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A phylogeny and taxonomy of the Thai-Malay Peninsula Bent-toed Geckos of the *Cyrtodactylus pulchellus* complex (Squamata: Gekkonidae): combined morphological and molecular analyses with descriptions of seven new species

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Abstract

An integrative taxonomic analysis using color pattern, morphology and 1497 base pairs of the ND2 mitochondrial gene and its five flanking tRNAs demonstrated that nine monophyletic species-level lineages occur within the *Cyrtodactylus pulchellus* complex (*Cyrtodactylus pulchellus sensu strictu* and *C. macrotuberculatus*) of the Thai-Malay Peninsula that have a sequence divergence between them ranging from 5.9–16.8%. Additionally, each lineage is discretely diagnosable from one another based on morphology and color pattern and most occur in specific geographic regions (upland areas or islands) that prevent or greatly restrict interpopulation gene flow. Six of these lineages were masquerading under the nomen *C. pulchellus* and are described as the following: *Cyrtodactylus astrum* sp. nov. from northwestern Peninsular Malaysia and southwestern Thailand; *C. langkawiensis* sp. nov., at this point endemic to Langkawi Island, Malaysia; *C. bintangrendah* sp. nov., a lowland species surrounding the Banjaran (=mountain range) Bintang of northwestern Peninsular Malaysia; *C. bintangtinggi* sp. nov., endemic to the upland regions of the Banjaran Bintang of northwestern Peninsular Malaysia; *C. trilatofasciatus* sp. nov., endemic to upland regions of Cameron Highlands in the central portion of the Banjaran Titiwangsa in Peninsular Malaysia; and *C. australotitiwangsaensis* sp. nov. from the more southerly upland regions of the Banjaran Titiwangsa. An additional species, *Cyrtodactylus lekaguli* sp. nov. from Satun, Trang, Surat Thani, and Phang-nga provinces in southern Thailand, was identified on the basis of morphology and color pattern and is hypothesized to be part of a clade containing *C. astrum* sp. nov. and *C. langkawiensis* sp. nov.

Key words: Taxonomy, Phylogeny, *Cyrtodactylus*, Gekkonidae, Malaysia, Thailand, Molecular systematics, New species

Introduction

The genus *Cyrtodactylus* is the most speciose group of gekkonid lizards to date (152 species at present count; see www.reptile-database.org plus Shea *et al.* 2011) and the remarkable frequency at which new species are being described shows no signs of abating (i.e., David *et al.* 2011; Iskandar *et al.* 2011; Ngo, 2011; Oliver *et al.* 2011; Schneider *et al.* 2011; Shea *et al.* 2011). The vast majority of these recent descriptions were born out of

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field work in unexplored areas throughout Southeast Asia and as such, the species having been described are known only from a few specimens from their type localities. The description of *C. macrotuberculatus* Grismer & Norhayati 2008 from an insular population in Malaysia previously considered to be *C. pulchellus* (Gray), was the first indication that some of the more widely distributed species of *Cyrtodactylus* may represent species complexes and that the close examination of other widespread taxa may reveal a hidden diversity within *Cyrtodactylus* not yet realized. Grismer (2011) went on to propose that the variation in color pattern and morphology in the remaining populations of *C. pulchellus* was additional evidence that this species was still a conglomerate of multiple, unnamed lineages.

As it is currently constituted, *Cyrtodactylus pulchellus* is a forest-dwelling scansorial, species ranging from southern Thailand south of the Isthmus of Kra, southward through Peninsular Malaysia. Most populations of *C. pulchellus* are known from lowland localities even though the species extends from sea level to over 1500 meters in elevation (Grismer 2011; Taylor 1963). Morphologically distinct populations have been noted from upland areas in different mountain ranges and from islands (Grismer 2011) where interpopulation gene flow is not possible. More surprising, however, is that morphologically distinct populations have been reported from lowland areas (Grismer 2011) despite this species' broad distribution throughout such regions west of the major mountain systems of the Thai-Malay Peninsula. Although mitochondrial DNA phylogenies have proven to be extremely valuable in delimiting species boundaries and identifying cryptic species, highly divergent haplotypes can persist within populations due to incomplete lineage sorting and introgression, resulting in phylogenies that are inconsistent with species histories (McGuire *et al.* 2007). Therefore, the addition of non-recombinant data sources (nuclear markers and/or morphology) to taxonomic analyses have proven to be highly informative in disentangling the lineages of species complexes (e.g. Malhotra *et al.* 2011). Therefore, we employed an integrative taxonomic approach (i.e. Padial *et al.* 2010) to test for, and to delimit species boundaries within the *C. pulchellus* complex (*C. pulchellus sensu strictu* and *C. macrotuberculatus*) in order to provide an evolutionary based taxonomy. A molecular phylogeny using 1497 base pairs of the ND2 mitochondrial gene and the flanking tRNAs was compared to color pattern and morphology from seven populations of *C. pulchellus* (n=43 individuals) and four populations of *C. macrotuberculatus* (n=17 individuals) from throughout their ranges. The results indicated that the geographic variation in color pattern and morphology between the populations of *C. pulchellus* was correlated with the existence of six exclusive lineages bearing sequence divergences from one another ranging from 5.9–16.8% and each occurred within a specific geographic region. These lineages plus one other are described here as new species.

Materials and Methods

Taxon Sampling and Outgroup Selection

Mitochondrial DNA.—The primary aim of this study was to investigate the taxonomy and phylogenetic relationships of the *Cyrtodactylus pulchellus* complex based on the mitochondrial marker NADH dehydrogenase subunit 2 (ND2) and its flanking tRNAs, Trp, Ala, Asn, Cys, Tyr (1497 base pairs). We sampled as widely as possible across the range of this complex, being sure to include multiple representatives from populations of the broadly characterized color pattern groups noted in Grismer (2011) and from all major physiographic regions from where this complex is known to occur. Unfortunately, we were unable to obtain tissues of any Thai populations. Based on Wood *et al.* (2012), we used *C. interdigitalis* (Smith), *C. elok* Dring, and *C. intermedius* (Smith) as the nearest outgroups to root the tree and *Tropiocolotes steudneri* (Peters), *Agamura persica* (Duméril), and *Hemidactylus frenatus* Schlegel were included as more distant outgroups. Taxon sampling for the ingroup included 60 individuals from 21 localities and for the outgroup eight individuals were included (Table 1). All sequences were deposited in Genebank (TABLE 1).

Morphological analysis.— 117 individuals from throughout the range of the species complex were examined. In order to assess species-level taxonomy, individuals were first grouped on the basis of locality and concordant color pattern variation as noted in Grismer (2011). A subsequent tree-based taxonomy (Wiens & Penkrot 2002) using the mitochondrial ND2 gene and adjacent flanking tRNA regions was then compared to the color pattern/ geographic groups. We considered populations whose haplotypes formed strongly supported lineages restricted to particular physiographic regions to be putative species. These lineages were then examined for additional corroborating diagnostic morphological characters.

TABLE 1. Taxon sampling for ingroup and outgroup, locality data, and Genebank accession numbers.

Voucher	Species	Locality	Gene Bank Accession No.
NC00155	*Hemidactylus frenatus*	unkown	JX519468
FMNH 247474	*Agamura persica*	Pakistan, Baluchistan Province, Makran District, Gwadar	JX440515
JB 28	*Tropiocolotes steudneri*	unkown	JX440520
LSUHC 9513	*C. intermedius*	Thailand, Chantaburi Province, Khao Khitchakut	JX519469
LSUHC 9514	*C. intermedius*	Thailand, Chantaburi Province, Khao Khitchakut	JX519470
LSUHC 6471	*C. elok*	West Malaysia, Pahang, Fraser's Hill, The Gap	JQ889180
FMNH 265806	*C.* sp.	Thailand, Loei, Phu Rua	JX519471
FMNH 255454	*C. interdigitalis*	Lao PDR, Khammouan Province, Nakai District	JQ889181
LSUHC 10024	*C. astrum* sp. nov.	West Malaysia, Perlis, Wang Kelian	JX519472
LSUHC 9215	*C. astrum* sp. nov.	West Malaysia, Perlis, Perlis State Park	JX519473
LSUHC 10023	*C. astrum* sp. nov.	West Malaysia, Perlis, Wang Kelian	JX519474
LSUHC 9962	*C. astrum* sp. nov.	West Malaysia, Perlis, Perlis State Park, Gua Wang Burma	JX519475
LSUHC 9986	*C. astrum* sp. nov.	West Malaysia, Perlis, Perlis State Park, Gua Wang Burma	JX519476
LSUHC 9987	*C. astrum* sp. nov.	West Malaysia, Perlis, Perlis State Park, Gua Wang Burma	JX519477
LSUHC 8807	*C. astrum* sp. nov.	West Malaysia, Perlis, Gua Kelam	JX519478
LSUHC 8808	*C. astrum* sp. nov.	West Malaysia, Perlis, Gua Kelam	JX519479
LSUHC 8809	*C. astrum* sp. nov.	West Malaysia, Perlis, Gua Kelam	JX519480
LSUHC 8806	*C. astrum* sp. nov.	West Malaysia, Perlis, Gua Kelam	JX519481
LSUHC 8815	*C. astrum* sp. nov.	West Malaysia, Perlis, Kuala Perlis	JX519482
LSUHC 8816	*C. astrum* sp. nov.	West Malaysia, Perlis, Kuala Perlis	JX519483
LSUHC 6637	*C. australotitiwangsaensi*s sp. nov.	West Malaysia, Pahang, Genting Highlands	JX519484
LSUHC 8087	*C. australotitiwangsaensi*s sp. nov.	West Malaysia, Pahang, Fraser's Hill	JX519485
LSUHC 8086	*C. australotitiwangsaensi*s sp. nov.	West Malaysia, Pahang, Fraser's Hill	JX519486
LSUHC 9984	*C. bintangrendah* sp. nov.	West Malaysia, Kedah, Bukit Palang	JX519487
LSUHC 9975	*C. bintangrendah* sp. nov.	West Malaysia, Perak, Lengong Valley	JX519488
LSUHC 9976	*C. bintangrendah* sp. nov.	West Malaysia, Perak, Lengong Valley	JX519489
LSUHC 9974	*C. bintangrendah* sp. nov.	West Malaysia, Perak, Lengong Valley	JX519490
LSUHC 9977	*C. bintangrendah* sp. nov.	West Malaysia, Perak, Lengong Valley	JX519491
LSUHC 9983	*C. bintangrendah* sp. nov.	West Malaysia, Kedah, Bukit Palang	JX519492
LSUHC 8862	*C. bintangtinggi* sp. nov.	West Malaysia, Perak, Bukit Larut	JX519493
LSUHC 9006	*C. bintangtinggi* sp. nov.	West Malaysia, Perak, Bukit Larut	JX519494
LSUHC 9435	*C. langkawiensis* sp. nov.	West Malaysia, Kedah, Pulau Langkawi, Wat Wanararm	JX519495
LSUHC 9125	*C. langkawiensis* sp. nov.	West Malaysia, Kedah, Pulau Langkawi, Wat Wanararm	JX519496
LSUHC 9437	*C. langkawiensis* sp. nov.	West Malaysia, Kedah, Pulau Langkawi, Wat Wanararm	JX519497
LSUHC 9434	*C. langkawiensis* sp. nov.	West Malaysia, Kedah, Pulau Langkawi, Wat Wanararm	JX519498
LSUHC 9124	*C. langkawiensis* sp. nov.	West Malaysia, Kedah, Pulau Langkawi, Wat Wanararm	JX519499
LSUHC 9123	*C. langkawiensis* sp. nov.	West Malaysia, Kedah, Pulau Langkawi, Wat Wanararm	JX519500
LSUHC 9122	*C. langkawiensis* sp. nov.	West Malaysia, Kedah, Pulau Langkawi, Wat Wanararm	JX519501

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Table 1. (Continued)

Voucher	Species	Locality	Gene Bank Accession No.
LSUHC 9120	*C. langkawiensis* sp. nov.	West Malaysia, Kedah, Pulau Langkawi, Wat Wanararm	JX519502
LSUHC 7560	*C. macrotuberculatus*	West Malaysia, Kedah, Pulau Langkawi, Gunung Machinchang	JX519503
LSUHC 9429	*C. macrotuberculatus*	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	JX519504
LSUHC 6829	*C. macrotuberculatus*	West Malaysia, Kedah, Pulau Langkawi, Lubuk Semilang	JX519505
LSUHC 9428	*C. macrotuberculatus*	West Malaysia, Kedah, Pulau Langkawi, Gunung Raya	JX519506
LSUHC 9448	*C. macrotuberculatus*	West Malaysia, Kedah, Pulau Langkawi, Gunung Machinchang	JX519507
LSUHC 7173	*C. macrotuberculatus*	West Malaysia, Kedah, Pulau Langkawi, Telaga Tuju	JX519508
LSUHC 9449	*C. macrotuberculatus*	West Malaysia, Kedah, Pulau Langkawi, Gunung Machinchang	JX519509
LSUHC 9671	*C. macrotuberculatus*	West Malaysia, Kedah, Hutan Lipur Sungai Tupah	JX519510
LSUHC 9672	*C. macrotuberculatus*	West Malaysia, Kedah, Hutan Lipur Sungai Tupah	JX519511
LSUHC 5999	*C. macrotuberculatus*	West Malaysia, Kedah, Gunung Jerai	JX519512
LSUHC 5939	*C. macrotuberculatus*	West Malaysia, Kedah, Gunung Jerai	JX519513
LSUHC 6000	*C. macrotuberculatus*	West Malaysia, Kedah, Gunung Jerai	JX519514
LSUHC 9980	*C. macrotuberculatus*	West Malaysia, Perlis, Perlis State Park	JX519515
LSUHC 9981	*C. macrotuberculatus*	West Malaysia, Perlis, Perlis State Park	JX519516
LSUHC 9693	*C. macrotuberculatus*	West Malaysia, Kedah, Hutan Lipur Sungai Tupah	JX519517
LSUHC 10038	*C. macrotuberculatus*	West Malaysia, Perlis, Bukit Chabang	JX519518
LSUHC 10037	*C. macrotuberculatus*	West Malaysia, Perlis, Bukit Chabang	JX519519
LSUHC 9667	*C. pulchellus*	West Malaysia, Penang, Pulau Pinang, Terjun Titi Kerawang	JX519520
LSUHC 9668	*C. pulchellus*	West Malaysia, Penang, Pulau Pinang, Terjun Titi Kerawang	JX519521
LSUHC 10022	*C. pulchellus*	West Malaysia, Penang,Pulau Pinang, Terjun Titi Kerawang	JX519522
LSUHC 6668	*C. pulchellus*	West Malaysia, Penang, Pulau Pinang, Empangan Air Itam	JX519523
LSUHC 6785	*C. pulchellus*	West Malaysia, Penang, Pulau Pinang, Moongate Trail	JX519524
LSUHC 6728	*C. pulchellus*	West Malaysia, Penang, Pulau Pinang, Moongate Trail	JX519525
LSUHC 6727	*C. pulchellus*	West Malaysia, Penang, Pulau Pinang, Moongate Trail	JX519526
LSUHC 6726	*C. pulchellus*	West Malaysia, Penang, Pulau Pinang, Moongate Trail	JX519527
LSUHC 6729	*C. pulchellus*	West Malaysia, Penang, Pulau Pinang, Moongate Trail	JX440552
LSUHC 10064	*C. trilatofasciatus* sp. nov.	West Malaysia, Pahang, Cameron Highlands	JX519529
LSUHC 10065	*C. trilatofasciatus* sp. nov.	West Malaysia, Pahang, Cameron Highlands	JX519530
LSUHC 10066	*C. trilatofasciatus* sp. nov.	West Malaysia, Pahang, Cameron Highlands	JX519531

Data

Mitochondrial DNA.— Genomic DNA was extracted from liver tissues stored in 95–100% ethanol following the standard protocol in the Qiagen DNeasy™ tissue kit (Valencia, CA, USA). The ND2 gene was amplified using a double-stranded Polymerase Chain Reaction (PCR). Included in the reaction were 2.5 µl genomic DNA, 2.5 µl light strand primer 2.5 µl heavy strand primer, 2.5 µl dinucleotide pairs, 2.5 µl 5x buffer, MgCl 10x buffer, 0.18 µl Taq polymerase, and 9.82 µl 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 50–55°C for 35 s, followed by a cycle extension at 72°C for 35 s, for 31 cycles (Greenbaum *et al.* 2007). All PCR products were visualized on a 1.5% agarose gel electrophoresis to check for distinct bands with the appropriate molecular weight. Successful PCR amplifications were purified using AMPure magnetic bead solution (Agentcourt Bioscience, Beverly, MA, USA) to remove any impurities. Purified PCR products were sequenced using Applied Biosystems BigDye™ Terminator v3.1 Cycle Sequencing ready reaction kit. Both internal and external primers were used for sequencing reactions (see Table 2). A Cleanseq magnetic bead solution (Agentcourt Bioscience, Beverly, MA, USA) was used to purify sequencing products. All purified sequencing reactions were analyzed using a ABI 3730XL automated sequencer. Sequences were analyzed from both the 3' and the 5' ends separately to confirm congruence between the reads. Both the forward and the reverse sequences were uploaded and edited in Geneious™ version v5.4 (Drummond *et al.*, 2011) and were edited therein. The protein-coding region of the ND2 sequence was aligned by eye. The flanking tRNA's were reconstructed using ARWEN v1.2 (Laslett & Canbäck 2008) and then adjusted by eye. MacClade v4.08 (Maddison & Maddison 2003) was used to calculate the correct amino acid reading frame and to confirm the lack of premature stop codons.

TABLE 2. Primer sequences for the ND2 gene.

Primer name	Primer reference		Sequence
L4437b	Macey & Schulte 1999	External	5'-AAGCAGTTGGGCCCATACC-3'
CyrtintF1	Siler *et al.* 2010	Internal	5'-TAGCCYTCTCYTCYATYGCCC-3'
CyrtintR1	Siler *et al.* 2010	Internal	5'-ATTGTKAGDGTRGCYAGGSTKGG-3'
L5002	Macey & Schulte 1999	External	5'-AACCAAACCCAACTACGAAAAAT-3'

Phylogenetic reconstructions were executed using three independent methods, a character-based Maximum Parsimony (MP) analysis and two model-based analyses, Maximum Likelihood (ML) and Bayesian Inference (BI). Maximum Parsimony (MP) phylogenetic reconstruction and bootstrap estimates for nodal support was executed in PAUP* v4.0 (Swofford 2002). Bootstrap support values (Felsenstein 1985) for nodal support in the MP trees were calculated using 1000 pseudoreplicates each including 10 random addition-sequence replicates using the TBR branch swapping algorithm. The 1000 bootstrap replicates were then summarized as a majority rule consensus tree. We considered bootstrap values of 70% or greater to represent strongly supported nodes.

Partitioned maximum likelihood (ML) analyses were implemented using RAxML HPC v7.2.3 (Stamatakis *et al.* 2008). The best fit evolutionary models were estimated in ModelTest v3.7 (Posada & Crandall 1998) for each codon position (see Table 3). The analyses were performed using the more complex model (GTR+I+G) applied to all partitions due to computer programming limitations (see Table 4 for selected models and models applied). Maximum likelihood inferences for the best tree were performed for 200 replicates and each inference was initiated with a random starting tree. All gaps were treated as missing data and clade confidence was assessed using 1000 bootstrap pseudoreplicates employing the rapid hill-climbing algorithm (<XREF>Stamatakis *et al.* 2008). We considered bootstrap values of 70% or greater to represent strongly supported nodes.

Partitioned Bayesian analyses were implemented in the program MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003) using default flat priors. The best fit model of nucleotide substitution was determined in ModelTest v3.7 (Posada & Crandall 1998) and was applied to each codon position (Table 3). Two simultaneous parallel runs were executed with eight chains per run, seven hot and one cold chain for 10,000,000 generations and sampled every 1000 generations from the Markov Chain Monte Carlo (MCMC). The Bayesian analysis was halted after the chains reached a stationary position and the standard split frequencies fell below 0.01. We employed the program Are We There Yet? (AWTY) (Nylander *et al.* 2008) to plot the log likelihood scores against the number of generations to assess convergence and to determine the appropriate number of burnin trees. We discarded the first 25% of the generations (2500 trees) as the burnin. A consensus tree was constructed from the two parallel runs using TreeAnnotator v1.6.1 (Drummond & Rambaut 2007). We considered Bayesian posterior probabilities of 0.95 or higher as strongly supported (Wilcox *et al.* 2002).

TABLE 3. Models of evolution selected by Model test v3.7 (Posada & Crandall 1998) and models applied for Bayesian analyses.

Gene	Model selected	Model applied
ND2		
1st pos	GTR+I+Γ	GTR+I+Γ
2nd pos	GTR+I	GTR+I
3rd pos	GTR+Γ	GTR+Γ
tRNAs	GTR+I+Γ	GTR+I+Γ

Morphological analysis.—Color notes were taken from digital images of living specimens of all age classes prior to preservation. The following measurements on the type series were taken with Mitutoyo dial calipers to the nearest 0.1 mm under a Nikon SMZ 1500 dissecting microscope on the left side of the body where appropriate: 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 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; inner orbital distance (IO), measured between the anterior edges of the orbit; ear length (EL), the greatest horizontal distance of the ear opening; and internarial distance (IN), measured between the nares across the rostrum. Additional character states evaluated on the type series and comparative material (Appendix) were numbers of supralabial and infralabial scales counted from the largest scale immediately posterior to the dorsal inflection of the posterior portion of the upper jaw to the rostral and mental scales, respectively; the presence or absence of tubercles on the anterior dorsal and ventral margins of the forearm; the number of paravertebral tubercles between limb insertions counted in a straight line immediately left of the vertebral column; the number of longitudinal rows of body tubercles counted transversely across the center of the dorsum from one ventrolateral fold to the other; the presence or absence of tubercles in the gular region, throat, and lateral margins of the abdomen; the number of longitudinal rows of ventral scales counted transversely across the center of the abdomen from one ventrolateral fold to the other; the shape of the subdigital lamellae proximal to the digital inflection; the number of subdigital lamellae beneath the fourth toe counted from the base of the first phalanx to the claw; the total number of femoro-precloacal pores (*i.e*., the contiguous rows of femoral and precloacal scales bearing pores combined as a single meristic referred to as the femoro-precloacal pores); the degree and arrangement of body tuberculation; the relative size and morphology of the subcaudal scales; the number of dark body bands between the nuchal loop (*fide* Grismer 1988) and the caudal constriction; the ratio of the width of the dark body bands divided by the width of the interspace between the bands; the presence or absence of a band outlined in white on the thigh; number of dark caudal bands on the original tail; the presence or absence of dark pigmentation infused in the white caudal bands of adults; and whether or not the posterior one-third of the original tails in hatchlings and juveniles less than 50 mm SVL was white or whitish and faintly banded or boldly banded.

Institutional abbreviations follow Sabaj Pérez (2010) except we retain ZRC the Zoological Research Collection of the Raffles Museum of Biodiversity, National University of Singapore. LSUHC refers to the La Sierra University Herpetological Collection, La Sierra University, Riverside, California, USA; LSUDPC refers to the La Sierra University Digital Photo Collection; and MS refers to the collection of Montri Sumontha, Ranong Marine Fisheries Station, 157 M. 1, Saphan-Pla Road, Paknam, Muang, Ranong 85000, Thailand.

