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Taxonomic status of two populations of Bent-toed Geckos of the *Cyrtodactylus irregularis* complex (Squamata: Gekkonidae) with description of a new species from Nui Chua National Park, southern Vietnam

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Abstract

Based on genetic, morphological and chromatical comparisons we evaluate the taxonomic status of two southern Vietnamese forest-dwelling populations of the *Cyrtodactylus irregularis* species complex. We confirm the allocation of the population from Binh Chau—Phuoc Buu Nature Reserve (Ba Ria—Vung Tau Province) to *C. cattienensis* and we describe the population of Nui Chua National Park (Ninh Thuan Province) as *Cyrtodactylus sangi* sp. nov. This brings to 18 the number of species within the *C. irregularis* complex and to 41 the number of described *Cyrtodactylus* species recorded from Vietnam.

Key words: *Cyrtodactylus cattienensis*, *Cyrtodactylus sangi* sp. nov., new species, taxonomy, Binh Chau—Phuoc Buu Nature Reserve, Nui Chua National Park

Introduction

Gymnodactylus peguensis var. *irregularis* Smith, 1921 was described from an open pine forest at Camly in the Langbian Plateau, Vietnam. Nazarov *et al.* (2008) showed that it belonged to a species complex, and described *C. ziegleri* Nazarov, Orlov, Nguyen & Ho. The species complex has recently been the subject of numerous morphological and molecular analyses, and so far 17 species have been described, along with several additional populations whose taxonomic status is still unresolved (Nazarov *et al.* 2008, 2012; Nguyen *et al.* 2013, 2014, 2017; Schneider *et al.* 2014; Luu *et al.* 2017). The complex currently includes the following taxa: *C. bidoupimontis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, 2012, *C. bugiamapensis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, 2012, *C. caovansungi* Orlov, Nguyen, Nazarov, Ananjeva & Nguyen, 2007, *C. cattienensis* Geissler, Nazarov, Orlov, Böhme, Phung, Nguyen & Ziegler, 2009, *C. cryptus* Heidrich, Rösler, Vu, Böhme & Ziegler, 2007, *C. cucdongensis* Schneider, Phung, Le, Nguyen & Ziegler, 2014, *C. dati* Ngo, 2013, *C. gialaiensis* Luu, Dung, Nguyen, Le & Ziegler, 2017, *C. huynhi* Ngo & Bauer, 2008, *C. irregularis*, *C. kingsadai* Ziegler, Phung, Le & Nguyen, 2013, *C. phuocbinhensis* Nguyen, Le, Tran, Orlov, Lathrop, MacCulloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, 2013, *C. pseudoquadrivirgatus* Rösler, Vu, Nguyen, Ngo & Ziegler, 2008, *C. takouensis* Ngo & Bauer, 2008, *C. taynguyenensis* Nguyen, Le, Tran, Orlov, Lathrop, MacCulloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, 2013, *C. yangbayensis* Ngo & Chan, 2010 and *C. ziegleri* Nazarov, Orlov, Nguyen & Ho, 2008.

In their review, Nazarov *et al.* (2012), based on morphological and mtDNA analyses, noted two unidentified populations of the *Cyrtodactylus irregularis* complex from southern Vietnam: (1) the Nui Chua National Park (below Nui Chua N.P.) population in Ninh Thuan Province was shown to be genetically distinct and closely related to *C. cattienensis*, and was regarded as *Cyrtodactylus* sp. 2 pending further taxonomic research; (2) the population of small-sized *Cyrtodactylus* from maritime forests of Binh Chau—Phuoc Buu Nature Reserve (below as Binh Chau—Phuoc Buu N.R.) was tentatively assigned to *C. cattienensis sensu lato* and was mentioned as *C. cf. cattienensis*. Later, Nguyen *et al.* (2013, 2014) also examined these populations and suggested that *Cyrtodactylus* sp. 2 from Nui Chua N.P. indeed likely represents a distinct taxon based both on evidence from mtDNA and nuDNA genetic markers; they also confirmed the assignment of *Cyrtodactylus* from Binh Chau—Phuoc Buu N.R. to *C. cattienensis*.

Recently, Nguyen *et al.* (2017) presented a large-scale review of differentiation within the *C. irregularis* species complex based on one mitochondrial (COI) and two nuclear DNA (RPL35, RAG1) markers. Their study provided solid genetic evidence for specific status of the highly diverged lineage of *Cyrtodactylus* sp. 2 from Nui Chua N.R., suggested attribution of maritime populations of *Cyrtodactylus* from Ba Ria—Vung Tau Province (Binh Chau—Phuoc Buu N.R. and Nui Dinh Mt.) to *C. cattienensis*, and also confirmed the specific status of *C. bugiamapensis* from Binh Phuoc Province, which was questioned by earlier studies (Nguyen *et al.* 2013). However, morphological characterizations of the populations from Nui Chua N.R. and Binh Chau—Phuoc Buu N.R. are still lacking.

In the present study, based on examination of additional material, these populations are morphologically and molecularly characterized and compared with all species of the *C. irregularis* complex.

Material and methods

Sampling. For the list of specimens accessed in our molecular analysis see Tables 1 and 2. A map showing the distribution of the *C. irregularis* species complex in Vietnam and the location of the sampling sites for the present work are provided in Fig. 1. The list of specimens we morphologically examined is given in the Appendix.

