Such a topology with concomitant weak nodal support would suggest a rapid radiation and diversification at the initial formation of these clades. All the species groups of the Indo-Chinese clade formed between approximately 23.8 and 18.0 Mya (Fig. 11). This was followed by generally long periods of differentiation and a subsequent, relatively rapid burst of speciation between approximately 9.6 and 3.5 Mya, giving rise to all the known current species in each group (Fig. 11).

One of the most notable features concerning the new species described herein is the remarkable degree of microendemism within the species groups and the sympatry of species from different species groups within the same karst formation. Sister species such as *Cyrtodactylus pharbaungensis* sp. nov. and *C. sanpelensis* sp. nov. are found no farther apart than 16.5 km along the same waterway are separated by at least 9.4% sequence divergence, statistically significant mean differences in meristics, discrete differences in colour pattern, and occupy non-overlapping areas in morphospace (Fig. 12; Fig. S5; Tables 4, 9). If these populations were located even farther apart along a continuous range of suitable habitat (see Fig. 11), a strong argument for conspecificity could be made that their differences (including sequence divergences) could be attributed to sampling error. However, none of these criteria are met and at this juncture we believe the preponderance of data argues for a hypothesis considering them separate species. The reciprocally monophyletic sister species of the other species groups are even more divergent genetically and morphologically (Fig. 12; Fig. S5; Tables 5, 6, 9) and thus we favour their specific recognition as well.

The fact that *C. sinyineensis* sp. nov. and *C. sadanensis* sp. nov. occur in different species groups that are not sister lineages yet these two species occur in sympatry on the same karst hill, indicates separate colonization events and a high degree of niche partitioning. No *C. sinyineensis* sp. nov. were found outside the cave where *C. sadanensis* sp. nov. were abundant. In fact,

this phenomenon may be more prevalent than we record here. At many of the areas we visited, we could only survey during the day due to safety concerns and we do not know if additional species occur outside the caves at night. It is clear from the preliminary natural history data presented herein that these habitats need to be surveyed both day and night for multiple species.

It is tempting to try to piece together a biogeographical scenario to account for the distribution and evolution of the Burmese species; however, this would be premature as we believe there are too many missing data points (taxa). The isolated karst habitats to where we were guided for sampling were only a few surrounded by tens if not hundreds of others dotting the landscape within our line of sight. Given that nearly every isolated karst area we visited had at least one endemic species, we can only surmise that many more species have yet to be discovered. Furthermore, since these species do not form a single monophyletic group but instead form species groups most closely related to taxa farther west in Thailand, Cambodia and Vietnam, indicates that their evolutionary history is not the result of a single environmental event followed by a subsequent adaptive radiation. Rather their origins are the result of independent speciation events, each with their own separate history. Until more populations are sampled and more branches put on the tree, trying to infer those histories would be premature. Plans have been made for additional sampling and the use of genomic data to address these questions in the next round of analyses.

Conservation

The high levels of biodiversity and site-endemism in limestone karst habitats rival that of many other habitats, yet karstic regions are rapidly becoming some of the most imperiled ecosystems in Southeast Asia (Clements *et al.*, 2006; Grismer *et al.*, 2016a; Luo *et al.*, 2016). Southeast Asia harbours more karst habitat than anywhere else in the world (Day & Urich, 2000) but unregulated and unsustainable quarrying practices continue to threaten the integrity of these landscapes and are the primary threat to the survival of karst-adapted species. This will no doubt amplify the ongoing biodiversity crisis in Southeast Asia whose overall rate of habitat loss is the highest among the world's tropical regions (Sodhi & Brook, 2006). A number of recent studies have shown that there are far more karst-associated vertebrates in Southeast Asia than previously reported (e.g. Luo *et al.*, 2016; Connette *et al.*, 2017) and the rate of discovery of new species of karst-adapted amphibians and reptiles shows no signs of levelling-off (see discussions in Grismer et al., 2016a, b, c; Wood *et al.*, 2017). The report here of 11 new species of site-restricted, karst-adapted species of *Cyrtodactylus* now moves the issues of conservation and management squarely into Myanmar whose karst ecosystems may be some of the most extensive and legally unprotected in all of Southeast Asia (Day & Urich, 2000). However, the situation in Myanmar may not be as dire as in other Southeast Asian nations. Many of the karst formations in which site-endemic species are located are religious retreats and protected places of worship that are occupied by Buddhist monasteries and guarded by vigilant monks (Grismer 2016). As such, they remain protected from the quarrying operations of industrial companies as well as commercial collecting.

