Zootaxa 5570 (1): 081–099
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5570.1.3
http://zoobank.org/urn:lsid:zoobank.org:pub:335A37F5-199F-4025-9DBA-8AF569B058E9

A New Species Belonging to the *Cyrtodactylus sadleiri* Complex (Squamata: Gekkonidae) Has Been Discovered in East Java, Indonesia

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Abstract

We describe a new species of *Cyrtodactylus* Gray from East Java (Maospati and Mojokerto), Indonesia that belongs to the *C. sadlieri* complex within the *C. darmandvillei* species group. It is a medium sized (SVL) species with adult males reaching 67.2 mm and females 59.0 mm, dorsal tubercles absent on brachium, present on antebrachium and along the ventrolateral fold; 18–20 irregular dorsal tubercle rows at midbody; 26–28 paravertebral tubercles per series; 28–34 ventral scale rows across belly; precloacal groove present with 32–37 precloacofemoral pores in males; enlarged femoral and precloacal scales arranged in a continuous series; abrupt transition between the enlarged femorals and the adjacent scales on the posterior margin of the thigh; subequal median subcaudal scales not transversely enlarged. The new species is genetically divergent from the other Javan congeners of the *C. darmandvillei* groupwith genetic divergences (p-distances) ranging from 7.7–12.1% for the mitochondrial ND2 gene.

Key words: phylogeny, *C. darmandvillei*, East Java, taxonomy

Introduction

Java is one of the most biodiverse hotspots on Earth (Cincotta *et al*. 2000) and it is the thirteenth largest island in the world (Dahl 1991) with an area of ~128,000 km^2 (Monk *et al*. 1997). Being almost entirely of volcanic origin, it is composed of 38 active volcanoes forming an east-west spine on the island (Whitten *et al*. 1996). This created the island's unique geographical and ecological conditions which have contributed to the evolution of Java's gekkonid fauna over millions of years, with many species becoming endemic to the island (O'Connell *et al*. 2019). Currently, there are four described bent-toed geckos of the genus *Cyrtodactylus* Gray known to occur on this island: *C. belanegara* Riyanto, Hikmah, Amarasinghe, Abinawanto & Hamidy, 2024, *C. marmoratus* Gray, 1831, *C. petani* Riyanto, Grismer & Wood, 2015, and *C. semiadii* Riyanto, Bauer & Yudha, 2014. *C. belenegara*, *C. marmoratus* and *C. semiadii* belong to the *C. marmoratus* group sensu Grismer *et al*. (2021), which is a complex of species, whereas *C. petani* belongs to the *C. darmandvillei* group (sensu Grismer *et al*. (2021)). Based on our comprehensive fieldwork in Java with subsequent integrative taxonomic studies, we have found and present genetic and morphological data that indicate specimens from Maospati and Mojokerto (East Java) represent an unrecognized species. Our genetic data place these specimens in the *C. darmanvillei* group (sensu Grismer *et al*. 2021) and belonging to *C. sadleiri* complex (sensu Reilly *et al*. 2023), and are described herein.

Accepted by M. Heinicke: 27 Nov. 2024; published: 16 Jan. 2025

Materials and Methods

Molecular analyses. In March and May 2023, we conducted a field trip in Java, and collected several *Cyrtodactylus* specimens from urban areas in Maospati and Mojokerto which have a flat topography raging in elevation from 200–750 m above sea level (Figure 1A). All specimens were euthanized with sodium pentobarbital, and fixed in 10% buffered formalin prior to storage in 70% ethanol. The liver tissue samples were preserved for DNA analysis in 95% ethanol. All specimens were permanently deposited at the Museum Zoologicum Bogoriense (MZB), National Research and Innovation Agency, Cibinong, West Java, Indonesia. New genetic sequences generated in this work were deposited in GenBank, and additional genetic data were downloaded from GenBank (Appendix 1). We follow Riyanto *et al*. (2020) and consider DNA sequences from specimens from Cibodas, West Java to represent true *C. marmoratus* and use *Gekko gecko* and *Hemidactylus frenatus* as outgroups. The genomic DNA from liver samples was extracted using a Qiagen DNeasy Extraction Kit. A partial mitochondrial sequence of the protein-encoding gene NADH dehydrogenase subunit 2 (ND2) was amplified with the primers following Oliver *et al*. (2016) M: 112F (5'–AAGCTTTCGGGGCCCATACC–3') and M1123R (5'–GCTTAATTAAAGTGTYTGAGTTGC–3'). The PCRs were performed in 25 µL total volumes using Top Taq by Qiagen comprising 1.0 µL DNA template, 2.5 µL 10X Top Taq PCR buffer, 0.5 µL 10mM dNTP mix, 2.5 µL 10X CoralLoad, 5 µL 5X Q solution, 1.0 µL light strand primer, 1.0 µL heavy strand primer, 0.125 µL Top Taq DNA polymerase with appropriate buffer and ddH2O to volume. PCR reactions were executed on an Eppendorf Mastercycler under the following conditions: initial denaturation at 94^{o}C for 9 min, second denaturation at 94^{o}C for 45 s, annealing at 60^{o}C for 45 s, and a cycle extension at 72^{o}C for 1 min, for 35 cycles. Purified PCR products were sequenced by 1st Base Asia, Singapore.

We assembled and aligned DNA sequences and available data from GenBank using Clustal W in MEGA X v10.1.7 (Kumar *et al*. 2018). The uncorrected *p*-distance (sequence divergence) was calculated in MEGA X, and all ambiguous positions were removed for each sequence pair (pairwise deletion option employed). The final alignment of ~ 997 bp was analyzed using Maximum Likelihood (ML), implemented in IQ-TREE (Nguyen *et al.* 2015). We used the function -m MFP+MERGE (Lanfear *et al*. 2017) to identify the partition strategy and molecular models (first codon position TPM2u+F+G4: second codon position HKY+F+G4: third codon position TPM3u+F+R2), and 5000 ultrafast bootstrap replicates (Hoang *et al.* 2017). Nodes with bootstrap values of 95% and above were considered highly supported (Minh *et al*. 2013).

Morphological data. Measurements and scale counts were made on the right side of each specimen (except on labials and if damaged) under an Am Scope dissecting microscope. Measurements were done by using a Mitutoyo digital calliper to the nearest 0.1 mm. The following measurement definitions were followed: Snout–vent length (SVL), tip of snout to vent; tail length (TailL), vent to tip of tail; head length (HL), tip of snout to posterior edge of retroarticular process of lower jaw; head width (HW), straight line between angles of jaw; head height (HH), maximum height of head between occiput and throat; snout length (SL), tip of snout to anteriormost edge of orbit; eye to ear distance (EE), edge of orbit to anterior edge of ear opening; ear length (EL), maximum length of ear opening; orbit diameter (OD), horizontal diameter of orbit; forearm length (ForL), taken on the ventral surface from the posterior margin of the elbow while flexed 90° to the inflection of the flexed wrist; axilla groin length (AGL), axilla to groin; tibia length (TibL), taken on the ventral surface from the posterior surface of the knee while flexed 90° to the base of the heel.

Meristic data were taken following Riyanto *et al*. (2022). We counted supralabial scales from the first scale behind the rostral scale to the largest scale immediately posterior to dorsal inflection of posterior portion of upper jaw; infralabial scales (number of labial scales of lower jaw, beginning with first scale bordering mental shield, ending with last enlarged scale bordering angle of jaw); dorsal tubercles (DorT), number of longitudinal tubercle rows on dorsum at midbody between ventrolateral folds; paravertebral tubercles (PVT), tubercles along paravertebral region, counted between postaxial margin of arm and pre-axial margin of leg; ventral scales (VS), number of ventral scales at midbody, counted in one row between ventrolateral folds across the belly; number of lamellae under fingers 1–5 ($F_{1–5}$, subdigital lamellae counted from point where interdigital skin contacts digit regardless of condition of scales under digit at this point, including fractured scales but not the elongate ungual scale at the base of the claw [claw sheath] or lamellae that extend onto the palm at base of digit); number of lamellae under toes 1–5 ($T_{1–5}$, subdigital lamellae counted from point where interdigital skin contacts digit regardless of condition of scales under digit at this point, including fractured scales but not including the elongate ungual scale at the base of the claw or lamellae that extend onto plantar surface at the base of the digit). Basal subdigital scales were counted