Results

Phylogenetic analysis.—The analysis generated a total of 1497 base pairs from the ND2 gene and the five tRNA flanking regions of which 473 were parsimony informative. ML, MP, and BI analyses produced the same tree with all nodes receiving posterior probabilities greater than 0.96 from the BI analysis as well as strong support from the ML (bootstrap proportions > 78) and MP (bootstrap proportions > 91) analyses with the exception of low support for one node within *Cyrtodactylus macrotuberculatus* from the BI and ML analysis and two nodes within *C. macrotuberculatus* from the MP analysis (Fig. 1). The mtDNA analysis was 100% concordant with the species-level morphological analysis and revealed that, as it is currently constituted, *C. pulchellus* is not only paraphyletic with respect to a monophyletic *C. macrotuberculatus* (Fig. 1), but composed of eight distinctive highly divergent species (see taxonomy below). Additionally, the genetic data show that the *C. pulchellus* complex is divisible into two strongly supported major clades, each with additional, well supported, phylogenetic substructuring (Fig. 1). One of these clades occurs in northern Malaysia and is composed of two strongly supported sister lineages, one from the island of Langkawi and the other from the state of Perlis on the adjacent peninsula (Figs. 1,2). The other clade comprises the remaining populations which are divisible into two strongly support lineages; one from the Bintang Mountain Range and its associated lowlands which itself is divisible into strongly supported upland and lowland lineages; and the other from the Titiwangsa Mountain Range, Penang Island, and three populations composing *C. macrotuberculatus* (Figs. 1,2). The Titiwangsa lineage is divisible into a Cameron Highlands group and a Fraser's Hill/Genting Highlands group leaving *C. pulchellus* from Penang Island as the sister species to *C. macrotuberculatus* (Figs. 1, 2).

Based on the corroborating evidence from the genetic and morphological analyses, we believe there are at least eight lineages (Fig. 1) within *Cyrtodactylus pulchellus sensu strictu* deserving of separate species status, all of which are morphologically discretely diagnosable from one another (Table 4) and bear large sequence divergences from one another as well (Table 5). The Langkawi Island *pulchellus* has a sequence divergence from all other *pulchellus* populations ranging from 9.3–16.0% and from its closest relative from the adjacent peninsula in Perlis, its divergence is 9.3%. Similarly, the lowland *pulchellus* populations from Perak in northern Peninsular Malaysia have a sequence divergence from all other *pulchellus* populations ranging from 6.9–15.8%. Within the Bintang Mountain Range lineage, the upland population from Bukit Larut has a sequence divergence of 6.9–15.1 from all other *pulchellus* populations and 6.9% and 8.0%, respectively, from the associated lowland populations from the Lenggong Valley and the Bukit Mertajam and Bukit Palong lineage. These latter three lowland populations form a monophyletic lineage and differ from each other by only 1.9–2.4% and are considered here as conspecific. The Titiwangsa Mountain Range lineage is composed of two well-supported lineages. The Cameron Highlands lineage has a sequence divergence of 5.9–16.8% from all other *pulchellus* populations and a divergence of 5.9–9.0% from its closest relative, the Fraser's Hill/Genting Highlands lineage. This latter lineage has a sequence divergence from all other *pulchellus* populations ranging from 5.9–15.0% but between Fraser's Hill and Genting Highlands the divergence is only 1.1–1.2%. Given this, and the fact lizards from these two localities are not morphologically diagnosable from one another, they are considered conspecific. The remaining *pulchellus* population from Penang Island has a sequence divergence of 6.8–16.2% from all other *pulchellus* and a divergence of 6.8–10.2% from its closest relative *C. macrotuberculatus.*

Taxonomy

Given that the phylogenetic relationships within *Cyrtodactylus pulchellus sensu strictu* show multiple, strongly supported lineages (Fig. 1) from discrete geographic areas (Figs. 2,3) that have considerably high percent sequence divergences between them (Table 5) and that all these lineages are morphologically discretely diagnosable from one another (Table 4), we describe seven of these lineages as new species. The type locality of the remaining species, *C. pulchellus sensu lato* is clarified.

FIGURE 1. Inferred phylogenetic relationships of the *Cyrtodactylus pulchellus* complex based on 1497 bp of mitochondrial ND2 gene. The tree is a Maximum likelihood topology (lnL -17497.532298) with Bayesian posterior probabilities (BPP), Maximum Likelihood bootstrap support values (ML), and Maximum Parsimony bootstrap support values (MP) respectively at the nodes.

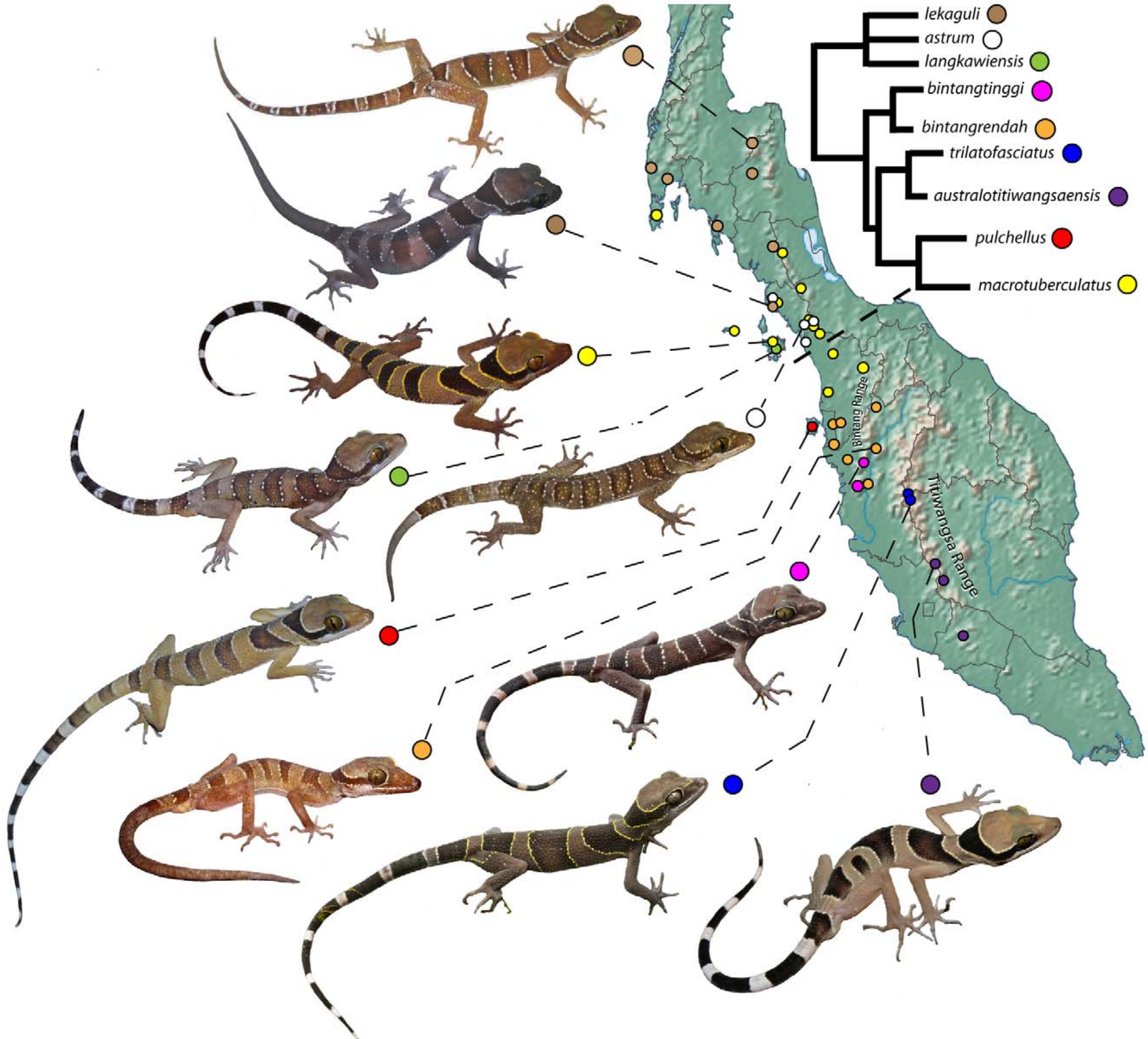

FIGURE 2. Phylogenetic relationships of the *Cyrtodactylus pulchellus* complex in relationship to the species' distribution on the Thai-Malay Peninsula. Dots represent localities from which genetic samples and/or specimens were examined. The thick dashed line represents the Kangar-Pattani Line.

Cyrtodactylus pulchellus Gray

Penang Island Bent-toed Gecko

Fig. 4

Cyrtodactylus pulchella Gray, J.E. 1827:56. A synopsis of the genera of saurian reptiles, in which some new genera are indicated, and the others reviewed by actual examination. Philosophical Magazine 2: 54–58. Type locality.— "India" restricted without comment to "Singapore" (Gray 1845:173) and further restricted here to Penang Island, Peninsular Malaysia (see below).

Gymnodactylus pulchellus Duméril and Bibron 1836:423; Günther 1864:113; Cantor 1847:631; Stoliczka 1873:118; Boulenger 1885:47; Flower 1896:863 (in part), 1899:626 (in part); Boulenger 1912:37 (in part); Smith 1930:13 (of Boulenger 1912).

Diagnosis.– Adult males reaching 114.1 mm SVL, adult females reaching 113.3 mm SVL; 9–11 supralabials, 8–10 infralabials; tubercles of dorsum moderately large, strongly keeled and widely separated with no intervening smaller tubercles; no tubercles on ventral surface of forelimbs, gular region, or in ventrolateral body fold or these regions may be weekly tuberculated; 33–43 paravertebral tubercles; 22–26 longitudinal rows of dorsal tubercles; 29–34 rows of ventral scales; 21–26 subdigital lamellae on fourth toe; 33–39 femoro-precloacal pores in males;

dorsum not bearing scattered, white tubercles; four dark body bands with a body band/interspace ratio of 0.75–1.25; 8–10 dark caudal bands on original tail; white caudal bands in adults immaculate; and posterior portion of tail hatchlings and juveniles not white (Table 4). These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

TABLE 4. Morphological data of *Cyrtodactylus pulchellus* from Pulau Pinang, Penang, Malaysia. m=male; f=female; SVL=snout-vent length; w=weak; 0=absence; 1=presence; /=data unavailable.

	LSUHC									ZRC			
	6668	6726	6727	6728	6729	6785	9967	9968	10022	2.117	2.5197	2.4854	2.4857
Sex	/	m	m	m	f	m	/	m	m	f	m	f	f
Supralabials	10	10	11	9	11	9	11	10	9	10	10	10	11
Infralabials	10	10	10	10	9	8	9	9	10	10	10	9	10
Tubercles on ventral surface of forelimbs	0	0	0	0	0	0	0	w	0	0	0	0	0
Tubercles in gular region	0	0	0	0	0	0	0	w	0	0	0	0	0
Ventrolateral fold tuberculate	0	0	0	0	0	0	0	w	0	0	0	0	0
No. of paravertebral tubercles	35	35	38	38	40	37	38	35	38	33	41	43	42
No. longitudinal rows of tubercles	22	23	25	24	22	22	23	26	22	24	22	24	22
No. of ventral scales	33	/	31	33	34	30	29	30	31	33	34	32	32
Proximal subdigital lamellae square	0	0	0	0	0	0	0	0	0	/	0	0	0
No. of subdigital lamellae on 4th toe	21	24	23	21	21	22	22	23	22	/	26	26	25
No. of femoro-precloacal pores	/	35	39	34	/	36	/	33	38	/	36	/	/
Bands on base of thigh	w	0	0	0	1	0	0	0	0	0	0	0	m
No. body bands	4	4	4	4	4	4	4	4	4	4	4	4	4
Band/interspace width	1.00	1.00	0.75	1.00	1.25	1.00	1.00	1.00	1.00	/	/	/	/
No. dark bands on original tail	10	/	/	9	/	9	8	/	/	/	/	/	/
Hatch./juv. with white tail tips	/	/	/	/	/	/	/	/	/	/	/	/	/
SVL	68.3	108.7	114.1	105.2	113.3	106.0	66.8	110.9	111.7	/	113.8	/	/

Distribution.– *Cyrtodactylus pulchellus* is endemic to Penang Island (=Pulau Pinang), Penang, Peninsular Malaysia (Fig. 3).

Remarks.– In his description of *Cyrtodactylus pulchellus*, Gray (1827) listed the type locality as “India” which, without comment, he later amended to “Singapore” (Gray 1845). Cantor (1847:633) noted that “no authenticated record exists of this species ever having been observed in Bengal” (*fide* Duméril & Bibron 1836) and further indicates that the specimen described by Gray (1827) and others, he (Cantor) had apparently examined and were “from the hills of Prince of Wales Island (Pulo Pinang)” and at the time of his writing prior to 1843 were in his personal collection. Additionally, confirmed records of this species in Singapore have never existed despite the extensive collections made on that island since the turn of the 20th Century (see Grismer 2011:81–87 for a review). We examined close-up, high resolution, digital color photographs (LSUDPC 6051–55) of the holotype (BM XXII.91.a; an adult female) which had diagnostic characters in accord with those of *C. pulchellus sensu lato* (Table 4) in having large, widely separated dorsal tubercles with no intervening smaller tubercles, 36 paravertebral tubercles, and lacking lightened centers in the body bands separating it from *C. astrum* sp. nov.; moderately large strongly keeled dorsal tubercles separating it from *C. lekaguli* sp. nov., *C. astrum* sp. nov. *C. langkawiensis* sp. nov., *C. bintangtinggi* sp. nov., and *C. trilatofasciatus* sp. nov.; no tubercles on ventral surface of forelimbs, gular region, or in the ventrolateral body fold separating it from *C. macrotuberculatus*; and four body bands the same width as the interspaces separating it from *C. trilatofasciatus* sp. nov. Therefore, in conformity with the International Code of Zoological Nomenclature's (ICZN 1999), Recommendation 76A.2 which states that "a type locality that is found to be erroneous should be corrected", we herein restrict the type locality of *Cyrtodactylus pulchellus* to Penang Island, Penang, Peninsular Malaysia.

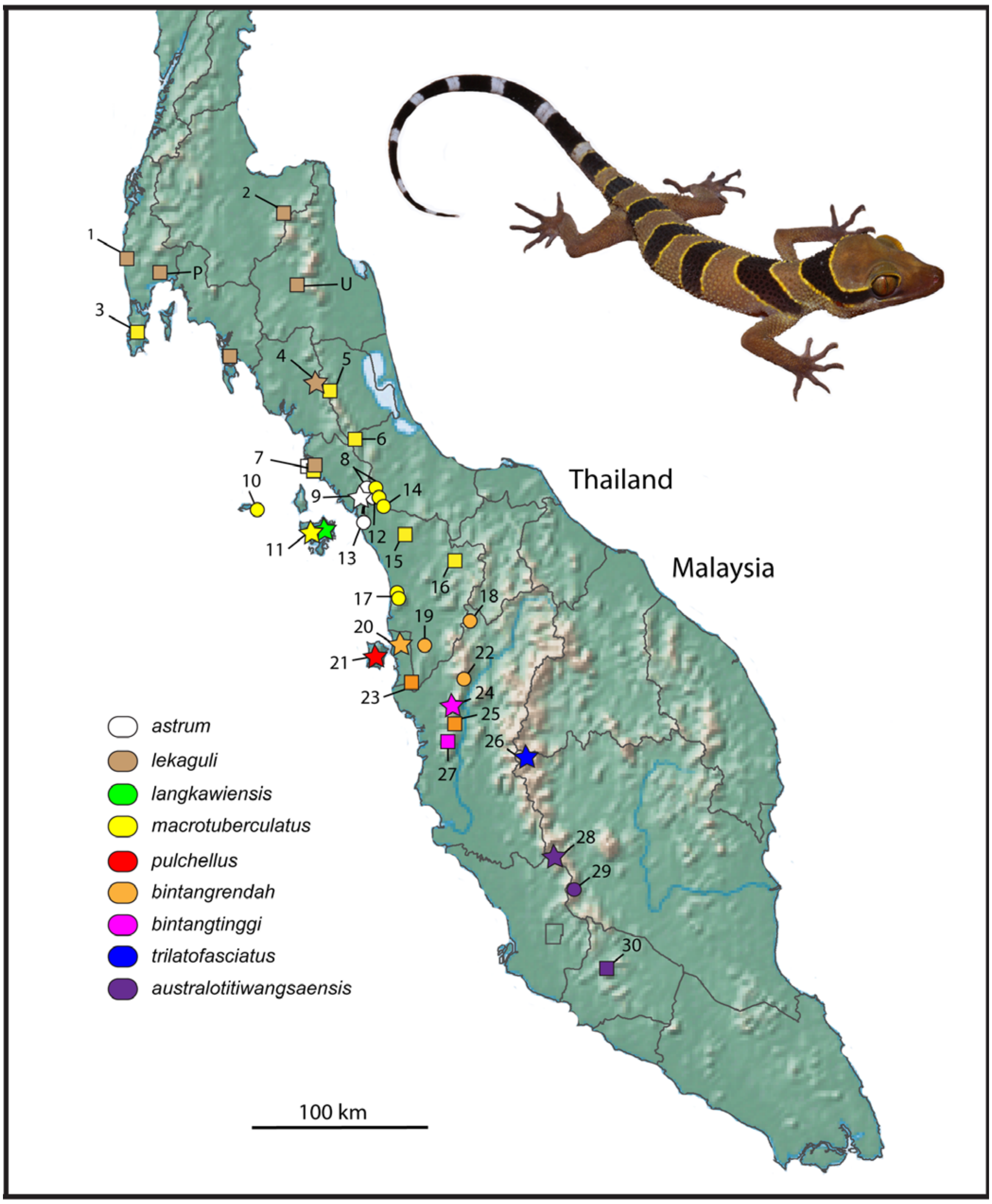

FIGURE 3. Distribution of the species of the *Cyrtodactylus pulchellus* complex. Closed circles represent localities from which specimens have been examined genetically and/or morphologically (see appendix and Table 1). Closed squares are localities from which specimens have been only examined morphologically or photographically (see appendix). Closed stars represent the type localities from where specimens have been examined genetically, morphologically and photographically. 1. Suwankuha Cave, Muang District, Phang-nga Province, Thailand. 2. Petch Phanomwung Cave, Kanchanadit District, Surat Thani Province, Thailand. 3. Phuket Island 4. Khao Chong waterfall, Khao Chamao, Khaochong District, Trang Province, Thailand. 5. Phattalung Province, Thailand. 6. Rattabhumi District, Songkhla, Thailand. 7. La-ngu District, Satun Province, Thailand (three squares). 8. Gua Wang Burma, Perlis State Park, Perlis, Malaysia (two circles). 9. Wang Kelian, Perlis, Malaysia. 10. Adang Island, Satun Province, Thailand. 11. Pulau Langkawi, Kedah, Malaysia (two stars). 12. Gua Kelam and Bukit Chabang, Malaysia (two circles). 13. Kuala Perlis, Perlis, Malaysia. 14. Chuping, Perlis, Malaysia. 15. Bukit Wang, Kedah, Malaysia. 16. Ulu Muda, Kedah, Malaysia. 17. Gunung Jerai and Hutan Lipur Sungai Tupah, Kedah, Malaysia (two circles). 18. Bukit Palong, Perak, Malaysia. 19. Ulu Paip, Kedah, Malaysia. 20. Bukit Mertajam, Penang, Malaysia. 21. Pulau Pinang, Penang, Malaysia. 22. Lengong Valley, Perak, Malaysia. 23. Bukit Panchor, Penang, Malaysia. 24. Bukit Larut, Perak, Malaysia. 25. Bukit Pondok, Perak, Malaysia. 26. Ringlet, Cameron Highlands, Pahang, Malaysia. 27. Gunung Bubu, Perak, Malaysia. 28. Fraser's Hill, Pahang, Malaysia. 29. Genting Highlands, Pahang, Malaysia. 30. Gunung Angsi, Negeri Sembilan, Malaysia. P = Tham Phung Chang Cave, Phang-nga City, Muang District, Phang-nga Province, Thailand. U = Nakon Si Thammarat Province; specific locality unknown.

TABLE 5. Uncorrected "P" distances for the *C. pulchellus* complex calculated from the mitochondrial gene ND2 (1497 bp). Percentages in bold on the diagonal represent intraspecific divergences.

	astrum	*australotitiwangsaensis*	*bintangtinggi*	*langkawiensis*	*macrotuberculatus*	*pulchellus*	*bintangrendah*	*trilatofasciatus*
astrum	**0.0–3.3**							
australotitiwangsaensis	13.2–15.0	**0.1–1.1**						
bintangtinggi	13.1–15.1	8.7–9.2	**0.04**					
langkawiensis	9.3–11.3	12.3–13.7	12.6–13.1	**0.0–1.4**				
macrotuberculatus	13.6–16.2	8.3–11.2	8.6–10.8	13.8–15.6	**2.6–6.8**			
pulchellus	13.8–16.2	9.4–10.9	9.6–11.1	13.8–15.3	6.8–10.2	**0.2–1.8**		
bintangrendah	13.6–15.8	8.8–10.0	6.9–8.0	13.4–14.3	9.2–11.4	10.4–11.9	**2.1–2.4**	
trilatofasciatus	13.6–16.8	5.9–9.0	9.9–12.7	13.2–16.0	8.2–13.4	10.0–13.5	9.6–13.1	**0.7–2.7**

FIGURE 4. *Cyrtodactylus pulchellus* from Penang Island, Penang, Malaysia. Upper left: LSUDPC 5435; adult male from the Botanical Gardens (photo by L. Grismer). Upper right: LSUDPC 6315; juvenile from Penang Hill (photo by E. Quah). Lower left: LSUDPC 6316; adult female from Air Terjun Titi Kerawang (photo by E. Ouah). Lower right: granite rock-forest microhabitat of *C. pulchellus* at Air Terjun Titi Kerawang (photo by E. Quah).

TABLE 6. Diagnostic characters separating the species of the *Cyrtodactylus pulchellus* complex. w=week, S=strong. Numbers in parentheses represent numbers of specimens.

	astrum	*australotitiwangsaensis*	*bintangtinggi*	*bintangrendah*	*langkawiensis*	*lekaguli*	*macrotuberculatus*	*pulchellus*	*trilatofasciatus*
Supralabials	10–12	9–12	9–13	8–12	9–12	10–12	9–12	9–11	10–12
Infralabials	9–12	9–13	8–11	8–10	8–10	9–11	7–11	8–10	8–11
Tubercles on ventral surface of forelimbs	No	No	No	No	No	No	Yes	No-w	No
Tubercles in gular region	No	No	No	No	No	No	Yes	No-w	No
Ventrolateral fold tuberculate	No	No	No	No-w	No	No	w-Yes	No-w	No
Paravertebral tubercles	40–57	37–45	31–42	33–44	34–44	30–50	31–44	33–43	34–38
Longitudinal rows of tubercles	20–29	22–30	21–26	22–25	21–25	20–24	19–27	22–26	23–27
Ventral scales	31–46	32–40	36–40	31–39	38–43	31–43	17–28	29–34	33–36
4th toe lamellae	20–24	21–25	21–24	20–24	19–21	20–25	20–24	21–26	22–27
Femoro-precloacal pores	31–38	39–45	38–41	41–46	30	30–36	28–40	33–39	41–46
Body bands	4	3(6) or 4(6)	3(1) or 4	4 or 5(2)	4 or 5(2)	4 or 5(2)	4	4	3
Band/interspace ratio	1.00–2.00	1.00–2.00	1.00–1.25	0.50–1.25	0.75–1.00	1.00–2.00	1.00–1.50	0.75–1.25	2.00–2.75
Hatchlings/juveniles with white tail tip	Yes	No	No	No	Yes	Yes	No	No	No
No. dark caudal bands on original tail	13 or 14	7 or 8	8–10	8–14	11–16	12–14	7–10	8–10	6 or 7
White caudal bands in adults immaculate	No	Yes	Yes	Yes	No	No	No	Yes	Yes
Maximum SVL	108.3	120.1	111.1	114.4	99.8	103.5	118.6	114.1	122.2
Sample size	11	13	14	10	10	13	29	13	6

***Cyrtodactylus astrum* sp. nov.**

Starry Bent-toed Gecko
Figs. 5,6

Cyrtodactylus pulchellus Chan, Grismer, Sharma, Belabut and Norhayati 2009:280; Chan, Grismer, Shahru, Quah, Grismer, Wood, Jr., Muin, & Norhayati 2011:255; Grismer 2011:415 (in part).