Morphological descriptions. Measurements and meristic counts follow Pauwels *et al.* (2014a, b, 2016). Paired meristic characters are given left/right. Numbers of supralabial and infralabial scales were 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 number of longitudinal rows of body tubercles was counted transversely across the center of the dorsum from one ventrolateral skin fold to the other. The number of longitudinal rows of ventral scales was counted transversely across the center of the abdomen from one ventrolateral skin fold to the other. The numbers of subdigital lamellae beneath the toes were counted from the base of the first phalanx to the claw. The following measurements were taken with a digital caliper to the nearest 0.1 mm: AG: axilla to groin length, 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; EarL: ear length, the greatest horizontal distance of the ear opening; ForeAL: forearm length, taken on the dorsal surface from the posterior margin of the elbow while flexed 90° to the inflection of the flexed wrist; HeadH: head height, the maximum depth of head between the occiput to the throat; HeadL: head length, from the posterior margin of the retroarticular process of the lower jaw to the tip of the snout; HeadW: head width, measured at the angle of the jaws; Internar: internarial distance, measured between the nares across the rostrum; Interorb: interorbital distance, measured between the anterior edges of the orbits; NosOrb: nostril to orbit distance, from the posterior margin of the external nares to the anterior margin of the orbit; OrbD: orbit diameter, the greatest horizontal diameter of the orbit; OrbEar: orbit to ear distance, from the anterior edge of the ear opening to the posterior edge of the orbit; RH: rostral height; RW: rostral width; SnOrb: snout to orbit distance, from the tip of the snout to the anteriormost margin of the orbit; SVL: snout-vent length, taken from the tip of snout to the vent; TailL: tail length, taken from the vent to the tip of the tail, original or regenerated; TailW: tail width, taken at the base of the tail immediately posterior to the postcloacal swelling; TibiaL: tibia length, taken on the ventral surface from the posterior surface of the knee while flexed 90° to the base of heel. Meristic characters abbreviations: DorTub: number of longitudinal rows of dorsal tubercles at midbody; EnlFemSc: enlarged femoral scales; FemPi: femoral pits; FemPo: femoral pores; IL: infralabial scales; InterorbSc: interorbital scales; ParaTub: number of paravertebral tubercles between the limbs insertions, counted in a straight line immediately left of the vertebral column; PreclPi: precloacal pits (shallow depressions without waxy exudates); PreclPo: precloacal pores (deeper than pits, and with waxy exudates); SL: supralabial scales; Ven: number of ventral scale rows. Institutions, collections and other acronyms: IEBR: Institute of Ecology and Biological Resources, Hanoi; ITBCZ: Institute of Tropical Biology Collection of Zoology, Hồ Chí Minh City; KIZ: Kunming

Institute of Zoology, Kunming; NAP: private research collection of N.A. Poyarkov (specimens will be deposited in ZMMU); PNKB: Phong Nha Ke Bang National Park; ROM: Royal Ontario Museum, Toronto; VNMN: Vietnam National Museum of Nature, Hanoi; ZISP: Zoological Institute, St. Petersburg; ZMMU: Zoological Museum, Moscow State University, Moscow.

Comparisons with congeneric species are based on literature data and on direct examination of preserved specimens (see Appendix).

DNA isolation, PCR and sequencing. For molecular phylogenetic analyses, total genomic DNA was extracted from ethanol-preserved femoral muscle tissue using standard phenol-chloroform — proteinase K (final concentration 1 mg/ml) extraction procedures with consequent isopropanol precipitation (protocols followed Hillis *et al.* 1996 and Sambrook *et al.* 1989). The isolated total genomic DNA was visualized in agarose electrophoresis in presence of ethidium bromide. The concentration of total DNA was measured in 1 μ l using NanoDrop 2000 (Thermo Scientific), and consequently adjusted to ca. 100 ng DNA/ μ L.

Following Nazarov *et al.* (2012, 2014) and Nguyen *et al.* (2013, 2014) we selected the mitochondrial cytochrome oxidase subunit I (COI) and nuclear non-coding ribosomal protein L35 Intron 2 (RPL35) as phylogenetic markers. We amplified 655 bp of Cytochrome oxidase I (COI), a mitochondrial marker widely used as a barcoding marker for vertebrates, including both reptiles and amphibians (Smith *et al.* 2008, Nagy *et al.* 2012, Murphy *et al.* 2013) and which proved to be useful for species identification in various groups of lizards (Solovyeva *et al.* 2011, Nazarov *et al.* 2012, 2014, Hartmann *et al.* 2013). Primers used both for PCR and sequencing were the VF1-d (5'-TTCTCAACCAACCACAARGAYATYGG-3') and the VR1-d (5'-TAGACTTCTGGGTGGCCRAARAAYCA-3') (Ivanova *et al.* 2006). The obtained fragments were sequenced in both directions for each sample, and a consensus sequence was generated. PCRs were performed in 25 μ l reactions using ca. 50 ng genomic DNA, 10 pmol of each primer, 15 nmol of each dNTP, 50 nmol additional MgCl₂, Taq PCR buffer (10 mM Tris-HCl, pH 8.3, 50 mM KCl, 1.1 mM MgCl₂ and 0.01% gelatine) and 1 U of Taq DNA polymerase. The PCR conditions for the COI gene fragment followed Nazarov *et al.* (2012) and included an initial denaturation step at 95° C for 3 min; 5 cycles at 95° C for 30 s, annealing at 45° C for 1 min, extension at 72° C for 2 min followed with 35 cycles at 95° C for 30 s, annealing at 51 for 1 min, extension at 72° C for 2 min and final extension of 5 min at 72° C.

