A phylogenetic taxonomy of the *Cyrtodactylus peguensis* group (Reptilia: Squamata: Gekkonidae) with descriptions of two new species from Myanmar (#27374)

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A phylogenetic taxonomy of the *Cyrtodactylus peguensis* group (Reptilia: Squamata: Gekkonidae) with descriptions of two new species from Myanmar

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A phylogenetic taxonomy of species in the *Cyrtodactylus peguensis* group from the Ayeyarwady Basin of Myanmar is constructed based on color pattern, morphology, and molecular systematic analyses using the mitochondrial gene ND2. Newly collected samples from the type locality of *C. peguensis* and other localities indicate that this clade is endemic to central Myanmar and contains at least seven species, four of which are undescribed. Three species, including *C. peguensis* occur in the low hills of the Bago Yoma Range within the central portion of the Ayeyarwady Basin. Two of these, *C. myintkyawthurai* sp. nov. from the northern and central Bago Yoma and *C. meersi* sp. nov. which is syntopic with *C. peguensis* in the southern Bago Yoma are described herein. As more lowland hilly areas bordering, and within the Ayeyarwady Basin are surveyed, more new species of this group are likely to be discovered. These discoveries continue the recent surge of descriptions of new species of *Cyrtodactylus* that are being discovered in Myanmar.

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ABSTRACT

A phylogenetic taxonomy of species in the *Cyrtodactylus peguensis* group from the Ayeyarwady Basin of Myanmar is constructed based on color pattern, morphology, and molecular systematic analyses using the mitochondrial gene ND2. Newly collected samples from the type locality of *C. peguensis* and other localities indicate that this clade is endemic to central Myanmar and contains at least seven species, four of which are undescribed. Three species, including *C. peguensis* occur in the low hills of the Bago Yoma mountain range within the central portion of the Ayeyarwady Basin. Two of these, *C. myintkyawthurai* sp. nov. from the northern and central Bago Yoma and *C. meersi* sp. nov. which is syntopic with *C. peguensis* in the southern Bago Yoma are described herein. As more lowland hilly areas bordering, and within the Ayeyarwady Basin are surveyed, more new species of this group are likely to be discovered. These discoveries continue the recent surge of descriptions of new species of *Cyrtodactylus* that are being discovered in Myanmar.

Subjects Herpetology, Molecular Phylogenetics, Taxonomy, Zoology

Keywords Myanmar, Geckos, Phylogeny, New Species

INTRODUCTION

The Gekkota (geckos) comprises one of the most diverse lizard lineages in the world, containing approximately 1777 species to date (*Uetz et al. 2018*). Within the Gekkota, Bent-toed Geckos (*Cyrtodactylus* Gray) are not only the most speciose genus, but the most rapidly growing in terms of the annual rate of newly described species. This is especially true throughout Indochina and Sundaland with the Southeast Asian nation of Myanmar being no exception. In fact, the number of new species of *Cyrtodactylus* discovered in Myanmar has increased from 19 to 34 (79%) in just the last year alone (*Grismer et al. 2017a, 2018*). Notably, this increase in diversity is not due to molecular analyses partitioning out species groups and adjusting the taxonomy accordingly but rather it is the result of discoveries made during recent expeditions into some of the more remote regions of the country.

One of the more enigmatic species in Myanmar, *Cyrtodactylus peguensis* (Boulenger, 1893), was described from two specimens (syntypes) collected by Signor L. Fea in 1887 from Palon [Hpa Lon], Bago Division in southern Myanmar. Unfortunately, one of the syntypes has been lost and apparently was never accessioned into the British Museum of Natural History (*Patrick Campbell in litt. 2018*). It is clear, however, that the specimen did exist and was available to Smith (1921) based on his statement that the syntypes have "two series of (6–8) large round spots on the back [referring to BMNH 1946.8.23] *or* [our italics] with the spots confluent transversely [referring to the specimen illustrated in *Boulenger* (*1893*)]”. Following its description, *C. peguensis* became somewhat of an unscrutinized taxonomic repository and began to accumulate populations from throughout Indochina ranging from Vietnam to Thailand (*Laidlaw, 1901; Boulenger, 1912; Annandale, 1913; Smith, 1916, 1921, 1930, 1935*). *Cyrtodactylus peguensis* is still reported to occur in western and southern Thailand (i.e., *Taylor, 1962, 1963; Manthey & Grossman, 1997; Chan-ard, et al., 2015*) and some (with no voucher) have even reported it from northern Peninsular Malaysia (*Ulber & Schäfer, 1989; Denzer & Manthey, 1991*). *Taylor* (*1962*) recognized one of the southern Thai populations from Nakhon Si Thammarat Province as *C. p. zebriacus* and another from Trang Province, 70 km to the south in the same mountain range as *C. p. peguensis.* Subsequent authors (e.g., *Manthey & Grossmann, 1997; Chan-ard, et al., 1999; Das, 2010*), however, implicitly considered both populations as *C. p. zebriacus* but did so without comment. In a recent phylogeny, *Grismer et al.* (*2017a*) noted that *C. p. zebriacus* is a member of a lineage they designated as the Indochinese clade and that it is only distantly related to species of the Indo-Burmese that contains true *C. peguensis* group species (i.e., *C. pyinyaungensis,* see discussion in *Grismer et al.,* [*2017*]), thus bringing into question the species identity of the Thai populations.

In order to construct a taxonomy of this group that is consistent with its evolutionary history, an understanding of the phylogenetic relationships of true *Cyrtodactylus peguensis* from the type locality to the other populations in Myanmar and to *C. p. zebriacus* is paramount. Therefore, we collected two specimens from the Myin Mo Shwe Taung Pagoda, 9.5 km east of Hpa Lon village (the type locality) in the western foothills of the southern portion of the Bago Yoma mountain range as this locality constitutes the closest, most suitable, habitat for *C. peguensis* (Fig. 1). To this we added eight samples from Mt. Popa from the northernmost section of the Bago Yoma Range (Mandalay Division). This population resembles *C. peguensis* in color pattern but has been referred to as *C. fea* (*Wood et al., 2012; Agarwal et al., 2014; Brennan et al. 2017*) but later informally re-identified as *C. peguensis* (see discussion in *Grismer et al.,* *2017:3*). We also included seven samples that were accessioned into the California Academy of Sciences (CAS) as *C. peguensis*: three from the central portion of the Bago Yoma Range (Bago Division), two from the Panlaung and Pyadalin Cave Wildlife Sanctuary (Shan State), one from Aung Ya Village (Rakhine State), and one from the Shwe Settaw Wildlife Sanctuary (Magway Division). Last, we included a sample of *C. p. zebriacus* from Nahkon Si Thammarat Province, Thailand and three samples of *C. pyinyaungensis* from Pyinyaung Village, Shan State which has been hypothesized to be closely related to *C. peguensis* (*Grismer et al., 2017a*). Tissues from these samples were used to construct a molecular phylogeny based on 1467 base pairs of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and its flanking tRNA regions. Morphological and color pattern data taken from specimens from the type locality (including the remaining syntype), Mt. Popa, the central Bago Yoma, and *C. pyinyaungensis* were analyzed and the results compared to the molecular phylogeny. We also examined 16 specimens of *C. p. zebriacus* from three localities in southern Thailand and compared them to species of the *peguensis* group. The results of these analyses corroborate one another and indicate that in order to bring the taxonomy of the *peguensis* group in line with its evolutionary history (*i.e.* phylogeny), at least four new species must be described and that *C. p. zebriacus* should be elevated to species status being that it is not closely related to or morphologically similar to any species in the *peguensis* group.

MATERIALS AND METHODS

Molecular data and analyses

The data set of *Grismer et al. (2017a),* which included exemplars of all the major *Cyrtodactylus* clades in *Agarwal et al. (2014),* was augmented with 17 samples purported to be *C. peguensis,* totaling 222 ingroup samples. *Hemidactylus angulatus* Hallowell*, H. frenatus* Duméril & Bibron*, H. garnotii* Duméril & Bibron*, H. mabouia* (Moreau de Jonnès), and *H. turcicus* (Linnaeus) served as outgroups following *Grismer et al. (2017a).* All new sequences were deposited in GenBank (Table 1). Genomic DNA was isolated from liver or skeletal muscle tissue stored in

95% ethanol using a Maxwell® RSC Tissue DNA kit on the Promega Maxwell® RSC extraction robot. 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 5x buffer (1.5 µM), MgCl 10x buffer (1.5 µM), 0.1 µl Taq polymerase (5u/µl), and 6.4 µl ultra-pure H_2O. PCR reactions were executed on Bio-Rad 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 48–52°C for 35 s, followed by a cycle extension at 72°C for 35 s, for 31 cycles. All PCR products were visualized using electrophoresis on a 1.0 % agarose gel. Successful PCR products were sent to GENEWIZ® for PCR purification, cycle sequencing, sequencing purification, and sequencing using the same primers as in the amplification step (Table 2). Sequences were analyzed from both the 3' and the 5' ends separately to confirm congruence between the reads. Forward and reverse sequences were uploaded and edited in Geneious^{TM} version v6.1.8. Following sequence editing we aligned the protein-coding region and the flanking tRNAs using the MAFTT v7.017 (*Katoh & Kuma, 2002*) plugin under the default settings in Geneious^{TM} (*Kearse et al., 2012*). 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 in the ND2 portion of the DNA fragment.

Two model-based phylogenetic analyses, maximum likelihood (ML) and Bayesian Inference (BI) were employed. The ML analysis was implemented in IQ-TREE (*Nguyen et al., 2015*) and used a Bayesian Information Criterion (BIC) to calculate that K3P+I+G4 was the best-fit model of evolution for the tRNA, TVM+F+I+G4 the best-fit model for the first codon position, TIM3F+I+G4 for the second codon position, and GTR+F+ASC+G4 for the third codon position. Shimodaira-Hasegawa-like approximate likelihood ratio test (LRT; *Guindon et al., 2010*) and Ultrafast Bootstrap Approximation (UFB; *Hoang et al., 2017*) using 1000 bootstrap replicates were used to construct a final consensus tree. Nodes with UFB values of 95 and above and LRT values of 0.80 and above were considered significantly supported. A BI analysis was implemented in MrBayes 3.2.3. on XSEDE (*Ronquist et al., 2012*) using CIPRES (Cyberinfrastructure for Phylogenetic Research; *Miller et al., 2010*) employing default priors and GTR + Gamma model of evolution for all codon positions. Two simultaneous runs were performed with four chains, three hot and one cold. The simulation ran for 10,000,000 generations, was sampled every 1000 generations using the Markov Chain Monte Carlo (MCMC), and the first 25% of each run were discarded as burn-in. Stationarity and .p files from each run were checked in Tracer v1.6 (*Rambaut et al., 2014*) to ensure effective sample sizes (ESS) were above 200 for all parameters. Nodes with Bayesian posterior probabilities (BPP) of 0.95 and above were considered well-supported (*Hulsenbeck et al., 2001; Wilcox et al., 2002*). After removing outgroup taxa, MEGA7 (*Kumar et al., 2016*) was used to calculate uncorrected pairwise sequence divergence of the ingroup species.

Morphological data and analyses

Color pattern notes were taken from living and preserved specimens and digital images of living specimens of all possible age classes prior to preservation. Measurements were taken on the right side of the body when possible to the nearest 0.1 mm by MSG using dial calipers under a Leica Wild M 10 stereo 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 90º to the inflection of the flexed wrist; tibia length (TBL), taken on the ventral surface from the posterior surface of the knee while flexed 90º 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 hind limb 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 eye-ball; eye to ear distance (EE), measured from the anterior edge of the ear opening to the posterior edge of the eye-ball; eye to snout distance (ES), measured from anteriormost margin of the eye-ball 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.