Holotype.—Adult male (ZRC 2.6962) collected on 24 March 2011 by L. L. Grismer, S. Anuar, E. S. H. Quah, Chan, K. O., and M. A. Muin from Wang Kelian, Perlis, Peninsular Malaysia (06°41.805 N, 100°10.751 E) at 150 meters above sea level.

Paratypes.—ZRC 2.6963, LSUHC 8810 and 8816 (adult male, female, and male, respectively) collected on 3 March 2008 by L. L. Grismer and Chan K. O. from Gua Kelam, Perlis, Peninsular Malaysia and an adult female (ZRC 2.6964) and adult male (ZRC 2.6965) collected on 11 October 2009 and 21 May 2010, respectively, by E. S. H. Quah, S. Anuar, and M. A. Muin from Gua Wang Burma, Perlis, Peninsular Malaysia (06°42.005 N, 100°11.878 E) at 180 meters in elevation.

FIGURE 5. *Cyrtodactylus astrum.* Upper left: ZRC 2.6962 (holotype); adult male from Wang Kelian, Perlis, Malaysia (photo by L. Grismer). Upper right: LSUDPC 6317; adult male from La-ngu District, Satun Province, Thailand (photo by M. Sumontha). Lower left: LSUHC 10024; hatchling from Wang Kelian, Perlis, Malaysia (photo by L. Grismer). Lower right: karst habitat of *C. astrum* in Perlis State Park, Perlis (photo by L. Grismer).

Diagnosis.—Adult males reaching 108.3 mm SVL, adult females reaching 104.8 mm SVL; 10–12 supralabials, 9–12 infralabials; tubercles of dorsum small to moderately large with several intervening smaller tubercles; no tubercles on ventral surfaces of forelimbs, gular region, or in ventrolateral body fold; 40–57 paravertebral tubercles; 20–29 longitudinal rows of dorsal tubercles; 31–46 rows of ventral scales; 20–24 subdigital lamellae on fourth toe; 31–38 femoro-precloacal pores in males; dorsum bearing a scattered pattern of white tubercles; four dark body bands in adults with lightened centers and light colored tubercles; band to interspace ratio 1.00–2.00; 13 or 14 dark caudal bands on original tail; white caudal bands in adults heavily infused with dark pigmentation, nearly indiscernible; and posterior portion of tail in hatchlings and juveniles white. These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

Description of holotype.— Adult male SVL 108.3 mm; head large, moderate in length (HL/SVL 0.39) and wide (HW/HL 0.69), somewhat flattened (HD/HL 0.38), distinct from neck, and triangular in dorsal profile; lores concave anteriorly, inflated posteriorly; frontal and prefrontal regions deeply concave; canthus rostralis sharply rounded anteriorly; snout elongate (ES/HL 0.45), rounded in dorsal profile, laterally constricted; eye large (ED/HL 0.23); ear opening round, moderate in size (EL/HL 0.10), vertically oriented; eye to ear distance greater than diameter of eye; rostral rectangular, divided dorsally by an inverted Y-shaped furrow, bordered posteriorly by left and right supranasals and large medial postrostral (=internasal), bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by a large anterior supranasal and small posterior supranasal, posteriorly by large single postnasal, ventrally by first supralabial; 12(R) 11(L) square supralabials extending to just beyond upturn of labial margin, tapering abruptly below midpoint of eye; second supralabial slightly larger than first; 10 (R,L) infralabials tapering in size posteriorly; scales of rostrum and lores flat to slightly raised, larger than granular scales on top of head and occiput, those on posterior portion of canthus rostralis largest; scales of occiput intermixed with small tubercles; large, boney frontal ridges bordering orbit confluent with boney, V-shaped, transverse, parietal ridge; dorsal superciliaries elongate, smooth, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by left and right, rectangular postmentals which contact medially for 65% of their length; one row of slightly enlarged, elongate sublabials extending posteriorly to 7th infralabial; small, granular, gular scales grading posteriorly into larger, flat, smooth, imbricate, pectoral and ventral scales.

FIGURE 6. Type series and additional specimens examined of *Cyrtodactylus astrum.* Upper: Type series from left to right; holotype ZRC 2.6962, paratypes ZRC 2.6963, LSUHC 8810, 8816, ZRC 2.6964, 2.6965. Lower: additional specimens examined.

Body relatively short (AG/SVL 0.39) with well-defined, non-tuberculate, ventrolateral folds; dorsal scales small, granular, interspersed with large, trihedral, regularly arranged, keeled tubercles separated by smaller keeled tubercles 50% their size; tubercles extend from occiput to caudal constriction and onto tail where they occur in transverse rows separated by 6–8 small, flat scales; caudal tubercles largest dorsally, weak laterally, and absent ventrally; tubercles absent from regenerated portion of tail; tubercles on occiput and nape relatively small, those on body largest; approximately 20 longitudinal rows of tubercles at midbody; 47 paravertebral tubercles; 46 flat imbricate ventral scales between ventrolateral body folds, ventral scales larger than dorsal scales; precloacal scales large, smooth; distinct precloacal groove.

Forelimbs moderate, relatively short (FL/SVL 0.16); scales on dorsal surfaces of forelimbs granular, intermixed with larger tubercles; scales of ventral surface of forearm flat, rounded, lacking tubercles; palmar scales rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae rectangular proximal to joint inflection, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.20), larger tubercles on dorsal surface of thigh separated by smaller granular scales, tubercles on dorsal surfaces of foreleg smaller; ventral scales of thigh flat, smooth, imbricate, larger than dorsal granular scales; ventral, tibial scales flat, smooth, imbricate; single row of greatly enlarged, flat, rectangular, imbricate, pore-bearing femoral scales extend from knee to knee through precloacal region where they are continuous with enlarged, pore-bearing precloacal scales; 32 contiguous, pore-bearing femoro-precloacal scales forming an inverted T bearing a deep, precloacal groove in which six pore-bearing scales are found (three on each side of groove); postfemoral scales immediately posterior to pore-bearing scale row small, forming an abrupt union with pore-bearing postfemoral scales on posteroventral margin of thigh; plantar scales low, slightly rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae proximal to joint inflection rectangular, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; 20 (R,L) subdigital lamellae on 4th toe.

Tail 99 mm in length, first 48 mm original, last 51 mm regenerated, 11.4 mm in width at base, tapering to a point; dorsal scales of original portion of tail flat, square; original portion segmented, 6–8 transverse scale rows per segment; posterior margin of segments bordered by 3–5 larger tubercles dorsally in anterior one-third of tail, fewer posteriorly; original subcaudal region bearing large, transverse scales; regenerated portion of tail covered with small, smooth to weakly keeled rectangular scales dorsally and ventrally; dorsal and lateral caudal furrows extend entire length of original tail; base of tail bearing hemipenial swellings; three small, postcloacal tubercles on hemipenial swellings; postcloacal scales smooth, flat, large, imbricate.

Coloration in life (Fig. 5). Dorsal ground color of head, body, limbs, and tail brown; wide, dark brown, nuchal band extends from posterior margin of one eye to posterior margin of other eye; nuchal band edged with thin, white, broken lines that are most prominent where they encompass tubercles, giving it a somewhat spotted appearance; four similarly colored dorsal bands with similar white edging occur between limb insertions, first band terminates at shoulders, second and third bands terminate just dorsal to ventrolateral fold, third band bifurcates on right side of body at vertebral column, fourth band terminates on anterior margin of hind limb insertions; body band/interspace ratio 1.50; one additional dark brown band posterior to hind limbs; no band on posterior margin of thigh; diffuse, indistinct bands extend onto original portion of tail becoming less discernable posteriorly; no bands on regenerated portion tail; all bands have light brown centers bearing yellowish to white tubercles, giving dorsum an overall “starry” appearance; ventral surfaces of head, limbs, and tail smudged with brown; abdomen immaculate, beige except for slightly darker, lateral regions.

Variation. The paratypes match the holotype in all aspects of dorsal banding and coloration (Fig. 6) except the third body band in the paratypes is not bifurcated. LSUHC 8810 and 8816 have a lighter overall color pattern and LSUHC 8816 has a unicolor regenerated tail. ZRC 2.6964 lacks a tail and its white, dorsal tuberculation is not as prominent. ZRC 2.6965 has a completely regenerated tail and an overall lighter dorsal pattern. ZRC 2.6963 has a slightly more contrasting dorsal pattern. Females (ZRC 2.6964) lack a precloacal groove and pore-bearing femoro-precloacal scales although enlarged homologous scales are present. Overall coloration lightens considerably at night. A significant degree of ontogenetic change in color pattern occurs with hatchlings and juveniles having a greatly contrasting banding pattern where the body bands are very dark and do not have lighten centers or encompass light colored tubercles. Furthermore, the bands are edged with thin yellow lines, there are no white tubercles in the interspaces, and the top of the head is yellowish (Fig. 5). Lastly the white colored portion of the tail is lost in adulthood.

Additional specimens examined. The posterior 50% of the tail in the juveniles LSUHC 8815 and 8808 (SVL 43 mm and 46 mm, respectively) from Gua Kelam and LSUHC 10024 (SVL 46 mm) from Wang Kelian are white (Fig. 6). Meristic differences in the type series and additional specimens examined are presented in Table 7.

Distribution. *Cyrtodactylus astrum* sp. nov. ranges from at least La-ngu District, Satun Province, Thailand south to Kuala Perlis, Perlis, Peninsular Malaysia (Fig. 3).

Natural history. *Cyrtodactylus astrum* sp. nov. is a saxicolous species inhabiting lowland forests of varying types and is closely associated with karst formations (Fig. 5). In Perlis, we have found lizards deep within the cave system of Gua Wang Burma as well as on karst walls at Wang Kelian and Kuala Perlis. At Wang Kelian we have collected specimens from the trunks of trees adjacent to karst towers and have seen hatchlings on the ground nearby karst towers during March. In Perlis State Park, *C. astrum* sp. nov. and *C. macrotuberculatus* are narrowly syntopic being that we have found both species within Gua Wang Burma. Generally however, these two species partition their habitat in that *C. astrum* sp. nov. is principally saxicolous but will opportunistically use tree trunks if nearby and *C. macrotuberculatus* generally occurs on vegetation but will opportunistically use rock surfaces (including karst) if nearby (Grismer 2011). Lizards observed in the La-ngu District of Satun Province, Thailand were also associated with karst formations. *Cyrtodactylus lekaguli* sp. nov. occurs at this locality as well (see below).

Grismer (2011) noted that juveniles bearing white tails will wave them over their head when threatened.

Etymology. The specific epithet *astrum* is Latin, meaning “a star” and is in reference to the starry pattern of the white dorsal tubercles.

TABLE 7. Morphological data of type series and additional specimens of *Cyrtodactylus astrum* from Perlis State, Malaysia. m=male; f=female; SVL=snout-vent length; TL=tail length; TW=tail width; FL=forelimb length; TBL=tibia length; AG=axilla-groin length; HL=head length; HW=head width; HD=head depth; ED=eye diameter; EE=eye to ear distance; ES=eye to snout distance; EN=eye to nostril distance; IO=interorbital distance; EL=ear length; and IN=internarial distance. B = broken; PR = partially regenerated; R = regenerated; /=data unavailable.

	LSUHC 8816 Paratype Kuala Perlis	ZRC 2.6963 Paratype Gua Kelam	LSUHC 8810 Paratype Gua Kelam	ZRC 2.6964 Paratype Kuala Perlis	ZRC 2.6962 Holotype Wang Kelian	ZRC 2.6965 Paratype Gua Wang Burma	LSUHC 8806 Gua Kelam	LSUHC 8808 Gua Kelam	LSUHC 8815 Gua Wang Burma	LSUHC 9125 Gua Wang Burma	LSUHC 10024 Wang Kelian
Sex	m	m	f	f	m	m	/	/	/	/	/
Supralabials	12	12	12	11	12	10	10	12	10	12	11
Infralabials	10	10	9	12	10	10	9	10	9	9	10
Tubercles on ventral surface of forelimbs	0	0	0	0	0	0	0	0	0	0	0
Tubercles in gular region	0	0	0	0	0	0	0	0	0	0	0
Ventrolateral fold tuberculate	0	0	0	0	0	0	0	0	0	0	0
No. of paravertebral tubercles	57	43	45	50	47	45	45	48	40	44	45
No. longitudinal rows of tubercles	26	22	22	23	20	22	28	23	29	23	22
No. of ventral scales	31	41	39	42	46	41	38	41	37	38	41
Proximal subdigital lamellae square	0	0	0	0	0	0	0	0	0	0	0
No. of subdigital lamellae on 4th toe	21	20	22	24	20	21	23	24	22	23	22
No. of femoro-precloacal pores	38	32	/	/	32	31	/	/	/	/	/
Bands on base of thigh	0	0	0	0	0	0	0	0	0	0	0
No. body bands	4	4	4	4	4	4	4	4	4	4	4
Band/interspace width	1	1	1	2.00	1.50	1	1	1	1	1.50	1
No. dark bands on original tail	/	/	/	/	/	/	/	/	/	13	14
Hatch./juv. with white tail tips	/	/	/	/	/	/	Yes	Yes	/	Yes	Yes
SVL	97.1	97.9	92.2	104.8	108.3	103.7	46.4	45.6	42.5	50.0	46.1
TL	91.8/R	109/PR	60.2/B	B	99/PR	102/R					
TW	8.7	10.4	8.1	8.8	11.4	10.7					
FL	17	17.4	16	17.6	17.3	18.5					
TBL	19.2	20.6	18.6	20.8	21.8	22.1					
AG	37.4	38.4	36.6	45.6	42.5	43.7					
HL	28.3	28.1	26.5	30.1	30.7	30					
HW	19.7	19.4	18.3	20.5	21.3	20.5					
HD	10.8	11	10.5	11.3	11.8	12.1					
ED	6.9	7.7	6.2	6.5	7.1	6.6					
EE	8.6	7.7	7.38	8.4	8.7	8.2					
ES	12.7	12.7	11.6	13.3	13.7	13.2					
EN	9.7	9.4	10	10.5	10.1	10.1					
IO	6.3	5.8	5.7	6.3	7	6.3					
EL	2.5	2.7	2.8	2.4	3	2.3					
IN	2.8	2.7	2.8	3	3	2.9					

Comparisons. *Cyrtodactylus astrum* sp. nov. is separated from all other members of the *Cyrtodactylus pulchellus* complex by its scattered pattern of white, dorsal tubercles. From *C. macrotuberculatus* it differs in lacking large tubercles on the dorsal surface of the head, body and limbs, on the underside of the forearms, in the gular region, and in the ventrolateral body fold; and having 31–46 ventral scales as opposed to 17–28 (Table 6). It differs from *C. trilatofasciatus* sp. nov. in having more than 39 paravertebral tubercles as opposed to having 38 tubercles or less. It differs further from *C. langkawiensis* sp. nov. and *C. lekaguli* sp. nov. in having dark body bands in adults with lightened centers as opposed to these bands being unicolor. From *C. trilatofasciatus* sp. nov. it differs in having four as opposed to three dark dorsal bands and in having a body band/interspace ratio of 1.00–2.00 vs. 2.00–2.75. It differs from all other species except *C. langkawiensis* sp. nov. and *C. lekaguli* sp. nov. in that hatchlings and juveniles have white tail tips as opposed to lacking white tail tips. *Cyrtodactylus astrum* sp. nov. has 13 or 14 dark caudal bands on the original tail which differentiates it from *C. australotitiwangsaensis* sp. nov., *C. bintangtinggi* sp. nov., *C. pulchellus*, *C. trilatofasciatus* sp. nov. and *C. macrotuberculatus* which have less than 11 caudal bands. Heavy dark mottling in the white caudal bands differentiate it from all other species except *C. langkawiensis* sp. nov., *C. lekaguli* sp. nov., and *C. macrotuberculatus.* The maximum SVL of 108.3 mm of *C. astrum* sp. nov. separates it from *C. australotitiwangsaensis* sp. nov., *C. bintangrendah* sp. nov., *C. macrotuberculatus, C. pulchellus* and *C. trilatofasciatus* sp. nov. whose maximum SVL is greater than 114.0 mm and from *C. langkawiensis* sp. nov. and *C. lekaguli* sp. nov. whose maximum SVL is less than 103.6 mm.

Remarks. The sister species relationship between *Cyrtodactylus astrum* sp. nov. and *C. langkawiensis* sp. nov. (Fig. 1) is in biogeographical accordance with that of other species found south of the Isthmus of Kra that range south into the Banjaran Nakawan along the northwestern portion of the Malaysian border and whose sister lineage occurs on the offshore extension of this range, Pulau (=island) Langkawi. Such taxa include *Cnemaspis roticanai* (Grismer 2011) and *Cryptelytrops venustus* (Grismer *et al*. in prep.).

Cyrtodactylus lekaguli sp. nov.

Tuk-kai Boonsong, Bent-toed Gecko
Figs. 7,8

Cyrtodactylus pulchellus Taylor 1963:714; Manthey and Grossmann 1997:226;
Cox, van Dijk, Nabhitabhata and Thirakhupt 1998:86; Pauwels *et al*. 2000:129–130, 2002:27.

Holotype.—Adult male (FMNH 215987) collected on 7 November 1979 by D. L. Damman from Khao Chong waterfall, Khao Chamao, Trang Province, Thailand at approximately 07°35.28 N, 99°50.25 E at 165 meters above sea level as estimated from Google Earth.

Paratypes.—Adult females (FMNH 215985–86) bear the same data as the holotype. The adult male FMNH 176885 was collected by E. H. Taylor from Khao Chao (date unknown). Adult female IRSNB 2678 collected on 21 July 1998 by O. S. G. Pauwels and Chucheep Chimsunchart from Tham Phung Chang (cave) Phang-nga City, Muang District, Phang-nga Province, Thailand.

Diagnosis.—Adult males reaching 103.5 mm SVL, adult females reaching 97.3 mm SVL; 10–12 supralabials, 9–11 infralabials; tubercles of dorsum moderate, with no intervening smaller tubercles; no tubercles on ventral surfaces of forelimbs, gular region, or in ventrolateral body fold; 30–50 paravertebral tubercles; 20–24 longitudinal rows of dorsal tubercles; 31–43 rows of ventral scales; 20–25 subdigital lamellae on fourth toe; 30–36 femoro-precloacal pores in males; dorsum not bearing a scattered pattern of white tubercles; four or five dark body bands in adults lacking lightened centers and light colored tubercles; body band to interspace ratio 1.00–2.00; 12–14 dark caudal bands; and white caudal bands infused with dark coloration and the posterior portion of the tail in hatchlings and juveniles is white. These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

Description of holotype.—Adult male SVL 92.2 mm; head large, moderate in length (HL/SVL 0.28) and wide (HW/HL 0.76), somewhat flattened (HD/HL 0.41), distinct from neck, and triangular in dorsal profile; lores concave anteriorly, inflated posteriorly; frontal and prefrontal regions deeply concave; canthus rostralis sharply rounded anteriorly; snout elongate (ES/HL 0.43), rounded in dorsal profile, laterally constricted; eye large (ED/HL

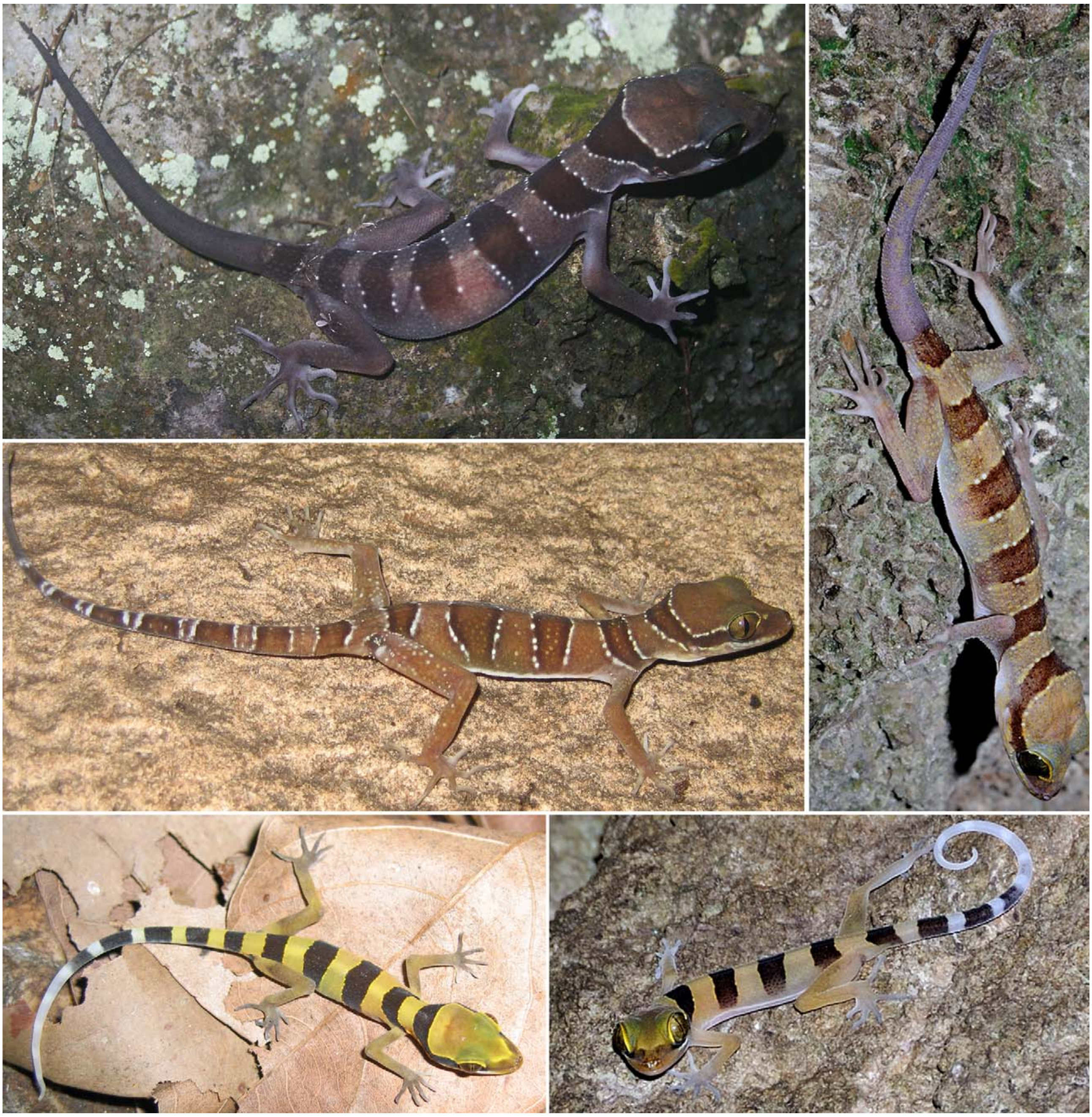

FIGURE 7. *Cyrtodactylus lekaguli.* Upper left: LSUDPC 6317; adult female (gravid) from La-ngu District, Satun Province, Thailand (photo by M. Sumontha). Right: LSUDPC 6325, Krabi, Krabi Province, Thailand (photo by N. Baker). Middle left: MS 519; adult male from Petch Phanomwung Cave, Kanchanadit District, Surat Thani Province, Thailand (photo by M. Sumontha). Lower left: LSUDPC 6327, Khamin Cave, Ban Nasan District, Surat Thani Province, Thailand (photo by M. Sumontha). Lower right: LSUDPC 6326, Krabi, Krabi Province, Thailand (photo by N. Baker).