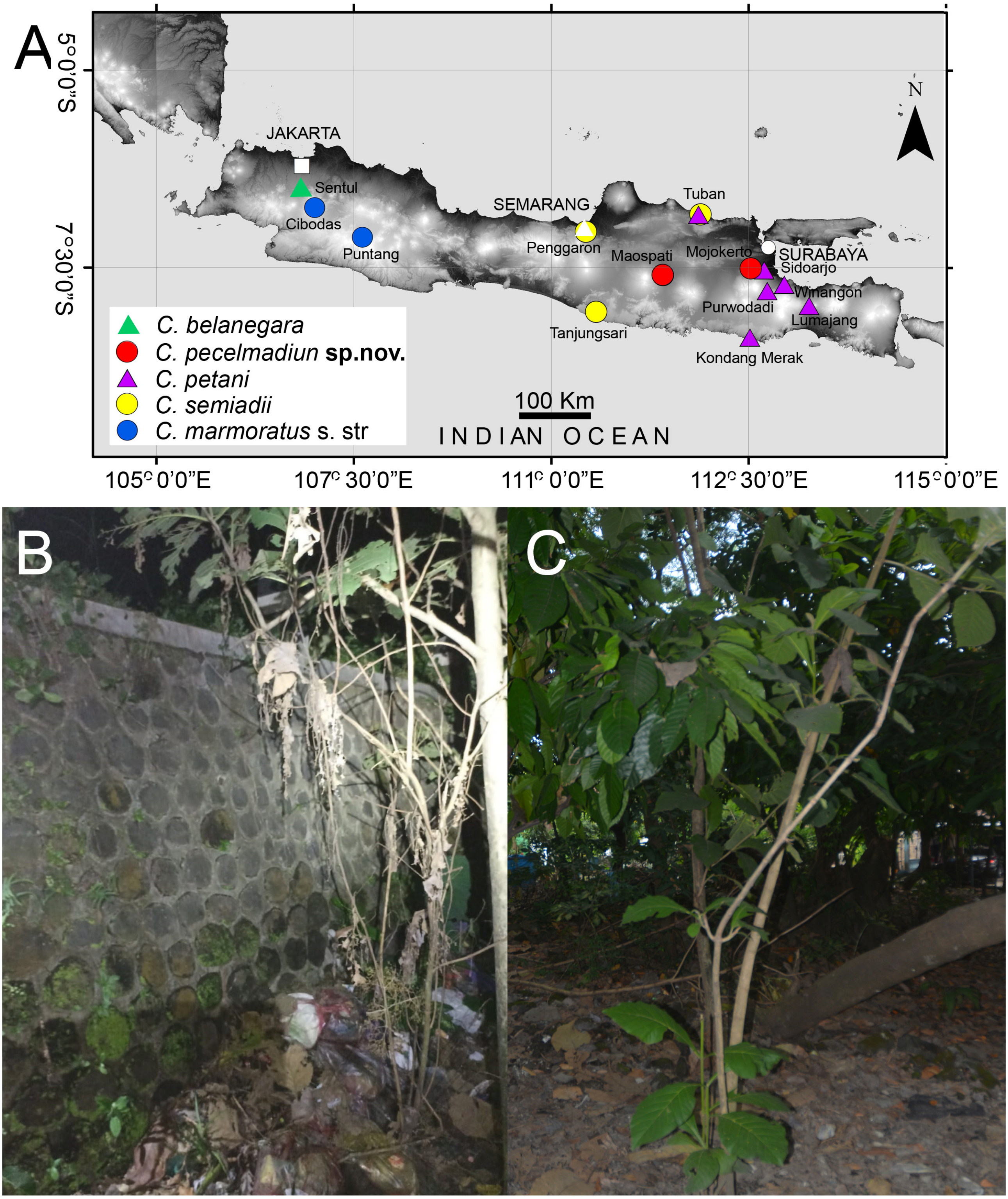

FIGURE 1. A. Map of Java illustrating the distribution of the members of *Cyrtodactylus darmanvillei* group and the *C. marmoratus* group. B. Type locality of *C. pecelmadiun* **sp. nov.** at Maospati, East Java. C. Paratype recorded at Mojokerto, East Java. Photographs by A. Riyanto.

from the most proximal scale at least twice as large as adjacent palmar scales following Bauer *et al*. (2010). Where relevant we also noted the following characters: presence of tubercles on the dorsal surfaces of the brachium (upper arm), antebrachium (forearm) and thigh; presence of enlarged precloacofemoral scales (EPFS), and extent to which these formed a continuous series; and presence of transversely enlarged median subcaudals. Following Grismer *et al*. (2016), we evaluated an abrupt contact between large and small postfemoral scales and ventral femoral scales versus smooth transition. We follow Mecke *et al*. (2016) in describing the morphology of precloacal depressions. Sex was determined as male if (1) preserved specimens showed enlarged hemipenial pockets, and confirmed by (2) viewing the hemipenes via a small lateral incision made at the base of the tail. In order to examine smaller characters such as keeling in the ventrals, we followed Amarasinghe *et al*. (2015) and Harvey *et al*. (2015) and applied the reversible stain methylene blue in 70% ethanol. Color notes were taken from digital images of living specimens prior to preservation. Comparative specimens examined in this paper are listed in Appendix 2.

Statistical analyses. Statistical analyses were conducted using R (R Core Team, 2021). Due to small sample size the statistically informative tests could not be performed on separate sexes (Zar 2010). Juveniles were excluded to avoid the bias of allometry for the statistical analysis. A separate t-test and analysis of variance test were performed to assess the morphometric variation between the new species (n=8) and *C. petani* (n=12). To remove potential effects of allometry in the morphometric characters, size was normalized using the following equation: $X_{adj} = \log(X) - \beta[\log(SVL) - \log(SVL_{mean})]$, where Xadj = adjusted value; X = measured value; β = unstandardized regression coefficient for each population; and SVLmean = overall average SVL of all populations (Thorpe 1975, 1983; Turan 1999; Lleonart *et al*. 2000) in the package GroupStruct (Chan & Grismer 2022). The morphometrics of each species were normalized separately and then concatenated so as not to conflate intra- with interspecific variation (Reist 1986). A multivariate analysis was conducted using Principal Component Analysis (PCA) on the scaled morphometrics above to reduce the highly correlated multidimensional data matrix into a few uncorrelated variables [i.e., principal components (PC)]. The prcomp function in the R statistical software program was used (v4.0.4; R Core Team 2021). Biplots of the first two principal component scores were used to examine the trajectory of the morphospatial differentiation between the species.

Results

Our molecular analysis showed that the *Cyrtodactylus* specimens from East Java (Maospati and Mojokerto) are nested within the *Cyrtodactylus darmandvillei* group (sensu Grismer *et al*. 2021) and specifically belong to the *C. sadleiri* complex (*sensu* Reilly *et al*. 2023). This population is the highly supported (99) sister species of a clade containing *C. batucolus* and *C. petani* (Figure 2) It differs from these by an uncorrected *p*-distance of 8.3–10.2% (Table 1).

TABLE 1. Uncorrected pairwise sequence divergence (%) for 997 base pairs of the ND2 protein-coding mitochondrial gene among *Cyrtodactylus sadleiri* complex.

Cyrtodactylus	*Cyrtodactylus*					
	pecelmadiun	*petani*	*batucolus*	*jatnai*	*sadleiri*	*seribuatensis*
pecelmadiun	0.0–3.9					
petani	8.3–10.2	0.1–1.6				
batucolus	7.7–9.6	6.2–7.0	0.0			
jatnai	9.0–10.2	9.3–10.1	10.2–10.5	0.0–0.6		
sadleiri	9.1–10.0	9.8–10.1	9.7–9.8	3.5–3.7	0.0	
seribuatensis	10.8–12.1	10.2–10.5	11.1	8.3–9.1	8.1–8.4	0.0

The t-test recovered statistically significant differences ($p \leq 0.05$) between the Maospati-Mojokerto population and *C. petani* (Table 2) in all morphometric characters and the meristic characters (DorT and VS), demonstrating that the population from Maospati-Mojokerto is relatively larger in all metrics than *C. petani* (Figure 3). The PCA analysis also showed distinct overall differences (Figure 4). Principal components 1 and 2 collectively explained 75.27% of the variation in the morphometric data (Table 3). The morphometric characters SVL, AGL, HL, HW, HH, SL, and OD loaded positively with principal component 1, whereas in component 2 there are five adjusted morphometric characters SVL, HL, HW, HH, and SL which loaded positively (Table 3). Given these results, we describe the Maospati-Mojokerto population as a new species.