Meristic characters taken were the numbers of supralabial (SL) and infralabial (IL) scales counted from the largest scale immediately below the middle 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 center of the dorsum from one ventrolateral fold to the other; the number of longitudinal rows of ventral scales (VS) counted transversely across the center of the abdomen from one ventrolateral fold to the other; and the total number of subdigital lamellae (4TL) beneath the fourth toe. 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; the number of precloacal pores in (PP) in males; the number of rows of post-precloacal scales (PPS) on the midline between the enlarged precloacal scales and the vent (see *Grismer et al., 2017a*:Fig. 4); number of body bands (BB) or large, transversely oriented, dark paravertebral spots between the nuchal loop (dark band running from eye to eye) and the hind limb insertions not including the nape or postsacral bands; 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 (see *Grismer et al., 2017a*:Fig. 6); and the relative length to width ratio of the transversely expanded, median subcaudal scales.

Color pattern characters (see *Grismer et al., 2017a*:Fig. 5) evaluated were the dorsal body bands bearing paired, paravertebral elements or fused medially; top of head bearing combinations of dark diffuse mottling or dark, distinct blotches overlain with a light-colored reticulating network or not; and light caudal bands encircling tail or not.

Following Levene's tests for homogeneity of variances (necessary for an analysis of variance [ANOVA] using unequal sample sizes), an ANOVA was performed to ascertain if statistically significant mean differences among meristic characters ($p<0.05$) existed among multiple populations. ANOVAs having a p-value less than 0.05, indicating that statistical differences existed in the data set, were subjected to a Tukey HSD test to ascertain which population pairs differed significantly from each other. Additionally, Student t-tests were performed on selected pairs of populations to search for significantly different ($p<0.05$) mean differences following F-tests for homogeneity of variances. Principal Component Analysis (PCA) and Discriminant Analysis of Principal Components (DAPC) using the ADEGENET package in R (*Jombart et al., 2010*) 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 their presence in only males. All PCA data were log-transformed prior to analysis and scaled to their standard deviation 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 nonlinearity. A biplot analysis implemented by the ggbiplot command in R was overlain on the PCA plot in order to visualize the degree to which certain characters co-varied and contributed to the overall variation in the data set. 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 et al., 2010*). DAPC relies on log transformed data from the PCA as a prior step to ensure that variables analyzed 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 analyses were performed using the platform R v 3.2.1 (*R Core Team 2015*).

Museum abbreviations follow *Sabaj* (2016) except for LSUHC referring to the La Sierra University Herpetological Collection, La Sierra University, Riverside, California, 92505, USA; and MS referring to Montri Sumontha, Ranong Marine Fisheries Station, Ranong 85000, Thailand. Ministry of Natural Resources and Environmental Conservation Forest Department of Myanmar provided collecting and export permits. The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:80F582E5-9FE4-4A1A-AAE8-035FA0708E11. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central and CLOCKSS

RESULTS

The ML and BI analyses produced trees with identical topologies and strong nodal support at nearly every node (Fig. 2). All but one of the Burmese populations included in the analyses that have been formally or informally considered conspecific with or allied to *Cyrtodactylus peguensis* are recovered as a monophyletic group. *Cyrtodactylus annandalei* Bauer was recovered as a closely related sister species to this monophyletic group and distantly related to all other species of the Indo-Burma clade (Fig. 2). As such, it and the other populations are referred to here as the *peguensis* group. The specimen (CAS 22143) not included in the *peguensis* group from Aung Ya Village, Rakhine State was recovered as an undescribed sister ~~species~~ to *C. ayeyarwadyensis* Bauer. Surprisingly, the two samples from the Myin Mo Shwe Taung Pagoda from near the type locality of *C. peguensis* were not each other's closest relatives and share an 10.3% uncorrected pairwise sequence divergence between them despite being collected within 200 m of one another (Table 3).

In comparing each specimen from the Myin Mo Shwe Taung Pagoda to the syntype of *Cyrtodactylus peguensis* (BMNH 1946.8.23.10), it is clear that LSUHC 13454 is much closer morphologically to the type than is LSUHC 13455 (Table 4). The syntype and LSUHC 13454 have 17–19 longitudinal rows of dorsal tubercles (LRT) vs. 13 in LSUHC 13455, 36 or 37 ventral scales (VS) vs. 32, 19 subdigital lamellae on the fourth toe (4TL) vs. 17, and three vs. two post-precloacal scale rows. Furthermore, the syntype and LSUHC 13454 group closely together in the PCA where 44% of the variation in the data set occurs along the first principal component (PC1) and loads most heavily for fourth toe lamellae and infralabial scales and 16% of the variation occurs along PC2 and loads most heavily for body bands (Table 5, Fig. 3). Additionally, the syntype and LSUHC 13454 are well-separated from LSUHC 13455 in both the PCA and DAPC analyses (Fig. 3). Therefore, we consider LSUHC 13454 to be *C. peguensis* and LSUHC 13455 to be a new species (described below). The analyses also recovered the Shan State specimens (CAS 226142–43) from the Pyadalin Cave region and CAS 226139 from the Shwe Settaw Wildlife Sanctuary, Magway Division to be distinct from one another and from all other *peguensis* group lineages and will be described elsewhere when specimens become available. The PCA and DAPC analyses recovered *C. pyinyaungensis* and *C. peguensis* as the most morphospatially distinct species in the *peguensis* group (Fig. 3) and the biplot analysis shows a distinct dichotomy along PC1 in character variation between the number body bands which do not covary with any of the remaining covarying characters. All species are widely separated in the DAPC analysis.

As predicted (*Grismer et al., 2017a*), *Cyrtodactylus pyinyaungensis* is the sister species of *C. peguensis*. Together, these sister species are most closely related to sister populations from the central Bago Yoma, Bago Division and Mt. Popa from the northern Bago Yoma, Mandalay Division. These reciprocally monophyletic sister populations overlap in morphospace (Fig. 3) and are not morphologically distinguishable from one another (Table 6). They share an uncorrected pairwise sequence divergence of 3.0–4.0% despite the samples being separated by approximately 230 km (Table 3). This is in stark contrast to *C. peguensis* (LSUHC 13454) and LSUHC 13455 from the Myin Mo Shwe Taung Pagoda which share an 10.3% sequence divergence yet were found only 200 m apart. Additionally, the latter two are morphospatially widely separated (Fig. 3). The central Bago Yoma and Mt. Popa populations are morphologically distinct from all other species in the *peguensis* group (Tables 7, 8) and differ from them by an uncorrected pairwise sequence divergence of 4.0–16.0% (Table 3). Despite the fact that Mt. Popa is an isolated volcano delimiting the disjunct northern limit of the Bago Yoma, the intervening lowlands contain scattered, low-lying hills and suitable habitat that may still provide opportunities for gene flow or at least very recent gene flow. As such, we consider these populations conspecific and are described below as a new species.

As previously hypothesized (*Grismer et al. 2017a, 2018a,b*), the molecular analyses indicate that *Cyrtodctylus peguensis zebraicus* of southern Thailand is not closely related to *C. peguensis* but nested within the *oldhami* group (*sensu* Connette *et al.* 2017) of the Indochinese clade and not with species of the *peguensis* group of the Indo-Burmese clade (Fig. 2). It is also shares a sequence divergence of 28.0–31.3% with species of the *peguensis* group (Table 3). Therefore, we remove *C. p. zebriacus* from the synonymy of *C. peguensis* and elevate it to the full species, *C. zebriacus* Taylor, 1962. Based on the examination of eight specimens of *Cyrtodactylys zebriacus* from Ko Samui Island, Surat Thani Province (CAS 23568–75), six specimens from Trang Province (FMNH 176851–54, 176857, 177328), and two specimens from Nakhon Si Thammarat, Province (FMNH 178286 and 215984), *C. zebriacus* differs from all members of the *peguensis* group by having larger and more strongly keeled body tubercles; no femoral pores; a dorsal pattern that is generally banded or has a more reticulated pattern as opposed to being composed of large, dark, paravertebral spots or hour glass-shaped bands; the top of the head bearing a diffuse, reticulated pattern as opposed to having large, dark, well-defined spots; having black and white caudal bands of nearly equal width as opposed to having dark-brown and yellow caudal bands of unequal width; and the light-colored (*i.e.* white) caudal bands encircling the tail as opposed to being incomplete in the subcaudal region (Fig 4).

SYSTEMATICS AND TAXONOMY

Species concept

We follow the general lineage concept of species (*de Queiroz 1998, 1999*) and consider allopatric populations that are morphologically *and* genetically diagnosable, as unique evolutionary lineages, and thus distinct species. We use phylogenetic relationships to delimit species boundaries and those limits are defined using fixed diagnostic character differences (both in color pattern and morphology), statistically significant mean differences among characters, and non-overlapping ranges in scale and color pattern meristics.

Below we define and diagnose the *Cyrtodactylus peguensis* group and describe two of the new species recovered in the phylogenetic and morphological analyses. We also re-describe *Cyrtodactylus peguensis* based on one of the syntypes (BM 1946.8.23.10) and the newly collected specimen (LSUHC 13454) from near the type locality. We do this in order to correct errors and omissions in the original description (*Boulenger, 1893*) and subsequent descriptions of the syntypes (*Smith, 1921*) as well as to present new characters used herein to diagnose different species in the *peguensis* group.

Cyrtodactylus peguensis group

Definition and diagnosis. The *Cyrtodactylus peguensis* group ranges throughout the low hills of the Ayeyarwady Basin and its low hilly margins from the Alaungdaw Kathapa National Park, Magwe Division in the northeastern foothills of the Chin Hills, eastward to the Panlaung and Pydalain Cave Wildlife Sanctuary, Shan State in the northwestern foothills of the Shan Hills, and southward through the Bago Yoma Range to the Myin Mo Shwe Taung Pagoda, Bago Division in the southern Bago Yoma Range (Fig. 1). This clade is composed of four nominal species *C. peguensis* (Boulenger), *C. annandalei* Bauer, *C. meersi* sp. nov., *C. myintkyawthurai* sp. nov., *C. pyinyaungensis* Grismer *et al.,* two undescribed species *Cyrtodactylus* sp. 1 and *Cyrtodactylus* sp. 2 and is defined by the following range of characters: seven or eight supralabials, 28–33 paravertebral scales, 13–23 longitudinal rows of dorsal tubercles, 32–43 ventral scales, 10–19 fourth toe lamellae, 12–22 femoral pores in males, 7–12 precloacal pores in males, two or three post-precloacal scales, 4–6 dark transverse body bands between limb insertions usually bearing paravertebral elements, 9–13 light and dark caudal bands, dorsal body tubercles domed and weakly keeled and conical to raised and moderately to strongly keeled, top of the head blotched or patternless never bearing a reticulated pattern, and a maximum SVL of at least 55–75.1 mm (Table 7).

Cyrtodactylus peguensis (Boulenger, 1893)

Pegu Bent-toed Gecko

(Fig. 5)

Gymnodactylus peguensis Smith 1921:29; 1935:52 in part. Wermuth 1965:63 in part.

Cyrtodactyuls peguensis Taylor 1963:728 in part; Denzer & Manthey 1991:314 in part; Cox et al. 1998:87 in part; Pianka & Vitt 2003:175 in part; Manthey & Grossmann 1997:225 in part; Das 2010:213 in part; Grismer et al. 2017a:91 in part; Brennan et al. 2017:3, in part.

Cyrtodactyulus (*Cyrtodactylys*) *peguensis* Rösler 2000:66 in part.

Other synonymies exist in several popular herpetoculrural outlets but are not listed here.