0.25); ear opening elliptical, moderate in size (EL/HL 0.10), vertically oriented; eye to ear distance greater than diameter of eye; rostral rectangular, divided dorsally by an inverted Y-shaped furrow, bordered posteriorly by left and right supranasals and medial postrostral (=internasal), bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by a large, anterior supranasal and smaller posterior supranasal, posteriorly by large single postnasal, ventrally by first supralabial; 10(R,L) square supralabials extending to just beyond upturn of labial margin, tapering abruptly below midpoint of eye; second supralabial not larger than first; 10,9(R,L) infralabials tapering in size posteriorly; scales of rostrum and lores flat, larger than granular scales on top of head and occiput, those on posterior portion of canthus rostralis largest; scales of occiput intermixed with small tubercles; large, boney frontal ridges bordering orbit confluent with boney, V-shaped, transverse, parietal ridge;

dorsal superciliaries elongate, smooth, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by left and right, rectangular postmentals which contact medially for 50% of their length; one row of slightly enlarged, elongate sublabials extending posteriorly to 5th infralabial; small, granular, gular scales grading posteriorly into larger, flat, smooth, imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.42) with well-defined, non-tuberculate, ventrolateral folds; dorsal scales small, granular, interspersed with large, trihedral, regularly arranged, keeled tubercles not separated by smaller intervening tubercles; tubercles extend from occipital region to caudal constriction and onto original portion of tail; tubercles on occiput and nape relatively small, those on body largest; approximately 23 longitudinal rows of tubercles at midbody; 35 paravertebral tubercles; 41 flat, imbricate ventral scales between ventrolateral body folds, ventral scales larger than dorsal scales; precloacal scales large, smooth; distinct precloacal groove.

Forelimbs moderate, relatively short (FL/SVL 0.16); scales on dorsal surface of forelimbs raised, intermixed with larger tubercles; scales of ventral surface of forearm flat, rounded, lacking tubercles; palmar scales rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae rectangular proximal to joint inflection, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.21), larger tubercles on dorsal surface of thigh separated by smaller granular scales, tubercles on dorsal surfaces of foreleg smaller; ventral scales of thigh flat, smooth, imbricate, larger than dorsal granular scales; ventral, tibial scales flat, smooth, imbricate; single row of greatly enlarged, flat, rectangular, imbricate, pore-bearing femoral scales extend from knee to knee through precloacal region where they are continuous with enlarged, pore-bearing precloacal scales; 33 contiguous, pore-bearing femoro-precloacal scales forming an inverted T bearing a deep, precloacal groove in which eight pore-bearing scales are found (four on each side of groove); postfemoral scales immediately posterior to pore-bearing scale row small, forming an abrupt union with pore-bearing postfemoral scales on posteroventral margin of thigh; plantar scales low, slightly rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae proximal to joint inflection rectangular, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; 23,24(R,L) subdigital lamellae on 4th toe.

Tail original, 125 mm in length, 9.0 mm in width at base, tapering to a point; dorsal scales small, square, weakly keeled, in transverse rows; subcaudal region bearing large, transverse scales for first half of tail, second half bearing smaller, irregularly shaped scales; base of tail bearing hemipenial swellings; four smaller, postcloacal tubercles on hemipenial swellings; postcloacal scales smooth, flat, large, imbricate.

Coloration in alcohol. Dorsal ground color of head, body, limbs, and tail brown; wide, dark brown, nuchal band extends from posterior margin of one eye to posterior margin of other eye; nuchal band edged with thin, white, lines; four similarly colored dorsal bands lacking lightened centers occur between limb insertions, first band terminates at shoulders, second and third bands terminate dorsal to ventrolateral fold, fourth band terminates at anterior margin of hind limb insertions; white edging on body bands generally restricted to the tubercles giving edging a spotted appearance; body band/interspace ratio 1.00; one additional dark brown band posterior to hind limbs; no band on posterior margin of thigh; 14 dark, caudal bands; 13 light caudal bands infused with dark pigment; scales of all ventral surfaces heavily stippled.

Variation. The paratypes closely approach the holotype in coloration (Fig. 8). FMNH 176885 (SVL 100.0 mm) and 215985 (SVL 80.5 mm) have a slightly lighter ground color and in FMNH 215985, the ends of the second and third body bands contact one another on the left side of the body just dorsal to the ventrolateral fold. IRSNB 2678 has an overall more faded color pattern (Fig. 8). Juveniles have white tail tips (Fig. 7).

Additional specimens examined. MS 441 and 442 from Khao Chong, Trang Province closely approximate the holotype in overall coloration other than being slightly darker (Fig. 8). MS 442 has a completely regenerated tail and MS 441 has relatively narrow body bands. MS 519 from Petch Phanomwung Cave, Kanchanadit District, Surat Thani Province, MS 79 from Suwankuha Cave, Muang District, Phang-nga Province, and IRSNB 16558 from Nakon Si Thammarat Province, Thailand are much lighter in overall coloration. Meristic differences between individuals of the type series and additional specimens examined are presented in Table 8. Taylor (1963) reported a male (No. 35747) from the Khao Chong Forest Station, Trang Province with a SVL of 102 mm and 38 femoro-precloacal pores.

FIGURE 8. Type series and additional specimens examined of *Cyrtodactylus lekaguli.* Upper row: type series from left to right FMNH 215987, 215895, 215986, 176885. Additional specimens examined from type locality from left to right: MS 441, 442. Lower row: additional specimens examined from Satun Province, Thailand from left to right: MS 401, 445, 446 and from Surat Thani Province, Thailand MS 519 and Phang-nga Province, Thailand MS 79; paratype IRSNB 2678 from Phang-nga Privince, Thailand.

Distribution. *Cyrtodactylus lekaguli* sp. nov. is known from the type locality at Khao Chong waterfall, Khao Chamao, Trang Province, from Petch Phanomwung Cave, Kanchanadit District, Surat Thani Province, Krabi, Krabi Province, and from Suwankuha Cave, Phung Chang Cave, Reusi Cave, Tham Phung Chang Cave, Phang-nga City, Muang District, Phang-nga Province, Thailand (Fig. 3).

Natural history. Taylor (1963) reported specimens being found at the Khao Chong Forest Station, Trang Province on the trunks of trees in the forest near streams, in the crevices of trees, and in the rest house. These data would suggest this population may be less confined to rocky areas than are other members of the *Cyrtodactylus pulchellus* complex. Specimens from Krabi, Phang-nga, and Surat Thani Provinces were found in association with karst boulders and caves. Pauwels *et al.* (2000) reported that during a one-hour visit in late July in Phung Chang Cave, six individuals were observed, and the species was abundant in Reusi Cave as well. They reported a female (IRSNB 15143) collected in July that contained two eggs of about 11 mm diameter, and another one collected on the same day that contained an egg of about 9 mm diameter and another much less developed. They also reported on a hatchling that hatched one day after its egg was collected deep from within the Reusi Cave on January 11th. That egg had been deposited along with 15 others, of which 11 had recently hatched, in a small fissure filled with soft soil. The eggs were about 16 mm by 13 mm. The hatchling (MNHN 1999.7706) had a SVL of 38 mm and a total length of 79 mm at birth and a white tail tip.

Etymology. The specific epithet *lekaguli* honors Dr. Boonsong Lekagul (1907–1992), biologist and conservationist of Thailand and the first biologist to suggest the Thai common name " Tuk-Kai " for geckos of the genus *Cyrtodactylus* (Lekagul 1977).

TABLE 8. Morphological data of type series and additional specimens of *Cyrtodactylus lekaguli* from Thailand. m=male; f=female; SVL=snout-vent length; TL=tail length; TW=tail width; FL=forelimb length; TBL=tibia length; AG=axilla-groin length; HL=head length; HW=head width; HD=head depth; ED=eye diameter; EE=eye to ear distance; ES=eye to snout distance; EN=eye to nostril distance; IO=interorbital distance; EL=ear length; and IN=internarial distance; B = broken; PR = partially regenerated; R = regenerated; /=data unavailable.

	FMNH	FMNH	FMNH	FMNH	IRSNB	MS	MS	MS	MS	MS	MS	MS	IRSBN
	176885	215985	215986	215987	2678	441	442	401	445	446	519	79	16558
	Paratype	Paratype	Paratype	Holotype	Paratype								
	Khao Chong	Khao Chong	Khao Chong	Khao Chong	Phang-nga	Khao Chong	Khao Chong	La-ngu	La-ngu	La-ngu	Surat Thani	Phang -nga	Nakkon Si Thammarat
Sex	m	f	f	m	f	m	f	f	m	f	m	m	m
Supralabials	11	11	12	10	11	11	10	11	12	12	12	12	11
Infralabials	9	10	9	10	9	9	10	10	9	9	9	11	9
Tubercles on ventral surface of forelimbs	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubercles in gular region	0	0	0	0	0	0	0	0	0	0	0	0	0
Ventrolateral fold tuberculate	0	0	0	0	0	0	0	0	0	0	0	0	0
No. of paravertebral tubercles	40	44	50	35	39	30	37	38	41	43	35	39	35
No. longitudinal rows of tubercles	22	22	22	23	22	21	22	20	20	20	24	22	22
No. of ventral scales	38	43	40	41	40	38	37	33	31	35	38	33	36
Proximal subdigital lamellae square	0	0	0	0	0	0	0	0	0	0	0	0	0
No. of subdigital lamellae on 4th toe	23	24	21	23	22	20	21	23	20	23	25	24	22
No. of femoro-precloacal pores	34	/	/	33	/	34	/	/	36	/	30	33	36
Bands on base of thigh	1	1	0	0	0	0	0	0	0	0	0	0	0
No. body bands	4	4	4	4	5	4	4	4	4	4	5	4	4
Band/interspace width	1.00	1.00	1.00	1.00	1.00	2.00	1.25	1.00	1.25	1.25	1.00	1.25	1.00
No. dark bands on original tail	/	/	12	14	/	/	/	/	/	/	/	/	/
Hatch./juv. with white tail tips	/	/	/	/	/	/	/	/	/	/	/	/	/
SVL	100.0	80.5	85.7	92.2	95.0	103.5	97.3	93.9	93.7	95.6	102.7	97.2	103.4
TL	82B	93R	115	125	97.8PR								
TW	9.4	7.2	6.9	9	7.5								
FL	17.3	13	13.6	14.8	15.4								
TBL	20	15.8	15.9	19.5	19.7								
AG	45	35.4	35.7	39	45.0								
HL	28.2	23	24	25.4	26.5								
HW	20	15.8	16.7	19.2	17.3								
HD	12.1	9.7	9	10.3	10.7								
ED	6.3	5	5.8	6.4	7.0								
EE	8.5	7.3	6.9	7.9	8.3								
ES	12.3	10	10.1	11	11.6								
EN	9.7	7.3	7.6	8.1	9.0								
IO	5.8	4.9	4.9	5.4	5.6								
EL	1.9	1.8	2	2.1	1.5								
IN	3.5	2.5	2.6	2.4	2.6								

Comparisons. *Cyrtodactylus lekaguli* sp. nov. is separated from *C. macrotuberculatus* in lacking large tubercles on the dorsal surface of the head, body and limbs, on the underside of the forearms, in the gular region, in the ventrolateral body fold, and in having 31–43 as opposed to 17–28 ventral scales. *Cyrtodactylus lekaguli* sp. nov. has fewer (20–24) longitudinal rows of dorsal tubercles than *C. trilatofasciatus* sp. nov. (23–27). *Cyrtodactylus lekaguli* sp. nov. is separated from *C. australotitiwangsaensis* sp. nov., *C. bintangtinggi* sp. nov., *C. bintangrendah* sp. nov., and *C. trilatofasciatus* sp. nov. in having less than less than 37 femoro-precloacal pores. From *C. trilatofasciatus* sp. nov., *C. lekaguli* sp. nov. differs in having four or five narrow body bands with a band/interspace ratio of 1.00–2.00 as opposed to having three wide body bands with a band/interspace ratio of 2.00–2.75 and it differs from *C. langkawiensis* sp. nov. in having wider body bands (1.00–2.00 vs. 0.75–1.00, respectively). It differs from *C. astrum* sp. nov. in lacking a scattered dorsal pattern of white tubercles. Having 12–14 dark caudal bands differentiates it from *C. australotitiwangsaensis* sp. nov., *C. bintangtinggi* sp. nov., *C. macrotuberculatus*, *C. pulchellus* and *C. trilatofasciatus* sp. nov. which have less than 11 dark caudal bands. Heavy dark mottling in the white caudal bands differentiate it from all other species except *C. astrum* sp. nov., and *C. langkawiensis* sp. nov. The small maximum SVL (103.5 mm) of *C. lekaguli* sp. nov. separates it from the larger species *C. astrum* sp. nov., *C. australotitiwangsaensis* sp. nov., *C. bintangtinggi* sp. nov., *C. bintangrendah* sp. nov., *C. macrotuberculatus* sp. nov., *C. pulchellus,* and *C. trilatofasciatus* sp. nov. that reach over 108 mm SVL.

Remarks. *Cyrtodactylus lekaguli* sp. nov., *C. langkawiensis* sp. nov. and *C. astrum* sp. nov., are the only species previously considered to be *C. pulchellus* that have white caudal bands infused with dark pigment. Like *C. langkawiensis* sp. nov., *C. lekaguli* sp. nov. is a relatively small species (neither reaches 104 mm SVL; [Taylor 1963]) and the hatchlings of all three species have white tail tips. Based on this, and the fact that these species are found collectively only in extreme northern Malaysia and southern Thailand, we hypothesize that *C. lekaguli* sp. nov. forms a close, but yet unresolved, phylogenetic relationship with *C. astrum* sp. nov. and *C. langkawiensis* sp. nov.

Three specimens from La-ngu, Satun Province, Thailand (MS 401, 445–446) 75 km south of the type locality are only weakly diagnosable from the three individuals of the type series and other individuals from Khao Chong, Phnag-nga, and Nakon Si Thammarat provinces on the basis of having fewer ventral scales (31–35 vs. 37–43) and fewer longitudinal rows of dorsal tubercles (20 vs. 22 or 23; Table 8). Dorsal tuberculation is generally weaker and the overall color pattern is less contrasted (Fig. 8). These morphological data suggest they may not be conspecific with *C. lekaguli* sp. nov. from the type locality and northward. However, until molecular evidence can be brought to bear on this hypothesis, we consider this population to be *C.* cf. *lekaguli.*

Cyrtodactylus langkawiensis sp. nov.

Langkawi Island Bent-toed Gecko
Figs. 9,10

Holotype.—Adult male (ZRC 2.6966) collected on 11 October 2008 by L. L. Grismer, Norhayati A., Chan, K. O., D. Belabut, and J. L. Grismer from Wat Wanaram, Pulau Langkawi, Kedah, Peninsular Malaysia (06°20.275 N, 99°52.507 E) at 35 meters above sea level.

Paratypes.—Adult females (ZRC LSUHC 2.6967–68 and LSUHC 9123–24) collected from same locality on the same date as the holotype and by the same collectors; adult female (ZRC 2.6969) collected at same locality as holotype by Chan, K. O., C. Johnson, and L. Grismer on 19 September 2009.

Diagnosis.—Adult males reaching 93.3 mm SVL, adult females reaching 99.8 mm SVL; 9–12 supralabials, 8–10 infralabials; tubercles of dorsum small to moderately large with no intervening smaller tubercles; no tubercles on ventral surfaces of forelimbs, gular region, or in ventrolateral body fold; 34–44 paravertebral tubercles; 21–25 longitudinal rows of dorsal tubercles; 38–43 rows of ventral scales; 19–21 subdigital lamellae on fourth toe; 30 femoro-precloacal pores in males; dorsum not bearing a scattered pattern of white tubercles; four rarely five dark body bands in adults lacking lightened centers and light colored tubercles; band to interspace ratio 0.75–1.00; 11–16 dark caudal bands on original tail; white caudal bands in adults infused with dark pigmentation; and posterior portion of tail in hatchlings and juveniles white. These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

FIGURE 9. *Cyrtodactylus langkawiensis* from Wat Wanaram, Pulau Langkawi, Kedah, Peninsular Malaysia. Upper left: LSUHC 9123, adult female. Upper right: LSUDPC 4694; gravid female. Lower left: LSUDPC 5196; adult male. Lower right: karst microhabitat of *C. langkawiensis* at Wat Wanaram, Kedah, Peninsular Malaysia. All photos by L. Grismer.

FIGURE 10. Type series and additional specimens examined of *Cyrtodactylus langkawiensis.* Upper row: type series from left to right; holotype ZRC 2.6966, paratypes from left to right ZRC 2.6967–68, LSUHC 9123–24, ZRC 2.6969. Lower row: additional specimens examined from type locality from left to right; LSUHC 9436, 9435 and three juveniles.

Description of holotype.—Adult male SVL 93.3 mm; head large, moderate in length (HL/SVL 0.27) and wide (HW/HL 0.70), somewhat flattened (HD/HL 0.47), distinct from neck, and triangular in dorsal profile; lores flat anteriorly, inflated posteriorly; frontal and prefrontal regions concave; canthus rostralis rounded anteriorly; snout elongate (ES/HL 0.50), rounded in dorsal profile, laterally constricted; eye large (ED/HL 0.28); ear opening elliptical, moderate in size (EL/HL 0.11), vertically oriented; eye to ear distance greater than diameter of eye; rostral rectangular, divided dorsally by an inverted Y-shaped furrow, bordered posteriorly by left and right supranasals, a medial postrostral (=internasal), and an anomalous series of granular scales extending into dorsal portion of rostral; rostral bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by a large anterior supranasal and small posterior supranasal, posteriorly by single postnasal, ventrally by first supralabial; 12(R) 11(L) square supralabials extending to just beyond upturn of labial margin, tapering abruptly below midpoint of eye; second supralabial slightly larger than first; 10(R) 9(L) infralabials tapering in size posteriorly, second and third left infralabials fused; scales of rostrum and lores flat to slightly raised, larger than granular scales on top of head and occiput, those on posterior portion of canthus rostralis slightly larger; scales of occiput intermixed with small tubercles; large, boney frontal ridges bordering orbit confluent with boney, V-shaped, transverse, parietal ridge; dorsal superciliaries elongate, smooth, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by left and right, rectangular postmentals which contact medially for 75% of their length; one row of slightly enlarged, elongate sublabials extending posteriorly to 7th infralabial; small, granular, gular scales grading posteriorly into larger, flat, smooth, imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.46) with well-defined, non-tuberculate, ventrolateral folds; dorsal scales small, granular, interspersed with large, trihedral, regularly arranged, keeled tubercles, smaller intervening tubercles absent; tubercles extend from occiput to caudal constriction and onto tail where they occur in transverse rows separated by 6–8 small, flat scales; caudal tubercles largest dorsally, weak laterally, and absent ventrally; caudal tubercles decrease in size posteriorly, absent from regenerated portion of tail; tubercles on occiput and nape relatively small, those on body largest; approximately 23 longitudinal rows of tubercles at midbody; 34 paravertebral tubercles; 41 flat imbricate ventral scales between ventrolateral body folds, ventral scales larger than dorsal scales; precloacal scales large, smooth; distinct precloacal groove.

Forelimbs moderate, relatively short (FL/SVL 0.16); scales on dorsal surfaces of forelimbs flat to granular, intermixed with a few larger tubercles; scales of ventral surface of forearm flat, rounded, lacking tubercles; palmar scales rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae rectangular proximal to joint inflection, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.20), larger tubercles on dorsal surface of thigh separated by smaller granular scales, tubercles on dorsal surfaces of foreleg smaller; ventral scales of thigh flat, smooth, imbricate, larger than dorsal granular scales; ventral, tibial scales flat, smooth, imbricate; single row of greatly enlarged, flat, rectangular, imbricate, pore-bearing femoral scales extend from knee to knee through precloacal region where they are continuous with enlarged, pore-bearing precloacal scales; 30 contiguous, pore-bearing femoro-precloacal scales forming an inverted T bearing a deep, precloacal groove in which five pore-bearing scales are found (three on right, two on left side of groove); postfemoral scales immediately posterior to pore-bearing scale row small, forming an abrupt union with pore-bearing postfemoral scales on posteroventral margin of thigh; plantar scales low, slightly raised; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae proximal to joint inflection rectangular, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; 20 (R,L) subdigital lamellae on 4th toe.

Tail 113 mm in length, first 72 mm original, last 41 mm regenerated, 9.3 mm in width at base, tapering to a point; dorsal scales of original portion of tail flat, square; original portion segmented, 6–8 transverse scale rows per segment; posterior margin of segments bordered by 3–5 larger tubercles dorsally in anterior one-third of tail, fewer posteriorly; original subcaudal region bearing large, transverse scales; regenerated portion of tail covered with small, smooth to weakly keeled rectangular scales dorsally and laterally and larger scales ventrally; dorsal and lateral caudal furrows extend nearly length of original tail; base of tail bearing hemipenial swellings; four small, postcloacal tubercles on hemipenial swellings; postcloacal scales smooth, flat, large, imbricate.

Coloration in life. Dorsal ground color of head, body, limbs, and tail brown; wide, dark brown, nuchal band extends from posterior margin of one eye to posterior margin of other eye; nuchal band edged with thin, white, broken lines that are most prominent where they encompass tubercles, giving it a somewhat spotted appearance; four similarly colored dorsal bands with similar white edging occur between limb insertions, first band terminates at shoulders, second and third bands terminate just dorsal to ventrolateral fold, fourth band terminates on anterior margin of hind limb insertions; body band/interspace ratio 1.00; one additional dark brown band posterior to hind limbs; no band on posterior margin of thigh; four diffuse, indistinct dark bands and five indistinct lighter bands extend onto original portion of tail; no bands on regenerated portion tail; no caudal or body bands have lighten centers or encompass yellowish to white tubercles; ventral surfaces of head, limbs, and tail smudged with brown; abdomen immaculate, beige except for slightly darker, lateral regions.

Variation. The paratypes closely match the holotype in all aspects of dorsal banding and coloration (Fig. 10). In LSUHC 9124 the dorsal bands are not as distinctly edged with thin white lines and in LSUHC 9123 the third dorsal band bifurcates on the left side at the vertebral region. ZRC 2.6967 has a few light colored tubercles within the lateral portions of the second, third, and fourth bands. ZRC 2.6968 is a gravid female with a slight more opaque overall pattern and there are some yellowish tubercles on the flanks and limbs. A significant degree of ontogenetic change in color pattern occurs with hatchlings and juveniles having a greatly contrasting banding pattern where the body bands are very dark and are edged with thin white lines and the white colored portion of the tail is lost in adulthood. Meristic differences in the type series and additional specimens examined are presented in Table 9.

Additional specimens examined.— Four additional specimens from the type locality were examined (Table 9) and of these three (LSUHC 9125, 9435–36) had bifurcations in the third band (Fig. 10). The posterior 50% of the tails in the juveniles LSUHC 9125 and 9437 (SVL 43 mm, 51 mm, and 51 mm, respectively) have a whitish wash (Fig. 10) and appear opaque in life.

Distribution. *Cyrtodactylus langkawiensis* sp. nov. is known only from Wat Wanaram, Pulau Langkawi, Peninsular Malaysia (Fig. 3).

Natural history. Like its sister species *Cyrtodactylus astrum* sp. nov., *C. langkawiensis* sp. nov. is a saxicolous species inhabiting lowland forests in close association with karst formations on which it maybe a substrate specialist (Fig. 9). Lizards were found at night on the sides of karst towers and in cracks from 1–3 meters above the forest floor. None were seen moving about on the ground. Gravid females carrying two eggs were found during October and juveniles were found during March, September, and October indicating *C. langkawiensis* sp. nov. may breed year round. No *C. macrotuberculatus* were observed at or near the type locality of *C. langkawiensis* sp. nov. and surveys throughout much of the forested areas of Pulau Langkawi lacking karst have resulted in the presence of only *C. macrotuberculatus*. The range of *C. langkawiensis* sp. nov. is almost certainly not restricted to the type locality and it is expected that this species will be discovered in additional regions with karst formations. Grismer (2011) noted that juveniles bearing white tails wave them over their head when threatened.

Etymology. The specific epithet, *langkawiensis*, refers to Langkawi Island to where this species was first discovered and may be endemic.