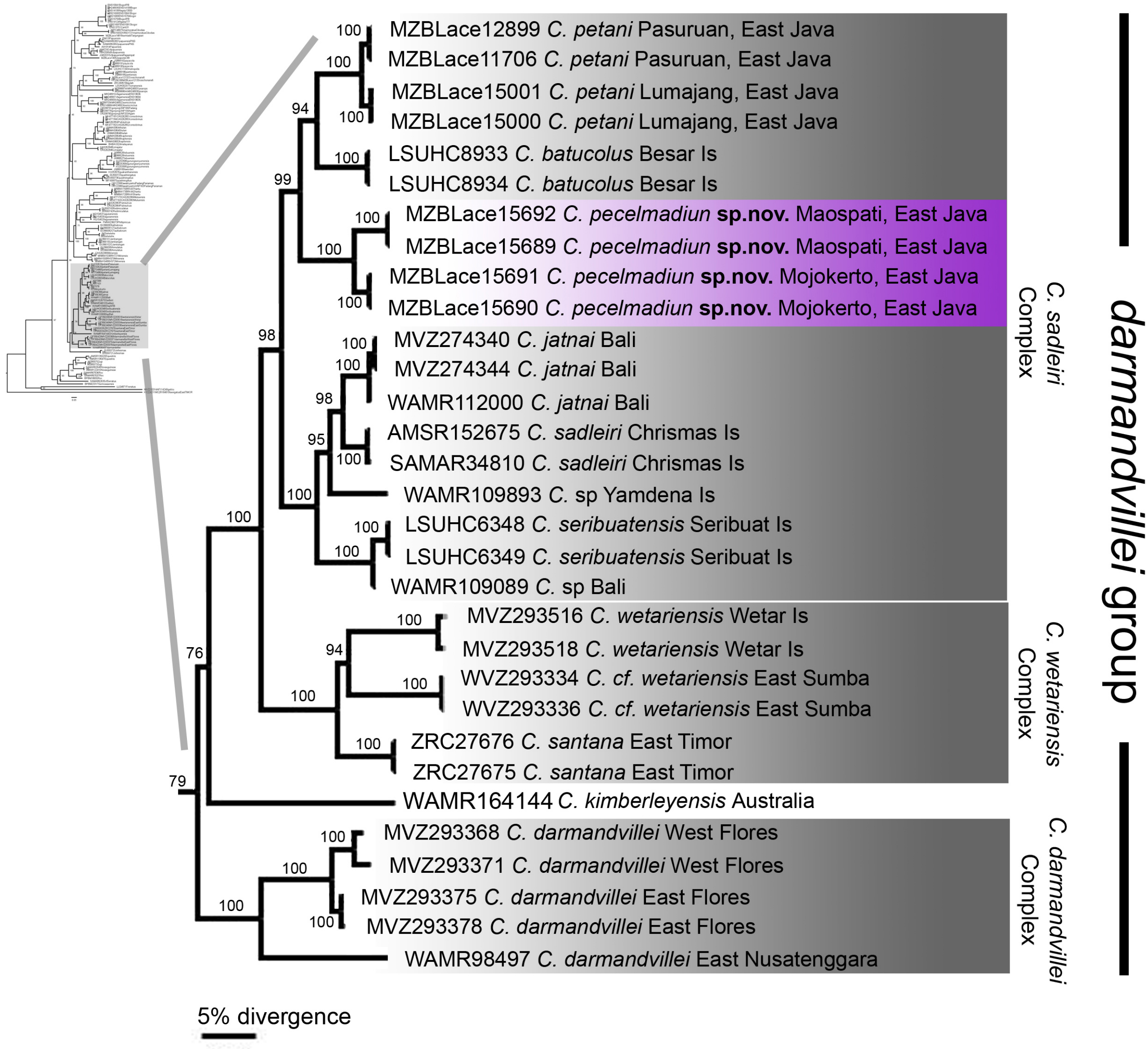

FIGURE 2. Consensus tree from the ML analysis showing the new species within the clade of *Cyrtodactylus darmandvillei* group and the *C. sadleri* complex using ~ 997 bp fragment of ND2 mitochondrial gene and its flanking tRNAs.; outgroup taxa, *Gekko gecko* and *Hemidactylus frenatus*, are not shown.

TABLE 2. Summary statistics and t-test resultson variation of morphometric between *C. pecelmadiun* **sp. nov**. and *C. petani*.

	C. pecelmadiun **sp.nov.** (n = 8)	*C. petani* n = 12)	T	*P* value
Scaled SVL	**1.802(±0.0181)**	**1.754(±0.0422)**	**3.4802**	**0.003105**
Scaled AGL	**1.443(±0.0118)**	**1.392(±0.0258)**	**6.3736**	**6.849e-06**
Scaled HL	**1.263(±0.0149)**	**1.217(±0.0219)**	**5.1911**	**6.288e-05**
Scaled HW	**1.109(±0.0141)**	**1.025(±0.0213)**	**10.387**	**5.017e-09**
Scaled HH	**0.882(±0.0513)**	**0.833(±0.2672)**	**2.5223**	**0.03254**
Scaled SL	**0.867(±0.0274)**	**0.800(±0.0207)**	**6.1353**	**6.586e-05**
Scaled OD	**0.641(±0.0601)**	**0.579(±0.0318)**	**2.7033**	**0.02285**
PVT	27.25000	27.58333	-0.48684	0.633
DorT	**19.25**	**18.25**	**2.2563**	**0.04159**
VS	**31.5**	**36.42**	**-5.0398**	**0.000122**
T_4	17.88	18.25	-0.7807	0.446

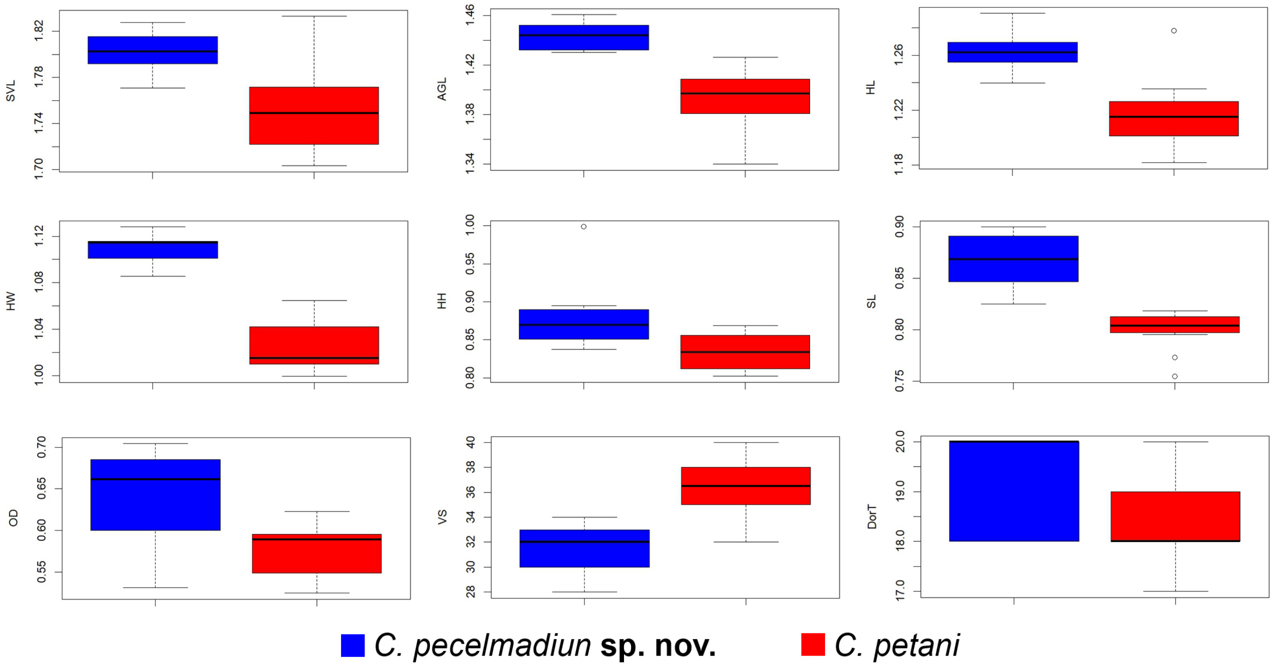

FIGURE 3. Box plots of adjusted SVL, AGL, HL, HW, HH, SL, OD, VS, and DorT showing differences between *Cyrtodactylus pecelmadiun* **sp. nov.** and *C. petani*.