For RPL35, amplification was also performed in a 25 μ l volume. Primers used both for PCR and sequencing were the Rpl35-F (5'-GCTAAACAAGCACAGAGTTGATCC-3') and Rpl35-R (5'-TCAGGCTCAGAAAGRACTATTATGG-3') (Siler *et al.* 2010). PCR procedures also followed Siler *et al.* (2010) and included initial denaturation at 95° C for 4 min, followed by 35 cycles of 95° C for 30 s, annealing at 56–58° C for 30 s, extension at 72° C for 1 min 30 s, and a final extension phase at 72° C for 7 min.

PCR products were loaded onto 1.5% agarose gels in presence of ethidium bromide and visualized in agarose electrophoresis. If distinct bands were produced, products were purified using 2 μ l, from a 1:4 dilution of ExoSapIt (Amersham), per 5 μ l of PCR product prior to cycle sequencing. A 10 μ l sequencing reaction included 2 μ L of template, 2.5 μ l of sequencing buffer, 0.8 μ l of 10 pmol primer, 0.4 μ l of BigDye Terminator version 3.1 Sequencing Standard (Applied Biosystems) and 4.2 μ l of water. The cycle sequencing reaction was 35 cycles of 10 sec at 96° C, 10 s at 50° C and 4 min at 60° C. Cycle sequencing products were purified by ethanol precipitation. Sequence data collection and visualization were performed on an ABI 3730xl automated sequencer (Applied Biosystems). The obtained sequences are deposited in GenBank under the accession numbers MG791876–MG791912 (Tables 1 and 2).

Phylogenetic analyses. For phylogenetic analyses we used the COI dataset of Nazarov *et al.* (2012) and Nguyen *et al.* (2013, 2014) and the RPL35 dataset of Nguyen *et al.* (2013) and Siler *et al.* (2010), with addition of the newly obtained sequences of *Cyrtodactylus* spp. from Ninh Thuan and Ba Ria—Vung Tau Provinces (see Table 1 for COI and Table 2 for RPL35 datasets). In total 94 sequences of the COI fragment and 49 sequences of RPL35 were included in the final alignment and subjected to phylogenetic analyses.

Mitochondrial and nuclear data were analyzed separately because of their differing modes of inheritance. Nucleotide sequences were initially aligned using ClustalX 1.81 (Thompson *et al.* 1997) with default parameters, and then optimized manually in BioEdit 7.0.5.2 (Hall 1999) and MEGA 6.0 (Tamura *et al.* 2013). Mean uncorrected genetic distances (*p*-distances) between sequences were determined with MEGA 6.0. MODELTEST v.3.06 (Posada & Crandall 1998) was used to estimate the optimal evolutionary models to be used for both COI and RPL35 datasets. The best-fitting model selected for COI dataset was GTR+ Γ for the first and the third codon positions and HKY+I for the second codon position. The best-fitting model for the RPL35 dataset was GTR+ Γ as suggested by the Akaike Information Criterion (AIC).