Syntype. Adult male BM 1946.8.23.10 collected in 1887 by Signor L. Fea from “Palon” [Hpa Lon], “Pegu” [Bago Region], Taikkyi Township, Yangon (north) District, Myanmar. Hpa-Lon is a small village in the Ayeyarwady Basin 9.5 km west of the western foothills of the southern portion of the Bago Yoma Range where Fea reported making zoological collections (*Fea, 1897*). Being that foothills are the closest suitable habitat for *Cyrtodactylus peguensis* east of Pa-Lon, we restrict the type locality to the Myin Mo Swhe Taung Pagoda, Bago Division, Taikkyi Township, Yangon (north) District, Myanmar (17.46272° N, 96.01624° E, elevation 162 m) situated within these foothills where we collected an additional specimen (LSUHC 13455). The other syntype could not be located.

Additional specimen. Subadult male (LSUHC 13454) collected by Myint Kwaw Thura on 18 May 2017 along a dirt road just below the Myin Mo Swhe Taung Pagoda.

Diagnosis. *Cyrtodactylus peguensis* differs from other species of the *peguensis* group by having the unique combination of seven supralabial and infralabial scales; 31 or 32 paravertebral tubercles; 17–19 longitudinal rows of body tubercles; 36 or 37 ventral scales; 19 subdigital lamellae on the fourth toe; 17–19 femoral pores in males; eight precloacal pores in males; three rows of post-precloacal scales; and domed to weakly conical and weakly keeled body tubercles; and a maximum SVL of 70 mm (Table 7).

Description based on BM 1946.8.23.10 and LSUHC 13454. Maximum SVL 70.0 mm; head moderate in length (HL/SVL 0.28–0.29), wide (HW/HL 0.57–0.65), somewhat flattened (HD/HL 0.44), distinct from neck, triangular in dorsal profile; lores inflated, prefrontal region concave, canthus rostralis rounded; snout elongate (ES/HL 0.38–0.42), rounded in dorsal profile; eye large (ED/HL 0.21–0.24); ear opening triangular, moderate in size (EL/HL 0.12); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally, bordered posteriorly by large left and right supranasals contacting on midline or separated by small internasal, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by large supranasal, posteriorly by two small postnasals, ventrally by first supralabial; seven (R,L) rectangular supralabials extending to below midpoint of eye; seven (R,L) infralabials tapering smoothly to below posterior margin of orbit; 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 supraciliaries not elongate or keeled; mental triangular, bordered laterally by first infralabials and posteriorly by large, left and right trapezoidal postmentals that contact medially for 40–60% of their length posterior to mental; one row of slightly enlarged chinshields extending posteriorly to fourth infralabial; and gular and throat scales small, granular, grading posteriorly into larger, flatter, smooth, subimbricate to imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.42–0.43) with weak ventrolateral folds; dorsal scales small, interspersed with small, domed to weakly conical, semi-regularly arranged weakly keeled tubercles; tubercles extend from occiput onto base of tail but no farther; tubercles on occiput and nape small, those on posterior portion of body larger and keeled; approximately 17–19 longitudinal rows of dorsal tubercles; 31 or 32 paravertebral tubercles; approximately 36 or 37 flat, imbricate, ventral scales larger than dorsal scales composing 36 or 37 rows; eight pore-bearing precloacal scales; three rows of large post-precloacal scales; and no deep precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.14–0.16); flat scales of forearm larger than those on body, not interspersed with tubercles; palmar scales flat to rounded and 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; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.17–0.18), covered dorsally by granular scales interspersed with slightly larger, weakly keeled tubercles and anteriorly by large, flat, imbricate scales; ventral scales of femora flat, imbricate, larger than dorsals, lacking a row of enlarged femoral scales; 8 or 9 (R) and 9 or 10 (L) pore-bearing femoral scales; small postfemoral scales form an abrupt union with large, flat ventral scales of posteroventral margin of thigh; subtibial scales flat, imbricate; plantar scales granular, slightly raised; digits relatively short, well-developed, inflected at basal, interphalangeal joints; 19 subdigital lamellae on fourth toe; and claws well-developed, base of claw sheathed by a dorsal and ventral scale; two or three enlarged postcloacal tubercles at base of tail; and postcloacal scales flat.

Regenerated tail (BM 1946.8.23.10), approximately 70.0 mm in length, 5.9 mm in width at base, tapering to a point; dorsal scales flat, imbricate, becoming larger posteriorly; subcaudal scales slightly larger than dorsal scales; two enlarged postcloacal tubercles at base of tail; and postcloacal scales flat. Original tail (LSUHC 13454) moderate in proportions, 46.0 mm in length, 3.9 mm in width at base, tapering to a point; dorsal scales of base of tail granular rapidly becoming flatter posteriorly; and median row of transversely enlarged subcaudal scales twice as wide as long not extending onto lateral margin of tail.

Coloration of LSUHC 13455 life (Fig. 5). Dorsal ground color of head body, and limbs light-brown; dorsal ground color of tail yellow; top of head bearing large, dark-brown, round blotches edged in yellow; dark-brown, wide, nuchal loop extending from posterior margin of one eye, across occiput, to posterior margin of other eye; nape bearing a large, dark-brown band edged in yellow with distinct paravertebral sections; five dark-brown body bands edged in yellow with distinct paravertebral sections between limb insertions; one dark-brown post-sacral band edged in yellow bearing a longitudinal yellow stripe; 13 dark-brown caudal bands wider than 12 yellow, hourglass-shaped, caudal bands with darkened centers; dorsal portion of forelimbs mottled with yellow; dorsal portion of hind limbs bearing large, elliptical, dark-brown blotches edges in yellow; flanks with a series of 9–11 dark-brown, round to irregularly shaped blotches edged in yellow. All ventral surfaces generally beige, immaculate except for ventral surfaces of forelimbs, forelegs, hands, feet, and posterior section of tail bearing dark pigment.

Distribution. *Cyrtodactylus peguensis* is known only from the type locality of Myin Mo Shwe Taung Pagoda, 9.5 km east of the village of Hpa Lon, Bago Division, Taikkyi Township, Yangon (north) District Myanmar (Fig. 1).

Natural History. No natural history data accompanied the description of the syntypes. LSUHC 13455 was collected in a region composed of low foothills and highly disturbed forest (Fig. 6). The specimen was collect at 2100 hours as it was crawling down an earthen bank covered with small rocks (< 1m in diameter) along the side of steep dirt road at the base of the Myin Mo Shwe Taung Pagoda.

Comparisons. We did not have access to the specimens from the Panlaung and Pyadalin Cave Wildlife Sanctuary, Shan State (CAS 226142–43) or the Shwe Settaw Wildlife Sanctuary, Magway Division (CAS 226139) that are illustrated in the phylogeny, and thus could not compare them to *Cyrtodactylus peguensis* or the new species described herein. It is clear however, that based on their phylogenetic relationships they are distinct from all the species discussed in this report. *Cyrtodactylus peguensis* is differentiated from *C. annandalei* by the top of the head being blotched as opposed to being patternless. *Cyrtodactylus peguensis* is most closely related to *C. pyinyaungensis* (Fig. 2) but differs from it by having significantly higher mean values of infralabial scales (IL; 7.0 vs. 6.0), longitudinal rows of dorsal tubercles (LRT; 18.0 vs. 16.4), post-precloacal scales (PPS; 3.0 vs. 2.0), fourth toe lamellae (4TL; 19.0 vs 17.0), and ventral scales (VS; 36.5, vs. 31.8) (Table 7, 8). *Cyrtodactylus peguensis* further differs from *C. myintkyawthurai* sp. nov. by having significantly higher mean value of post-precloacal scales (PPS; 3.0 vs. 2.0), and fourth toe lamellae (4TL; 19.0 vs 17.6) and domed to weakly conical and weakly keeled body tubercles vs. raised and moderately keeled body tubercles (Table 6, 7). From *Cyrtodactylus meersi* sp. nov., it differs by having significantly higher mean number of longitudinal rows of dorsal body tubercles (LRT; 18.0 vs. 13.0) and significantly more post-precloacal scales (PPS; 3.0 vs. 2.0) (Tables 7, 8). *Cyrtodactylus peguensis* is widely separated from *C. pyinaungensis* and *C. meersi* sp. nov. in the PCA and DAPC analyses and shares a 3.3% and 10.3% uncorrected pairwise sequence divergence, respectively, from them. It shares a 4.0–5.0% sequence divergence with *C. myintkyawthurai* sp. nov. (Table 3).

Remarks. *Boulenger* (*1893*) listed *Cyrtodactylus peguensis* as having nine supralabials and seven or eight infralabials and *Smith* (*1921*) reports 9–11 supralabials and 7–9 infralabilas whereas we report seven supralabials and infralabials in the syntype. Boulenger's and Smith's totals were a result of counting all the granular scales along the labial margins posterior to the enlarged labial scales which was not done here. *Boulenger (1893)* reports the syntypes as having

43–45 ventral scales across the belly whereas we report 37 scales in the syntype between the ventrolateral folds. *Boulenger (1893)* did not indicate how his counts were made. *Boulenger* (*1893*) states that femoral pores were absent in the syntypes, however, we counted nine femoral pores on the right leg and 10 on the left. Femoral pores in species of the *peguensis* group are difficult to see because they are small and not imbedded within enlarged femoral scales as in other *Cyrtodactylus*. Additionally, the pores on the pore-bearing scales generally lie hidden beneath the posterior edges of the scales of the scale row immediately anterior to the pore-bearing row. *Boulenger* (*1893*) described the dorsal pattern as consisting of two series of large dorsal spots. This is true for the syntype BMNH 1946.8.23.10 however based on his illustration of the lost syntype, the spots are confluent on the midline as they are in LSUHC 13455 (Fig. 5). This description was made even more confusing by *Smith* (*1921:428*) who accurately noted the difference between the syntypes but provides an Illustration of a specimen of *C. zebriacus* from southern Thailand bearing a very different color pattern which he referred to as the “Forma typica”.

Cyrtodactylus meersi **sp. nov.**

Bago Yoma Bent-toed Gecko

(Fig. 7)

Holotype. Juvenile male LSUHC 13455 collected on 18 May 2017 at 2000 hrs by Mark. W. Herr from Myin Mo Swhe Taung Pagoda, Bago Division, Taikkyi Township, Yangon (north) District, Myanmar (17.46272° N, 96.01624° E, elevation 162 m)

Diagnosis. *Cyrtodactylus meersi* sp. nov. differs from other species of the *peguensis* group by having the unique combination of seven supralabials and eight infralabials; 32 paravertebral tubercles; 13 longitudinal rows of body tubercles; 32 ventral scales; 17 subdigital lamellae on the fourth toe; 12 femoral pores; eight precloacal pores; two rows of post-precloacal scales; and domed to weakly conical and weakly keeled body tubercles (Table 7).

Description of holotype. Juvenile, SVL 36.0 mm; head moderate in length (HL/SVL 0.27), wide (HW/HL 0.67), somewhat flattened (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; eye large (ED/HL 0.27); ear opening elliptical to triangular, moderate in size (EL/HL 0.09); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally, bordered posteriorly by large left and right supranasals separated by small internasal, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by large supranasal, posteriorly by two small postnasals, ventrally by first supralabial; seven (R,L) rectangular supralabials extending to below midpoint of eye; eight (R,L) infralabials tapering smoothly to below posterior margin of orbit; 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 supraciliaries not elongate or keeled; 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, grading posteriorly into larger, flatter, smooth, subimbricate to imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.45) with weak ventrolateral folds; dorsal scales small, interspersed with small, domed to weakly conical, semi-regularly arranged weakly keeled tubercles; tubercles extend from occiput onto base of tail but no farther; tubercles on occiput and nape small, those on posterior portion of body larger and keeled; approximately 13 longitudinal rows of dorsal tubercles; 32 paravertebral tubercles; approximately 32 flat, imbricate, ventral scales larger than dorsal scales; eight pore-bearing precloacal scales; two rows of large post-precloacal scales; and no deep precloacal groove or depression.