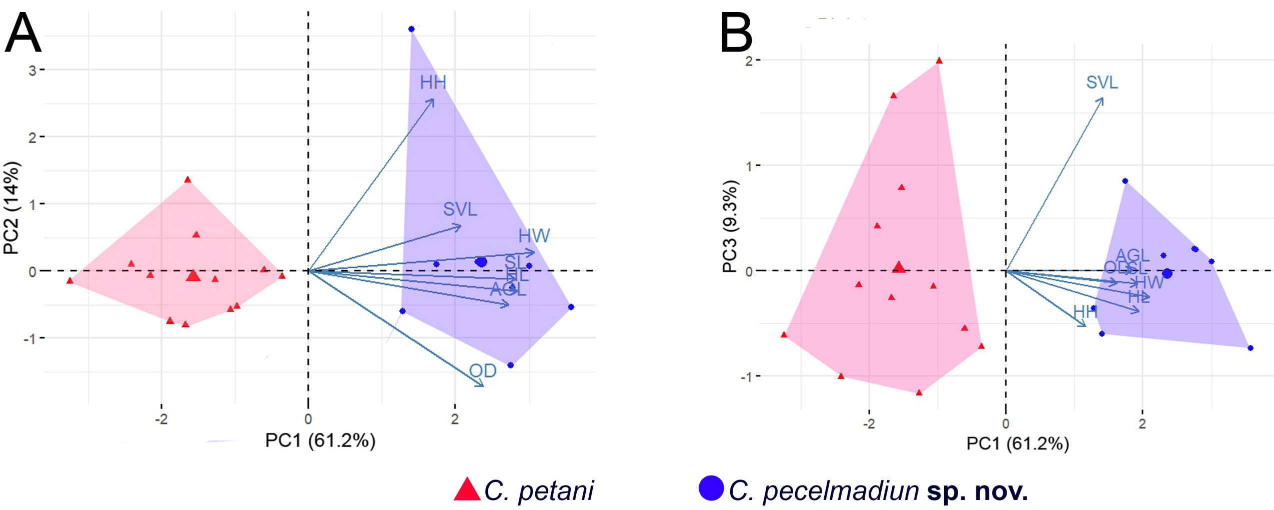

FIGURE 4. PCA plots of the adjusted morphometric variation between the new species (blue circle) and *Cyrtodactylus petani* (red triangle).

TABLE 3. Principal component analysis (PCA) and factor loadings of PC1 and PC2. Principal component 1 (PC 1) and PC 2 collectively account for 75.27% of the variation in the data set.

PCA variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Standard deviation	2.0706	0.9908	0.8070	0.6501	0.5554	0.4938	0.3237
Proportion of Variance	0.6125	0.1403	0.0930	0.0604	0.0441	0.0348	0.0150
Cumulative Proportion (%)	61.25	75.27	84.58	90.61	95.02	98.50	100.00
Loading							
Scaled SVL	0.307	0.209	0.914	0.000	0.136	0.000	0.000
Scaled AGL	0.403	-0.157	0.000	-0.691	-0.421	0.239	0.319
Scaled HL	0.420	0.000	-0.217	-0.140	0.654	-0.459	0.331
Scaled HW	0.453	0.000	-0.141	-0.185	0.146	0.128	-0.833
Scaled HH	0.252	0.795	-0.297	0.211	0.000	0.316	0.270
Scaled SL	0.417	0.000	0.000	0.394	-0.587	-0.564	0.000
Scaled OD	0.352	-0.532	0.000	0.514	0.102	0.545	0.133

Systematics

Cyrtodactylus pecelmadiun **sp. nov.**
English Common Name: Pecelmadiun's Bent-toed Gecko
Indonesia Common Name: Cecak Jari Bengkok Pecel Madiun
urn:lsid:zoobank.org:act:2DDA0FF0-1D85-4E10-ADDB-77C43549C178
(Figs. 5 & 6)

Holotype. MZB Lace 15689, adult male (Fig. 5A) from Tanjungsepreh Village, Maospati District, Magetan Regency, East Java Province, Indonesia (7.59701S; 111.4141E; 137 m asl), collected 9 May 2023 by Awal Riyanto and Asrael Racho.

Paratypes. MZB Lace 15690 (Fig. 5B), adult male, MZB Lace 15691, sub adult female from Pekukuhan Village, Mojosari, Mojokerto Regency, East Java Province, Indonesia (7.51245S; 112.527E; 60 m asl), collected 11 March 2023 by Awal Riyanto, Richo Firmansyah, Nanang Kamaludin and Faturrahman; MZB Lace 15692, female, from Tanjungsepreh Village, Maospati District, Magetan Regency, East Java Province, Indonesia (7.59619S; 111.41171E; 137 m asl), collected 12 March 2023 by Awal Riyanto, Richo Firmansyah, Nanang Kamaludin and Faturrahman Sidiq; MZB Lace 15693, 15694, 15695, 15696 and 15697, males, same data as holotype.

Diagnosis. The following combination of characters distinguishes *C. pecelmadiun* **sp. nov.** from all other congeners: adult males reaching 67.2 mm SVL and females 59.0 mm SVL; dorsal tubercles absent on brachium, present on antebrachium and within the ventrolateral fold; 18–20 irregular dorsal tubercle rows at midbody; 26–28 paravertebral tubercles per series; 28–34 ventral scale rows across belly; precloacal groove present with 32–37 precloacofemoral pores in males, absent in females; enlarged femoral and precloacal scales arranged in a continuous series; abrupt transition between the enlarged femorals and the adjacent scales on the posterior margin of the thigh; and subequal median subcaudal scales not transversely enlarged.

Description of holotype. Moderate-sized species, 64.5 mm SVL; head triangular in dorsal view, distinct from neck; tubercles present on the occiput and dorsolateral of head; head long (HL/SVL 0.28), rather wide (HW/SVL 0.20), head wider than high (HW/HH 1.67); snout elongate (SL/HL 0.39); canthus rostralis rounded, distance between eye-to-naris greater than the diameter of orbit (EE/OD 1.26); eye large (OD/HL 0.25); supraciliaries extending from anterior-ventral to posterior-dorsal edge of eye, longest at the anterior-dorsal part; ear opening small, dorsoventrally oblong, and oriented about 45 degrees to apex of rictus.

Rostral rectangular, incompletely divided dorsally by a Y-shaped shallow groove, wider than hight (RW/RH 1.54), bordered posterolaterally by first supralabials and naris, and dorsally by three postrostral scales; naris oval, bordered anteriorly by rostral, anterodorsally by 1 postrostral, posteriorly by three scales in right side and by three scales in left side, and ventrally by first supralabials; orbit separated from supralabials by two rows of small lorilabial scales; 11 supralabial scales to angle of jaw in right side, 10 in left side; 8 infralabial scales right side, 7 in left side . Mental triangular, slightly wider than long (ML/MW 0.76); bordered laterally by first infralabials, posteriorly by a pair of enlarged first postmentals, which contact medially over about 58.7% of their length; second postmentals ovoid, about one-third of the first postmentals and separated from each another by 4 granular scales; gular sales small, granular, grading to slightly smaller size posteriorly.

Body elongate (AGL/SVL 0.43); dorsal scales small and granular, interspersed with relatively high, keeled to rounded tubercles irregularly arranged in 20 longitudinal rows at midbody; ventrolateral body folds with blunt conical tubercles; 26 paravertebral tubercles in each row. Ventral scales larger than dorsal scales, smooth, flat, imbricate, 30 ventral scale rows between ventrolateral body folds across the belly; enlarged scales immediately anterior to the cloacal opening absent.

Forelimbs relatively short (ForL/SVL 0.15); dorsal scales on forelimbs and upper arms tri-keeled, forelimbs bearing tubercles, antebrachium lacking tubercles; palmar scales flat, smooth, subimbricate; digits well develop, inflected at basal interphalangeal joints, digits slightly narrower distal to inflection; subdigital lamellae transversely expanded along the entire length of each digit, but slightly compressed in both length and width immediately distal to interphalangeal inflection; subdigital lamellae on digits of manus: I(16), II(17), III(16), IV(15), V(14); claws well developed, sheathed by 2 dorsal scales and 1 ventral scale.