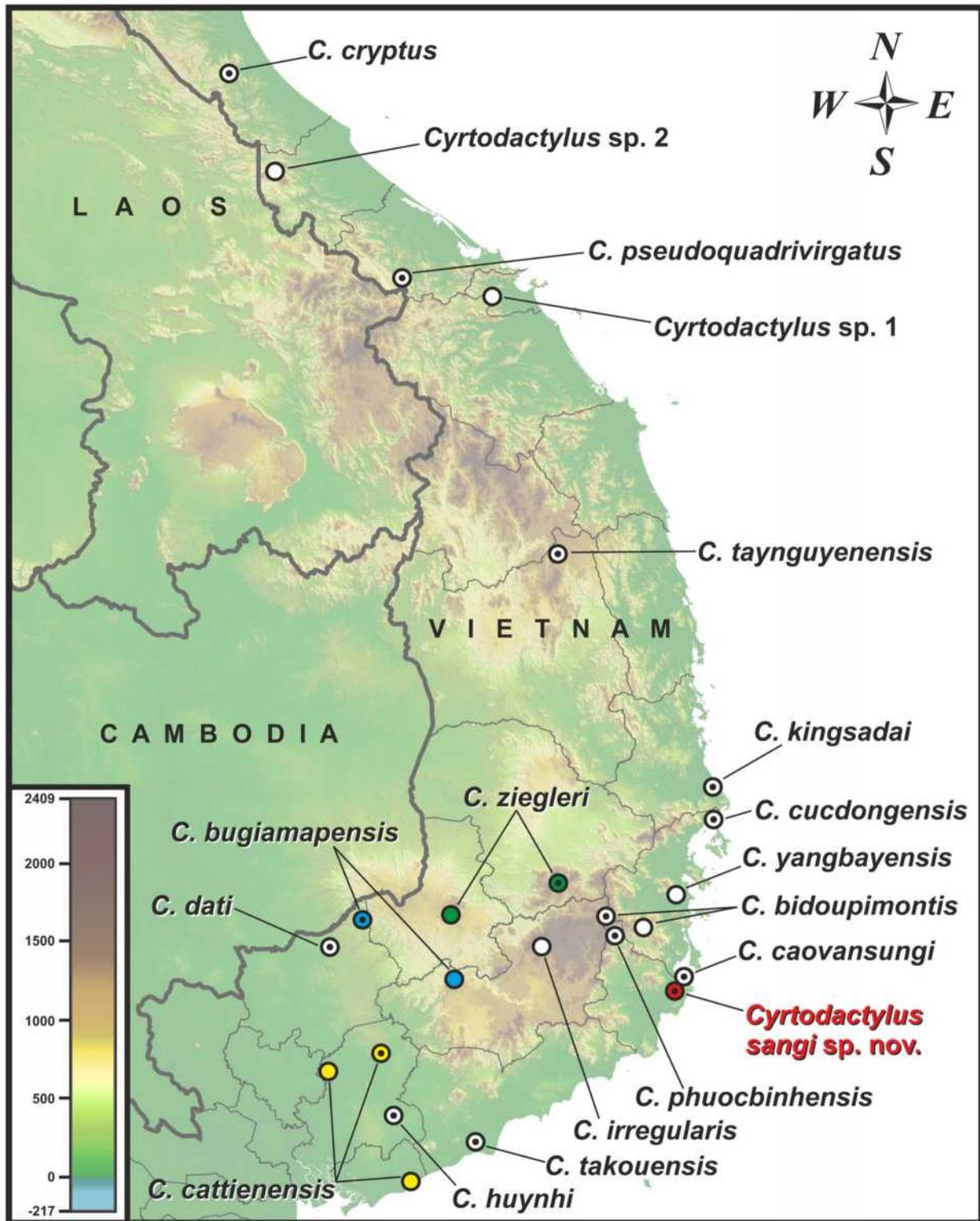


FIGURE 1. Distribution of the *Cyrtodactylus irregularis* complex in South Vietnam, with the type locality of *Cyrtodactylus sangi sp. nov.*

TABLE 1. Specimens and sequences of *Cyrtodactylus* representatives used in molecular analyses of the COI mtDNA gene fragment. AN—GenBank accession number.

No.	GenBank AN	Specimen ID	Species	Locality	Reference
1	KF169958	ITBCZ-1536	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nguyen <i>et al.</i> 2013
2	KF169959	ITBCZ-1537	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nguyen <i>et al.</i> 2013
3	KF169960	ITBCZ-1539	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nguyen <i>et al.</i> 2013
4	HQ967214	ZMMU NAP-01018*	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nazarov <i>et al.</i> 2012
5	HM425560	ZMMU NAP-01121	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nazarov <i>et al.</i> 2012
6	MG791877	ZMMU R-13515 (NAP-01413)	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	this paper
7	MG791876	ZMMU R-11445-8	<i>C. cf. bidoupimontis</i>	Hon Ba N.R., Khanh Hoa Prov., Vietnam	this paper
8	HQ967216	ZMMU R-13369-1 (NAP-00078)	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nazarov <i>et al.</i> 2012
9	HQ967215	ZMMU R-13369-2 (NAP-00080)	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nazarov <i>et al.</i> 2012
10	KC016071	ZMMU R-13369-3 (NAP-00103)	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nazarov <i>et al.</i> 2012
11	MG791878	ZMMU R-13831-1 (NAP-01321)	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	this paper
12	MG791879	ZMMU R-13831-2 (NAP-01322)	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	this paper
13	MG791880	ZMMU R-13832 (NAP-01742)	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	this paper
14	KF169961	ITBCZ-1562	<i>C. bugiamapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2013
15	KF169967	KIZ-179	<i>C. bugiamapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2013
16	KF169965	KIZ-45	<i>C. bugiamapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2013
17	KF169966	KIZ-98	<i>C. bugiamapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2013
18	HM425553	ZMMU R-13439 (NAP-00360)	<i>C. bugiamapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	Nazarov <i>et al.</i> 2012
19	MG791881	ZMMU NAP-02861	<i>C. bugiamapensis</i>	Loc Bac, Lam Dong Prov., Vietnam	this paper
20	MG791882	ZMMU NAP-02862	<i>C. bugiamapensis</i>	Loc Bac, Lam Dong Prov., Vietnam	this paper
21	HQ967200	ZMMU R-13093-1	<i>C. bugiamapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	Nazarov <i>et al.</i> 2012
22	HM888459	ZMMU R-13093-2	<i>C. bugiamapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	Nazarov <i>et al.</i> 2012
23	KF219680	ITBCZ-1113	<i>C. caovansungi</i>	Ninh Thuan Prov., Vietnam	Ziegler <i>et al.</i> 2013
24	KF219678	ITBCZ-908	<i>C. caovansungi</i>	Ninh Thuan Prov., Vietnam	Ziegler <i>et al.</i> 2013
25	KF219679	ITBCZ-932	<i>C. caovansungi</i>	Ninh Thuan Prov., Vietnam	Ziegler <i>et al.</i> 2013

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TABLE 1. (Continued)