Comparisons. *Cyrtodactylus langkawiensis* sp. nov. is separated from *C. macrotuberculatus* in lacking large tubercles on the sp. nov. dorsal surface of the head, body and limbs, on the underside of the forearms, in the gular region, in the ventrolateral body fold; and having 38–43 as opposed to 17–28 ventral scales. From *C. pulchellus*, *C. macrotuberculatus*, and *C. trilatofasciatus* sp. nov., *C. langkawiensis* sp. nov. differs in having more than 37 ventral scales as opposed to having 36 or less. It differs further from *C. australotitiwangsaensis* sp. nov., *C. trilatofasciatus* sp. nov. in having 19–21 as opposed to 21–25 and 22–27 fourth toe lamellae, respectively. *Cyrtodactylus langkawiensis* sp. nov. has 30 femoro-precloacal pores, separating it from *C. astrum* sp. nov., *C. australotitiwangsaensis* sp. nov., *C. bintangtinggi* sp. nov., *C. bintangrendah* sp. nov., *C. pulchellus* and *C. trilatofasciatus* sp. nov. which have 31 or more pores. It differs further from *C. trilatofasciatus* sp. nov. in having four or five body bands with a band/interspace ratio of 0.75–1.00 as opposed to having three bands with a ratio of 2.00–2.75. From *C. astrum* sp. nov. it differs in lacking a scattered dorsal pattern of white dorsal tubercles. *Cyrtodactylus langkawiensis* sp. nov. differs from all other species except *C. astrum* sp. nov. and *C. lekaguli* sp. nov. in that hatchlings and juveniles have white tail tips as opposed to lacking white tail tips. Hatchlings and juveniles of *C. trilatofasciatus* sp. nov. have not been observed. Having 11–16 dark caudal bands separates it form *C. australotitiwangsaensis* sp. nov., *C. bintangtinggi* sp. nov., *C. macrotuberculatus*, *C. pulchellus*, and *C. trilatofasciatus* sp. nov. which have less than 11 dark caudal bands. The heavy infusion of dark mottling in the white caudal bands of adults differentiates *C. langkawiensis* sp. nov. from *C. australotitiwangsaensis* sp. nov., *C. bintangtinggi* sp. nov., *C. bintangrendah* sp. nov., *C. pulchellus*, and *C. trilatofasciatus* sp. nov. which have immaculate white caudal bands. *Cyrtodactylus langkawiensis* sp. nov. has a maximum SVL of 99.8 mm which separates for all other species, except *C. lekaguli* sp. nov., that have maximum SVLs greater than 108.3 mm.

TABLE 9. Morphological data of type series and additional specimens of *Cyrtodactylus langkawiensis* form Pulau Langkawi, Kedah, Malaysia. m=male; f=female; SVL=snout-vent length; TL=tail length; TW=tail width; FL=forelimb length; TBL=tibia length; AG=axilla-groin length; HL=head length; HW=head width; HD=head depth; ED=eye diameter; EE=eye to ear distance; ES=eye to snout distance; EN=eye to nostril distance; IO=interorbital distance; EL=ear length; and IN=internarial distance; /=data unavailable.

	ZRC 2.6966 Holotype	ZRC 2.6967 Paratype	ZRC 2.6968 Paratype	LSUHC 9123 Paratype	LSUHC 9124 Paratype	ZRC 2.6969 Paratype	LSUHC 9125	LSUHC 9435	LSUHC 9436	LSUHC 9437
Sex	m	f	f	f	m	f	/	f	f	/
supralabials	12	9	11	10	10	12	11	12	11	11
Infralabials	10	8	9	9	9	9	8	10	9	10
Tubercles on ventral surface of forelimbs	0	0	0	0	0	0	0	0	0	0
Tubercles in gular region	0	0	0	0	0	0	0	0	0	0
Ventrolateral fold tuberculate	0	0	0	0	0	0	0	0	0	0
No. of paravertebral tubercles	34	36	40	44	44	35	34	40	36	37
No. longitudinal rows of tubercles	23	21	25	25	23	23	21	21	23	22
No. of ventral scales	41	42	41	43	40	42	/	39	38	40
Proximal subdigital lamellae square	0	0	1	0	0	0	0	1	0	0
No. of subdigital lamellae on 4th toe	20	20	20	21	20	20	20	19	21	20
No. of femoro-precloacal pores	30	/	/	/	30	/	/	/	/	/
Bands on base of thigh	0	0	0	0	0	0	0	0	0	0
No. body bands	4	5	4	5	4	4	4	4	4	4
Band/interspace width	1.00	1.00	1.00	1.00	0.75	1.00	1.00	1.00	0.75	1.00
No. dark bands on original tail	/	/	15	16	11	/	13	/	15	/
Hatch./juv. with white tail tips	/	/	/	/	/	/	Yes	Yes	Yes	Yes
SVL	93.3	97.9	90.1	99.8	85.2	96.7	42.3	77.6	79.4	49.5
TL	113	87	125	133	120	111				
TW	9.3	7.8	7.8	7.7	7.4	8.1				
FL	15.2	18.4	16.1	14.6	13.8	16				
TBL	19	17.7	18.4	19.4	16.7	18.7				
AG	42.8	44.8	41.2	42.5	37	39.2				
HL	25.4	28.2	25	27.2	24	28.2				
HW	17.8	17.8	16.4	17.6	16.1	18.1				
HD	11.9	10.5	11.3	10	8.7	9.6				
ED	7	6.9	5.6	6.2	5.2	5.7				
EE	7.3	7	7.2	7.7	7.2	7.3				
ES	12.7	12.2	11.7	12.1	10	12.2				
EN	9.4	8.3	9.1	8.8	8.2	9.7				
IO	6.3	5.2	6.1	5.4	4.6	5.8				
EL	2.9	2	2.2	2.2	1.8	2.5				
IN	2.7	2.1	2.9	2.3	2.3	2.8				

***Cyrtodactylus bintangtinggi* sp. nov.**
Bintang Mountain Bent-toed Gecko
Figs. 11,12

Gymnodactylus pulchellus Flower 1899:626 (in part); Boulenger 1903:148, 1912:36 (in part); Smith 1930:13.
Cyrtodactylus pulchellus Grismer *et al.* 2010:149, 2011:416 (in part).

Holotype.—Adult male (ZRC 2.6970) collected on 24 March 2008 by L. Grismer and R. Johnson from Bukit Larut, Peninsular Malaysia (04°51.715 N, 100°47.993) at 1151 meters above sea level.

Paratypes.—All paratypes come from the same locality as the holotype. Adult male (ZRC 2.6971) bears the same collection data as the holotype. The adult females (ZRC 9008 and 9010) and the adult males (ZRC 2.6972 and LSUHC 9006–07, 9009) were collected on 16 June 2008 by J. Grismer, P. Wood, Jr., R. Gregory, and L. Grismer.

Diagnosis.—Adult males reaching 111.1 mm SVL, adult females reaching 108.3 mm SVL; 9–13 supralabials, 8–11 infralabials; tubercles of dorsum small to moderate with no intervening smaller tubercles; no tubercles on ventral surfaces of forelimbs, gular region, or in ventrolateral body fold; 31–42 paravertebral tubercles; 21–26 longitudinal rows of dorsal tubercles; 36–40 rows of ventral scales; 21–24 subdigital lamellae on fourth toe; 39–41 femoro-precloacal pores in males; dorsum not bearing a scattered pattern of white tubercles; four (rarely three; one of 14 specimens examined) very dark body bands in adults lacking lightened centers and light colored tubercles; band to interspace ratio 1.00–1.25; 8–10 dark caudal bands on original tail; white caudal bands in adults immaculate; and posterior portion of tail in hatchlings and juveniles banded not white. These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

Description of holotype.—Adult male SVL 104.2 mm; head large, moderate in length (HL/SVL 0.28) and wide (HW/HL 0.72), somewhat flattened (HD/HL 0.37), distinct from neck, and triangular in dorsal profile; lores concave anteriorly, inflated posteriorly; frontal and prefrontal regions deeply concave; canthus rostralis sharply rounded anteriorly; snout elongate (ES/HL 0.44), rounded in dorsal profile, laterally constricted; eye large (ED/HL 0.07); ear opening elliptical, moderate in size (EL/HL 0.70), vertically oriented; eye to ear distance greater than diameter of eye; rostral rectangular, divided dorsally by a small postrostral (=internasal) and inverted V-shaped furrow, bordered posteriorly by left and right supranasals, a medial postrostral, bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by a large anterior supranasal and small posterior supranasal, posteriorly by single postnasal, ventrally by first supralabial; 9(R,L) square supralabials extending to just beyond upturn of labial margin, tapering abruptly below midpoint of eye; first supralabial largest; 9(R,L) infralabials tapering in size posteriorly; scales of rostrum and lores flat, larger than granular scales on top of head and occiput, those on posterior portion of canthus rostralis larger; scales of occiput intermixed with small tubercles; large, boney frontal ridges bordering orbit confluent with boney, V-shaped, transverse, parietal ridge; dorsal superciliaries elongate, smooth, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by left and right, rectangular postmentals which contact medially for 45% of their length; two rows of enlarged, elongate sublabials extending posteriorly to 6th infralabial; small, granular, gular scales grading posteriorly into larger, flat, smooth, imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.43) with well-defined, non-tuberculate, ventrolateral folds; dorsal scales small, granular, interspersed with large, trihedral, regularly arranged, keeled tubercles, smaller intervening tubercles absent; tubercles extend from occiput to caudal constriction and onto tail where they occur in transverse rows separated by five small, flat scales; caudal tubercles largest dorsally, absent laterally and ventrally; caudal tubercles decrease in size posteriorly; tubercles on occiput and nape relatively small, those on body largest; approximately 25 longitudinal rows of tubercles at midbody; 35 paravertebral tubercles; 37 flat imbricate ventral scales between ventrolateral body folds, ventral scales larger than dorsal scales; precloacal scales large, smooth; distinct precloacal groove.

Forelimbs moderate, relatively short (FL/SVL 0.18); scales on dorsal surfaces of forelimbs flat to granular, intermixed with a few larger tubercles; scales of ventral surface of forearm flat, subimbricate, lacking tubercles; palmar scales rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae rectangular proximal to joint inflection, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.28), larger tubercles on dorsal surface of thigh separated by smaller granular scales, tubercles on dorsal surfaces of foreleg same size as those on thigh; ventral scales of thigh flat, smooth, imbricate, larger than dorsal granular scales; ventral, tibial scales flat, smooth, imbricate; single row of greatly enlarged, flat, rectangular, imbricate, pore-bearing femoral scales extend from knee to knee through precloacal region where they are continuous with enlarged, pore-bearing precloacal scales; 38 contiguous, pore-bearing femoro-precloacal scales forming an inverted T bearing a deep, precloacal groove in which eight pore-bearing scales are found (four on each side of groove); postfemoral scales immediately posterior to pore-bearing scale row small, forming an abrupt union with pore-bearing postfemoral scales on posteroventral margin of thigh; plantar scales low, slightly raised; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae proximal to joint inflection rectangular, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; 23 (R,L) subdigital lamellae on 4th toe.

FIGURE 11. *Cyrtodactylus bintangtinggi.* Upper left: ZRC 2.6970 (holotype); adult male from Bukit Larut, Perak, Malaysia (photo by L. Grismer). Upper right: LSUDPC 5357; hatchling from Bukit Larut, Perak, Malaysia (photo by L. Grismer). Lower left: LSUDPC 6319; adult female from Gunung Bubu, Perak, Malaysia (photo by D. Belabut). Lower right: granite rock microhabitat of *C. bintangtinggi* at Bukit Larut, Perak, Malaysia (photo by L. Grismer).

Tail 124 mm in length, 9.6 mm in width at base, tapering to a point; dorsal scales of tail flat, squarish; tail segmented with five transverse scale rows per segment; posterior margin of segments bordered by four larger tubercles dorsally in anterior one-third of tail, fewer posteriorly; subcaudal region bearing large, transverse scales; dorsal and lateral caudal furrows extend nearly entire length of tail; base of tail bearing hemipenial swellings; three small, postcloacal tubercles on hemipenial swellings; postcloacal scales smooth, flat, large, imbricate.

Coloration in life (Fig. 11). Dorsal ground color of head, body, limbs, and tail dark brown; faint, white chevron on rostrum; wide, nearly black, nuchal band extends from posterior margin of one eye to posterior margin of other eye; nuchal band edged with prominant thin, white, lines; four similarly colored dorsal bands between limb insertions with immaculate, white, edging most prominent where it encompasses tubercles resulting in a somewhat spotted appearance; first band terminates at shoulders, second and third bands terminate just dorsal to ventrolateral fold, fourth band terminates on anterior margin of hind limb insertions; body band/interspace ratio 1.00; one additional dark brown band posterior to hind limbs; no band on posterior margin of thigh; seven dark caudal bands at least twice the width of seven white caudal bands extend onto tail; no caudal or body bands have lightened centers or encompass yellowish to white tubercles; ventral surfaces of head, limbs, and tail smudged with brown; gular scales stippled; abdomen immaculate, beige except for slightly darker, lateral regions, and weakly stippled ventral scales.

Variation. The paratypes approximate the holotype in all aspects of dorsal banding and coloration (Fig. 12). LSUHC 8862, 9008, and 9010 lack a white chevron marking on the rostrum. LSUHC 9009 has three dorsal bands. Portions of the tail of LSUHC 8862 and 9008 are regenerated. The white edging of the dark dorsal bands is not as prominent in LSUHC 9006 and it is even less so in LSUHC 9007. LSUHC 9007 is also missing its tail. The color pattern of hatchlings and juveniles has a greatly contrasting banding pattern where the body bands are nearly solid black, only faintly edged in yellow, and the interspaces and top of the head are yellow (Fig. 11). Meristic differences in the type series and additional specimens examined are presented in Table 10.

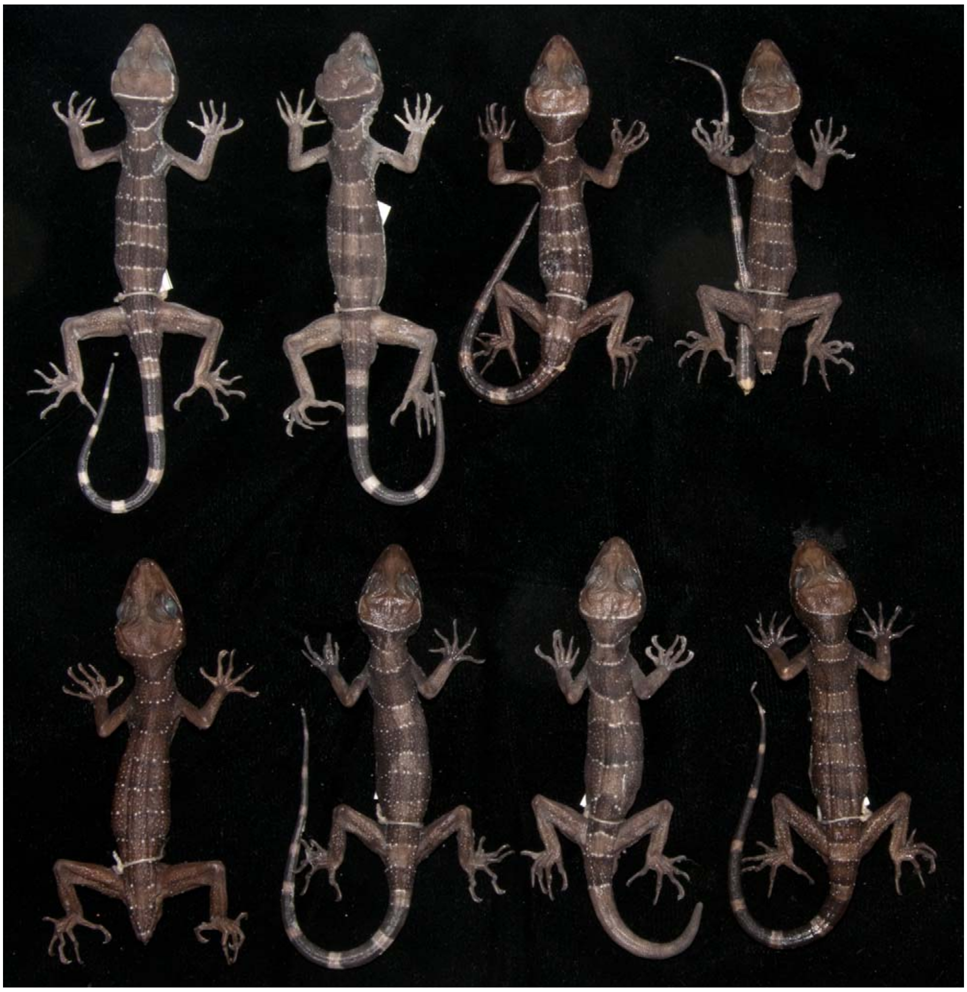

FIGURE 12. Type series of *Cyrtodactylus bintangtinggi*. Upper row from left to right: holotype ZRC 2.6970, paratypes from left to right ZRC 2.6971–72, LSUHC 9006. Lower row: paratypes from left to right LSUHC 9007, 9008, 9009, 9010.

Additional specimens examined.—The posterior 50% of the tails in the juveniles LSUDPC 4780 and 5357 were banded not white (Fig. 11).

Distribution. *Cyrtodactylus bintangtinggi* sp. nov. is known from the type locality of Bukit Larut, Perak and from Gunung Bubu, Perak 20 km to the southwest in Peninsular Malaysia (Grismer 2011; Grismer *et al.* 2010a; Fig. 3). It is likely, however, this species ranges throughout the Banjaran Bintang farther north into Thailand, similar to the upland Banjaran Bintang endemic *Cnemaspis mcguirei* (Grismer *et al.* 2008b).

Natural history. *Cyrtodactylus bintangtinggi* sp. nov. is a nocturnal upland species inhabiting hill dipterocarp and montane forests (Fig. 11) ranging up to 1500 m in elevation (Grismer 2011). It is always found in the vicinity of granite rocks where lizards take refuge in cracks and occasionally beneath rocks on the ground. Lizards can be found climbing on vegetation but only if the vegetation is in the vicinity of rocks. Grismer (2011) reports finding lizards in houses and often occurring in male female pairs. Gravid females carrying two eggs and hatchlings have been found during March (Grismer 2011).

TABLE 10. Morphological data of type series and additional specimens of *Cyrtodactylus bintangtinggi* form Bukit Larut, Perak, Malaysia. m=male; f=female; SVL=snout-vent length; TL=tail length; TW=tail width; FL=forelimb length; TBL=tibia length; AG=axilla-groin length; HL=head length; HW=head width; HD=head depth; ED=eye diameter; EE=eye to ear distance; ES=eye to snout distance; EN=eye to nostril distance; IO=interorbital distance; EL=ear length; and IN=internarial distance. /=data unavailable.

	ZRC 2.6970 Holotype	ZRC 2.6971 Paratype	ZRC 2.6972 Paratype	LSUHC 9006 Paratype	LSUHC 9007 Paratype	LSUHC 9008 Paratype	LSUHC 9009 Paratype	LSUHC 9010 Paratype	ZRC 2.1174	ZRC 2.1171	ZRC 2.5658	ZRC 2.5659	ZRC 2.5666	ZRC 2.4864
Sex	m	m	m	m	m	f	m	f	f	m	m	m	m	m
Supralabials	9	12	11	11	10	10	12	12	9	13	11	10	12	12
Infralabials	9	10	8	10	10	9	9	10	10	9	11	10	11	11
Tubercles on ventral surface of forelimbs	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tubercles in gular region	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ventrolateral fold tuberculate	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. of paravertebral tubercles	35	37	31	40	42	39	32	40	35	32	37	34	33	38
No. longitudinal rows of tubercles	25	24	24	21	23	26	24	25	24	24	22	24	25	24
No. of ventral scales	37	40	36	38	39	38	/	39	39	40	36	38	39	26
Proximal subdigital lamellae square	0	0	0	0	0	0	0	0	/	/	0	0	0	0
No. of subdigital lamellae on 4th toe	23	23	23	23	23	24	24	22	/	/	23	21	24	23
No. of femoro-precloacal pores	38	39	40	41	41	/	41	/	/	/	40	37	39	41
Bands on base of thigh	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. body bands	4	4	4	4	4	4	3	4	4	4	4	4	4	4
Band/interspace width	1.00	1.00	1.25	1.25	1.00	1.25	1.25	1.25	/	/	/	/	/	/
No. dark bands on original tail	8	/	/	8	/	10	/	9	/	/	/	/	/	/
Hatch./juv. with white tail tips	/	/	/	/	/	/	/	/	/	/	/	/	/	/
SVL	104.2	107.8	103.9	100.2	111.1	102.6	104.7	108.3	/	/	/	110.1	/	/
TL	124	113	104	137	/	135	65	137						
TW	9.6	10.3	10.1	9	10.4	8.7	10.4	9						
FL	18.8	17.3	17.1	15.8	18.8	17.9	16.4	17.5						
TBL	20.5	20.8	20.3	19.7	22.4	19.3	20.6	20.4						
AG	42.1	47.3	43.6	42.3	46.8	46.4	42.5	49.9						
HL	29.3	29.9	30.1	27.8	31.7	29.8	29.8	30.5						
HW	21.2	22	21.5	20.3	22.2	20.4	21.4	20.8						
HD	10.8	11.2	11.1	11.5	11.6	11.9	11	11.4						
ED	6.9	6.7	7	6.4	7.8	6.8	6.5	7.2						
EE	8.8	8.8	9.3	8.1	8.8	8.3	8.6	9.3						
ES	12.9	12.7	13.7	12.6	15	13.5	13.6	13.6						
EN	9.8	8.6	10.1	9.8	11.2	10	9.7	9.8						
IO	6.1	5.6	7	7.2	6.9	6.5	6.4	6.3						
EL	2.1	2.2	2.6	2	2.7	1.9	2.3	2.2						
IN	3.1	3.5	3.4	3.5	3.6	3.2	2.9	3.2						

Etymology. The word *bintangtinggi* is a combination of the Malaysian words *bintang* meaning star and *tinggi* meaning tall or high and is in reference to the upland regions of the Bintang Mountain Range to where this species is presumably endemic; *bintangtinggi* is a noun in apposition and is thus invariable.

Comparisons. *Cyrtodactylus bintangtinggi* sp. nov. is separated from *C. macrotuberculatus* in lacking large tubercles on the dorsal surface of the head, body and limbs, on the underside of the forearms, in the gular region, and in the ventrolateral body fold. From *C. macrotuberculatus* and *C. pulchellus* it differs in having more than 35 ventral scales. Having 38–41 femoro-precloacal pores separates it from *C. langkawiensis* sp. nov. and *C. lekaguli* sp. nov. which have less than 37 pores and from *C. astrum* sp. nov. which has 31–38 pores (overlapping by one scale at 38). It differs from *C. trilatofasciatus* sp. nov. by having four (only one specimen of 14 having three) body bands with a band/interspace ratio of 1.00–1.25 as opposed to having three bands with a band/interspace ratio of 2.00–2.75. *Cyrtodactylus bintangtinggi* sp. nov. is further separated from *C. astrum* sp. nov. in lacking a scattered dorsal pattern of white tubercles. From *C. astrum* sp. nov., *C. langkawiensis* sp. nov., and *C. lekaguli* sp. nov., *C. bintangtinggi* sp. nov. differs in not having hatchlings and juveniles with white tail tips. *Cyrtodactylus bintangtinggi* sp. nov. is further differentiated from *C. astrum* sp. nov., *C. langkawiensis* sp. nov, and *C. lekaguli* sp. nov. in having fewer than 11 dark caudal bands and from *C. trilatofasciatus* sp. nov. it differs in having more than seven dark caudal bands. The white caudal bands of *C. bintangtinggi* sp. nov. are immaculate which differentiates it from *C. astrum* sp. nov., *C. langkawiensis* sp. nov., *C. lekaguli* sp. nov.**,** and *C. macrotuberculatus* whose white caudal bands are infused with dark pigment. The SVL of 111.1 mm separates *C. bintangtinggi* sp. nov. from *C. australotitiwangsaensis* sp. nov., *C. macrotuberculatus*, and *C. trilatofasciatus* sp. nov. whose SVLs are greater than 117 mm and it is separated from *C. langkawiensis* sp. nov. and *C. lekaguli* sp. nov. whose SVLs are less than 104 mm.