Hindlimbs longer than forelimbs (TibL/SVL 0.18); covered dorsally by granular scales interspersed with larger, keeled tubercles; anterioroventral scales of thigh rounded, smooth, flat, subimbricate to juxtaposed; enlarged femoral and precloacal scales arranged in a continuous series, the largest in femoral part; precloacal groove present;

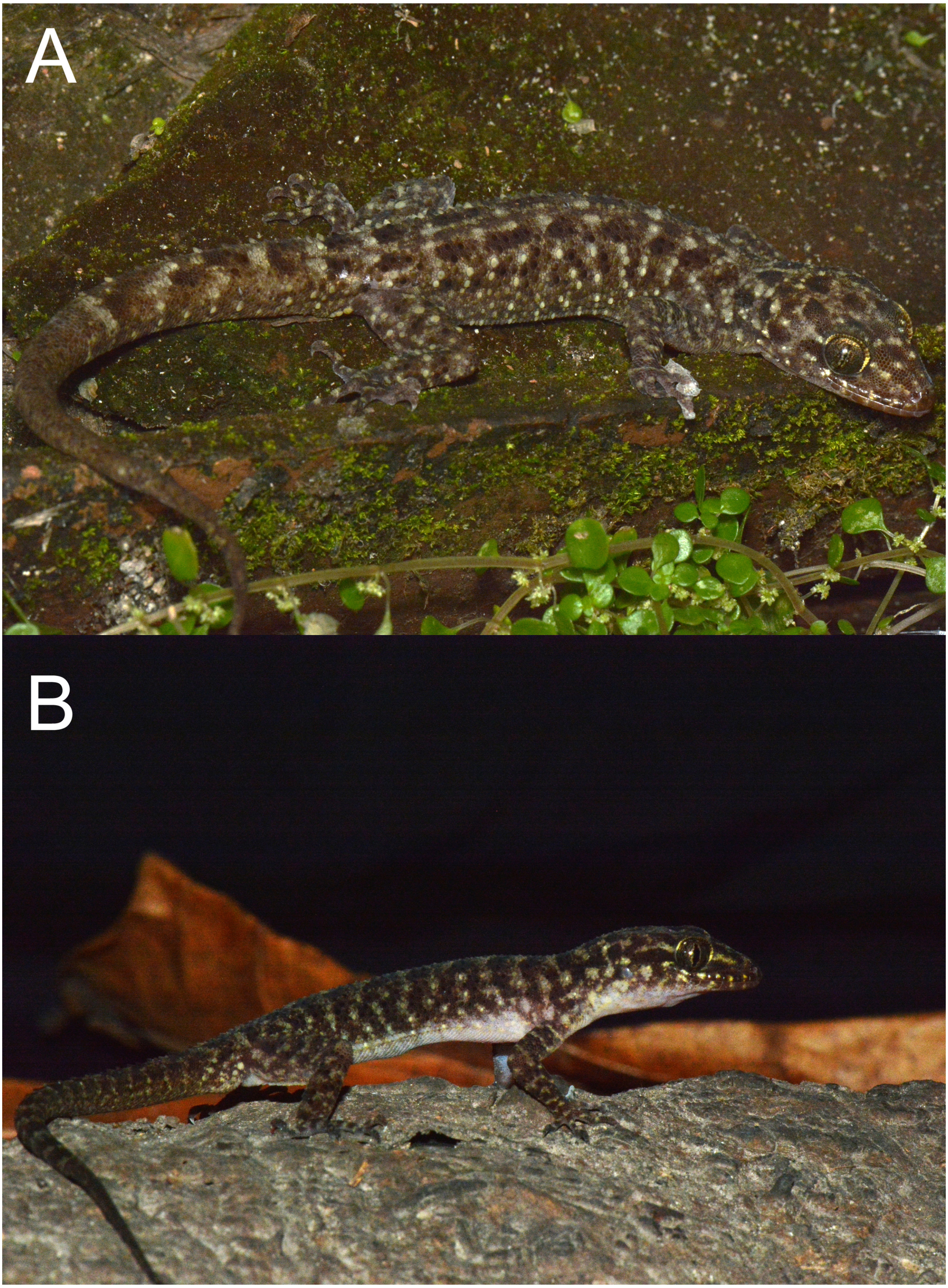

FIGURE 5. Living specimens of the Javanese *Cyrtodactylus*, (A) adult male of *Cyrtodactylus pecelmadiun* **sp. nov.** from Maospati district, Magetan regency, East Java (holotype, MZB.Lace.15689), (B) adult male from Mojokerto, East Java (paratype, MZB.Lace.15690). Photos by A. Riyanto.

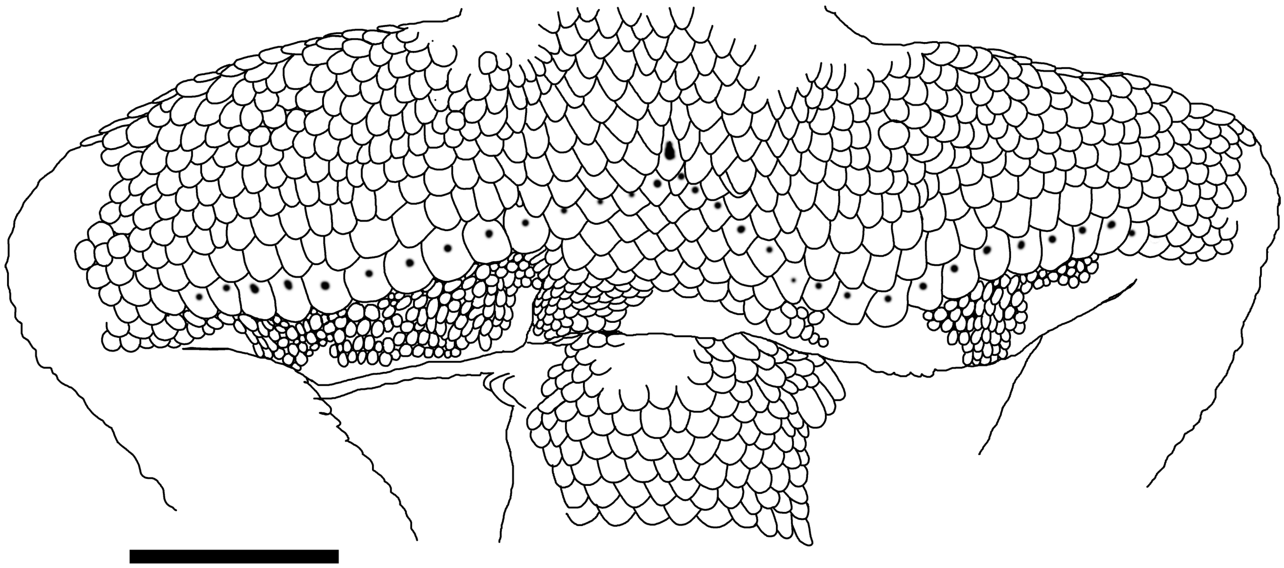

FIGURE 6. Precloacal depression and enlarged precloacofemoral scales of *Cyrtodactylus pecelmadiun* **sp. nov.** Illustration by A. Riyanto. Scale = 5 mm.

32 precloacofemoral pores in Λ-shape (Figure 6); ventral scales on tibia smooth, flat, subimbricate; plantar scales slightly raised; digits well developed, inflected at basal metapodial-phalangeal joints, digits slightly narrower distal to inflection; subdigital lamellae transversely expanded along the entire length of each digit, but slightly compressed in both length and width immediately distal to interphalangeal inflection; subdigital lamellae on digits of pes: I(12), II(16), III(16), IV(18), V(17); claws well developed, sheathed by 2 dorsal scales and 1 ventral scale.

Tail regenerated, 85.9 mm length; on the original part segmented, dorsally with keeled tubercles arranged in transverse rows forming whorls and original part of subcaudal without enlarged transverse plates; three postcloacal tubercles (spur) on each side in both sexes.

Coloration in life. Ground coloration overlain with brown markings widely edged in black. On the flanks, tubercles edging the brown; dorsal markings are frequently bright-yellow, sharply contrasting with the adjacent color. The anterior supraciliaries are also yellow with some black areas. The rostral, mental, narial region, and labials are mostly charcoal to black, with yellow spots on the rostral and narial regions, and the labials are marked by widely spaced distinctive yellow spots. Dorsally, paired subcircular blotches cover the nape and extend to the original tail where they transform into irregularly shaped bands; seven paravertebral blotches between axilla to groin and five on original tail; on the flanks thin blotches bordered by a thin yellow line occur between paired blotches. The iris is greenish yellow, edged in yellow and bearing a black reticulum.

Variation. Males have precloacofemoral pores and a precloacal groove, whereas females do not. The last one-half to the tail in the holotype is regenerated but complete in paratype (MZBLace 15690) (Fig. 5B). Detailed variation of mensural and meristic characters of the type series are presented in Table 4.

Etymology. The specific epithet is a noun in apposition "pecel" and 'madiun". Pecel is a traditional chili sauce that is originally from East Java, and made from chili pepper, peanuts, garlic, lime, and palm sugar with various boiled vegetables (such as spinach, water spinach, casava leaves, papaya leaves, long beans, bean sprouts, or sesban flowers) and peanut brittle or anchovies as the secondary ingredients, and served in a plate made from banana leaves. Madiun refers to the name of the city that is famous for this traditional pecel culinary delight.