No.	GenBank AN	Specimen ID	Species	Locality	Reference
26	KF169956	ITBCZ-1532	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	Nguyen <i>et al.</i> 2013
27	KF169957	ITBCZ-1533	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	Nguyen <i>et al.</i> 2013
28	KF929506	ITBCZ-1534	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2014
29	KF929507	ITBCZ-1535	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2014
30	KF169955	ITBCZ-707	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	Nguyen <i>et al.</i> 2013
31	KF169968	KIZ-13674	<i>C. cattienensis</i>	Ma Da (Vinh Cuu) N.R., Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
32	KF169973	ROM-37887	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
33	KF169974	ROM-37888	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
34	HQ57272	ZMMU NAP-00111	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nazarov <i>et al.</i> 2012
35	HQ967197	ZMMU NAP-00115	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nazarov <i>et al.</i> 2012
36	MG791896	ZMMU NAP-00116	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	this paper
37	HQ967198	ZMMU NAP-00117	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nazarov <i>et al.</i> 2012
38	MG791897	ZMMU NAP-01948	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	this paper
39	MG791898	ZMMU NAP-01959	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	this paper
40	MG791889	ZMMU R-14508-1 (NAP-02548)	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	this paper
41	MG791890	ZMMU R-14508-2 (NAP-02549)	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	this paper
42	MG791891	ZMMU R-14508-5 (NAP-02554)	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	this paper
43	MG791892	ZMMU R-14509 (NAP-03141)	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	this paper
44	MG791893	ZMMU R-13777-1 (NAP-03185)	<i>C. cattienensis</i>	Ma Da (Vinh Cuu) N.R., Dong Nai Prov., Vietnam	this paper
45	MG791894	ZMMU R-13777-2 (NAP-03187)	<i>C. cattienensis</i>	Ma Da (Vinh Cuu) N.R., Dong Nai Prov., Vietnam	this paper
46	MG791895	ZMMU R-13780 (NAP-00704)	<i>C. cattienensis</i>	Ma Da (Vinh Cuu) N.R., Dong Nai Prov., Vietnam	this paper
47	KC016075	ZMMU R-13824 (NAP-02149)	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	this paper
48	KF169969	PNKB-1	<i>C. cryptus</i>	U Bo, Phong Nha-Ke Bang N.P., Quang Binh Prov., Vietnam	Nazarov <i>et al.</i> 2012
49	KF169970	PNKB-2	<i>C. cryptus</i>	U Bo, Phong Nha-Ke Bang N.P., Quang Binh Prov., Vietnam	Nguyen <i>et al.</i> 2013
50	KF169971	PNKB-3	<i>C. cryptus</i>	U Bo, Phong Nha-Ke Bang N.P., Quang Binh Prov., Vietnam	Nguyen <i>et al.</i> 2013
51	KF169972	PNKB-4	<i>C. cryptus</i>	U Bo, Phong Nha-Ke Bang N.P., Quang Binh Prov., Vietnam	Nguyen <i>et al.</i> 2013

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TABLE 1. (Continued)

No.	GenBank AN	Specimen ID	Species	Locality	Reference
52	KJ403846	IEBR-A.2013.104	<i>C. cucdongensis</i>	Cuc Dong, Ninh Hoa Distr., Khanh Hoa Prov., Vietnam	Schneider <i>et al.</i> 2014
53	KJ403845	VNMIN- A.2013.18	<i>C. cucdongensis</i>	Cuc Dong, Ninh Hoa Distr., Khanh Hoa Prov., Vietnam	Schneider <i>et al.</i> 2014
54	MG791883	VNMIN-2101	<i>C. cucdongensis</i>	Cuc Dong, Ninh Hoa Distr., Khanh Hoa Prov., Vietnam	this paper
55	MG791884	VNMIN-2142	<i>C. cucdongensis</i>	Cuc Dong, Ninh Hoa Distr., Khanh Hoa Prov., Vietnam	this paper
56	KJ403847	ZFMK-95513	<i>C. cucdongensis</i>	Cuc Dong, Ninh Hoa Distr., Khanh Hoa Prov., Vietnam	Schneider <i>et al.</i> 2014
57	KF929508	ITBCZ-2537	<i>C. dati</i>	Bu Dop, Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2014
58	KF929509	ITBCZ-2538	<i>C. dati</i>	Bu Dop, Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2014
59	KF929510	ITBCZ-2539	<i>C. dati</i>	Bu Dop, Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2014
60	KF929511	ITBCZ-2540	<i>C. dati</i>	Bu Dop, Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2014
61	KF169947	ITBCZ-511	<i>C. huynhi</i>	Chua Chan, Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
62	KF169948	ITBCZ-513	<i>C. huynhi</i>	Chua Chan, Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
63	KF169949	ITBCZ-515	<i>C. huynhi</i>	Chua Chan, Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
64	KF169950	ITBCZ-530	<i>C. huynhi</i>	Chua Chan, Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
65	MG791886	ITBCZ-10016	<i>C. irregularis</i>	Lac Duong, Lam Dong Prov., Vietnam	this paper
66	MG791885	ITBCZ-10023	<i>C. irregularis</i>	Lac Duong, Lam Dong Prov., Vietnam	this paper
67	MG791887	ITBCZ-10025	<i>C. irregularis</i>	Lac Duong, Lam Dong Prov., Vietnam	this paper
68	KF188432	IEBR-A.2013.3	<i>C. kingsadai</i>	Dai Lanh Cape, Tuy Hoa Distr., Phu Yen Prov., Vietnam	Ziegler <i>et al.</i> 2013
69	KF169953	ITBCZ-1518	<i>C. phuoocbinhensis</i>	Phuoc Binh N.P., Ninh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2013
70	KF169954	ITBCZ-1529	<i>C. phuoocbinhensis</i>	Phuoc Binh N.P., Ninh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2013
71	KF169963	ITBCZ-3001	<i>C. pseudoquadrivirgatus</i>	A Luoi, Thua Thien-Hue Prov., Vietnam	Nguyen <i>et al.</i> 2013
72	KF169964	ITBCZ-3002	<i>C. pseudoquadrivirgatus</i>	A Luoi, Thua Thien-Hue Prov., Vietnam	Nguyen <i>et al.</i> 2013
73	KF929533	ITBCZ-2527	<i>C. takouensis</i>	Ta Kou N.R., Binh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2014
74	KF929534	ITBCZ-2528	<i>C. takouensis</i>	Ta Kou N.R., Binh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2014
75	KF169978	ROM-32119	<i>C. taynguyenensis</i>	Krong Pa Village, K Bang Dist., Gia Lai Prov., Vietnam	Nguyen <i>et al.</i> 2013
76	KF169979	ROM-32120	<i>C. taynguyenensis</i>	Krong Pa Village, K Bang Dist., Gia Lai Prov., Vietnam	Nguyen <i>et al.</i> 2013
77	KJ403848	VNMIN-3373	<i>C. yangbavensis</i>	Nha Trang, Khanh Hoa Prov., Vietnam	Schneider <i>et al.</i> 2014