Forelimbs moderate in stature, relatively short (FL/SVL 0.13); 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; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.17), covered dorsally by granular scales interspersed with slightly larger, weakly keeled tubercles and anteriorly by large, flat, imbricate scales; ventral scales of femora flat, imbricate, larger than dorsals, lacking a row of enlarged femoral scales; six (R,L) weakly developed, pore-bearing femoral scales; small postfemoral scales form an abrupt union with large, flat ventral scales of posteroventral margin of thigh; subtibial scales flat, imbricate; plantar scales flat but slightly raised; digits relatively short, well-developed, inflected at basal, interphalangeal joints; 17 subdigital lamellae on fourth toe; and claws well-developed, base of claw sheathed by a dorsal and ventral scale; two enlarged postcloacal tubercles at base of tail; and postcloacal scales flat

Original tail moderate in proportions, 38.0 mm in length, 3.6 mm in width at base, tapering to a point; dorsal scales of base of tail granular rapidly becoming flatter posteriorly; and median row of transversely enlarged subcaudal scales twice as wide as long, not extending onto lateral margin of tail.

Coloration in life (Fig. 7). Dorsal ground color of head body, limbs, and tail straw-colored; top of head bearing small, dark-brown spots, those in center of head well-defined and edged in yellow; dark-brown, wide, nuchal loop extending from posterior margin of one eye, across occiput, to posterior margin of other eye; three large, dark-brown spots edged in yellow on nape; five dorsal bands between limb insertions; anteriormost band composed of the three transversely arranged, dark-brown blotches edged in yellow; remaining bands composed of paired, separate, paravertebral, dark-brown blotches edged in yellow; postsacral band composed of three, dark-brown blotches edge in yellow; dorsal surface of limbs mottled with yellow spots and larger, poorly defined, dark blotches; 13 dark bands on tail, anteriormost bifurcated medially; 13 light-colored, yellowish bands on tail; tail-tip white; flanks bearing 8–10 small, diffuse, dark spots. All ventral surfaces generally beige, immaculate except for ventral surfaces of forelimbs, forelegs, hands, feet, and posterior section of tail bearing dark pigment. Based on ontegenetic changes in color pattern observed in *Cyrtodactylus pyinyaungensis,* it is likely that with an increase in SVL, blotches on the flanks and the top of the head would become slightly larger and more defined.

Distribution. *Cyrtodactylus meersi* sp. nov. is known only from the type locality of Myin Mo Shwe Taung Pagoda, 9.5 km east of the village of Hpa Lon, Bago Division, Taikkyi Township, Yangon (north) District Myanmar (Fig. 1).

Etymology. The specific epithet, *meersi,* is named in honor of Mr. John Meers whose generous private donations to Fauna & Flora International's in the name of karst conservation have resulted in the continuation of karst biology research in Indochina.

Natural History. The holotype was collected in a region composed of low foothills and highly disturbed forest (Fig. 6). The specimen was encountered at 2000 hours as it was sitting in the middle of an ant trail, presumably preying on the ants. The fact that the specimen is a juvenile suggests the reproductive season is prior to May.

Comparisons. *Cyrtodactylus meersi* sp. nov. is differentiated from *C. annandalei* by the top of the head being blotched as opposed to being patternless. Differences between *C. meersi* sp. nov. and *C. peguensis* are reported in the comparisons section of the latter. *Cyrtodactylus meersi* sp. nov. differs from *C. pyinyaungensis* in having significantly higher mean number of infralabial scales (IL; 8.0 vs. 6.0), fourth toe lamellae (4TL; 17.0 vs 15.0), and having domed to weakly conical and weakly keeled body tubercles vs. raised and moderately keeled body tubercles (Tables 7, 8). It differs from *C. myintkyawthurai* sp. nov. by having significantly higher mean number of infralabial scales (IL; 8.0 vs. 6.5) and a significantly lower mean number of longitudinal rows of dorsal tubercles (LRT; 13 vs. 18.6). *Cyrtodactylus meersi* sp. nov. is widely separated from all other species in both the PCA and DAPC and has an uncorrected pairwise sequence divergence from them of 10–13.7% (Table 3).

***Cyrtodactylus myintkyawthurai* sp. nov.**

Mt. Popa Bent-toed Gecko

(Fig. 8)

Cyrtodactylus fea Wood et al., 2012:995; Agarwal et al., 2014:147; Brennan et al., 2017:3.

Holotype. Adult male LSUHC 13808 collected on 27 October 2017 at 1030 hrs by Evan S. H. Quah, Perry L. Wood, Jr., Matthew L. Murdoch, Myint Kyaw Thura, Aung Lin, Robert E. Espinoza, Tun Oo, and L. Lee Grismer from Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Division, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).

Paratypes. LSUHC 13500–02, 13505, 13806–07, 13809 bear the same collection data as the holotype. CAS 245200–03 collected on 1 August 2007 by A.K. Shein, S.W. Kyi, and J.V. Vindum from Central Bago Yoma Range, between Pallan Gyi Forest Camp and summit, Bago Division, Myamnar (18.92108° N, 95.814027° E, 268 m). CAS 222147 collected on 11 August 2001 by H. Win and A.K. Shein from the Kyetshar Elephant Camp, Kyet Shar Village, Aok Twin Township, Bago Division, Myanmar (18.88094° N, 96.07922° E, 263 m elevation). CAS 222128 collected on 31 July 2001 by H. Win, A.K. Shein and H. Tun from the Ka Baung Reserve, Aok Twin Township, Taung Oo District, Bago Division, Myanmar (18.834750°N, 96.18638° E, 160 m elevation).

Diagnosis. *Cyrtodactylus myintkyawthurai* sp. nov. differs from other species in the *peguensis* group by having the unique combination of six or seven supralabials and six or seven infralabials; 28–33 paravertebral tubercles; 17–23 longitudinal rows of body tubercles; 32–36 ventral scales; 17–19 subdigital lamellae on the fourth toe; 12–20 femoral pores in males; 7–9 precloacal pores in males; two rows of post-precloacal scales; raised, moderately to strongly keeled body tubercles; and a maximum SVL of 75.1 mm (Table 7).

Description of holotype. Adult male, SVL 57.6 mm; head moderate in length (HL/SVL 0.28), wide (HW/HL 0.70), somewhat flattened (HD/HL 0.43), 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; eye large (ED/HL 0.27); ear opening triangular, moderate in size (EL/HL 0.13); eye to ear distance greater than diameter of eye; rostral rectangular, partially divided dorsally, bordered posteriorly by large left and right supranasals separated an internasal, laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by large supranasal, posteriorly by two postnasals, ventrally by first supralabial; six (R,L) rectangular supralabials extending to below midpoint of eye; six (R,L) infralabials tapering smoothly to below posterior margin of orbit; 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 supraciliaries not elongate or keeled; 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 third infralabial; and gular and throat scales small, granular, grading posteriorly into larger, flatter, smooth, subimbricate to imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.47) with weak ventrolateral folds; dorsal scales small, interspersed with larger, moderately to strongly keeled, semi-regularly arranged keeled tubercles; tubercles extend from occiput onto base of tail but no farther; tubercles on occiput and nape smaller than those on posterior portion of body that are larger and keeled; approximately 17 longitudinal rows of dorsal tubercles; 31 paravertebral tubercles; approximately 35 flat, imbricate, ventral scales larger than dorsal scales; seven pore-bearing precloacal scales; two 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 tubercles; palmar scales raised; digits slightly narrower distal to inflections; claws well-developed, sheathed by a dorsal and ventral scale; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.15), covered dorsally by granular scales interspersed with slightly larger, weakly keeled tubercles and anteriorly by large, flat, imbricate scales; ventral scales of femora flat, imbricate, larger than dorsals, lacking a row of enlarged femoral scales; six (R,L) pore-bearing femoral scales; small postfemoral scales form an abrupt union with large, flat ventral scales of posteroventral margin of thigh; subtibial scales flat, imbricate; plantar scales raised; digits relatively short, well-developed, inflected at basal, interphalangeal joints; 17 subdigital lamellae on fourth toe; and claws well-developed, base of claw sheathed by a dorsal and ventral scale; two enlarged postcloacal tubercles at base of tail; and postcloacal scales flat.

Original tail moderate in proportions, 64.0 mm in length, 5.9 mm in width at base, tapering to a point; dorsal scales of base of tail granular rapidly becoming flatter posteriorly; and intermittent rows of transversely enlarged, median, subcaudal scales twice as wide as long, not extending onto lateral margin of tail.

Coloration in life (Fig. 8). Dorsal ground color of head body, limbs, and tail yellow; top of head bearing large, dark-brown, irregularly shaped blotches edged in yellow; dark-brown, wide, nuchal loop extending from posterior margin of one eye, across occiput, to posterior margin of other eye; nape bearing a large, dark-brown band edged in yellow; four wide, dark-brown body bands between limb insertions edged in yellow with paravertebral sections; one dark-brown post-sacral band edged in yellow bearing paravertebral sections; 10 dark-brown caudal bands wider than 11 yellow, caudal bands with darkened centers; dorsal portion of forelimbs darkly banded; dorsal portion of hind limbs bearing irregularly shaped, dark-brown blotches edges in yellow; flanks with a series of 8–10 dark-brown, round to irregularly shaped blotches of varying sizes edged in yellow. All ventral surfaces generally beige, immaculate except for ventral surfaces of forelimbs, forelegs, hands, feet, and posterior section of tail bearing dark pigment.

Variation. Variation in the paratypes of *Cyrtodactylus myintkyawthurai* sp. nov. is most notable in the dorsal banding pattern. Specimens from the central Bago Yoma Range tend to have dorsal bands that are divided along the midline, thus manifesting distinct paravertebral elements (CAS 222147, 245201–03) although this is not so evident in CAS 245200 and CAS 222128 has somewhat of an anomolus pattern with some elongate, irregularly shape blotches. The banding pattern in specimens from Mt Popa lacks complete midline bifurcation although the dorsal bands have distinct paravertebral elements. The dorsal bands of all the paratypes except CAS 245200 and 245203, LSUHC 13505 are relatively wider than those of the holotype LSUHC 13808.

Specimens CAS 245200, 245202 and LSUHC 13500–02, 13806, and 13809 have regenerated tails bearing dark mottling. Specimens CAS 222128 and LSUHC 13505 have broken tails. Adult females have dimpled scales or 0–8 femoral pores. Other meristic mensural variation in the type series is presented in Table 6.

Distribution. *Cyrtodactylus myintkyawthurai* sp. nov. ranges throughout Mt. Popa, Mandalay Division and the central section of the Bago Yoma Range, Bago Division (Fig. 2).

Etymology. The specific epithet, *myintkyawthurai,* is a patronym honoring Myint Kyaw Thura for his contributions to the study of herpetology in Myanmar, his discovery of several new species, and collaboration with foreign researchers.

Natural History. At both Mt. Popa and in the central Bago Yoma Range, *Cyrtodactylus myintkyawthurai* sp. nov. occurs in hilly regions covered in deciduous dipterocarp forest up to 978 m in elevation (Fig. 9). The Mt. Popa specimens were collected at night from 0.05–1 m above the ground on rocks, the trunks of small trees, on leaves or on the ground amongst small rocks.

Comparisons. See previous comparison sections.

DISCUSSION

Members of the *peguensis* group all appear to be habitat generalists within the hilly regions they inhabit. *Cyrtodactylus pyinyaungensis* have been found crawling on karst boulders in dry secondary forest as well as highly disturbed, burned over lowland forests/agricultural areas. *Cyrtodactylus myintkwawthurai* sp. nov. is know from dry deciduous forests and mixed dipterocarp forests and *C. meersi* sp. nov. and *C. peguensis* occur in highly disturbed lowland forests bordering agricultural fields. No natural history data were provided with the description of *C. annandalei.* This lack of microhabitat preference suggests that additional populations of this species group are very likely to be found in other hilly areas both within and along the fringes of the Ayeyarwady Basin.