Comparison. *Cyrtodactylus pecelmadiun* **sp. nov.** differs statistically ($p<0.05$) from is sister species *C. petani* in the morphometric characters of SVL, AGL, HL, HW, HH, SL and OD, and the meristic characters DorT and VS. From more distantly related species in Java it differs from *C. marmoratus*, it can be differentiated by smaller adult body size in SVL (67.2 mm *versus* 85.7 mm), fewer ventral scales (30–35 versus 34–46), precloacal groove in Λ-shape (*versus* a deep inverse Y-shape), and fewer precloacofemoral pores (32–35 *versus* 24–52) and fewer subdigital lamellae under the fourth toe (17–18 *versus* 20–24 lamellae). It differs from *C. semiadii* in having a larger adult body size (known maximum SVL 67.2 mm *versus* 51.4 mm), precloacofemoral pores (*versus* precloacal pores), and abrupt transition (*versus* lacking). It differs from *C. belanegara* in having a larger adult body size (known maximum SVL 67.2 mm *versus* 53.8 mm), fewer ventral scales (28–34 *versus* 37–40, and precloacofemoral pores (*versus* discontinued precloacal and femoral pores).

TABLE 4. Meristic and morphometric data of the type series of *C. pecelmadiun* **sp. nov**., measurements in mm.

Characters	*C. pecelmadiun* **sp. nov.**								
MZB Lace	15689	15690	15691	15692	15693	15694	15695	15696	15697
Status	holotype	paratype	paratype	paratype	paratype	paratype	paratype	paratype	paratype
Sex	male	male	female, subadult	female	male	male	male	male	male
Tubercles on occiput	present	present	present	present	present	present	present	present	present
Tubercles on upper arms	absent	absent	absent	absent	absent	absent	absent	absent	absent
Enlarged transverse median subcaudal	absent	absent	absent	absent	absent	absent	absent	absent	absent
Precloacal depression	groove	no	no	groove	groove	groove	groove	groove	groove
SVL	64.5	61.1	55.5	59.0	67.2	63.2	62.7	65.4	63.7
TL/SVL	reg	1.40	reg	broken	reg	reg	reg	reg	1.26
AGL/SVL	0,42	0.46	0.42	0.44	0.43	0.45	0,43	0.43	0,44
HL/SVL	0.28	0,31	0.29	0,29	0.28	0.28	0.28	0.29	0.29
HW/SVL	0.21	0.21	0.19	0.19	0.19	0.20	0.21	0.20	0.21
HW/HH	1.72	1.64	1.63	1.62	1.79	1.87	1.29	1.76	1.90
SL/HL	0.44	0.40	0.40	0.38	0.39	0.42	0.38	0.39	0.41
EE/OD	1.26	1.24	1.24	1.23	1.53	1.04	1.40	1.23	1.49
DorT	20	20	18	20	18	20	20	18	18
PVT	26	27	26	28	28	27	28	28	26
VS	30	34	34	34	28	30	32	32	32
PFP	32	37	32	35	32	37	35	35	37
T_4	19	18	19	19	18	18	16	17	18

It differs from *Cyrtodactylus batucolus* Grismer, Onn, Grismer, Wood & Belabut, 2008 from Malaysia by having fewer precloacofemoral pores (32–37 *versus* 43–46) and a smaller maximum adult SVL (67.2 mm *versus* 75.2 mm). From *C. seribuatensis* Youmans & Grismer, 2006 from Malaysia it differs in having fewer precloacofemoral pores (32–37 *versus* 40–44) and a smaller maximum adult SVL (67.2 mm *versus* 75 mm). Detailed comparison among other species of the *C. sadleiri* complex are presented in Table 5.

Distribution and natural history. *Cyrtodactylus pecelmadiun* **sp. nov.** was collected in the lowlands of East Java. The type series was collected from a variety of habitats, i.e. paddy field embankments, a pile of building tiles left over from the building near the bushes and gardens in the village (Figure 1B & C). All were found no more than 40 cm above the ground. Given these observations, we consider this species as a habitat generalist (*sensu* Grismer *et al*. 2021).

Discussion

Our findings underscore that the diversity of Javanese *Cyrtodactylus* is still underestimated. This and other undescribed findings regarding the Javan group *C. marmoratus* (O'Connell *et al*. 2019; Riyanto at al., in prep) support this supposition. We strongly advocate for the use of an integrative taxonomic approach which has helped to uncover the cryptic diversity of *Cyrtodactylus* from Java and elsewhere. Many studies in Java have proven that this approach greatly increases the statistical defensibility of our species hypotheses. Among amphibians, the description of *Leptophryne javanica* by Hamidy *et al*. (2018), *Chirixalus pantaiselatan* by Munir *et al*. (2021), *Theloderma pseudohorridum* by Kurniawan *et al*. (2023), and *Zhangixalus faritsalhadii* by Gonggoli *et al*. (2024) all used an integrative taxonomic approach. Among reptiles, studies such as the description of *C. petani* (Riyanto *et al*. 2015), *Cnemaspis muria* (Riyanto *et al*. 2018) and *C. belanegara* (Riyanto *et al*. 2024) continue to underscore the need for this approach. Moreover, the number of sampling locations will also open up more opportunities to discover new findings.

TABLE 5. The selected diagnostic characters separating *Cyrtodactylus pecelmadiun* **sp.nov**. from other species of the *C. sadleiri* complex. ? = unknown or not assessable.

	C. pecelmadiun **sp.nov**.	*C. batucolus*	*C. darmandvillei*	*C. jatnai*	*C. petani*	*C. sadleiri*	*C. seribuatensis*
Source	This study (n=9)	Grismer *et al.* 2008	Chan *et al.* 2023	Amarasinghe *et al.* 2020; This study (n=8)	This study (n=12)	Chan *et al.* 2023	Youmans & Grismer 2006
Max SVL (mm)	67.2	75.2	75	66.8	69	88	75
DorT	18–20	?	?	17–19	15–20	?	?
PVT	26–28	30–35	17–20	24–29	26–33	22–25	27–35
VS	28–34	38–42	36–40	40–48	32–40	34–42	28–39
Precloacal depression	groove	pit	absent	pit	groove	groove	no
EPFS	present	present	present	present	present	present	present
PFP	32–37	43–46	?	40–43	30–40	—	40–44
Tubercles on lateral skin folds	present	?	present	present	absent	absent	absent
Abrupt transition	present	present	present	abrupt	present	?	abrupt
Enlarged median subcaudal scales	absent	absent	present	absent	absent	absent	absent
T_4	16–19	17–19	?	17–19	17–20	19–24	19–22

The new species is the second description of a species in the *C. darmandvillei* group occurring in Java following *C. petani.* These two species are distributed in lowland and degraded habitats. The distribution of the *C. darmandvillei* group is unique in that it occurs on islands off the east and west coast of Pennisular Malaysia and then again in East Java, Bali and the Lesser Sunda with no known related species as yet from the intervening areas such as Borneo.

Acknowledgments

We are grateful to the National Research and Innovation Agency Republic of Indonesia (BRIN), Nanang Kamaludin (Diponegoro University), Fathurrahman Sidiq (Semarang University), Muhammad Alif Fauzi and Richo Firmansyah (Brawijaya University), and Asrael Racho (Palangka Raya University) for their excellent help with logistics and hospitality during fieldwork. We also thank anonymous reviewers for helpful comments on an earlier version of this MS. This work was support by the Directorate of Research and Development, Universitas Indonesia under PUTI Q1 programme (grant NKB-449/UN2.RST/HKP.05.00/2023), and Degree by Research Scholarships (DBR)- BRIN.

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APPENDIX 1. Summary of *Cyrtodactylus* specimens corresponding to genetic samples included in the study, general locality, and GenBank accession.