Contrary to the premise of Connette *et al.*'s (2017) report that deforestation will threaten karst-adapted *Cyrtodactylus*, our data have shown that deforestation has little to no effect on the survival of any karst-adapted geckos. This is patently clear in Myanmar where the karst tower and hill localities of the 11 newly described species in Mon and Kayin States are completely surrounded by rice paddies. Elsewhere, *C. metropolis* Grismer, Wood, Chan, Aunar and Muin from the karst tower of Batu Caves in Peninsular Malaysia is completely surrounded by urbanization (Grismer *et al.*, 2014) and the small karst hill in Peninsular Malaysia wherein *C. hidupselamanya* Grismer, Wood, Anuar, Grismer, Quah, Murdoch, Muin, Davis, Aguilar, Klabacka, Cobos, Aowpho, and Sites is endemic is completely surrounded by oil palms (Grismer *et al.*, 2016b). Grismer (2011) noted additional examples in karst-adapted species of *Cnemaspis* Strauch and other species of *Cyrtodactylus* in Peninsular Malaysia. Connette *et al.* (2017) misquoted Grismer *et al.* (2016b) by stating Grismer *et al.* (2016b) indicated that oil palm plantations threatened karst-adapted species in Peninsular Malaysia when only quarrying operations were the identified threat. Therefore, if *C. payarhtanensis* and *C. lenya*—the new species described in Connette *et al.* (2017)—are site-specific karst-adapted endemics as they indicate, their claim that deforestation of the surrounding landscape will threaten their survival is likely to be untrue. The real danger here is that the broad-brush approach of 'save the rainforest' may not enhance the survival of karst-adapted geckos if karst formations are allowed to be quarried. One of us (L.L.G.) has visited sites in Sarawak, East Malaysia and elsewhere where roads have been cut through healthy intact forest specifically to access and quarry hidden karst formations. Protecting karst-adapted species requires a focused understanding of their microhabitat structure linked to a basic understanding of their natural history (e.g. Grismer *et al.*, 2014, 2016b) so that appropriate conservation measures can be conceived

KEY TO THE SPECIES OF *CYRTODACTYLUS* IN MYANMAR

1a. Deep precloacal (pubic) sulcus present ..... *C. rubidus*
1b. Precloacal sulcus present. 2
2a. Enlarged pore-bearing post-precloacal scales in males ..... *C. chrysophylos*
2b. No enlarged post-precloacal pore-bearing scales 3
3a. Ventral scales large, approximately equal in number to longitudinal rows of dorsal tubercles ..... *C. aequalis*
3b. Ventral scales small, exceed number of longitudinal rows of dorsal tubercles 4
4a. No precloacal or femoral pores in males 5
4b. Precloacal and/or femoral pores in males 6
5a. Light dorsal bands narrower and regularly shaped ..... *C. lenya*
5b. Light dorsal bands jagged, zigzagged or composed of irregularly shaped markings ..... *C. payarhtansis*
6a. Males with precloacal pores only, no femoral pores 7
6b. Males bearing femoral pores 16
7a. Femoral scales larger than surrounding scales 8
7b. Femoral scales same size as surrounding scales 13
8a. Dark dorsum overlain with light markings 9
8b. Light dorsum overlain with dark markings..... 10
9a. Light transverse dorsal bands; light reticulum on head ..... *C. feae*
9b. Light markings composed of spots or lines arranged longitudinally; no light reticulum on head ..... *oldhami*
10a. Dorsal pattern composed of large, round to elongate or hourglass-shaped dark markings 11
10b. Thin dark dorsal bands edged with light colouring 12
11a. 31–36 ventral scales ..... *C. pyinyaungensis* sp. nov.
11b. 43–45 ventral scales ..... *C. peguensis*
12a. Top of head unicolour ..... *C. wakeorum*
12b. Top of head bearing dark markings ..... *C. consobrinoides*
13a. Median subcaudal scales 2–3 times wider than long ..... *C. variegatus*
13b. Median subcaudal scales not transversely enlarged 14
14a. Digits short, subcaudal scales granular ..... *C. brevidactylus*
14b. Digits normal; subcaudal scales not granular 15
15a. Precloacal pore series in males acutely angled, recessed in a shallow groove; females bearing precloacal pores ..... *C. gansi*
15b. Precloacal pore series more nearly straight, absent in females ..... *C. ayerarwadyensis*
16a. 34–41 enlarged femoral scales 17
16b. 14–23 enlarged femoral scales 18
17a. 13–15 longitudinal rows of dorsal tubercles ..... *C. sadanensis* sp. nov.
17b. 22 longitudinal rows of dorsal tubercles ..... *C. russeilli*
18a. 8–16 femoral pores in males ..... *C. sanpelensis* sp. nov.
18b. 20–22 femoral pores in males 19
19a. 43 rows of ventral scales ..... *C. annandalei*
19b. 27–34 rows of ventral scales 20
20a. 12–14 precloacal pores in males ..... *C. sadansinensis* sp. nov.
20b. 6–10 precloacal pores in males 21
21a. Maximum SVL > 100 mm 22
21b. Maximum SVL < 100 mm 24
22a. 18–21 longitudinal rows of dorsal scales; fully regenerated tail not spotted 23
22b. 13–18 longitudinal rows of dorsal scales; fully regenerated tail spotted ..... *C. linnwayensis* sp. nov.
23a. Dorsal pattern consisting of wide, dark bands ..... *C. shwetaungorum* sp. nov.
23b. Dorsal pattern consisting of dark, paravertebral markings ..... *C. slowinskii*
24a. Enlarged proximal femoral scales ~1/2 size or smaller than of distal femorals 25
24b. Enlarged proximal femoral scales same size as distal femorals 27
25a. Maximum SVL > 90 mm 26
25b. Maximum SVL < 90 mm 27