The rapidly growing awareness of the diversity of karst-associated species of *Cyrtodactylus* and other gekkonids in Myanmar (*Grismer et al., 2017a,b, 2018a,b*) mirrors that in other Southeast Asian nations (see discussions in *Grismer et al., 2016a,b,c; Wood et al., 2017*) but is in no way surprising given Myanmar's vast regions of unexplored karstic habitats. What is surprising, however, is the diversity within lineages restricted to the relatively featureless Ayeyarwady Basin. The *peguensis* group collectively account for at least seven species of a monophyletic group that ranges disjunctly from the eastern foothills of the Chin Hills along the western fringe of the Ayeyarwady Basin to the western foothills of the Shan Hills along the eastern fringe of the basin (Fig. 1). Additionally, the low hills of the centrally located Bago Yoma are inhabited by *C. peguensis, C. myintkyawthurai* sp. nov., and *C. meersi* sp. nov. The allopatric distribution of these species is likely due to range fragmentation resulting from sedimentation from the numerous river courses—the Ayeyarwady and Sittaung being the largest—since at least the Lower Miocene-Upper Pliocene (*Agarwal et al., 2014*). The other eight species found within the Ayeyarwady Basin or along its mountainous fringes that are not part of the *peguensis* group (*Bauer, 2003; Mahoney, 2009*) do not form a monophyletic group but are nested within lineages containing Indian, Bangladeshi, and Himalayan taxa from farther west, indicating that colonization of the Ayeyarwady Basin is the result of multiple invasions since at least the Upper Miocene (*Agarwal et al., 2014*).

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- L. Lee Grismer conceived, designed, and ran the analyses, wrote the paper, prepared the figures and tables, reviewed drafts of the paper, and helped in the field.
- Perry L. Wood Jr conceived, designed, and ran the analyses, reviewed drafts of the paper, and helped in the field.
- Evan S. H. Quah helped in the field and reviewed drafts of the paper.
- Matthew L. Murdoch helped in the field and reviewed drafts of the paper.
- Marta S. Grismer generated the morphological and color pattern data, helped in the field, and reviewed drafts of the paper.
- Mark W. Herr helped in the field and reviewed drafts of the paper.
- Robert E. Espinoza helped in the field and reviewed drafts of the paper.
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Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers): Brigham Young University's Institutional Animal Care and Use Committee (IACUC) has approved the animal use protocol for this study (protocol # 160401).

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New Species Registration

The following information was supplied regarding the registration of a newly described species:

to be completed after acceptance of the manuscript.

Publication ID:

urn:lsid:zoobank.org:author:xxxxxxxx

urn:lsid:zoobank.org:act:xxxxxx

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Figure 1(on next page)

Distribution map of the *Cyrtodactylus peguensis* group.

Distribution of the species of the *Cyrtodactylus peguensis* group in the Ayeyarwady Basin and the adjacent foothills of the Chin Hills and Shan Hills in Myanmar.

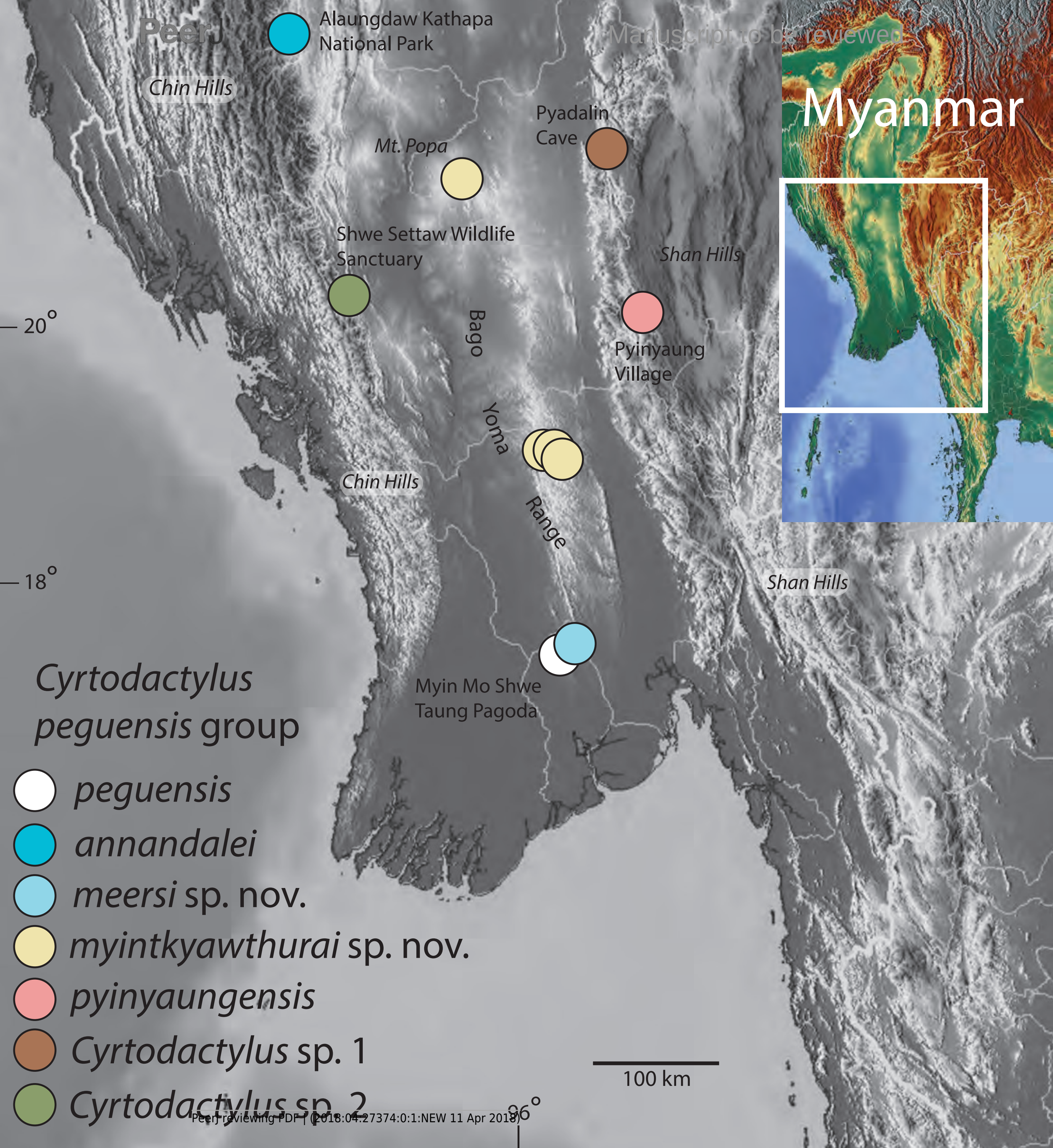
Alaungdaw Kathapa National Park
Chin Hills
Myanmar
Pyadalin Cave
Mt. Popa
Shwe Settaw Wildlife Sanctuary
Shan Hills
20°
Bago
Pyinyaung Village
Yoma
Chin Hills
Range
18°
Shan Hills
Myin Mo Shwe Taung Pagoda
Cyrtodactylus peguensis group
peguensis
annandalei
meersi sp. nov.
myintkyawthurai sp. nov.
pyinyaungensis
Cyrtodactylus sp. 1
Cyrtodactylus sp. 2
100 km
96°

Figure 2(on next page)

Phylogenetic relationships of the species of the *Cyrtodactylus peguensis* and *C. oldhami* groups.

Maximum likelihood consensus tree topology of *Cyrtodactylus* highlighting the distant phylogenetic position of the *peguensis* and *oldhami* groups. Black dots denote nodes with BPP ≥ 0.95, LRT ≥ 0.80, and UFB ≥ 95. The grey dot connotes a node with BPP ≥ 0.95, LRT ≤ 0.80, and UFB ≥ 95. The white dot connotes a node with BPP ≤ 0.95, LRT ≤ 0.80, and UFB ≥ 95. Red arrow and red circle denote the node of the Indo-Burma clade (*sensu Agarawal et al. 2014*. Blue arrow and blue circle denote the node of the Indochinese clade (*sensu Grismer 2017a*).

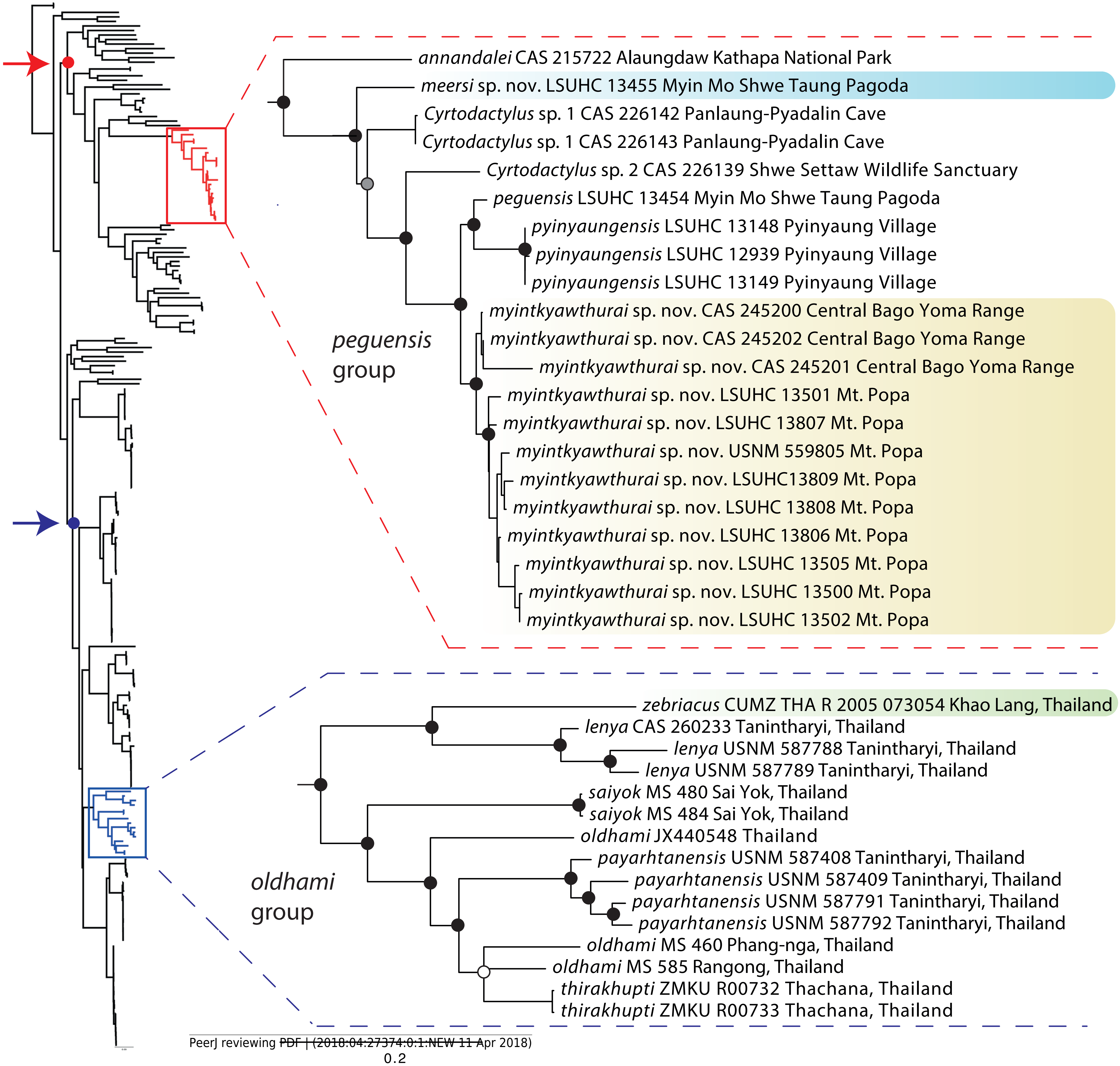
annandalei CAS 215722 Alaungdaw Kathapa National Park
meersi sp. nov. LSUHC 13455 Myin Mo Shwe Taung Pagoda
Cyrtodactylus sp. 1 CAS 226142 Panlaung-Pyadalin Cave
Cyrtodactylus sp. 1 CAS 226143 Panlaung-Pyadalin Cave
Cyrtodactylus sp. 2 CAS 226139 Shwe Settaw Wildlife Sanctuary
peguensis LSUHC 13454 Myin Mo Shwe Taung Pagoda
pyinyaungensis LSUHC 13148 Pyinyaung Village
pyinyaungensis LSUHC 12939 Pyinyaung Village
pyinyaungensis LSUHC 13149 Pyinyaung Village
myintkyawthurai sp. nov. CAS 245200 Central Bago Yoma Range
myintkyawthurai sp. nov. CAS 245202 Central Bago Yoma Range
myintkyawthurai sp. nov. CAS 245201 Central Bago Yoma Range
myintkyawthurai sp. nov. LSUHC 13501 Mt. Popa
myintkyawthurai sp. nov. LSUHC 13807 Mt. Popa
myintkyawthurai sp. nov. USNM 559805 Mt. Popa
myintkyawthurai sp. nov. LSUHC13809 Mt. Popa
myintkyawthurai sp. nov. LSUHC 13808 Mt. Popa
myintkyawthurai sp. nov. LSUHC 13806 Mt. Popa
myintkyawthurai sp. nov. LSUHC 13505 Mt. Popa
myintkyawthurai sp. nov. LSUHC 13500 Mt. Popa
myintkyawthurai sp. nov. LSUHC 13502 Mt. Popa
peguensis group
zebriacus CUMZ THA R 2005 073054 Khao Lang, Thailand
lenya CAS 260233 Tanintharyi, Thailand
lenya USNM 587788 Tanintharyi, Thailand
lenya USNM 587789 Tanintharyi, Thailand
saiyok MS 480 Sai Yok, Thailand
saiyok MS 484 Sai Yok, Thailand
oldhami JX440548 Thailand
payarhtanensis USNM 587408 Tanintharyi, Thailand
payarhtanensis USNM 587409 Tanintharyi, Thailand
payarhtanensis USNM 587791 Tanintharyi, Thailand
payarhtanensis USNM 587792 Tanintharyi, Thailand
oldhami MS 460 Phang-nga, Thailand
oldhami MS 585 Rangong, Thailand
thirakhupti ZMKU R00732 Thachana, Thailand
thirakhupti ZMKU R00733 Thachana, Thailand
oldhami group
0.2