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TABLE 1. (Continued)

No.	GenBank AN	Specimen ID	Species	Locality	Reference
78	KC016081	ZMMU R-131090-1	<i>C. yangbayensis</i>	Ba Ho, Khanh Hoa Prov., Vietnam	Nazarov <i>et al.</i> 2012
79	KF169946	UNS-5006	<i>C. zieglerei</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nguyen <i>et al.</i> 2013
80	KF169945	UNS-5007	<i>C. zieglerei</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nguyen <i>et al.</i> 2013
81	KF169975	VNMN-2014	<i>C. zieglerei</i>	Na Nung, Dak Nong Prov., Vietnam	Nguyen <i>et al.</i> 2013
82	KF169976	VNMN-2015	<i>C. zieglerei</i>	Na Nung, Dak Nong Prov., Vietnam	Nguyen <i>et al.</i> 2013
83	KF169977	VNMN-2016	<i>C. zieglerei</i>	Na Nung, Dak Nong Prov., Vietnam	Nguyen <i>et al.</i> 2013
84	KF929535	ZISP-36424	<i>C. zieglerei</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nguyen <i>et al.</i> 2014
85	HQ967210	ZMMU R-131116-3	<i>C. zieglerei</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nazarov <i>et al.</i> 2012
86	HQ967211	ZMMU R-131116-4	<i>C. zieglerei</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nazarov <i>et al.</i> 2012
87	HQ967212	ZMMU R-131116-5	<i>C. zieglerei</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nazarov <i>et al.</i> 2012
88	HQ967213	ZMMU R-131116-6	<i>C. zieglerei</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nazarov <i>et al.</i> 2012
89	KF169951	ITBCZ-1150	<i>Cyrtodactylus sangi</i> sp. nov.	Nui Chua, Ninh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2013
90	KF169952	ITBCZ-965	<i>Cyrtodactylus sangi</i> sp. nov.	Nui Chua, Ninh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2013
91	KC016080	ZMMU R-11503-2	<i>Cyrtodactylus sangi</i> sp. nov.	Nui Chua, Ninh Thuan Prov., Vietnam	Nazarov <i>et al.</i> 2012
92	KF169962	ITBCZ-2532	<i>Cyrtodactylus</i> sp. 1	Ba Na, Da Nang City, Vietnam	Nguyen <i>et al.</i> 2013
93	MG791888	ZMMU R-13095-2	<i>Cyrtodactylus</i> sp. 2	Ban Cup, Quang Tri Prov., Vietnam	this paper
94	KC016076	ZMMU R-11213-1	<i>C. intermedius</i>	Phnom Bakor N.P., Cambodia	Nazarov <i>et al.</i> 2012

* NAP—research collection numbers of N.A. Poyarkov; specimens will be deposited in ZMMU.

TABLE 2. Specimens and sequences of *Cyrtodactylus* representatives used in molecular analyses of the RPL35 nuDNA fragment. AN—GenBank accession number.