Remarks. *Cyrtodactylus bintangtinggi* sp. nov. and *C. bintangrendah* sp. nov. are sister species forming what is referred to here as the Bintang clade. Like other lineages associated with the Banjaran Bintang, the Bintang clade is most closely related to lineages within the Banjaran Titiwangsa, namely the Titiwangsa clade containing the sister species *C. trilatofasciatus* sp. nov. and *C. australotitiwangsaensis* sp. nov. This common biogeographic pattern is seen between the bufonids *Ansonia malayana* Inger and *A. jeetsukumarani* Wood, Grismer, Norhayati & Senawi (Wilkinson *et al*. 2012), the agamids *Acanthosaura bintangensis* Wood, Grismer, Grismer, Norhayati, Chan & Bauer and *A. titiwangsaensis* Wood, Grismer, Grismer, Norhayati, Chan & Bauer (Wood *et al.* 2009), the gekkonids *Hemiphyllodactylus harterti* Werner and *H. titiwangsaensis* Zug (Zug 2010), and populations of the colubrids *Asthenodipsas vertebralis* (Boulenger) (Laredo *et al*. in prep), *Collorhabdium williamsoni* Smedley, *Lycodon butleri* Boulenger, and *Macrocalamus chanardi* David & Pauwels. The sister lineages are likely to have initially diverged during periods of lowered sea levels that created warming and drying trends in the intervening lowlands and forced cool, more mesic adapted lowland forests to migrate upslope into current montane areas thus bifurcating lowland lineages that initially retreated with the forests to their respective upland refugia.

Cyrtodactylus bintangrendah sp. nov.

Bintang Lowland Bent-toed Gecko
Figs. 13,14

Cyrtodactylus pulchellus Grismer 2011:416 (in part).

Holotype.—Adult male (ZRC 2.6973) collected on 29 October 2011 by E. S. H. Quah, Fatim, S. B. M., Nor Amira, B. A. R. and Yusof O. from Bukit Mertajam, Seberang Perai, Penang, Peninsular Malaysia (05°35.698 N, 100°49.253 E) at 451 meters above sea level.

Paratypes.—Paratypes LSUHC 9974–76 (adult female, adult male, and adult female respectively) were collected from Lenggong, Perak. ZRC 2.6974 (adult male) was collected on 1 October 2010 by E. S. H. Quah from the type locality. Adult male (LSUHC 10520) bears the same collection data as the holotype. Juvenile female (ZRC 2.6975) collected on 20 June 2010 by E. S. H. Quah from Bukit Palong, Kedah, Peninsular Malaysia (5°36.140 N 100°55.190 E) at 238 meters in elevation. Adult male (LSUHC 10331) collected on 26 July 2011 by E. S. H. Quah at Ulu Paip, Kedah (5°24.630 N 100°38.419 E) at 200 meters above sea level as estimated from Google Earth.

Diagnosis.—Adult males reaching 114.4 mm SVL, adult females reaching 103.1 mm SVL; 8–12 supralabials, 8–10 infralabials; tubercles of dorsum small to moderate with no intervening smaller tubercles; no tubercles on ventral surfaces of forelimbs, gular region, or in ventrolateral body fold; 33–44 paravertebral tubercles; 22–25 longitudinal rows of dorsal tubercles; 31–39 rows of ventral scales; 20–24 subdigital lamellae on fourth toe; 41–46 femoro-precloacal pores in males; dorsum not bearing a scattered pattern of white tubercles; four, rarely five, body bands in adults lacking lightened centers and light colored tubercles; band to interspace ratio 0.50–1.25; 8–14 dark caudal bands on original tail; light caudal bands in adults not heavily infused with dark pigment; and posterior portion of tail in hatchlings and juveniles banded not white. These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

Description of holotype.—Adult male SVL 114.4 mm; head large, moderate in length (HL/SVL 0.27) and wide (HW/HL 0.81), somewhat flattened (HD/HL 0.49), distinct from neck, and triangular in dorsal profile; lores concave anteriorly, inflated posteriorly; frontal and prefrontal regions deeply concave; canthus rostralis rounded anteriorly; snout elongate (ES/HL 0.45), rounded in dorsal profile, laterally constricted; eye large (ED/HL 0.24); ear opening elliptical, moderate in size (EL/HL 0.05), vertically oriented; eye to ear distance greater than diameter of eye; rostral rectangular, divided dorsally by a large postrostral (=internasal), bordered posteriorly by left and right supranasals, a medial postrostral, bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by a large anterior supranasal and small posterior supranasal, posteriorly by two postnasals, ventrally by first supralabial; 9,10(R,L) square supralabials extending to just beyond upturn of labial margin, tapering abruptly below midpoint of eye; first supralabial largest; 8(R,L) infralabials tapering in size posteriorly; scales of rostrum and lores slightly raised, larger than granular scales on top of head and occiput, those on posterior portion of canthus rostralis slightly larger; scales of occiput and top of head posterior to eyes intermixed with small tubercles; large, boney frontal ridges bordering orbit confluent with boney, transverse, parietal ridge; dorsal superciliaries elongate, smooth, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by left and right, rectangular postmentals which contact medially for 30% of their length; two rows of enlarged, elongate sublabials extending posteriorly to 6th infralabial; small, granular, gular scales grading posteriorly into larger, flat, smooth, imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.44) with well-defined, weakly tuberculate, ventrolateral folds; dorsal scales small, granular, interspersed with large, trihedral, regularly arranged, keeled tubercles; smaller intervening tubercles generally absent; tubercles extend from top of head posterior to eyes to caudal constriction and onto tail where they occur in transverse rows separated by 6–8 small, flat scales; caudal tubercles largest dorsally, absent laterally and ventrally; caudal tubercles decrease in size posteriorly; tubercles on occiput and nape relatively small, those on body largest; approximately 24 longitudinal rows of tubercles at midbody; 39 paravertebral tubercles; 36 flat imbricate ventral scales between ventrolateral body folds, ventral scales larger than dorsal scales; precloacal scales large, smooth; distinct precloacal groove.

Forelimbs moderate, relatively short (FL/SVL 0.16); scales on dorsal surfaces of forelimbs raised, intermixed with larger tubercles; scales of ventral surface of forearm flat, subimbricate, lacking tubercles; palmar scales rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae rectangular proximal to joint inflection, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.20), larger tubercles on dorsal surface of thigh separated by smaller granular scales, tubercles on dorsal surfaces of foreleg same size as those on thigh; ventral scales of thigh flat, smooth, imbricate, larger than dorsal granular scales; ventral, tibial scales flat, smooth, imbricate; single row of greatly enlarged, flat, rectangular, imbricate, pore-bearing femoral scales extend from knee to knee through precloacal region where they are continuous with enlarged, pore-bearing precloacal scales; 42 contiguous, pore-bearing femoro-precloacal scales forming an inverted T bearing a deep, precloacal groove in which 13 pore-bearing scales are found (six on right, seven on left side of groove); postfemoral scales immediately posterior to pore-bearing scale row small, forming an abrupt union with pore-bearing, postfemoral scales on posteroventral margin of thigh; plantar scales low, slightly raised; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae proximal to joint inflection rectangular, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; 23(R) 24(L) subdigital lamellae on 4th toe.

Tail 140 mm in length, 10.1 mm in width at base, tapering to a point; dorsal scales of tail flat, squarish; tail segmented with 6–8 transverse scale rows per segment; posterior margin of segments bordered by 4–6 larger tubercles dorsally in anterior one-third of tail, fewer posteriorly; subcaudal region bearing large, transverse scales; shallow dorsal and lateral caudal furrows extend entire length of tail; base of tail bearing hemipenial swellings; 3,2(R,L) small, postcloacal tubercles on hemipenial swellings; postcloacal scales smooth, flat, large, imbricate.

FIGURE 13. *Cyrtodactylus bintangrendah.* Upper left: ZRC 2.6974 (paratype); adult male from Bukit Mertajam, Penang, Malaysia (photo by E. Quah). Upper right: LSUDPC 6320; adult female from Bukit Panchor, Penang, Malaysia (photo by E. Quah). Middle left: LSUHC 9974 adult male (paratype) from Lenggong Valley, Perak, Peninsular Malaysia (photo by M. Muin). Middle right: LSUHC 9977; juvenile from Bukit Mertajam, Penang, Malaysia (photo by E. Quah). Lower left: granite habitat of *C. bintangrendah* at Bukit Mertajam, Penang, Malaysia (photo by E. Quah). Lower right: karst habitat of *C. bintangrendah* at Gua Puteri, Lenggong Valley, Perak, Malaysia (photo by M. A. Muin).

Coloration in life. Dorsal ground color of head, body, limbs, and tail tan; no white chevron on rostrum; wide, brown, nuchal band extends from posterior margin of one eye to posterior margin of other eye, edged with prominent thin, yellow, lines; four similarly colored dorsal bands between limb insertions with immaculate, yellow, edging; first band terminates at shoulders, second and third bands terminate just dorsal to ventrolateral fold, fourth band terminates on anterior margin of hind limb insertions; body band/interspace ratio 1.25; one additional dark brown band posterior to hind limbs; no band on posterior margin of thigh; four wide, dark bands approximately three times the width of four white bands on original potion of tail; all bands encircle tail; regenerated portion of tail dark brown, immaculate; no bands on tail or body have lighten centers or encompass prominent yellowish to white tubercles; ventral surfaces of head, limbs, and tail beige; gular scales stippled; abdomen immaculate, except for slightly darker, lateral regions, and weakly stippled ventral scales.

Variation. ZRC 2.6975 (subadult female; SVL 67 mm from Bukit Palong, Kedah) closely approaches the holotype in general aspects of coloration except that its dorsal pattern is more contrasting being that the specimen is not an adult (Fig. 14). The paratypes from Lenggong, Perak (LSUHC 9974–76) have an overall orangish brown dorsal coloration like the holotype but are less contrasting in that the light edging of the bands is less distinct, and their dorsal tubercles are lower in profile and less distinct. Additionally, LSUHC 9974 and 9976 have five body bands and LSUHC 9975 has 14 dark and 13 whitish caudal bands, respectively. Meristic differences in the type series and additional specimens examined are presented in Table 11.

Additional specimen examined.—One additional specimen (LSUHC 9977) is a subadult female (SVL 74 mm) from Lenggong which is also lighter overall but has a more contrasting color pattern with more distinctive band edging with respect to the adults from Lenggong owing to its smaller size (Fig. 14).

FIGURE 14. Type series and additional specimens examined of *Cyrtodactylus bintangrendah.* Upper row from left to right: holotype ZRC 2.6973 and paratypes LSUHC 10520 and ZRC 2.6974 from Bukit Mertajam; paratypes ZRC 2.6975 from Palong, LSUHC 10331 from Ulu Paip, ZRC 2.117. Additional specimen examined; ZRC 2.1177 from Gunung Pondok. Lower row: paratypes LSUHC 9974, 9975, 9976 from Lenggong Valley. Additional specimen examined; LSUHC 9977 from Lenggong Valley.

Distribution. *Cyrtodactylus bintangrendah* sp. nov. is presumed to range throughout lowland forests up to 450 meters in elevation through the foothills and lower slopes surrounding the Bintang Mountain Range. Along the west side of the mountains it ranges from at least Bukit Mertajam, Seberang Perai, Penang in the south to Bukit Palong, Kedah in the north (Fig. 3). East of the Bintang range, it is known only from the Lenggong Valley, Perak (Fig. 3). Grismer (2011:424) reported lowland populations of *C. pulchellus sensu strictu* from much farther south in Selangor, Negeri Sembilan, and Johor which may indicate that *C. bintangrendah* sp. nov. shares a similar distribution pattern proposed for other lowland species found west of the Banjaran Titiwangsa (Grismer 2011).

Natural history. *Cyrtodactylus bintangrendah* sp. nov. is a nocturnal species found in lowland and lower hill dipterocarp forest below 500 meters elevation. At Bukit Mertajam, Penang, specimens were encountered on large rocks and boulders especially along forest streams at night (Fig. 13). Lizards were also observed on tree trunks and vines close to boulders but escaped into crevices in the rocks when approached. ZRC 2.6974 was found crawling on a retaining rock wall along a road cut at night at Bukit Mertajam. At Bukit Panchor, Penang, a male and a female (LSUDPC 6320) were collected at night crawling over large granite boulders that formed cave-like environments in lowland forest. Farther north at Bukit Palong, Kedah, the single subadult female (ZRC 2.6975) was found in lower hill dipterocarp forest at night clinging onto a sapling about 30cm above the ground. Other specimens were observed crawling on rocks and tree trunks. The male from Ulu Paip, Kedah (LSUHC 10331), was found on the side of a tree trunk at night approximately 1m off the ground near a river edged with boulders. Another specimen was observed in the vicinity on another tree trunk but ran into a crevice at the base of the trunk when approached. East of the Bintang Range at Lenggong Valley, Perak, *C. bintangrendah* sp. nov. is saxicolous and found on limestone karst outcrops and around the mouths of limestone caves. During the day geckos are occasionally observed hiding in cracks and crevices of the outcrops. At night, lizards emerge and can be found perched or crawling over the walls of the cave 1–3m above the ground.

Etymology. The word *bintangrendah* is a combination of the Malaysian words *bintang* meaning star and *rendah* meaning low and is in reference to the lowland regions surrounding the Bintang Mountain Range wherein this species occurs; *bintangrendah* is a noun in apposition and is thus invariable.

TABLE 11. Morphological data of type series and additional specimens of *Cyrtodactylus bintangrendah* form Perak State, Malaysia. m=male; f=female; SVL=snout-vent length; TL=tail length; TW=tail width; FL=forelimb length; TBL=tibia length; AG=axilla-groin length; HL=head length; HW=head width; HD=head depth; ED=eye diameter; EE=eye to ear distance; ES=eye to snout distance; EN=eye to nostril distance; IO=interorbital distance; EL=ear length; and IN=internarial distance; w=weak; /=data unavailable.

	LSUHC 9974 Lenggong Valley Paratype	LSUHC 9975 Lenggong Valley Paratype	LSUHC 9976 Lenggong Valley Paratype	ZRC 2.6974 Bukit Mertajam Paratype	ZRC 2.6975 Bukit Palong Paratype	ZRC 2.6973 Bukit Mertajam Holotype	LSUHC 10520 Bukit Mertajam Paratype	LSUHC 10331 Ulu Paip Paratype	LSUHC 9977 Lenggong Valley	ZRC 2.1177 Gunung Pondok
Sex	m	f	m	m	f	m	m	m	f	m
Supralabials	10	10	11	9	12	9	9	8	11	9
Infralabials	10	9	8	9	9	8	8	8	9	10
Tubercles on ventral surface of forelimbs	0	0	0	0	0	0	0	0	0	0
Tubercles in gular region	0	0	0	0	0	0	0	0	0	0
Ventrolateral fold tuberculate	0	0	0	0	0	w	0	w	0	0
No. of paravertebral tubercles	36	38	41	38	44	39	33	36	36	33
No. longitudinal rows of tubercles	23	25	24	23	22	24	25	25	22	24
No. of ventral scales	33	32	32	31	32	36	34	36	32	39
Proximal subdigital lamellae square	0	0	0	0	0	0	0	0	0	0
No. of subdigital lamellae on 4th toe	21	20	22	24	23	23	21	23	23	22
No. of femoro-precloacal pores	41	/	41	45	/	42	41	46	/	44
Bands on base of thigh	0	0	0	0	0	0	0	0	0	0
No. body bands	5	4	5	4	4	4	4	4	4	4
Band/interspace width	0.50	1.00	0.75	1.00	1.25	1.25	1.25	1.25	1.25	1.25
No. dark bands on original tail	/	14	/	8	9	/	/	/	/	/
Hatch./juv. with white tail tips	/	/	/	/	/	/	/	/	/	/
SVL	100.0	103.1	102.2	98.3	67.2	114.4	106.6	111.7	74.4	105.1
TL	97	132	100	130	82	140	151	/		
TW	8.4	8.7	8.5	9.7	4.8	10.1	10.6	10.3		
FL	16.2	7.8	16.6	16.6	11.2	17.8	17.6	17.8		
TBL	19.2	20	19.8	19.1	12.8	22.9	21.4	21		
AG	44.7	45.5	44.1	41.9	29.9	49.9	48.2	50.1		
HL	28.6	29.6	28.6	27.6	18.8	31.2	32.3	31.6		
HW	20	26.5	20.9	20.1	13.2	25.3	23.8	23.5		
HD	10.9	11.9	11.3	10.9	7.8	15.4	14	14.1		
ED	6.8	6.4	6.8	6	6.6	7.4	7.7	7.5		
EE	8.3	9.4	8	8.7	5.8	9.7	10.1	9.6		
ES	12.9	13	12.8	12.3	8.6	14	13.6	12.9		
EN	9.7	10.2	9.6	9.3	6.2	10.1	10	9.6		
IO	6.9	6.5	5.9	5.8	3.4	7.5	7.8	8		
EL	2.8	2	2.2	2.3	1.4	1.7	2.5	2		
IN	2.6	2.8	2.9	2.7	2.2	3.5	3.2	3.6		

Comparisons. *Cyrtodactylus bintangrendah* sp. nov. is separated from *C. macrotuberculatus* in lacking large tubercles on the dorsal surface of the head, body and limbs, on the underside of the forearms, in the gular region, and having 31–39 ventral scales as opposed to 17–28 ventral scales. From *C. astrum* sp. nov., *C. langkawiensis* sp. nov., *C. lekaguli* sp. nov. and *C. pulchellus*, *C. bintangrendah* sp. nov. differs in having more than 40 femoro-precloacal pores. It differs from *C. trilatofasciatus* sp. nov. in having four or five body bands with a band/ interspace ratio of 0.50–1.25 as opposed to having three bands with a band/interspace ratio of 2.00–2.75. *Cyrtodactylus bintangrendah* sp. nov. is further separated from *C. astrum* sp. nov. in lacking a scattered dorsal pattern of white tubercles. Hatchling and juvenile *C. bintangrendah* sp. nov. do not have a white tail tip which separates it from *C. astrum* sp. nov., *C. langkawiensis* sp. nov. and *C. lekaguli* sp. nov. whose hatchlings and juveniles do. *Cyrtodactylus bintangrendah* sp. nov. is separated from *C. trilatofasciatus* sp. nov. by having 8–14 dark caudal bands vs. six or seven in *C. trilatofasciatus* sp. nov. Its larger maximum SVL of 114.4 mm differentiates it further from *C. langkawiensis* sp. nov. and *C. lekaguli* sp. nov. which do not reach over 104 mm SVL and from the much larger *C. trilatofasciatus* sp. nov. (maximum SVL 122.2 mm). *Cyrtodactylus bintangrendah* sp. nov. cannot be discretely separated from *C. bintangtinggi* sp. nov. based on morphology. However, student *t*-test indicates the mean number of femoro-precloacal pores in *C. bintangrendah* sp. nov. (42.8) is significantly greater ($p < 0.003$) than that of *C. bintangtinggi* sp. nov. (39.7). Additionally the average sequence divergence between these two species is 6.9–8.0%.

Remarks. Along the west side of the Banjaran Bintang, *Cyrtodactylus bintangrendah* sp. nov. is associated with granite outcroppings in lowland forest. However, the population in the Lenggong Valley, Perak occurs along the eastern side of the Banjaran Bintang in karst formations and the color pattern of the lizards from this area has converged to some extent on that of the other karst dwelling species, *C. astrum* sp. nov., *C. langkawiensis* sp. nov. and *C. lekaguli* sp. nov. in being generally lighter overall and have a significantly higher number of dark caudal bands.

Cyrtodactylus trilatofasciatus sp. nov.

Cameron Highlands Bent-toed Gecko
Fig. 15,16

Cyrtodactylus pulchellus Lim *et al*. 2002:51; Grismer 2011:420 (in part).

Holotype.—Adult male (ZRC 2.6976) collected on 29 March 2011 by L. Grismer and Chan, K. O. from Ringlet, Cameron Highlands, Pahang, Peninsular Malaysia (04°24.516 N, 100°22.591 E) at 1109 meters above sea level.

Paratypes.—Paratypes ZRC 2.6977–78, and LSUHC 0461 (adult female, adult male and adult female, respectively) have the same collection data as the holotype.

Diagnosis.—Adult males reaching 122.2 mm SVL, adult females reaching 119.1 mm SVL; 10–12 supralabials, 8–11 infralabials; tubercles of dorsum small to moderate with no intervening smaller tubercles; no tubercles on ventral surfaces of forelimbs, gular region, or in ventrolateral body fold; 34–38 paravertebral tubercles; 23–27 longitudinal rows of dorsal tubercles; 33–36 rows of ventral scales; 22–27 subdigital lamellae on fourth toe; 41–46 femoro-precloacal pores in males; dorsum not bearing a scattered pattern of white tubercles; three body bands in adults lacking lightened centers and light colored tubercles; body band to interspace ratio 2.00–2.75; six or seven wide, dark, caudal bands on original tail; white caudal bands in adults not heavily infused with dark pigment; and posterior portion of tail in hatchlings and juveniles banded not white. These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

Description of holotype.—Adult male SVL 122.2 mm; head large, moderate in length (HL/SVL 0.26) and wide (HW/HL 0.89), somewhat flattened (HD/HL 0.38), distinct from neck, and triangular in dorsal profile; lores concave anteriorly, inflated posteriorly; frontal and prefrontal regions deeply concave; canthus rostralis rounded anteriorly; snout elongate (ES/HL 0.44), rounded in dorsal profile, laterally constricted; eye large (ED/HL 0.23); ear opening elliptical, moderate in size (EL/HL 0.07), obliquely oriented; eye to ear distance greater than diameter of eye; rostral rectangular, divided dorsally by an inverted Y-shaped furrow, bordered posteriorly by left and right supranasals, a medial postrostral (=internasal), bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by a large anterior supranasal and small posterior supranasal, posteriorly by two small postnasals, ventrally by first supralabial; 11(R,L) square supralabials extending to just beyond upturn of labial margin, tapering abruptly below midpoint of eye; first supralabial largest; 11(R,L) infralabials tapering in size posteriorly; scales of rostrum and lores flat, larger than granular scales on top of head and occiput, those on posterior portion of canthus rostralis slightly larger; scales of occiput and top of head between eyes intermixed with small tubercles; large, boney frontal ridges bordering orbit confluent with boney, V-shaped, transverse, parietal ridge; dorsal superciliaries elongate, smooth, largest anteriorly, damaged on right; mental triangular, bordered laterally by first infralabials and posteriorly by left and right, rectangular postmentals which contact medially for 50% of their length; single row of enlarged, elongate sublabials extending posteriorly to 3rd infralabial; small, granular to flat, gular scales grading posteriorly into larger, flat, smooth, imbricate, pectoral and ventral scales.

FIGURE 15. *Cyrtodactylus trilatofasciatus* from Ringlet, Cameron Highlands, Pahang, Malaysia. Upper left: LSUHC 10461 (paratype); adult female. Upper right: LSUDPC 5892; adult female. Lower left: ZRC 2.6976 (holotype); adult male. Lower right: Lower montane forest habitat of *C. trilatofasciatus* at Cameron Highlands, Pahang, Malaysia. All photos by L. Grismer.

Body relatively short (AG/SVL 0.47) with well-defined, non-tuberculate, ventrolateral folds; dorsal scales small, granular, interspersed with larger, trihedral, regularly arranged, keeled tubercles, smaller intervening tubercles generally absent; tubercles extend from top of head from between eyes to caudal constriction and onto tail where they occur in transverse rows separated by six or seven small, flat scales; caudal tubercles largest dorsally, absent laterally and ventrally; caudal tubercles decrease in size posteriorly; tubercles on occiput and nape small, those on body largest; approximately 24 longitudinal rows of tubercles at midbody; 38 paravertebral tubercles; 34 flat imbricate ventral scales between ventrolateral body folds, ventral scales larger than dorsal scales; precloacal scales large, smooth; distinct precloacal groove.