Figure 3(on next page)

PCA and DAPC analyses of the *Cyrtodactylus peguensis* group.

PCA biplot (left) and DAPC (righ) analyses showing the morphospatial relationships of the species of the *peguensis* group as well as the overlap of the reciprocally monophyletic populations of *Cyrtodactylus myintkyawthurai* sp. from Mt. Popa (MP) and the Bago Yoma (BY).

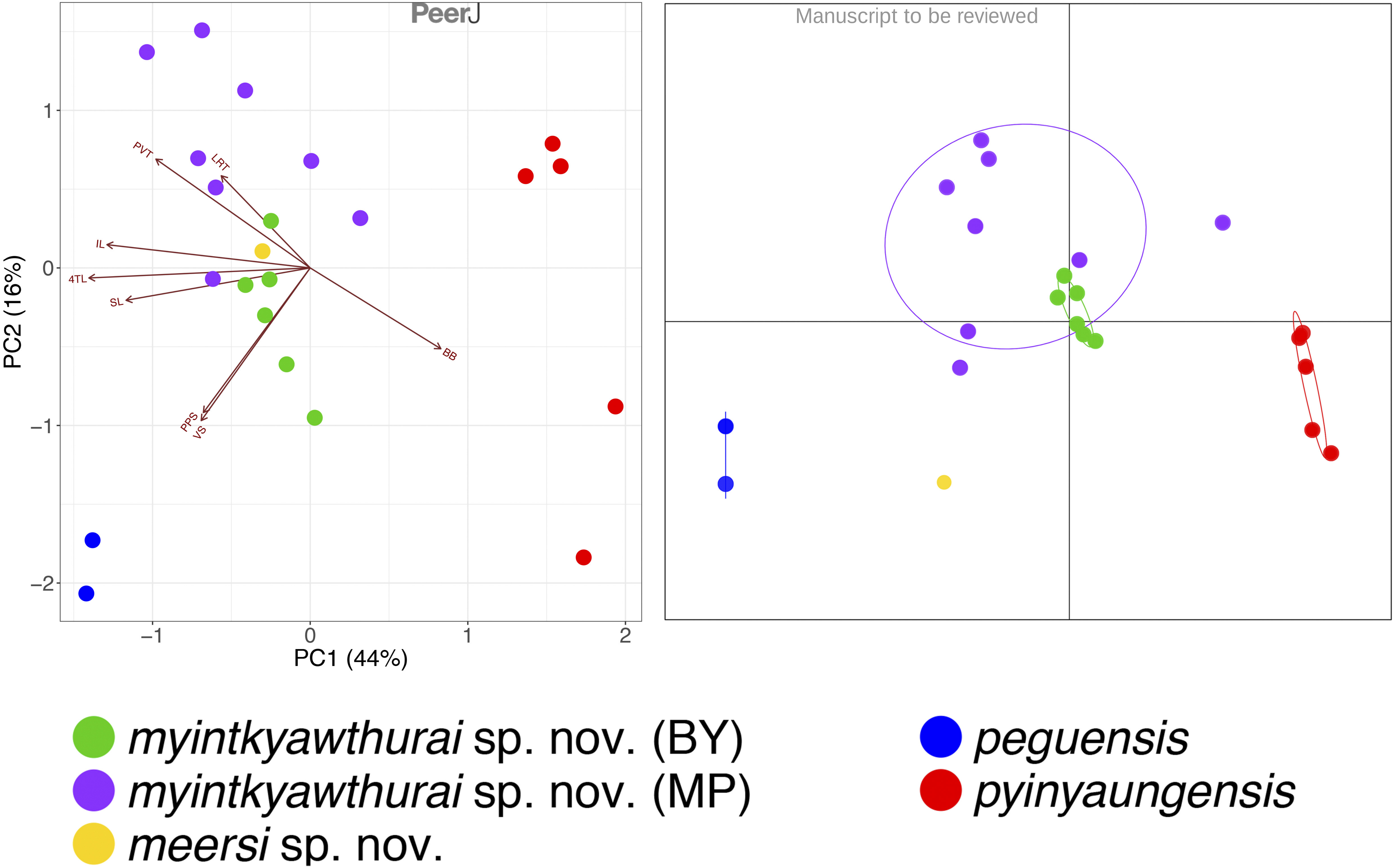
PC2 (16%)
1
0
−1
−2
PC1 (44%)
−1
0
1
2
PVT
LRT
IL
4TL
SL
BB
PPS
VS
● *myintkyawthurai* sp. nov. (BY)
● *myintkyawthurai* sp. nov. (MP)
● *meersi* sp. nov.
● *peguensis*
● *pyinyaungensis*

Figure 4(on next page)

Cyrtodactylus zebriacus and *C. pyinyaungensis*.

A. Uncollected specimen of *Cyrtodactylus zebriacus* (LSUDPC 10080) from Kanchandt, Surat Thani Province, Thailand. B. *Cyrtodactylus pyinyaungensis* (LSUHC 13150) from Pyinyaung Village, Mandalay Division, Myanmar.

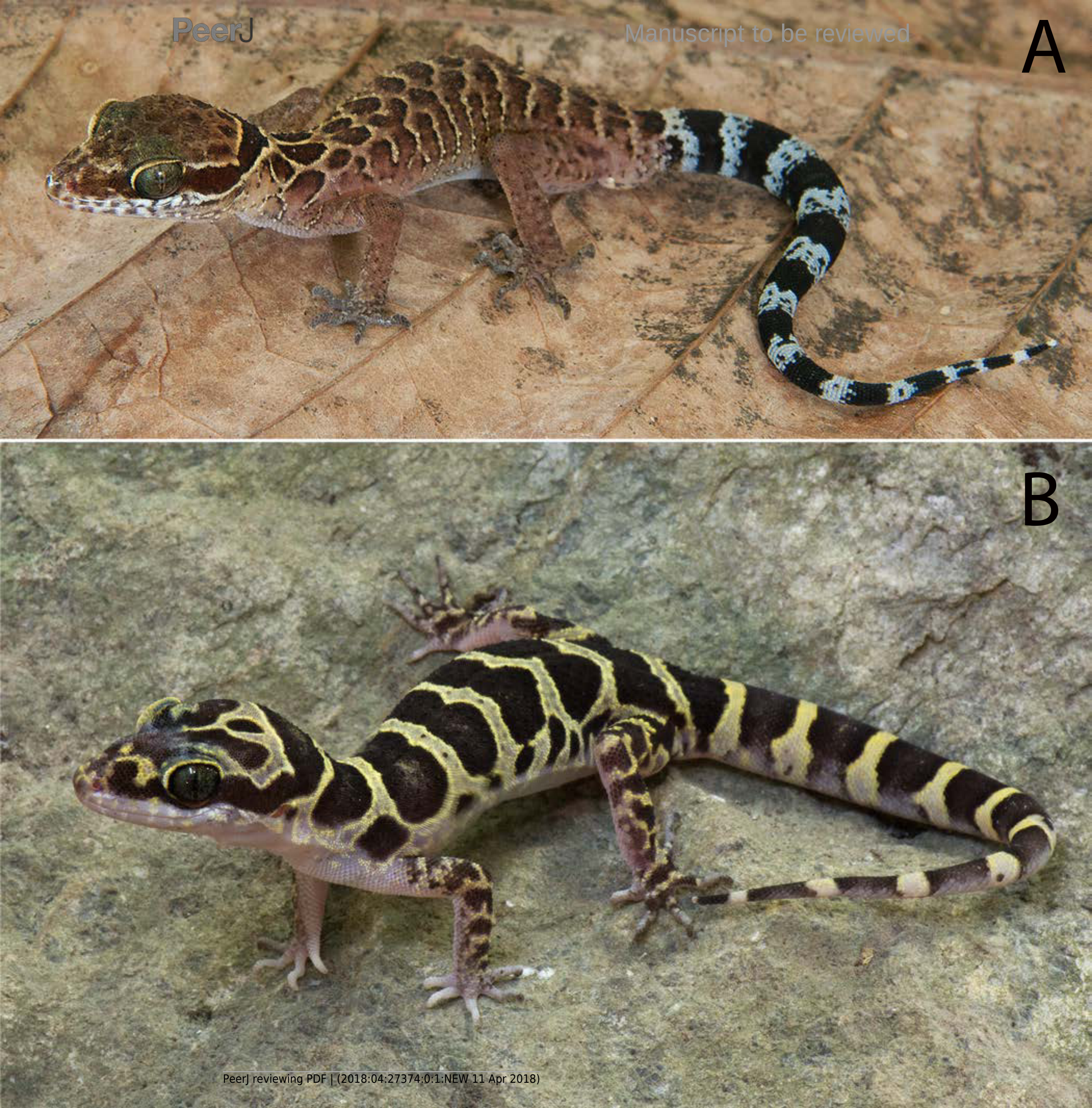
A
B

Figure 5(on next page)

Type specimens and additional specimen of *Cyrtodactylus peguensis*.