Species	Voucher	Locality	GenBank Acc	Sources
C. agamensis	ENS19636	Indonesia, Sumatra	MH248910	O'Connel *et al*. 2019
C. agamensis	ENS19694	Indonesia, Sumatra	MH248907	O'Connel *et al*. 2019
C. agamensis	ENS 19635	Indonesia, Sumatra	MH248909	O'Connel *et al*. 2019
C. agusanensis	KU320015	Philippines. Mindanao Island	HQ154531	Welton *et al*. 2010b
C. agusanensis	KU320009	Philippines. Mindanao Island	HQ154529	Welton *et al*. 2010b
C. agusanensis	KU320014	Philippines, Mindanao Island	HQ154530	Welton *et al*. 2010b
C. annulatus	KU 309363	Philippines, Camiguin Sur Island, Municipality of Mambajao	GU366099	Davis *et al*. 2020
C. annulatus	KU 309365	Philippines, Camiguin Sur Island, Municipality of Mambajao	GU366098	Davis *et al*. 2020
C. awalriyantoi	UNP 154	Indonesia, West Sumatra, Padang Pariaman	OR122990	Ahda *et al*. 2023
C. awalriyantoi	UNP 163	Indonesia, West Sumatra, Padang Pariaman	OR122989	Ahda *et al*. 2023
C. batucolus	LSUHC 8933	Malaysia, Peninsular Malaysia, Melaka, Pulau Besar	JQ889178	Johnson *et al*. 2012
C. batucolus	LSUHC 8934	Malaysia, Peninsular Malaysia, Melaka, Pulau Besar	JQ889179	Johnson *et al*. 2012
C. consobrinus	CAS 262851	Malaysia, Borneo, Sarawak, Bau, Gua Angin	MK477181	Davis *et al*. 2019
C. consobrinus	CAS 262852	Malaysia, Borneo, Sarawak, Bau, Gua Angin	MK477182	Davis *et al*. 2019
C. consobrinus	CAS 262853	Malaysia, Borneo, Sarawak, Bau, Gua Angin	MK477184	Davis *et al*. 2019
C. consobrinus	CAS 262854	Malaysia, Borneo, Sarawak, Bau, Gua Angin	MK477183	Davis *et al*. 2019
C. darmandvillei	WAM R98497	Indonesia, East Nusa Tenggara	KU232616	Riyanto *et al*. 2015
C. darmandvillei	MVZ293368	Indonesia, West Flores	OP356429	Reilly *et al*. 2023
C. darmandvillei	MVZ293371	Indonesia, West Flores	OP356430	Reilly *et al*. 2023
C. darmandvillei	MVZ293375	Indonesia, East Flores	OP356426	Reilly *et al*. 2023
C. darmandvillei	MVZ293378	Indonesia, East Flores	OP356422	Reilly *et al*. 2023
C. equestris	ASMR135520	PNG	KT835458	Oliver *et al*. 2016
C. equestris	ASMR119547	PNG	KT835457	Oliver *et al*. 2016
C. gonjong	UNP 194	Indonesia, West Sumatra, Padang Pariaman	OR208778	Nugraha *et al*. 2023
C. gonjong	UNP 165	Indonesia, West Sumatra, Padang Pariaman	OR208791	Nugraha *et al*. 2023
C. gonjong	UNP 203	Indonesia, West Sumatra, Padang Pariaman	OR208780	Nugraha *et al*. 2023
C. gunungsenyumensis	LSUHC 12201	West Malaysia, Pahang, Hutan Lipur Gunung Senyum	KU253585	Grismer *et al*. 2016
C. gunungsenyumensis	LSUHC 12204	West Malaysia, Pahang, Hutan Lipur Gunung Senyum	KU253586	Grismer *et al*. 2016

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APPENDIX 1. (Continued)

Species	Voucher	Locality	GenBank Acc	Sources
C. gunungsenyumensis	LSUHC 12205LLL	West Malaysia, Pahang, Hutan Lipur Gunung Senyum	KU253584	Grismer *et al*. 2016
C. hantu	BRK 437	Malaysia, Sarawak, Pelagus, Pelagus Resort	MN884175	Davis *et al*. 2020
C. hantu	BRK 415	Malaysia, Sarawak, Pelagus, Pelagus Resort	MN884172	Davis *et al*. 2020
C. hantu	BRK 442	Malaysia, Sarawak, Pelagus, Pelagus Resort	MN884173	Davis *et al*. 2020
C. *hutan*	UNIMAS 9644	Malaysia, Serawak, Gunung Mulu National Park	OP480051	Davis *et al*. 2023
C. hutan	UNIMAS 9645	Malaysia, Serawak, Miri, Gunung Mulu National Park	OP480052	Davis *et al*. 2023
C. hutan	UNIMAS 9646	Malaysia, Serawak, Miri, Gunung Mulu National Park	OP480053	Davis *et al*. 2023
C. jambangan	KU314793	Philippines, Mindanao Island	GU366100	Welton *et al*. 2010a
C. jambangan	KU314806	Philippines, Mindanao Island	GU366101	Welton *et al*. 2010a
C. jambangan	KU314835	Philippines, Mindanao Island	GU366102	Welton *et al*. 2010a
C. jatnai	MVZ274340	Indonesia, Bali	OP356366	Reilly *et al*. 2023
C. jatnai	MVZ274344	Indonesia, Bali	OP356365	Reilly *et al*. 2023
C. jatnai	WAMR112000	Indonesia, Bali	KU232624	Riyanto *et al*. 2015
C. jellesmae	RMB 1672	Indonesia, Sulawesi Island, Eastern Sulawesi, Siuna	GU550721	Siler *et al*. 2010
C. jellesmae	RMB 1692	Indonesia, Sulawesi Island, Eastern Sulawesi, Siuna	GU550720	Siler *et al*. 2010
C. kapitensis	UNIMAS 9653	Malaysia, Serawak, Kapit	OP480056	Davis *et al*. 2023
C. kapitensis	UNIMAS 9654	Malaysia, Serawak, Kapit	OP480057	Davis *et al*. 2023
C. kapitensis	UNIMAS 9656	Malaysia, Serawak, Kapit	OP480058	Davis *et al*. 2023
C. kimberleyensis	WAM R164144	Australia, Western Australia, East Montalivet Island	JX440544	Wood *et al*. 2012
C. limajalur	CAS 262946	Malaysia, Sarawak, Serian	MK477177	Davis *et al*. 2019
C. limajalur	CAS 262848	Malaysia, Sarawak, Serian	MK477178	Davis *et al*. 2019
C. majulah	ZRC 26951	Singapore, Nee Soon Swamp	JX988529	Grismer *et al*. 2012
C. malayanus	BABAO 024	Indonesia, Kalimantan, Sungai Babao	MK477159	Davis *et al*. 2019
C. marmoratus	ABTC48075	Indonesia, West Java, Cibodas	JQ820292	Oliver *et al*.2012
C. marmoratus	ENS15932	Indonesia, West Java, Cibodas	KR921721	O'Connel *et al*. 2019
C. metropolis	LSUHC 11343	Malaysia, Selangor, Batu Caves	KU253578	Grismer *et al*. 2016
C. miriensis	BRK721	Malaysia, Sarawak, Lawas	MN884153	Davis *et al*. 2021
C. miriensis	BRK 79	Malaysia, Sarawak, Lambir Hills	MN884155	Davis *et al*. 2021
C. miriensis	BRK572		MN884154	Davis *et al*. 2021

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APPENDIX 1. (Continued)