No.	GenBank AN	Specimen ID	Species	Locality	Reference
1	GU458137	KU-311133	<i>C. agusanensis</i>	Baybay, Leyte Island, Philippines	Siler <i>et al.</i> 2010
2	GU458132	KU-311195	<i>C. agusanensis</i>	Baybay, Leyte Island, Philippines	Siler <i>et al.</i> 2010
3	GU458089	KU-311157	<i>C. annulatus</i>	Baybay, Leyte Island, Philippines	Siler <i>et al.</i> 2010
4	GU458095	TNHC-56457	<i>C. annulatus</i>	San Juan, Siquijor Island, Philippines	Siler <i>et al.</i> 2010
5	GU458060	SPM-06906	<i>C. baliuensis</i>	Kinabalu N.P., Sabah, Malaysia	Siler <i>et al.</i> 2010
6	KF169996	ITBCZ-1536	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nguyen <i>et al.</i> 2013
7	KF169997	ITBCZ-1537	<i>C. bidoupimontis</i>	Bidoup - Nui Ba N.P., Lam Dong Prov., Vietnam	Nguyen <i>et al.</i> 2013
8	KF170001	ITBCZ-1562	<i>C. bugianapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	Nguyen <i>et al.</i> 2013
9	MG791901	ZMMU NAP-02861*	<i>C. bugianapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	this paper
10	MG791902	ZMMU NAP-02862	<i>C. bugianapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	this paper
11	MG791899	ZMMU R-13093-1	<i>C. bugianapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	this paper
12	MG791900	ZMMU R-13093-2	<i>C. bugianapensis</i>	Bu Gia Map N.P., Binh Phuoc Prov., Vietnam	this paper
13	KF169994	ITBCZ-1532	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	Nguyen <i>et al.</i> 2013
14	KF169995	ITBCZ-1533	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	Nguyen <i>et al.</i> 2013
15	KF169990	ITBCZ-707	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	Nguyen <i>et al.</i> 2013
16	KF170007	KIZ-13674	<i>C. cattienensis</i>	Ma Da (Vinh Cuu) N.R., Dong Nai Prov., Viet Nam	Nguyen <i>et al.</i> 2013
17	MG791906	ZMMU NAP-02548	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	this paper
18	MG791907	ZMMU NAP-02549	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	this paper
19	MG791908	ZMMU NAP-03141	<i>C. cattienensis</i>	Binh Chau - Phuoc Buu N.R., Ba Ria - Vung Tau Prov., Vietnam	this paper
20	MG791903	ZMMU R-13777-1 (NAP-03185)	<i>C. cattienensis</i>	Ma Da (Vinh Cuu) N.R., Dong Nai Prov., Viet Nam	this paper
21	MG791905	ZMMU R-13777-2 (NAP-03187)	<i>C. cattienensis</i>	Ma Da (Vinh Cuu) N.R., Dong Nai Prov., Viet Nam	this paper
22	MG791904	ZMMU R-13824 (NAP-02149)	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	this paper
23	KF170014	ROM-37887	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
24	KF170015	ROM-37888	<i>C. cattienensis</i>	Cat Tien N.P., Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
25	GU458047	FMNH-230113	<i>C. consobrinus</i>	Lahad Datu Distr., Sabah, Malaysia	Siler <i>et al.</i> 2010
26	GU458046	FRIM-1142	<i>C. consobrinus</i>	Kepong, Selangor, West Malaysia, Malaysia	Siler <i>et al.</i> 2010

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TABLE 2. (Continued)

No.	GenBank AN	Specimen ID	Species	Locality	Reference
27	KF170008	PNKB-1	<i>C. cryptus</i>	U Bo, Phong Nha-Ke Bang N.P., Quang Binh Prov., Vietnam	Nguyen <i>et al.</i> 2013
28	KF170010	PNKB-3	<i>C. cryptus</i>	U Bo, Phong Nha-Ke Bang N.P., Quang Binh Prov., Vietnam	Nguyen <i>et al.</i> 2013
29	KF169984	ITBCZ-511	<i>C. huynhi</i>	Chua Chan, Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
30	KF169985	ITBCZ-513	<i>C. huynhi</i>	Chua Chan, Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
31	KF169986	ITBCZ-516	<i>C. huynhi</i>	Chua Chan, Dong Nai Prov., Vietnam	Nguyen <i>et al.</i> 2013
32	GU458108	KU-314824	<i>C. jambangan</i>	Zamboanga, Mindanao Island, Philippines	Siler <i>et al.</i> 2010
33	GU458109	KU-314825	<i>C. jambangan</i>	Zamboanga, Mindanao Island, Philippines	Siler <i>et al.</i> 2010
34	GU458183	KU-302643	<i>C. philippinicus</i>	Pandan, Panay Island, Philippines	Siler <i>et al.</i> 2010
35	GU458242	KU-308524	<i>C. philippinicus</i>	Paluan, Mindoro Island, Philippines	Siler <i>et al.</i> 2010
36	KF169993	ITBCZ-1518	<i>C. phuoocbinhensis</i>	Phuoc Binh N.P., Ninh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2013
37	KF170000	ITBCZ-1529	<i>C. phuoocbinhensis</i>	Phuoc Binh N.P., Ninh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2013
38	KF170002	ITBCZ-3001	<i>C. pseudoquadrivirgatus</i>	A Luoi, Thua Thien-Hue Prov., Vietnam	Nguyen <i>et al.</i> 2013
39	GU458063	KU-309329	<i>C. redimiculus</i>	Brooke's Point, Palawan Island, Philippines	Siler <i>et al.</i> 2010
40	GU458061	PNM-1468	<i>C. redimiculus</i>	Palawan Island, Philippines	Siler <i>et al.</i> 2010
41	KF169983	UNS-5007	<i>C. ziegleri</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nguyen <i>et al.</i> 2013
42	MG791911	ZMMU R-13116-3	<i>C. ziegleri</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	this paper
43	MG791912	ZMMU R-13116-4	<i>C. ziegleri</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	this paper
44	KF169992	ITBCZ-1150	<i>Cyrtodactylus sangi sp. nov.</i>	Chu Yang Sin N.P., Dak Lak Prov., Vietnam	Nguyen <i>et al.</i> 2013
45	KF169991	ITBCZ-965	<i>Cyrtodactylus sangi sp. nov.</i>	Nui Chua, Ninh Thuan Prov., Vietnam	Nguyen <i>et al.</i> 2013
46	MG791909	ZMMU R-11503-1	<i>Cyrtodactylus sangi sp. nov.</i>	Nui Chua, Ninh Thuan Prov., Vietnam	this paper
47	MG791910	ZMMU R-11503-2	<i>Cyrtodactylus sangi sp. nov.</i>	Nui Chua, Ninh Thuan Prov., Vietnam	this paper
48	KF169999	SNN-2013	<i>Cyrtodactylus sp. 1</i>	Ba Na, Da Nang City, Vietnam	Nguyen <i>et al.</i> 2013
49	KF169988	ITBCZ-609	<i>C. intermedius</i>	Nui Cam, An Giang Prov., Vietnam	Nguyen <i>et al.</i> 2013

* NAP—research collection numbers of N.A. Poyarkov; specimens will be deposited in ZMMU.