Forelimbs moderate, relatively short (FL/SVL 0.16); scales on dorsal surfaces of forelimbs slightly raised, intermixed with larger tubercles; scales of ventral surface of forearm flat, subimbricate, lacking tubercles; palmar scales rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae rectangular proximal to joint inflection, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.18), larger tubercles on dorsal surface of thigh separated by smaller granular scales, tubercles on dorsal surface of foreleg same size as those on thigh; ventral scales of thigh flat, smooth, imbricate, larger than dorsal granular scales; ventral, tibial scales flat, smooth, imbricate; single row of greatly enlarged, flat, rectangular, imbricate, pore-bearing femoral scales extend from knee to knee through precloacal region where they are continuous with enlarged, pore-bearing precloacal scales; 41 contiguous, pore-bearing femoro-precloacal scales forming an inverted T bearing a deep, precloacal groove in which 10 pore-bearing scales are found (five on each side of groove); postfemoral scales immediately posterior to pore-bearing scale row small, forming an abrupt union with pore-bearing postfemoral scales on posteroventral margin of thigh; plantar scales low, slightly raised; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae proximal to joint inflection rectangular, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; 25(R) 24(L) subdigital lamellae on 4th toe.

Tail 150 mm in length, 11.1 mm in width at base, tapering to a point; dorsal scales of tail flat, squarish; tail segmented with six or seven transverse scale rows per segment; posterior margin of segments bordered by four larger tubercles dorsally in anterior one-third of tail, fewer posteriorly; subcaudal region bearing large, transverse scales; shallow dorsal and lateral caudal furrows extend entire length of tail; base of tail bearing hemipenial swellings; three small, postcloacal tubercles on left hemipenial swellings, two on right; postcloacal scales smooth, flat, large, imbricate.

Coloration in life (Fig. 15). Dorsal ground color of head, body, limbs, and tail dark brown; no white chevron on rostrum; wide, very dark brown nearly black, nuchal band extends from posterior margin of one eye to posterior margin of other eye, edged with prominent thin, white, dotted lines of tubercles; three wide, similarly colored dorsal bands between limb insertions with immaculate, white tubercles forming a dotted line edging the bands; first band terminates at shoulders, second band terminates just dorsal to ventrolateral fold midway between limb insertions, third band terminates on anterior margin of hind limb, groin, and the area anterior to the groin; body band/interspace ratio 2.75; one additional dark brown band posterior to hind limbs; oblique band outlined with white tubercles on posterior margin of thigh; six wide, dark bands approximately four times the width of five white bands extend onto tail; all bands encircle tail, no bands on tail or body have lighten centers or encompass yellowish to white tubercles; ventral surfaces of head, limbs, and tail heavily smudged with brown; gular scales stippled; abdomen immaculate, beige except for slightly darker, anterolateral regions, and weakly stippled ventral scales.

Variation. The dorsal color pattern of the paratypes (LSUHC 10064–65, 10461 female, male and female, respectively) is generally more vivid overall, especially in LSUHC 10065 (Fig. 16). Grismer (2011:420) illustrated a juvenile from Cameron Highlands with an anomalous dorsal pattern and seven black caudal bands. Additionally, the posterior one-half of the tail of LSUHC 10065 is regenerated. LSUDPC 6612–13 are newly born captive specimens with completely banded tails. Meristic differences in the type series and additional specimens examined are presented in Table 12.

Additional specimens examined. ZRC 2.1178 has a completely regenerated tail that lacks a pattern and its interspaces between the dorsal bands are slightly wider (Fig. 16).

Distribution. *Cyrtodactylus trilatofasciatus* sp. nov. is known only from the type locality at Ringlet, Cameron Highlands, Pahang, Malaysia (Fig. 3). This species most certainly occurs in other localities throughout the upland regions of Cameron Highlands and to the north where rocks are present.

Natural history. *Cyrtodactylus trilatofasciatus* sp. nov. occurs in hill dipterocarp and montane forests from approximately 1000–1500 meters in elevation. In these habitats lizards emerge at night and forage among rocks or on nearby vegetation (Fig. 15). This species has not been found in forested areas where rocks are absent.

Etymology. The specific epithet *trilatofasciatus* comes from the Latin words *ter* meaning three, *latus* meaning wide, and *fasciatus* meaning banded and refers the diagnostic character state of having three wide bands.

Comparisons. *Cyrtodactylus trilatofasciatus* sp. nov. is separated from *C. macrotuberculatus* in lacking large tubercles on the dorsal surface of the head, body and limbs, on the underside of the forearms, in the gular region, and in the ventrolateral body fold. From *C. astrum* sp. nov. it differs in having 34–38 paravertebral tubercles as opposed to 40–57. It differs from *C. lekaguli* sp. nov. in having 23–27 longitudinal rows of dorsal tubercles as opposed to 20–24 rows of tubercles. It is separated from *C. bintangtinggi* sp. nov. and *C. langkawiensis* sp. nov. in having less than 37 ventral scales (overlapping with *C. bintangtinggi* sp. nov. by one scale at 36) and from *C. macrotuberculatus* by having more than 32 ventral scales. It differs from all species except *C. australotitiwangsaensis* sp. nov. and *C. bintangrendah* sp. nov. in having more than 40 femoro-precloacal pores (overlapping with *C. bintangtinggi* sp. nov. by one pore at 41). It differs from all species except *C. australotitiwangsaensis* sp. nov. by having three body bands as opposed to four or more (one specimen [LSUHC 9009] out of 14 *C. bintangtinggi* sp. nov. has three bands). It differs from all species by having body band/ interspace ratio of 2.00–2.75 as opposed to a ratio of 2.00 or less (one specimen [ZRC 2.6964] of 11 *C. astrum* sp. nov., two specimens [LSUHC 9107–08] of 13 *C. australotitiwangsaensis* sp. nov., and one specimen [MS 441] of 16 *C. lekaguli* sp. nov. have a ratio of 2.00). *Cyrtodactylus trilatofasciatus* sp. nov. is further separated from *C.*

astrum sp. nov. in lacking a scattered dorsal pattern of white tubercles. *Cyrtodactylus trilatofasciatus* sp. nov. differs from all species except *C. australotitiwangsaensis* sp. nov. and *C. macrotuberculatus* by having no more than seven dark caudal bands. *Cyrtodactylus trilatofasciatus* sp. nov. differs from all species except *C. australotitiwangsaensis* sp. nov. and *C. macrotuberculatus* in having a maximum SVL greater than 115 mm.

TABLE 12. Morphological data of *Cyrtodactylus trilatofasciatus* from Pahang State, Malaysia. m=male; f=female; SVL=snout-vent length; TL=tail length; TW=tail width; FL=forelimb length; TBL=tibia length; AG=axilla-groin length; HL=head length; HW=head width; HD=head depth; ED=eye diameter; EE=eye to ear distance; ES=eye to snout distance; EN=eye to nostril distance; IO=interorbital distance; EL=ear length; and IN=internarial distance B = broken; PR = partially regenerated; R = regenerated; /=data unavailable.

	ZRC 2.6977 Paratype	ZRC 2.6978 Paratype	ZRC 2.6976 Holotype	LSUHC 10461 Paratype	ZRC 2.1178	ZRC 2.1179
Sex	f	m	m	f	m	f
Supralabials	10	12	11	10	10	10
Infralabials	10	10	11	8	11	11
Tubercles on ventral surface of forelimbs	0	0	0	0	0	0
Tubercles in gular region	0	0	0	0	0	0
Ventrolateral fold tuberculate	0	0	0	0	0	0
No. of paravertebral tubercles	36	36	38	38	37	34
No. longitudinal rows of tubercles	27	24	24	23	25	23
No. of ventral scales	33	36	34	33	33	35
Proximal subdigital lamellae square	0	0	0	0	0	0
No. of subdigital lamellae on 4th toe	22	25	25	23	27	27
No. of femoro-precloacal pores	/	44	41	/	46	/
Bands on base of thigh	1	1	1	1	0	0
No. body bands	3	3	3	3	3	3
Band/interspace width	2.25	2.00	2.75	2.25	2.50	2.50
No. dark bands on original tail	6	/	6	7	6	6
Hatch./juv. with white tail tips	/	/	/	/	/	/
SVL	119.1	115.6	122.2	113.7	114.3	99.1
TL	141	128R	150	153		
TW	9	9.4	11.1	9		
FL	19.8	20.4	19.8	17.8		
TBL	23.3	21.9	22.1	22		
AG	52.7	49.8	57.8	52.4		
HL	32.3	30.3	31.7	31.1		
HW	21.5	21.3	28.2	21.8		
HD	12.3	11.4	12.1	12.1		
ED	7.5	7.8	7.2	6.4		
EE	9.7	9.2	10	10.3		
ES	14.1	13.3	13.9	12.6		
EN	10.3	9.9	10.5	9.2		
IO	6.7	6.4	6.9	6.9		
EL	1.9	2.2	2.3	2.3		
IN	3	3.2	3.3	3.2		

FIGURE 16. Type series and additional specimens examined of *Cyrtodactylus trilatofasciatus.* Upper row: type series from left to right; holotype ZRC 2.6976, paratypes ZRC 2.6977–78, LSUHC 10461. Lower row: additional specimens examined from type locality from left to right: LSUHC ZRC 2.1178, 2.1179.

Remarks. Despite the fact that *Cyrtodactylus trilatofasciatus* sp. nov. from Cameron Highlands, Pahang and *C. australotitiwangsaensis* sp. nov. from Fraser's Hill and Genting Highlands, Pahang are sister species separated by only 76 km of continuous upland forest, the genetic distance between them ranges from 6.0–9.3%. This biogeographical pattern of well-differentiated sister lineages is consistent with other taxa from these areas such as *Cnemaspis flavolineata* (Grismer et al. in prep), *Larutia miodactyla* (Boulenger) (Grismer 2011:592), and *Sphenomorphus bukitensis* Grismer (Grismer 2011:631) as well as with the general high degree of herpetological endemism in Cameron Highlands (e.g. the megophryid *Kalophrynus youngi* Matsui; the microhylid *Leptolalax kecil* Matsui, Belabut, Norhayati & Yong; the agamid *Pseudocalotes flavigula* Smith; the scincid *Sphenomorphus cameronicus* Smith; the colubrids Smedley*; Macrocalamus schulzi* Vogel & David and *M. tweediei* Lim; and the viperid *Popeia nebularis* Vogel, David & Pauwels). Reasons for this high level of endemism are uncertain but it may have to do with the fact that the upland plateau of Cameron Highlands is extensive whereas the regions of Fraser's Hill and Genting Highlands are much more restricted, being little more than montane peaks.

***Cyrtodactylus australotitiwangsaensis* sp. nov.**
Southern Titiwangsa Bent-toed Gecko
Figs. 17,18

Cyrtodactylus pulchellus Lim *et al.* 2002:51; Grismer 2011:420 (in part).

Holotype.—Adult male (ZRC 2.6979) collected on 27 August 2006 by L. Grismer. P. Wood, Jr., and T. Youmans on the back road up to Fraser's Hill, Pahang, Peninsular Malaysia (03° 43.1699 N, 101° 45.4789 E) at 1059 meters above sea level.

Paratypes.—Paratypes ZRC 2.6980 and LSUHC 8088–90 (adult female and adult males, respectively) have the same collection data as the holotype. Paratype LSUHC 6637 (adult male) was collected on 18 August 2004 by P. Wood, Jr., and T. Youmans at Genting Highlands, Pahang, Peninsular Malaysia (03° 25.2388 N, 101° 47.3300 E) at 1346 meters above sea level.

Diagnosis.—Adult males reaching 120.1 mm SVL, adult females reaching 97.2 mm SVL; 9–12 supralabials, 9–13 infralabials; tubercles of dorsum small to moderately large with no intervening smaller tubercles; no tubercles on ventral surfaces of forelimbs, gular region, or in ventrolateral body fold; 37–45 paravertebral tubercles; 22–30 longitudinal rows of dorsal tubercles; 32–40 rows of ventral scales; 21–25 subdigital lamellae on fourth toe; 39–45 femoro-precloacal pores in males; dorsum not bearing a scattered pattern of white tubercles; three or four body bands in adults lacking lightened centers and light colored tubercles; band to interspace ratio 1.00–2.00; seven or eight dark, caudal bands on original tail; white caudal bands in adults immaculate; and posterior portion of tail in hatchlings and juveniles banded not white. These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

Description of holotype.—Adult male SVL 118.2 mm; head large, moderate in length (HL/SVL 0.28) and wide (HW/HL 0.73), somewhat flattened (HD/HL 0.37), distinct from neck, and triangular in dorsal profile; lores concave anteriorly, inflated posteriorly; frontal and prefrontal regions deeply concave; canthus rostralis sharply rounded anteriorly; snout elongate (ES/HL 0.40), rounded in dorsal profile, laterally constricted; eye large (ED/HL 0.22); ear opening elliptical, moderate in size (EL/HL 0.06), obliquely oriented; eye to ear distance greater than diameter of eye; rostral rectangular, divided dorsally by an inverted Y-shaped furrow, bordered posteriorly by left and right supranasals, and three small medial postrostrals (=internasals), bordered laterally by first supralabials; external nares bordered anteriorly by rostral, dorsally by a large anterior supranasal and small posterior supranasal, posteriorly by two smaller postnasals, ventrally by first supralabial; 11(R,L) rectangular supralabials extending to just beyond upturn of labial margin, tapering abruptly below midpoint of eye; first supralabial largest; 11(R) 10(L) infralabials tapering in size posteriorly; scales of rostrum and lores flat, larger than granular scales on top of head and occiput, those on posterior portion of canthus rostralis slightly larger; scales of occiput and top of head between eyes intermixed with small tubercles; large, boney frontal ridges bordering orbit confluent with boney, V-shaped, transverse, parietal ridge; dorsal superciliaries elongate, smooth, largest anteriorly; mental triangular, bordered laterally by first infralabials and posteriorly by left and right, rectangular postmentals which contact medially for 50% of their length; single row of enlarged, elongate sublabials extending posteriorly to seventh infralabial; small, granular to flat, gular scales grading posteriorly into larger, flat, smooth, imbricate, pectoral and ventral scales.

Body relatively short (AG/SVL 0.47) with well-defined, non-tuberculate, ventrolateral folds; dorsal scales small, granular, interspersed with larger, trihedral, regularly arranged, keeled tubercles, smaller intervening tubercles absent; tubercles extend from top of head from between eyes to caudal constriction and onto tail where they occur in transverse rows separated by six or seven small, flat scales; caudal tubercles largest dorsally, absent laterally and ventrally; caudal tubercles decrease in size posteriorly; tubercles on occiput and nape small, those on body largest; approximately 30 longitudinal rows of tubercles at midbody; 45 paravertebral tubercles; 38 flat imbricate ventral scales between ventrolateral body folds, ventral scales larger than dorsal scales; precloacal scales large, smooth; distinct precloacal groove.

Forelimbs moderate, relatively short (FL/SVL 0.18); scales on dorsal surfaces of forelimbs subimbricate, intermixed with larger tubercles; scales of ventral surface of forearm flat, subimbricate, lacking tubercles; palmar scales rounded; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae rectangular proximal to joint inflection, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; hind limbs more robust than forelimbs, moderate in length (TBL/SVL 0.20), larger tubercles on dorsal surface of thigh separated by smaller granular scales, tubercles on dorsal surfaces of foreleg same size as those on thigh; ventral scales of thigh flat, smooth, imbricate, larger than dorsal granular scales; ventral, tibial scales flat, smooth, imbricate; single row of greatly enlarged, flat, rectangular, imbricate, pore-bearing femoral scales extend from knee to knee through precloacal region where they are continuous with enlarged, pore-bearing precloacal scales; 43 contiguous, pore-bearing femoro-precloacal scales forming an inverted T bearing a deep, precloacal groove in which eight pore-bearing scales are found (four on each side of groove); postfemoral scales immediately posterior to pore-bearing scale row smaller, forming an abrupt union with pore-bearing postfemoral scales on posteroventral margin of thigh; plantar scales low, slightly raised; digits well-developed, inflected at basal, interphalangeal joints; subdigital lamellae proximal to joint inflection rectangular, only slightly expanded distal to inflection; digits more narrow distal to joints; claws well-developed, sheathed by a dorsal and ventral scale; 24(R,L) subdigital lamellae on 4th toe.

Tail 146 mm in length, 9.8 mm in width at base, tapering to a point; dorsal scales of tail flat, squarish; tail segmented with six or seven transverse scale rows per segment; posterior margin of segments bordered by four larger tubercles dorsally in anterior one-third of tail, fewer posteriorly; subcaudal region bearing large, transverse scales; shallow dorsal and lateral caudal furrows extend entire length of tail; base of tail bearing hemipenial swellings; three small, postcloacal tubercles on hemipenial swellings; postcloacal scales smooth, flat, large, imbricate.

Coloration in life. Dorsal ground color of head, body, limbs, and tail dark beige; no white chevron on rostrum; wide, dark brown nuchal band extends from posterior margin of one eye to posterior margin of other eye, edged with prominent thin, cream-colored, lines; three wide, similarly colored dorsal bands between limb insertions with immaculate, white tubercles forming a dotted line edging the bands; first band terminates at shoulders, second band terminates just dorsal to ventrolateral fold midway between limb insertions, third band terminates in groin and on anterior margin of hind limb; body band/interspace ratio of 1.25; one additional dark brown band posterior to hind limbs; no band on posterior margin of thigh; seven wide, dark bands approximately twice the width of seven white bands extend onto tail; all bands encircle tail, no bands on tail or body have lighten centers or encompass yellowish to white tubercles; ventral surfaces of head, limbs, and tail dull white; gular scales stippled; abdomen immaculate, beige; weakly stippled ventral scales.

Variation. The dorsal color of the paratypes closely matches that of the holotype although there is some departure in pattern (Fig. 18). The second and third body bands of LSUHC 6637 are broken just left of the midline and are offset. The second body band in LSUHC 8090 and ZRC 2.6980 is broken laterally with a fragment occurring on the right and left side of the midline respectively. LSUHC 6637 and 8089 have four instead of three body bands LSUHC 8089 has a regenerated tail, and LSUHC 6637 has eight instead of six dark caudal bands. Meristic differences in the type series are presented in Table 13.

Additional specimens examined. Variation in meristic characters for the type series and the additional specimens examined is listed in Table 13. Juveniles have a much bolder and contrasted color pattern than adults (Fig. 18).

Distribution. *Cyrtodactylus australotitiwangsaensis* sp. nov. ranges along the upland areas of the southern portion of the Titiwangsa Mountains from at least Fraser's Hill, Pahang in the north to Gunung Angsi, Negeri Sembilan in the south. Presumably it ranges farther to the north where it is likely to come in contact with its sister species *C. trilatofasciatus* sp. nov. and as far south perhaps as Gunung Ledang, Johor.

Natural history. *Cyrtodactylus australotitiwangsaensis* sp. nov. occurs in hill dipterocarp and lower montane forests (Fig. 17) from approximately 1000–1500 meters in elevation. It is a saxicolous lizard that emerges at night to forage among rocks or on nearby vegetation. At Fraser's Hill and Genting Highlands, Pahang, lizards are quite common along rocky road cuts. This species does not occur in forested areas where rocks are absent. Juveniles from Fraser's Hill have been collected in June (Grismer 2011).

Etymology. The specific epithet adjective *australotitiwangsaensis* is derived from the combination of the Latin *australis* meaning southern and the name of the mountain range, Titiwangsa, in which this species is endemic and refers to its occurrence in the southern portion of this range.

Comparisons. *Cyrtodactylus australotitiwangsaensis* sp. nov. is separated from *C. macrotuberculatus* in lacking large tubercles on the dorsal surface of the head, body and limbs, on the underside of the forearms, in the gular region, and in the ventrolateral body fold, and in having 32–40 ventral scales vs. 17–28. It is separated from *C. astrum* sp. nov., *C. langkawiensis* sp. nov., *C. lekaguli* sp. nov., and *C. pulchellus* in having more than 38 femoro-precloacal pores (it overlaps with *C. pulchellus* by one pore at 39). It differs from *C. trilatofasciatus* sp. nov. with a body band/interspace ratio of 1.00–2.00 (three specimens [LSUHC 9107–08, ZRC 2.5396] out of 13 had a ratio of 2.00) vs. 2.00–2.75. *Cyrtodactylus australotitiwangsaensis* sp. nov. is further separated from *C.*

astrum sp. nov. in lacking a scattered dorsal pattern of white tubercles. Having hatchlings and juveniles that lack white tail tips separate it from *C. astrum* sp. nov., *C. lekaguli* sp. nov., and *C. langkawiensis* sp. nov. Having less than nine dark caudal bands differentiates *C. australotitiwangsaensis* sp. nov. from *C. astrum* sp. nov., *C. langkawiensis* sp. nov., and *C. lekaguli* sp. nov. It is further separated from *C. astrum* sp. nov., *C. langkawiensis* sp. nov., *C. lekaguli* sp. nov., and *C. macrotuberculatus* by having immaculate white caudal bands as adults as opposed to white bands that are infused with dark pigment. Its large size (maximum SVL 120.1 mm) separates it from *C. astrum* sp. nov., *C. bintangtinggi* sp. nov., *C. langkawiensis* sp. nov., and *C. lekaguli* sp. nov. in that these species do not reach over 111.1 mm SVL.

FIGURE 17. Upper: *Cyrtodactylus australotitiwangsaensis* (LSUDPC 6431) from Fraser's Hill, Pahang, Malaysia. Lower left: *Cyrtodactylus australotitiwangsaensis* (LSUHC 8090) from Fraser's Hill, Pahang, Malaysia. Lower right: Lower montane forest habitat of *C. australotitiwangsaensis* at Fraser's Hill, Pahang, Malaysia. All photos by L. Grismer.

FIGURE 18. Type series and additional specimens examined of *Cyrtodactylus australotitiwangsaensis*. Upper row: type series from left to right; holotype ZRC 2.6979, paratypes LSUHC 8089–90, ZRC 2.6980, LSUHC 8088, 6637. Lower row: additional specimens examined from type locality from left to right; LSUHC 8087, 9107, 9108, from Genting Highlands from left to right ZRC 2.5396, from Gunung Angsi from left to right ZRC 2.1181, 2.1180.

Cyrtodactylus macrotuberculatus Grismer & Norhayati 2008
Large Tubercled Bent-toed Gecko
Fig. 19

Diagnosis.—Adult males reaching 118.6 mm SVL, adult females reaching 113.4 mm SVL; 9–12 supralabials, 7–11 infralabials; tubercles of dorsum very large with no intervening smaller tubercles; tubercles on ventral surfaces of forelimbs, in gular region, and in ventrolateral body fold; 31–44 paravertebral tubercles; 19–27 longitudinal rows of dorsal tubercles; 17–28 rows of ventral scales; 20–24 subdigital lamellae on fourth toe; 28–40 femoro-precloacal pores in males; dorsum not bearing a scattered pattern of white tubercles; four body bands in adults lacking lightened centers and light colored tubercles; band to interspace ratio 1.00–1.50; 7–10 dark, caudal bands on original tail; white caudal bands in adults infused with dark pigment; and posterior portion of tail in hatchlings and juveniles banded not white. These characters are scored across all species of the *Cyrtodactylus pulchellus* complex in Table 6.