26a. 27–29 ventral scales ..... *C. sinyineensis* sp. nov.
26b. 37 ventral scales ..... *C. tamaiensis*
27a. 25–30 ventral scales 28
27b. 30–38 ventral scales 29
28a. 36 femoral pores in males ..... *C. dammthetensis* sp. nov.
28b. 20 femoral pores in males ..... *C. welpyanensis* sp. nov.
29a. Dorsal bands jagged ..... *C. linnoensis* sp. nov.
29b. Dorsal bands straight or regular 30
30a. 30–32 ventral scale rows ..... *C. yathepyanensis* sp. nov.
30b. 34–38 ventral scale rows ..... *C. pharbaungensis* sp. nov.

and put into place to specifically protect the karst habitats.

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SUPPORTING INFORMATION

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

Figure S1. Type series of *Cyrtodactylus pyinyaungensis* sp. nov. LSUHC 13147–50 from 5.7 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region, Myanmar. LSUHC 12939 = BYU 52234 from 5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region, Myanmar.

Figure S2. Type series of *Cyrtodactylus linnwayensis* sp. nov. from Yum Twing Gyi, Yae Htwat and Lay Htwat caves, Linn-Way Village, 12.7 km north-east of Ywangan, Taunggyi District, Shan State, Myanmar. Upper row illustrates the colour pattern morph with wide, more irregularly shaped, dorsal bands and the lower row illustrates the morph with more narrow, even (straight-edged), dorsal bands. LSUHC 12982 and 12985 = BYU 52213–14, respectively.

Figure S3. Type series of *Cyrtodactylus shwetaungorum* sp. nov. from 5.0 and 5.3 km north of Pyinyaung Village at the Apache Cement factory mining site, Mandalay Region, Myanmar. LSUHC 12899, 12936 and 12938 = BYU 52225–27, respectively.

Figure S4. Type series of *Cyrtodactylus sadansinensis* sp. nov. from Sadan Sin Cave, 10.5 km north-west of Mawlamyine, Mawlamyine District, Mon State, Myanmar. LSUHC 12854 = BYU 52220.
Figure S5. Discriminant analyses of principle components (DAPC) of the species of the *sadansinensis* species group, *yathepyanensis* species group and *sinyineensis* species group showing complete separation of all species.
Figure S6. Type series of *Cyrtodactylus pharbaungensis* sp. nov. from Pharbaung Cave, 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar. LSUHC 12872 = BYU 52215.
Figure S7. Type series of *Cyrtodactylus sanpelensis* sp. nov. from Sanpel Cave, 21.3 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar. LSUHC 12876, 12882, 12884 and 12888 = BYU 52221–24, respectively.
Figure S8. Type series of *Cyrtodactylus dammathethensis* sp. nov. from Dammathet Cave, 38.4 km south-east of Mawlamyine, Mawlamyine District, Mon State, Myanmar.
Figure S9. Type series of *Cyrtodactylus sinyineensis* sp. nov. from Sin Yine Cave, 18.5 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar.
Figure S10. Type series of *Cyrtodactylus welpyanensis* sp. nov. from Welpyan Cave, 35 km north of Hpa-an, Hpa-an District, Kayin State, Myanmar.
Figure S11. Type series of *Cyrtodactylus yathepyanensis* sp. nov. from the type locality of Yathe Pyan Cave, 9 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar. LSUHC 12819–20 = BYU 52228–29, respectively.
Figure S12. Type series of *Cyrtodactylus linnoensis* sp. nov. from the type locality of Linno Cave region, 5 km south-west of Hpa-an, Hpa-an District, Kayin State, Myanmar. LUSHC 12827–28 and 12830–31 = BYU 52230–33, respectively.
Figure S13. Type series of *Cyrtodactylus sadanensis* sp. nov. from Sadan Cave, 17 km south-east of Hpa-an, Hpa-an District, Kayin State, Myanmar. LSUHC 12838, 12840, 12850–51 = BYU 52216–19, respectively.
Table S1. Summary statistics and principal component analysis scores for the species of the *linnwayensis* group. Abbreviations are listed in the Material and Methods.
Table S2. Summary statistics and principal component analysis scores for the species of the *sadansineensis* group.
Table S3. Summary statistics and principal component analysis scores for the species of the *sinyineensis* group.
Table S4. Summary statistics and principal component analysis scores for the species of the *yathepyanensis* group. Abbreviations are listed in the Material and Methods.