Cyrtodactylus peguensis. A. Boulenger’s (1893) illustration of the lost syntype from the type locality of Hpa Lon, Bago Division, Myanmar. B. Syntype BM 1946.3.23 from the type locality. C. LSUHC 13454 from the Myin Mo Shwe Taung Pagoda, 9.5 km east of Hpa Lon, Bago Division, Myanmar.


A
2
Peter Smit del. et lith.
Mintern Bros. imp.
2. Gymnodactylus peguensis.
B
29
C

Figure 6(on next page)

Type locality of *Cyrtodactylus peguensis*.

Habitat of *Cyrtodactylus peguensis* on the road just below the Myin Mo Shwe Taung Pagoda, Bago Division, Myanmar.

Figure 7(on next page)

Holotype of *Cyrtodactylus meersi*.

Holotype of *Cyrtodactylus meersi* sp. nov. from the type locality of the Myin Mo Shwe Taung Pagoda, Bago Division, Myanmar.

Figure 8(on next page)

Type specimens of *Cyrtodactylus myintkyawthurai* sp. nov.

Cyrtodactylus myintkyawthurai sp. nov. from the type locality of Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Division, Myanmar. A. Adult male holotype LSUHC 13808. B. Adult male paratype LSUHC 13807. C. Subadult male paratype 13806. D. Juvenile male paratype LSUHC 13809.


A
B
C
D

Figure 9(on next page)

Habitat of *Cyrtodactylus myintkyawthurai* sp. nov.

Mixed dry dipterocarp forest habitat of *Cyrtodactylus myintkyawthurai* sp. nov. near the type locality of Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Division, Myanmar.

Table 1(on next page)

Locality data and GenBank numbers of specimens used in this analysis.

GenBank accession numbers for the newly recorded specimens of the *peguensis* group used for the molecular phylogenetic analyses. Accession numbers for outgroups are in *Agarwal et al*. (*2014*) and for the other specimens of *Cyrtodactylus* of the Indochina clade see *Grismer et al.* (*2017a, 2018*).

Table 1. GenBank accession numbers for the newly recorded specimens of the *peguensis* group used for the molecular phylogenetic analyses. Accession numbers for outgroups are in *Agarwal et al*. (*2014*) and for the other specimens of *Cyrtodactylus* of the Indochina clade see *Grismer et al.* (*2017a, 2018*).

Taxon	**Catalog no.**	**Locality**	**GenBank no.**
Cyrtodactylus meersi sp. nov. holotype	LSUHC 13455	Myin Mo Swhe Taung Pagoda, Bago Division, Taikkyi Township, Yangon (north) District, Myanmar (17.46272° N, 96.01624° E, elevation 162 m)	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	CAS 245200	Central Bago Yoma, between Pallan Gyi Forest Camp and summit, Bago Division, Myamnar (18.92108° N, 95.814027° E, 268 m).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	CAS 245201	Central Bago Yoma, between Pallan Gyi Forest Camp and summit, Bago Division, Myamnar (18.92108° N, 95.814027° E, 268 m).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	CAS 245202	Central Bago Yoma, between Pallan Gyi Forest Camp and summit, Bago Division, Myamnar (18.92108° N, 95.814027° E, 268 m).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	LSUHC 135100	Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Region, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	LSUHC 135101	Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Region, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	LSUHC 135102	Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Region, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	LSUHC 135105	Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Region, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	USNM 559805	Popa Mountain Park, Mandalay Division, Myanmar	JX440536
Cyrtodactylus myintkyawthurai sp. nov.	LSUHC 13806	Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Region, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov. holotype	LSUHC 13807	Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Region, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	LSUHC 13808	Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Region, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).	xxxxxxxxx
Cyrtodactylus myintkyawthurai sp. nov.	LSUHC 13809	Taung Twin Chaung camp, Mt. Popa, Kyauk-pa-taung Township, Mandalay Region, Myanmar (20.93087°N, 95.22580°E; 978 m in elevation).	xxxxxxxxx
Cyrtodactylus pyinyaungensis	LSUHC 13139	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).	
Cyrtodactylus pyinyaungensis	LSUHC 13148	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).	
Cyrtodactylus pyinyaungensis	LSUHC 13149	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).	
Cyrtodactylus peguensis	LSUHC 13454	Myin Mo Swhe Taung Pagoda, Bago Division, Taikkyi Township, Yangon (north) District, Myanmar (17.46272° N, 96.01624° E, elevation 162 m)	
Cyrtodactylus sp. 1	CAS 226142	Panlaung-Pyadalin Cave Wildlife Sanctuary, Ywa Ngan Township, Shan State, Myanmar (21.11581° N, 96.36069° E, 346 m in elevation).	xxxxxxxxx
Cyrtodactylus sp. 1	CAS 226143	Panlaung-Pyadalin Cave Wildlife Sanctuary, Ywa Ngan Township, Shan State, Myanmar (21.11581° N, 96.36069° E, 346 m in elevation).	xxxxxxxxx
Cyrtodactylus sp. 2	LSUHC 226139	Shwe Settaw Wildlife Sanctuary, Min Bu Township, Magway Division: Myanmar (20.059805°N, 94.59606°E, 137 m in elevation).	xxxxxxxxx

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Table 2(on next page)

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

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

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’
H5934	(*Macey et al., 1997*)	External	5' -AGRGTGCCAATGTCTTTGTGRTT-3'

Table 3(on next page)

Percent uncorrected pair-wise sequence divergence among individuals and species of the *Cyrtodactylus peguensis* group and *C. zebriacus* calculated from 1467 base pairs of the mitochondrial gene ND2.

Percent uncorrected pair-wise sequence divergence among individuals and species of the *Cyrtodactylus peguensis* group and *C. zebriacus* calculated from 1467 base pairs of the mitochondrial gene ND2.

Table 3 Percent uncorrected pair-wise sequence divergence among individuals and species of the *Cyrtodactylus peguensis* group and *C. zebriacus* calculated from 1467 base pairs of the mitochondrial gene ND2.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1. *zebriacus* CUMZ 2005 073054	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
2. *Cyrtodactylus* sp.1 CAS 226139	0.303	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
3. *Cyrtodactylus* sp.2 CAS 226142	0.283	0.097	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
4. *Cyrtodactylus* sp.2 CAS 226143	0.280	0.093	0.003	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
5. *meersi* sp. nov. LSUHC 13455	0.283	0.100	0.110	0.107	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
6. *myintkyawthurai* sp. nov. Bago Yoma CAS 245200	0.293	0.117	0.097	0.093	0.113	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
7. *myintkyawthurai* sp. nov. Bago Yoma CAS 245202	0.293	0.113	0.093	0.090	0.110	0.003	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
8. *myintkyawthurai* sp. nov. Bago Yoma CAS 245201	0.303	0.123	0.103	0.100	0.117	0.013	0.010	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
9. *myintkyawthurai* sp. nov. Mt. Popa LSUHC 13500	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	***	***	***	***	***	***	***	***	***	***	***	***	***	***
10. *myintkyawthurai* sp. nov. Mt. Popa LSUHC 13502	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	0.000	***	***	***	***	***	***	***	***	***	***	***	***	***
11. *myintkyawthurai* sp. nov. Mt. Popa LSUHC 13809	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	0.000	0.000	***	***	***	***	***	***	***	***	***	***	***	***
12. *myintkyawthurai* sp. nov. Mt. Popa LSUHC 13806	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	0.000	0.000	0.000	***	***	***	***	***	***	***	***	***	***	***
13. *myintkyawthurai* sp. nov. Mt. Popa LSUHC 13808	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	0.000	0.000	0.000	0.000	***	***	***	***	***	***	***	***	***	***
14. *myintkyawthurai* sp. nov. Mt. Popa LSUHC 13807	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	0.000	0.000	0.000	0.000	0.000	***	***	***	***	***	***	***	***	***
15. *myintkyawthurai* sp. nov. Mt. Popa LSUHC 13505	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	0.000	0.000	0.000	0.000	0.000	0.000	***	***	***	***	***	***	***	***
16. *myintkyawthurai* sp. nov. Mt. Popa LSUHC 13501	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	***	***	***	***	***	***	***
17. *myintkyawthurai* sp. nov. Mt. Popa USNM 559805	0.313	0.117	0.103	0.100	0.120	0.033	0.030	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	***	***	***	***	***	***
18. *peguensis* LSUHC 13454	0.293	0.093	0.093	0.090	0.103	0.043	0.040	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	***	***	***	***	***
19. *pyinyaungensis LSUHC 12939*	0.293	0.100	0.093	0.090	0.117	0.047	0.043	0.053	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.033	***	***	***	***
20. *pyinyaungensis* LSUHC 13149	0.293	0.100	0.093	0.090	0.117	0.047	0.043	0.053	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.033	0.000	***	***	***
21. *pyinyaungensis* LSUHC 13148	0.293	0.100	0.093	0.090	0.117	0.047	0.043	0.053	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.050	0.033	0.000	0.000	***	***
22. *annandalei* CAS 215722	0.280	0.103	0.143	0.140	0.137	0.153	0.150	0.160	0.153	0.153	0.153	0.153	0.153	0.153	0.153	0.153	0.153	0.150	0.143	0.143	0.143	***

Table 4(on next page)

Meristic, mensural, and color pattern data for *Cyrtodactylus peguensis* and *C. meersi sp.* nov.

Meristic, mensural, and color pattern data for *Cyrtodactylus peguensis* and *C. meersi sp.* nov.

Table 4 Meristic, mensural, and color pattern data for *Cyrtodactylus peguensis* and *C. meersi sp.* nov.

	BM	LSUHC	LSUHC
	1946 8.23.10	13454	13455
	syntype		holotype
	peguensis	*peguensis*	*meersi* sp. nov.
sex	m	m	juvenile
supralabials	7	7	7
infralabials	7	7	8
body tubercles low and rounded (dome-shaped)	yes	yes	yes
body tubercles pointed and strongly keeked (triangular)	no	no	no
no. of paravertebral tubercles	32	31	32
no. longitudinal rows of tubercles	17	19	13
tubercles on at least anterior 1/3 of tail	/	no	no
no. of ventral scales	37	36	32
subdigital lamellae on 4th toe	19	19	17
total number of femoral pores in males	19	17	12
number of precloacal pores in males	8	8	8
post-precloacal scales rows	3	3	2
transeverse subcaudal 2–3 times wider than long	/	yes	yes
dorsal pattern with paravertebrtal elements	yes	variable	yes
paravertebral elements not in contact	yes	variable	yes
number of body bands	5	5	5
number of light bands on tail	/	12	11
number of dark bands on tail	/	13	10
SVL	70	44	36
TL	5.9	46	38
TW	6.6		
FL	10		
TBL	12.3		
AG	30		
HL	20.2		
HW	11.5		
HD	8.9		
ED	4.2		
EE	5.7		
ES	7.7		
EN	6.2		
IO	5.1		

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Table 5(on next page)

Summary statistics and principal component analysis scores for the species of the *peguensis* group.

Summary statistics and principal component analysis scores for the species of the *peguensis* group. Abbreviations are listed in the Materials and methods.

Table 5 Summary statistics and principal component analysis scores for the species of the *peguensis* group. Abbreviations are listed in the Materials and methods.