Remarks. *Cyrtodactylus macrotuberculatus* was sampled from the type locality on Langkawi Island and five additional peninsular localities including Perlis State Park and Bukit Chabang, Perlis; and Gunung Jerai (including Hutan Lipur Sungai Tupah), Kedah (Fig. 3). Although the Langkawi population is monophyletic (exclusive), its overall sequence divergence from the remaining populations is relatively modest (2.2–5.9%) and it is not morphologically diagnosable from them (Tables 14–16). Although all four populations form a strongly supported monophyletic group, the relationships between them remain unresolved as indicated by the low support values from all three analyses (Fig. 1). Therefore at this point, we refrain from considering them different species. Additionally, the relationships between the peninsular populations was somewhat inconsistent with their pattern of distribution given that a Gunung Jerai specimen (LSUHC 9693) grouped with samples from Bukit Chabang, precluding exclusivity (reciprocal monophyly) between these lineages as well as the polytomus relationships of the three major *C. macrotuberculatus* lineages (Fig. 1). We consider the failure of haplotypes from a given locality to cluster together as evidence for potential gene flow between these localities. Lastly, these two groups are not morphologically diagnosable from one another (Tables 14–16) and we know of geographically intervening populations that we were unable to sample and suspect that gene flow here is highly likely. As such, we leave the taxonomy of *C. macrotuberculatus* unchanged. With tissue samples and specimens from the Thai populations, additional taxonomic interpretations may be necessary even though at this point, the few samples of the Thai populations (Tables 14–16) are not morphologically distinct from the Malaysian populations.

FIGURE 19. *Cyrtodactylus macrotuberculatus.* Upper left: LSUDPC 1461; subadult male from Gunung Machinchang, Pulau Langkawi (photo by L. Grismer). Upper right: LSUHC 9673; adult female from Hutan Lipur Sungai Pachat at the base of Gunung Jerai, Kedah, Malaysia (photo by L. Grismer). Middle left: LSUHC 9432; adult female from Gunung Raya, Pulau Langkawi, Kedah, Malaysia (photo by L. Grismer). Middle right: LSUDPC 6322; adult male from Songkhla, Thailand (photo by M. Sumontha). Lower left: LSUDPC 6323; hatchling from Ulu Muda, Kedah, Malaysia (photo by E. Quah). Lower right: LSUDPC 6324; adult male from La-ngu District, Satun Province, Thailand (photo by M. Sumontha).

Biogeography

Although the completely resolved and strongly supported relationships within the *Cyrtodactylus pulchellus* complex (Fig. 1) coupled with the geographically circumscribed distribution of the newly described species (Fig. 3) make it tempting to construct a historical biogeographical scenario to account for the evolution and distribution of the lineages of this group, such a scenario is premature at this juncture. We know very little about the distribution and taxonomy of this complex in the northern half of its range (i.e. that portion of Thailand between the Isthmus of Kra and the Thai-Malay border). Given the degree of this group's the local endemism in the hilly and mountainous areas of Peninsular Malaysia, it is logical to infer much the same occurs throughout its range in Thailand. To date, we have no tissue samples from specimens from any Thai populations nor have we examined

TABLE 13. Morphological data of type series and additional specimens of *Cyrtodactylus australotitiwangsaensis* from Pahang State, Malaysia. m=male; f=female; SVL=snout-vent length; TL=tail length; TW=tail width; FL=forelimb length; TBL=tibia length; AG=axilla-groin length; HL=head length; HW=head width; HD=head depth; ED=eye diameter; EE=eye to ear distance; ES=eye to snout distance; EN=eye to nostril distance; IO=interorbital distance; EL=ear length; and IN=internarial distance. B = broken; PR = partially regenerated; R = regenerated; /=data unavailable.

	ZRC 2.6980 Fraser's Hill Paratype	LSUHC 8088 Fraser's Hill Paratype	LSUHC 8089 Fraser's Hill Paratype	LSUHC 8090 Fraser's Hill Paratype	ZRC 2.6979 Fraser's Hill Holotype	LSUHC 6637 Genting Highlands Paratype	LSUHC 8087 Fraser's Hill	LSUHC 9107 Fraser's Hill	LSUHC 9108 Fraser's Hill	ZRC 2.5396 Genting Highlands	ZRC 2.1180 Gunung Angsi	ZRC 2.1181 Gunung Angsi
Sex	f	m	m	m	m	m	f	/	/	/	f	/
Supralabials	12	10	10	10	11	11	11	12	12	10	10	9
Infralabials	11	9	10	9	11	11	11	11	11	10	11	13
Tubercles on ventral surface of forelimbs	0	0	0	0	0	0	0	0	0	0	0	0
Tubercles in gular region	0	0	0	0	0	0	0	0	0	0	0	0
Ventrolateral fold tuberculate	0	0	0	0	0	0	0	0	0	0	0	0
No. of paravertebral tubercles	39	40	42	40	45	40	40	44	41	37	39	39
No. longitudinal rows of tubercles	29	27	28	27	30	24	27	26	27	28	26	22
No. of ventral scales	37	37	39	38	38	32	40	/	/	38	33	38
Proximal subdigital lamellae square	0	0	0	0	0	0	0	0	0	0	0	0
No. of subdigital lamellae on 4th toe	23	22	22	21	24	24	22	25	25	23	25	/
No. of femoro-precloacal pores	/	39	42	45	43	42	/	/	/	/	/	/
Bands on base of thigh	0	0	0	0	0	0	0	1	1	0	/	/
No. body bands	3	3	4	3	3	4	4	3	4	3	4	4
Band/interspace width	1.25	1.00	1.25	1.50	1.25	1.00	1.25	2.00	2.00	2.00	1.25	/
No. dark bands on original tail	7	/	/	7	7	8	8	/	/	7	/	/
Hatch./juv. with white tail tips	/	/	/	/	/	/	/	/	/	/	/	/
SVL	97.2	105.9	120.1	109.3	118.2	105.0	79.3	53.5	53.4	50.6	119.8	62.4
TL	125	/	113R	130	146	134						
TW	13	/	11.9	9.4	9.8	4.4						
FL	17	/	18.5	19.1	21.2	19.5						
TBL	19.1	/	23	21.2	23.9	22						
AG	41.8	/	52.8	49.9	55	44.2						
HL	26.8	/	33.5	29.2	33.1	31.2						
HW	19.3	/	25.2	21.2	24.3	20.7						
HD	10.3	/	14.7	11.4	12.8	11.2						
ED	5.6	/	12.5	7.5	7.4	6.8						
EE	8.9	/	10.5	8.8	10.2	9.2						
ES	11.5	/	14.5	13.1	13.3	12.7						
EN	8.6	/	12	10.1	10.6	10.7						
IO	5.7	/	7.8	6.2	6.5	7.3						
EL	2.3	/	2.1	1.9	2.1	2.8						
IN	3.1	/	3.8	3.6	3.9	3.2						

TABLE 14. Morphological data of *Cyrtodactylus macrotuberculatus* from Pulau Langkawi, Kedah, Malaysia. m=male; f=female; SVL=snout-vent length.

	LSUHC 6829	LSUHC 7532	LSUHC 7560	LSUHC 9133	LSUHC 9428	LSUHC 9429	LSUHC 9432	LSUHC 9448	LSUHC 9449	LSUHC 9450
Sex	/	f	/	m	m	f	m	/	f	f
Supralabials	10	11	11	11	10	11	9	10	11	10
Infralabials	9	8	8	9	8	9	8	9	9	9
Tubercles on ventral surface of forelimbs	1	1	1	1	1	1	1	1	1	1
Tubercles in gular region	1	1	1	1	1	1	1	1	1	1
Ventrolateral fold tuberculate	1	1	1	1	1	1	1	1	1	1
No. of paravertebral tubercles	36	40	39	40	39	42	41	38	35	39
No. longitudinal rows of tubercles	20	22	20	19	21	23	20	21	20	21
No. of ventral scales	23	21	/	20	19	24	21	17	22	23
No. of subdigital lamellae on 4th toe	20	24	20	21	22	20	21	23	22	21
No. of femoro-precloacal pores	/	/	/	31	28	/	31	/	/	/
Bands on base of thigh	0	0	0	0	0	0	0	0	0	0
No. body bands	4	4	4	4	4	4	4	4	4	4
Band/interspace width	1.00	1.00	1.00	1.00	1.00	1.00	1.25	1.00	1.25	1.00
No. dark bands on original tail	8	/	8	8	/	/	9	/	/	9
Hatch./juv. with white tail tips	0	/	0	/	/	/	/	/	/	/
SVL	44.9	106.1	48.8	88.2	113.7	111.3	108.6	48.0	111.5	89.0

specimens from any upland areas in the Nakhon Si Thammarat or Sankalakhiri mountains which are contiguous with the Banjaran Bintang and Banjaran Titiwangsa of Peninsular Malaysia. Additionally, trying to date these nodes with only a single mitochondrial gene would most likely inflate their ages and result large degrees of overlap (Matsui *et al.* 2010). These shortcomings notwithstanding, however, we can offer some inference on the evolution of the major clades within Peninsular Malaysia so as to at least establish testable hypotheses to be revised with an expanded morphological and molecular (including nuclear genes) data set (Grismer & Wood in prep.).

During the last 2.5 million years the Sundaic Region has been one of the most dynamically evolving landscapes in Southeast Asia (Bird *et al.* 2005; Cannon *et al.* 2009; Hall 1998, 2001, 2002; Outlaw & Voelker 2008; Reddy 2008; Woodruff 2003, 2010). The areal portions of this region only represent approximately 50% of the Sundaic landmass—the remaining 50% (the Sunda Plains) lying beneath the South China Sea—and this geographic configuration has persisted for only about 2% of the last two million years (Woodruff 2010). The cyclical, fluctuating changes in sea levels and complete submergence of the Sunda Plains coupled with concomitant changes in climate, have had a dramatic impact on the diversity and patterns of distribution of the Sundaic flora and fauna—patterns which cannot be surmised from current geography alone. These changes have been most pronounced along what is today the Thai-Malay Peninsula. The long, rocky spine of this unique physiographic feature is sculpted by a series of isolated, imbricating mountain ranges whose upland areas have provided cool refugia from the warmer, intervening lowland regions during Pleistocene interglacial episodes (Cannon *et al.* 2009; Woodruff 2010) when lower sea levels transformed the Thai-Malay Peninsula into a sky-island archipelago of mountain tops. The genetic signatures of such isolation events can be recovered in the fauna that they impacted and often manifest themselves in deep divergences between sister lineages on adjacent mountain ranges (Bell *et al.* 2010, 2011) that are usually corroborated by discrete morphological differences. Bell *et al.* (2011) demonstrated that multiple sister lineages on adjacent mountain ranges often result from repeated sequential vicariant episodes occurring over long periods of time. During cooler, glacial maxima, genetic admixture may occur between some of these previously relict, upland populations who migrate downslope with the advancing montane forest (Bell *et al.* 2010). Bell *et al.* (2010) suggest that a lack of such admixture is evidence that the relict populations remained in place during glacial episodes, however a more parsimonious explanation is that these relict populations developed reproductive incompatibility in isolation, migrated downslope with the advancing forest, but did not exchange genes when secondary contact occurred.

TABLE 15. Morphological data of *Cyrtodactylus macrotuberculatus* from Perlis State, Malaysia. m=male; f=female; SP=state park; SVL=snout-vent length.

	LSUHC 9214 Perlis	LSUHC 9980 Perlis	LSUHC 9981 Perlis	LSUHC 10067 Perlis	ZRC 2.4869 Perlis	LSUHC 9686 Bukit Chabang	LSUHC 10037 Bukit Chabang	LSUHC 10038 Bukit Chabang	ZRC 2.1919 Chuping
Sex	f	m	m	m	m	f	/	/	m
Supralabials	9	10	10	11	10	9	9	12	10
Infralabials	8	8	9	10	11	9	7	9	10
Tubercles on ventral surface of forelimbs	1	1	1	1	1	1	1	1	1
Tubercles in gular region	1	1	1	1	1	1	1	1	1
Ventrolateral fold tuberculate	1	1	1	1	1	1	1	1	1
No. of paravertebral tubercles	40	39	38	37	49	41	39	34	44
No. longitudinal rows of tubercles	23	23	21	23	27	21	22	19	24
No. of ventral scales	26	24	22	26	27	21	22	21	28
No. of subdigital lamellae on 4th toe	22	22	21	21	20	22	20	20	22
No. of femoro-precloacal pores	/	32	33	37	20	/	/	/	37
Bands on base of thigh	0	0	0	0	41	0	0	0	/
No. body bands	4	4	4	4	4	4	4	4	/
Band/interspace width	1.25	1.25	1.50	1.00	1.50	1.25	1.50	1.50	/
No. dark bands on original tail	9	/	/	/		/	/	/	/
Hatch./juv. with white tail tips	/	/	/	/		/	/	/	/
SVL	75.1	99.9	89.2	106.8	/	111.3	76.7	65.4	118.6

We hypothesize that the ecology of the ancestral species of the *Cyrtodactylus pulchellus* complex was that of warm-adapted lowland taxon given that there are only two cool-adapted upland lineages (*C. bintangtinggi* sp. nov. and the *C. trilatofasciatus* sp. nov.-*C. australotitiwangsaensis* sp. nov. lineage) that do not form a monophyletic group and are embedded within the phylogeny of the warm-adapted, lowland lineage species (Fig. 1). The mitochondrial phylogeny recovered a highly structured geographic pattern of diversity within the *C. pulchellus* complex with a deep basal split between northern and southern lineages (13.1–16.8% average sequence divergence) along the Kangar-Pattani Line—a region some authors recognize as the boundary between the Indochina and Sundaic ecoregions (Wikramanayake et al. 2002; Fig. 2). The northern lineage contains the insular endemic *C. langkawiensis* sp. nov. from Langkawi Island and *C. astrum* sp. nov. from the adjacent peninsula (*Cyrtodactylus lekaguli* sp. nov. is hypothesized to be a part of this clade but of unknown relationships). Their separation could have happened any time within the last 2.5 million years with one of the ~50 glacial cycles that caused sea levels to change ±50 m (Woodruff 2010), isolating the Langkawi landmass. Genetic divergence estimates (9.3–11.3%) would suggest this split happened very early on. The next major split occurs between two lineages composed of both lowland and upland sister taxa that show an average sequence divergence from one another of 8.6–13.1%. One of these lineages is associated with the Banjaran Bintang and contains the lowland *C. bintangrendah* sp. nov. and the upland *C. bintangtinggi* sp. nov. (Figs. 2,3). The other lineage contains the lowland sister species *C. pulchellus* (endemic to Penang Island) and *C. macrotuberculatus* of adjacent peninsular regions and their sister lineage composed of the upland sister species *C. trilatofasciatus* sp. nov. in the central Titiwangsa Range and *C. australotitiwangsaensis* sp. nov. in the southern portion of the Titiwangsa Range (Figs. 2,3). Early representatives of each one of these major lineages are likely to have migrated independently upslope with the retreating montane forests during one of the warmer interglacial periods and speciated *in situ* thus, producing sister lineages with both lowland and upland representatives. The lowland and upland sister lineages in the Bintang group (*C. bintangtinggi* sp. nov. and *C. bintangrendah* sp. nov., respectively) have a sequence divergence of 6.9–8.0% from one another. The divergence between the upland lineage of Titiwangsa group (*C. trilatofasciatus* sp. nov.-*C. australotitiwangsaensis* sp. nov. and the lowland lineage of *C. macrotuberculatus*-*C. pulchellus*) is 8.2–13.5%, suggesting that this speciation event occurred earlier than the speciation event giving rise to the Bintang lineages. In the case of the Titiwangsa group, further speciation occurred in the upland lineage while the lowland lineage expanded northward through the warm western lowland forests onto Penang Island and farther into Thailand, secondarily overlapping the *astrum-langkawiensis-lekaguli* clade (Fig. 3).

Discussion

Using an integrative taxonomic approach to discover deeply divergent lineages within a putatively single, wide ranging species is not novel (see Avise 2000; Padial *et al.* 2010) but it has never been applied to species of *Cyrtodactylus*—a genus whose species composition is already increasing at a rate faster than that of any other gekkonid lizard. The discovery here of seven additional species under the single nomen of *Cyrtodactylus pulchellus sensu strictu* may indicate that not only is the diversity of this genus increasing because of several newly discovered, unique, endemic lineages with highly restrictive distributions, but that many of its more common, widely distributed species may be composites of still more unnamed, species-level lineages. The results of this study add to a growing body of data on the hidden lizard diversity in Peninsular Malaysia and Singapore (see Grismer 2011). This is especially true for common, widely distributed species, which upon close examination, often prove to be complexes of multiple species (Grismer *et al.*, 2008; 2010b). *Cyrtodactylus quadrivirgatus* Taylor is proving to be just such a species. Johnson *et al.* (2012) and Grismer *et al.* (2012) noted that the swamp dwelling species *C. payacola* Johnson, Quah, Anuar, Muin, Wood, Grismer, Greer, Chan, Norhayati, Bauer & Grismer from western Peninsular Malaysia and *C. majulah* Grismer, Wood & Lim from Singapore and Indonesia, respectively, were previously considered part of *C. quadrivirgatus*. These studies serve as indicators that other wide-ranging common species could also be species complexes and if we are to truly understand and effectively and efficiently manage the biodiversity of the Thai-Malay Peninsula, then a closer inspection of many of these species should be undertaken. More importantly, however, is that such inspection need not await a molecular analysis, as the tens of newly described species from the Malay Peninsula and from this study were originally distinguished by morphological analyses (see Grismer, 2011 and Grismer *et al.* 2010b). At this point, there are far more specimens in museums awaiting examination than there are tissue samples in freezers.

Key to the species of the *Cyrtodactylus pulchellus* complex

The following key can be used as a guide to the identification of the species of the *Cyrtodactylus pulchellus* complex. However, it should be used in conjuction with the descriptions, diagnoses, and distribution sections in the text. The nature of the interspecific variation in morphology and color pattern within this group does not allow for all age groups of all species to be unequivocally diagnosed. Additionally, some diagnostic characters occur only in males, juveniles, or only on an original tail.

1. Tubercles in gular region. . . . . *macrotuberculatus*
   Tubercles not in gular region. 2

2. Centers of dorsal body bands in adults lighter in color than edges; posterior portion of tail in hatchlings and juveniles white . 3
Dorsal bands solid; hatchilngs and juveniles bearing fully banded tails throughtout length 5
3. Dorsum bearing scattered white dorsal spots between body bands in adults . . . . *astrum*
Dorsum not as above 4
4. 19–21 lamellae beneath 4th toe; occurs in the Langkawi Archipelago . . . .*langkawiensis*
20–25 lamellae beneath 4th toe; does not in the Langkawi Archipelago. . . . . *lekaguli*
5. Three wide dorsal bands (band/interspace ratio 2.00–2.75) . . . . *trilatofasciatus*
Four (rarely three) more narrow dorsal bands (band/interspace ratio ≤ 2.00 6
6. Maximun SVL 120.1 mm; from southern section of the Titiwangsa Range from Fraser's Hill south . . .*australotitiwangsaensis*
Maximun SVL < 115 mm; does not occur in the Titiwangsa Range 7
7. 29–34 ventral scales; from Pulau Pinang . . . .*pulchellus*
36–40 ventral scales; not from Pulau Pinang 8
8. 38–41 femero-precloacal pores; from the upper elevations (>800m) of the Bintang Range . . . . *bintangtinggi*
41–46 femero-precloacal pores; from the lowlands (<200m) surrounding the Bintang Range . . . .*bintangrendah*

TABLE 16. Morphological data of *Cyrtodactylus macrotuberculatus* from Kedah State, Malaysia and Thailand. m=male; f=female; SVL=snout-vent length.

	LSUHC 9671 Gunung Jerai	LSUHC 9672 Gunung Jerai	LSUHC 9673 Gunung Jerai	LSUHC 9690 Gunung Jerai	LSUHC 9693 Gunung Jerai	LSUHC 10330 Bukit Wang	LSUHC 10329 Bukit Wang	MS 402 Songkhla, Thailand	MS 443 Phattalung, Thailand	MS 444 Adang Island Thailand
Sex	m	m	f	f	f	m	m	m	f	m
Supralabials	10	9	10	9	10	10	11	10	9	10
Infralabials	9	10	10	9	11	9	8	9	8	10
Tubercles on ventral surface of forelimbs	1	1	1	1	1	1	1	1	1	1
Tubercles in gular region	1	1	1	1	1	1	1	1	1	1
Ventrolateral fold tuberculate	1	1	1	1	1	1	1	1	w	w
No. of paravertebral tubercles	38	37	37	39	36	36	36	40	31	39
No. longitudinal rows of tubercles	22	23	23	20	22	20	22	22	22	22
No. of ventral scales	23	22	22	20	26	22	23	21	22	26
No. of subdigital lamellae on 4th toe	21	22	23	24	22	22	22	20	22	22
No. of femoro-precloacal pores	/	39	/	/	/	40	34	35	/	38
Bands on base of thigh	1	0	0	1	0	0	/	0	0	0
No. body bands	4	4	4	4	4	4	4	4	4	4
Band/interspace width	1.25	1	1	1.5	1.25	1.25	1	1.25	1	1
No. dark bands on original tail	/	/	7	/	8	10	/	/	/	/
Hatch./juv. with white tail tips	/	/	/	/	/	/	/	/	/	/
SVL	85.5	105.1	113.4	106.2	110.3	84.1	104.0	111.7	100.7	117.7

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Appendix

The following preserved specimens and photographs were examined. For locality data of individuals from 22 other species of Sundaland *Cyrtodactylus* examined, see Grismer *et al*. (2010).

Cyrtodactylus pulchellus. Malaysia—Penang: Pulau Pinang; Empangan Air Itam LSUHC 6668; Moongate Trail LSUHC 6726–29, 6785; Air Terjun Titi Kerawang LSUHC 9967–68, 10022; Penang Hill ZRC 2.117, 2.5197, 2.4854, 2.5857.

Cyrtodactylus astrum. Malaysia—Perlis: Kuala Perlis LSUHC 8816, ZRC 2.6964; Gua Kelam LSUHC 8806, 8808, 8810, ZRC 2.6963; Wang Kelian LSUHC 10023–24; Gua Wang Burma LSUHC 8815, 9125, ZRC 2.6965. Thailand—Satun Province; La –ngu District LSUDPC 6317.

Cyrtodactylus lekaguli. Thailand—Trang Province; Khao Chong FMNH 176885, 21585–87, MS 441–42. Satun Province; La-ngu District MS 401, 445–46. Surat Thani Province: Kanchanadit District, Petch Phanomwung Cave MS 519. Phang-nga Province: Muang District, Suwankuha Cave MS 79. Nakkon Si Thammarat Province IRSNB 16558.

Cyrtodactylus langkawiensis. Malaysia—Kedah; Pulau Langkawi; Wat Wanaram LSUHC 9123–25, 9435–37, ZRC 2.6966–69.

Cyrtodactylus bintangtinggi. Malaysia—Perak: Bukit Larut ZRC 2.6970–72, LSUHC 9006–10.

Cyrtodactylus bintangrendah. Malaysia—Kedah: Bukit Palong ZRC 2.6975; Ulu Paip LSUHC 10331. Penang: Bukit Mertajam ZRC 2.6973–74, LSUHC 10520. Perak: Lenggong Valley LSUHC 9974–77; Gunung Pondok ZRC 2.1177.

Cyrtodactylus trilatofasciatus. Malaysia—Pahang: Cameron Highlands, Ringlet ZRC 2.1178–79, ZRC 2.6976–78, LSUHC 10461.

Cyrtodactylus australotitiwangsaensis. Malaysia—Pahang; Fraser's Hill LSUHC 8087–90; ZRC 2.6979–80; Genting Highlands LSUHC 6637, ZRC 2.5396–97; Gunung Angsi ZRC 2.118, 2.1181.

Cyrtodactylus macrotuberculatus. Malaysia—Kedah: Pulau Langkawi; Lubuk Semilang LSUHC, Gunung Raya LSUHC 7532, 9428–29, 9432, Gunung Machinchang LSUHC 7560, 9133, 9448–50, Hutan Lipur Sungai Tupah LSUHC 9671–73, 9690, 9693; Bukit Wang 10329–30, Ulu Muda LSUDPC 6323. Perlis: Perlis State Park LSUHC 9214, 9980–81, 10067, ZRC 2.4869; Bukit Chabang LSUHC 9686, 10037–38; Chuping ZRC 2.1919. Thailand—Phattalung Province: MS 443. Satun Province: Adang Island MS 444, La-ngu District LSUDPC 6324. Songkhla Province: Rattabhumi District LSUDPC 6322, MS 402.