Species	Voucher	Locality	GenBank Acc	Sources
C. miriensis	CAS 262989	Malaysia, Serawak, Mulu, Gua Lang	MK477175	Davis *et al*. 2021
C. muluensis	CAS 262983	Malaysia, Serawak, Mulu, Gua Lang	MK477163	Davis *et al*. 2019
C. muluensis	CAS 262984	Malaysia, Serawak, Mulu, Gua Lang	MK477170	Davis *et al*. 2019
C. novaeguinea	SAMAR62648	PNG, Libano	JQ820302	Oliver *et al*. 2012
C. novaeguinea	ASMR122410	PNG, Waro	Q820301	Oliver *et al*. 2012
C. pantiensis	LSUHC 8905	Malaysia, Johor, Gunung Panti FR, Bunker Trail	JQ889186	Johnson *et al*. 2012
C. pantiensis	LSUHC 8906	Malaysia, Johor, Gunung Panti FR, Bunker Trail	JQ889185	Johnson *et al*. 2012
C. papeda	MZBLace 14052	Indonesia, Moluccas, Obi Island	OM158779	Riyanto *et al*. 2022
C. papuensis	AA1914	Indonesia, Papua, Fak Fak	OM517149	Tallowin *et al*. 2018
C. papuensis	PMO3	PNG	OM517150	Tallowin *et al*. 2018
C. papuensis	SAMA R62651	PNG, Western Province, Libano	Q820321	Oliver *et al*. 2012
C. papuensis	SAMA R62652	PNG, Western Province, Libano	JQ820320	Oliver *et al*. 2012
C. cf. *papuensis*	JAM 2242	Indonesia, Buru Island	MF169967	Brennan *et al*. 2017
C. cr. *papuensis*	TNHC59549		JX440546	Wood *et al*. 2012
C. cf. *papuensis*	MZB.Lace. 5419	Indonesia, Papua Barat, Raja Ampat	JQ820315	Oliver *et al*. 2012
C. payacola	LSUHC9982	Malaysia, Penang, Bukit Panchor	JQ889192	Johson *et al*. 2012
C. payacola	LSUHC10071	Malaysia, Penang, Bukit Panchor	JQ889191	Johson *et al*. 2012
C. payacola	LSUHC10070	Malaysia, Penang, Bukit Panchor	JQ889190	Johson *et al*. 2012
C. pecelmadiun **sp.nov.**	MZBLace15691	Indonesia, East Java, Mojokerto	PQ591470	This study
C. pecelmadiun **sp.nov.**	MZBLace15690	Indonesia, East Java, Mojokerto	PQ591471	This study
C. pecelmadiun **sp.nov.**	MZBLace15692	Indonesia, East Java, Maospati	PQ591469	This study
C. pecelmadiun **sp.nov.**	MZBLace15689	Indonesia, East Java, Maospati	PQ591468	This study
C. petani	MZBLace 11706	Indonesia, East Java, Pasuruan	KU232620	Riyanto *et al*. 2015
C. petani	MZBLace 12899	Indonesia, East Java, Pasuruan	KU232619	Riyanto *et al*. 2015
C. petani	MZBLace 15000	Indonesia, Jawa Timur Province, Lumajang Regency, Danau Klakah	MT704864	Riyanto *et al*. 2020
C. petani	MZBLace 15001	Indonesia, Jawa Timur Province, Lumajang Regency, Danau Klakah	MT704865	Riyanto *et al*. 2020
C. philippinicus	FMNH 236073	Philippines, Romblon Island	JX440550	Wood *et al*. 2012
C. psarops	MZBLace 9686	Indonesia, Sumatra, Lampung	MH248930	O'Connel *et al*. 2019
C. psarops	MZBlace 9687	Indonesia, Sumatra, Lampung	MH248931	O'Connel *et al*. 2019
C. pubisulcus	CAS 262963	Malaysia, Serawak, Bau, Gua Angin	MK1447166	Davis *et al*. 2019
C. pubisulcus	CAS 262964	Malaysia, Serawak, Bau, Gua Angin	MK1447165	Davis *et al*. 2019

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APPENDIX 1. (Continued)

Species	Voucher	Locality	GenBank Acc	Sources
C. quadrivirgatus	LSUHC 9013	Malaysia, Perak, Bukit Larut	GU550723	Johnson *et al*. 2012
C. quadrivirgatus	LSUHC 9864	Malaysia, Perak, Bukit Larut	GU550736	Johnson *et al*. 2012
C. quadrivirgatus	LSUHC 4813	Pulau Tioman, Pahang	MF169975	Brennan *et al*. 2017
C. redimiculus	KU309328	Philippines, Palawan Island	GU550742	Siler *et al*. 2010
C. redimiculus	KU309327	Philippines, Palawan Island	GU550743	Siler *et al*. 2010
C. rosichonarieforum	MZBLace 12133	Indonesia, Great Natuna Island	KP256188	Riyanto *et al*. 2015
C. rosichonarieforum	MZBLace 12132	Indonesia, Great Natuna Island	KP256187	Riyanto *et al*. 2015
C. sadleiri	AMSR152675	Christmas Is	MH105037	Oliver *et al*. 2018
C. sadleiri	SAMAR34810	Christmas Is	JQ820309	Oliver *et al*. 2012
C. santana	ZRC27676	Indonesia, East Timor	OP650035	Chan *et al*. 2023
C. santana	ZRC27675	Indonesia, East Timor	OP650034	Chan *et al*. 2023
C. semiadii	MZBLace 14818	Indonesia, Daerah Istimewa Yogyakarta, Gunung Kidul regency, Tanjungsari district	MT704866	Riyanto *et al*. 2020
C. semicinctus	ENS 14966	Indonesia, Sumatra, Kerinci	MH248924	O'Connel *et al*. 2019
C. semicinctus	MZBLace 9703	Indonesia, Sumatra, Kerinci	KR921715	Harvey *et al*. 2015
C. sp	ENS14199	Indonesia, Lampung	MH248935	O'Connel *et al*. 2019
C. sp	ENS15784	Indonesia, West Java, Bogor	KR921689	O'Connel *et al*. 2019
C. sp	ENS15841	Indonesia, West Java, Bogor	KR921690	O'Connel *et al*. 2019
C. sp	ENS15759	Indonesia, West Java, Bogor	MH248933	O'Connel *et al*. 2019
C. sp	ENS12124	Indonesia, Sumatra, Lampung	MH248932	O'Connel *et al*. 2019
C. sp	ENS15813	Indonesia, West Java, Bogor	KR921697	O'Connel *et al*. 2019
C. sp	ENS13751	Indonesia, Sumatra, Lampung	MH248942	O'Connel *et al*. 2019
C. seribuatensis	LSUHC6348	Malaysia, Peninsular Malaysia, Johor, Pulau Mentigi	JX440557	Brennan *et al*. 2017
C. seribuatensis	LSUHC6349	Malaysia, Peninsular Malaysia, Johor, Pulau Mentigi	MF169976	Brennan *et al*. 2017
C. sp	WAMR109893	Yamdena Is	KU232621	Riyanto *et al*. 2015
C. sp	WAMR 109089	Bali Is	KU232625	Riyanto *et al*. 2015
C. sworderi	LSUHC 7685	Malaysia, Johor, Endau-Rompin, Peta, Sungai Kawal	JQ889189	Grismer *et al*. 2013
C. tautbatorum	KU 309320	Philippines, Palawan Island, Municipality of Brooke's Point	GU366082	Siler *et al*. 2010
C. tautbatorum	KU309321	Philippines, Palawan Island, Municipality of Brooke's Point	GU366081	Siler *et al*. 2010
C. tebuensis	LSUHC10901	Malaysia, Trengganu	JX988526	Grismer *et al*. 2013
C. tebuensis	LSUHC10903	Malaysia, Trengganu	JX988528	Grismer *et al*. 2013
C. tebuensis	LSUHC10902	Malaysia, Trengganu	JX988527	Grismer *et al*. 2013
C. tehetehe	MZBLace15613	Indonesia, East Kalimantan, Maratua Island	PP092502	Wiradarma *et al*. 2024
C. tehetehe	MZBLace15614	Indonesia, East Kalimantan, Maratua Island	PP092503	Wiradarma *et al*. 2024

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APPENDIX 1. (Continued)

Species	**Voucher**	**Locality**	**GenBank Acc**	**Sources**
C. tiomanensis	LSUHC 6251	West Malaysia, Pahang, Pulau Tioman, Tekek-Juara Trail	JX440563	Wood *et al*. 2012
C. wetariensis	MVZ293516	Indonesia, Wetar Is	OP356306	Reilly *et al*. 2023
C. wetariensis	MVZ293518	Indonesia, Wetar Is	OP356310	Reilly *et al*. 2023
C. cf. wetariensis	MVZ293334	Indonesia, East Sumba	OP356349	Reilly *et al*. 2023
C. cf. wetariensis	MVZ293336	Indonesia, East Sumba	OP356348	Reilly *et al*. 2023
C.zugi	MZBLace5575	Indonesia, Batanta, Raja Ampat Is	JQ820306	Oliver at al. 2012
C. zugi	MZBLace5573	Indonesia, Batanta, Raja Ampat Is	JQ820305	Oliver *et al*. 2012
G. gecko	MVZ215314	Thailand, Patong Beach, Kathu District, Phuket Island, Phuket Province	AF114249	Macey *et al*. 1999
H. frenatus	LSUHC4871	Malaysia, Pahang, Bukit Bakong	GQ458049	Bauer *et al*. 2010

APPENDIX 2. Comparative material examined.

Cyrtodactylus jatnai. MZBLace 8726, 8729, 8731, UIMZ0081, 0082,0101, adult males, MZBLace 8725, 8728, adult females, Teluk Menjangan, Bali, Indonesia.

Cyrtodactylus marmoratus. MZBLace 9709, AR10001, adult males, 9706-08, 9710-11, adult females, Cibodas, West Java, Indonesia.

Cyrtodactylus petanii. MZBLace 15000, 15001, adult males, Lumajang, East Java; MZBLace 11706, 11708-10, 11712, 11713, 12143, 12899, adult males, Pasuruan, East Java; MZBLace11707, 11711, adult females, Pasuruan, East Java, Indonesia.

Cyrtodactylus semiadii. MZBLace 9104, adult male, Tuban, East Java; MZBLace15675, adult male, Gunungpati, Semarang, Central Java; MZBLace 15676-77, adult males, Lamongan, East Java; MZBLace 10827, adult female, Bantul, Jogjakarta, Indonesia.