Standard deviation	1.87977	1.14550	1.04649	0.88399	0.76149	0.58707	0.45129	0.38658
Proportion of Variance	0.44171	0.16402	0.13689	0.09768	0.07248	0.04308	0.02546	0.01868
Cumulative Proportion	0.44171	0.60572	0.74261	0.84029	0.91278	0.95586	0.98132	1.00000
Eigenvalue	3.53357	1.31218	1.09514	0.78144	0.57987	0.34466	0.20366	0.14944
SL	-0.41562	-0.11994	0.43799	-0.04827	0.26991	-0.29239	0.58088	0.35060
IL	-0.45874	0.08613	0.18604	0.25940	0.15835	-0.26483	-0.74375	0.17843
PVT	-0.34827	0.40331	-0.21661	0.45143	0.04823	0.61796	0.20295	0.19983
LRT	-0.20080	0.34158	-0.71353	-0.29496	0.03732	-0.45765	0.09269	0.16560
VS	-0.24605	-0.56588	-0.26397	-0.43539	0.33955	0.43168	-0.17252	0.16900
4TL	-0.49952	-0.03722	-0.03150	-0.00330	0.07709	-0.03537	0.11926	-0.85244
PPS	-0.24112	-0.53611	-0.23620	0.34100	-0.66325	-0.13589	0.08476	0.12963
BB	0.29492	-0.29969	-0.30170	0.57768	0.58068	-0.21672	0.09186	-0.07646

Table 6(on next page)

Meristic, mensural, and color pattern data for *Cyrtodactylus myintkywathurai* sp. nov.

Meristic, mensural, and color pattern data for *Cyrtodactylus myintkywathurai* sp. nov. r = regenerated; / = data unobtainable.

Table 6 Meristic, mensural, and color pattern data for *Cyrtodactylus myintkywathurai* sp. nov. r = regenerated; / = data unobtainable.

	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC
	13808	13502	13501	13500	13505	13807	13809	13806
	holotype	paratype	paratype	paratype	paratype	paratype	paratype	paratype
	myintkyawthurai sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.
	Mt. Popa	Mt. Popa	Mt. Popa	Mt. Popa	Mt. Popa	Mt. Popa	Mt. Popa	Mt. Popa
sex	m	f	m	m	f	m	f	m
supralabials	6	6	6	7	7	7	7	7
infralabials	6	7	7	7	7	7	7	7
body tubercles low and rounded (dome-shaped)	no	no	no	no	no	no	no	no
body tubercles pointed and keeked (triangular)	yes	yea	yes	yes	yes	yes	yes	yes
no. of paravertebral tubercles	31	33	33	31	32	33	31	30
no. longitudinal rows of tubercles	17	21	23	21	19	18	17	18
no. of ventral scales	35	34	35	32	32	35	32	33
subdigital lamellae on 4th toe	17	18	17	17	19	18	19	18
enlarged femoral scales and precloacal scales continuous	/	/	/	/	/	/	/	/
total number of femoral pores	12	dimples	16	20	0 (juv)	14	8	12
number of precloacal pores in males	7	5	8	8	0(juv)	7	8	8
post-precloacal scales rows	2	2	2	2	2	2	2	2
transeverse subcaudal 2–3 times wider than long	no	/	no	no	no	no	no	no
dorsal pattern with paravertebrtal elements	yes	variable	no	yes	yes	yes	yes	yes
paravertebral elements not in contact	no	no	no	no	no	no	no	no
number of body bands	4	6	5	4	4	6	5	4
number of light bands on tail	11	/	/	/	9	12	/	/
number of dark bands on tail	10	/	/	/	10	11	/	/
SVL	57.6	75.1	63	58.8	41.7	57	53.3	51.2
TL	64	r	r	r		68	r	r
TW	5.9	6.7	7.3	6.4	3.5	5	5.1	4.7
FL	9	9.9	8.4	8.2	7	8.3	7.3	7.9

TBL	8.8	12.3	10.4	10.3	7.4	10.1	9	8.8
AG	27.2	35.8	27.3	24.2	18.1	27.7	23.7	23.3
HL	16.1	18.4	16.6	17.1	12.4	15.5	14.8	13.5
HW	11.3	14.1	10.7	11.2	7.7	10.8	10.1	9.6
HD	7	8.8	7.4	6.8	4.9	6.1	6.7	6.5
ED	4.3	4.5	3.6	3.3	2.7	3.3	4.1	4
EE	4.5	5.8	4.2	4.6	3.3	4.3	4	4
ES	6.4	8.2	6.8	6.3	5	6.3	6.7	5.9
EN	5.6	5.6	4.5	4.5	3.2	4.7	5.9	4.7
IO	4.7	6.7	5.2	4.7	3.6	5	4.8	3.9
EL	2.1	2.1	1.7	2.1	1.4	1.8	2.1	1.9
IN	2.1	2.7	2.4	2.2	2	2.2	2.3	1.8

Table 6 continued.

	CAS	CAS	CAS	CAS	CAS	CAS
	245200	245202	222147	245203	222128	245201
	paratype	paratype	paratype	paratype	paratype	paratype
	myintkyawthurai sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.	*myintkyawthurai* sp. nov.
	Bago Yoma	Bago Yoma	Bago Yoma	Bago Yoma	Bago Yoma	Bago Yoma
sex	f	f	f	f	m	m
supralabials	7	7	7	7	7	7
infralabials	6	6	6	6	6	6
body tubercles low and rounded (dome-shaped)	no	no	no	no	no	no
body tubercles pointed and keeked (triangular)	yes	yes	yes	yes	yes	yes
no. of paravertebral tubercles	28	29	32	30	32	31
no. longitudinal rows of tubercles	17	19	17	17	18	18
no. of ventral scales	36	35	35	36	34	35
subdigital lamellae on 4th toe	17	18	17	17	17	18
enlarged femoral scales and precloacal scales continuous	no	no	no	no	no	no
total number of femoral pores	4	1	0	1	16	13
number of precloacal pores in males	9	5	8	7	9	9
post-precloacal scales rows	2	2	2	2	2	2
transeverse subcaudal 2–3 times wider than long	/	yes	yes	yes	/	yes
dorsal pattern with paravertebrtal elements	yes	yes	yes	yes	yes	yes
paravertebral elements not in contact	no	no	no	yes	variable	no
number of body bands	5	5	5	5	~5	5
number of light bands on tail	/	/	11	11	/	11
number of dark bands on tail	/	/	11	12	/	11
SVL	70	69.6	68.3	55.3	61.3	47.6
TL	r	r	76.1	58.5	b	50.7
TW	6	5.4	6.3	4.8	6.5	4.6
FL	9.8	10	9.4	8.6	9.1	7.6

TBL	11.6	10.5	11.6	9.5	10.6	8.8
AG	30.6	34.4	34.8	22.5	26.8	23.4
HL	18.8	19.1	18.3	14.7	16.8	13.6
HW	11.6	11.2	11.9	9.7	10.5	8.2
HD	7.5	7.7	9.4	5.8	6.8	5.4
ED	4.5	4.2	4.7	3.9	4.4	4.1
EE	4.3	4.8	5.3	3.9	4.4	3.3
ES	6.8	6.8	6.9	6.2	6.6	4.7
EN	4.6	5.4	5.4	4.5	5.3	3.4
IO	5	4.5	4.5	3.8	3.9	3.1
EL	2	2.2	1.6	1.9	2.4	1.5
IN	2.4	2.3	2.2	1.7	2.4	1.8

Table 7(on next page)

Summary statistics and diagnostic characters of the species from the *peguensis* species groups.

Summary statistics and diagnostic characters of the species from the *peguensis* species groups. SD = standard deviation, and N = sample size. * = data come from Bauer (2003).

Table 7 Summary statistics and diagnostic characters of the species from the *peguensis* species groups. SD = standard deviation, and N = sample size. * = data come from Bauer (2003).

	peguensis	*meersi* sp. nov.	*myintkywathurai* sp. nov.	*pyinyaungensis*	*annandalei**
supralabial scales (SL)					
Mean	7	7	6.9	8.0	/
SD	0	0	±0.36	0	/
Range	7	7	6 or 7	8	7 or 8
N	2	1	14	5	3
infralabial scales (IL)					
Mean	7	8	6.5	6	9
SD	0	0	±0.52	0	0
Range	7	8	6 or 7	6	9
N	2	1	14	5	3
paravertebral tubercles (PVT)					
Mean	31.5	32	31.1	28.2	/
SD	±0.7	0	±1.51	2.49	/
Range	31 or 32	32	28–33	25–30	/
N	2	1	14	5	/
longitudunal rows of body tubercles (LRT)					
Mean	18.0	13	18.6	16.4	/
SD	±1.41	0	±1.87	1.14	/
Range	17–19	13	17–23	15–18	16–18
N	2	1	14	5	3
ventral scales (VS)					
Mean	36.5	32	32.4	31.8	/
SD	±0.71	0	±01.42	2.49	/
Range	36 or 37	32	32–36	30–36	43
N	2	1	14	5	3
4th toe lamellae (4TL)					
Mean	19.0	17.0	17.6	15.0	/
SD	0	0	±0.74	0	/
Range	19	17	17–19	15	10
N	2	1	14	5	3
femoral pores in males (FP)					
Mean	18.0	12	14.9	17.5	/
SD	±1.00	0	±2.97	±1.00	/
Range	17–19	12	12–20	17 or 18	20–22
N	2	1	7	2	3
precloacal pores in males (PP)					
Mean	8	8	8	8	/
SD	0	0	±0.82	0	/
Range	8	8	7–9	8	11 or 12
N	2	1	2	2	3
enlarged post-precloacal scales (PPS)					
Mean	3	2	2	2	/
SD	0	0	0	0	/
Range	3	2	2	2	/
N	2	1	14	5	/
body bands (BB)					

Mean	5	5	4.9	5.8	/
SD	0	0	±0.66	0.45	/
Range	5	5	4–6	5 or 6	4
N	2	1	14	5	3
light caudal bands (LCB)					
Mean	12.5	11	10.8	10.8	/
SD	±0.50	0	±0.98	1.71	/
Range	12 or 13*	11	9–12	9–13	11
N	2	1	6	4	1
dark caudal bands (DCB)					
Mean	13	10	10.8	11.0	/
SD	0	0	±0.75	1.63	/
Range	13	10	10–12	9–13	12
N	2	1	6	4	1
Morphology					
body tubercles domed to weakly conical and weakly keeled	yes	yes	no	no	yes
body tubercles raised, moderately to strongly keeled	no	no	yes	yes	no
Color Pattern					
top of head patternless or blotched	blotched	blotched	blotched	blotched	patternless
paravertebral elements of dorsal bands confluent	variable	yes	variable	yes	yes
maximum SVL (mm)	70	36.0	75.1	71.7	55

Table 8(on next page)

Pairwise comparison of characters with statistically significant mean differences among species of the *peguensis* group.

Pairwise comparison of characters with statistically significant mean differences among species of the *peguensis* group. The raw data for *Cyrtodactylus annandaeli* were unavailable.

Table 8 Pairwise comparison of characters with statistically significant mean differences among species of the *peguensis* group. The raw data for *Cyrtodactylus annandaeli* were unavailable.

	meersi sp. nov.	*myintkyawthurai* sp. nov.	*peguensis*	*pyinyaungensis*
meersi sp. nov.	***	***	***	***
myintkyawthurai sp. nov.	IL	***	***	***
peguensis	LRT	PPS,4TL	***	***
pyinyaungensis	IL,4TL	BB,IL,PV,4TL	IL,LRT,PPS,4TL,VS	***

Table 9(on next page)

New species of *Cyrtodactylus* from Myanmar

CONCLUSIONS

A phylogenetic taxonomy of species in the *Cyrtodactylus peguensis* group from the Ayeyarwady Basin of Myanmar recovers at least seven species, four of which are undescribed. Three species, including *C. peguensis* occur in the low hills of the Bago Yoma mountain range one of which, *C. meersi* sp. nov., is syntopic with *C. peguensis*. As more lowland hilly areas associated with the Ayeyarwady Basin are surveyed, more new species of this group are likely to be discovered. These discoveries continue the recent surge of descriptions of new species of *Cyrtodactylus* that are being discovered in Myanmar.