Phylogenetic trees were inferred using two different methods: Bayesian inference (BI) and Maximum Likelihood (ML). BI was conducted in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003); Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run with one cold chain and three heated chains for four million generations and sampled every 1,000 generations. Five independent MCMCMC runs were performed and 1,000 trees were discarded as burn-in. The remaining trees were combined, and a 50% majority consensus tree was generated. Confidence in tree topology was assessed by posterior probability (PP) (Huelsenbeck & Ronquist 2001). The ML analyses were conducted using Treefinder (Jobb *et al.* 2004). Confidence in tree topology was tested by non-parametric bootstrap analysis (BS) with 1000 replicates (Felsenstein 1985). We *a priori* regarded tree nodes with bootstrap (BS) values 70% or greater and posterior probabilities (PP) values over 0.95 as sufficiently resolved, those BS between 70% and 50% (PP between 0.95 and 0.90) were regarded as tendencies, those BS below 50% (PP below 0.90) were considered to be unresolved (Huelsenbeck & Hillis 1993, Felsenstein 2004).

Results

Genetic differentiation. Sequence data. The final alignment of the examined COI mtDNA gene fragment consisted of 677 sites: 430 sites were conserved and 242 sites were variable, of which 231 were found to be parsimony-informative. The transition–transversion bias (R) was estimated as 3.74. Nucleotide frequencies were A = 23.21%, T = 24.77%, C = 32.30%, and G = 19.72% (all data given for ingroup only). The RPL35 nuDNA intron fragment consisted of 580 sites in its final alignment: 462 sites were conserved and 107 sites were variable, of which 71 were found to be parsimony-informative. The transition-transversion bias (R) was estimated as 1.55. Nucleotide frequencies were A = 28.74%, T = 25.52%, C = 19.08%, and G = 26.62% (all data given for ingroup only).

Phylogenetic relationships as inferred from mtDNA marker. Bayesian and Maximum Likelihood analyses resulted in essentially similar topologies (see Fig. 2) slightly differing from each other only in associations at several poorly supported basal nodes. In general, data on genetic differentiation of *Cyrtodactylus irregularis* species group members is consistent with the results reported in previous studies by Nazarov *et al.* (2014), Nguyen *et al.* (2013, 2014), Ziegler *et al.* (2013) and Schneider *et al.* (2014). Though the partial fragment of the COI gene is herein applied primarily as a DNA-barcoding marker, and should not be used as a single tool for reconstructing phylogenetic relationships (Murphy *et al.* 2013), the examined fragment still had certain phylogenetic signal which infers the following set of genealogical relationships among the examined taxa:

The *C. irregularis* species group comprises a clade which includes the following *Cyrtodactylus* taxa: *C. bidoupimontis*, *C. bugiamapensis*, *C. caovansungi*, *C. cattienensis*, *C. cryptus*, *C. cucdongensis*, *C. dati*, *C. gialaiensis*, *C. huynhi*, *C. irregularis sensu stricto*, *C. kingsadai*, *C. phuocbinhensis*, *C. pseudoquadrivirgatus*, *C. takouensis*, *C. taynguyenensis*, *C. yangbayensis*, *C. ziegleri*, the population of *Cyrtodactylus* sp. from Nui Chua Mt. (Ninh Thuan Province), and two mtDNA lineages from Da Nang City and Quang Tri Province (hereafter indicated as *Cyrtodactylus* sp. 1 and *Cyrtodactylus* sp. 2, respectively) (see Fig. 2). Monophyly of this clade gets high support from BI (BPP = 1.0), whereas node support in ML analysis is low (BS = 62%). These data are concordant with the results by Nguyen *et al.* (2014).

Lineages encompassing *C. cattienensis* from lowland monsoon forests of southern Vietnam and the *Cyrtodactylus* sp. population from Nui Chua Mt. are reciprocally monophyletic; together they comprise a clade (1.0/78%; hereafter node support values are given for BPP/BS, respectively), which is a sister-group with respect to the clade joining all other members of *C. irregularis* species complex (0.96/72%) (see Fig. 2).

A significant differentiation is observed within *C. cattienensis* with two distinct mtDNA lineages recovered: one is restricted exclusively to the dry maritime dipterocarp forests of Binh Chau—Phuoc Buu N.R. (Ba Ria—Vung Tau Province), and the second lineage joins all other known populations of this species from Dong Nai Province (including the type locality in Cat Tien National Park) (see Fig. 2). The existence of these two distinct mtDNA lineages was first reported by Nguyen *et al.* (2013, 2014).

Within the remaining members of the *C. irregularis* species group, *C. phuocbinhensis* is the sister lineage to all other members of the clade (see Fig. 2) with moderate support (0.97/45). This contradicts its phylogenetic position in the results of Nguyen *et al.* (2014), where this species is grouped with *C. cattienensis* and *Cyrtodactylus* sp. from Nui Chua Mt., though only for BI analysis (1.0 for BPP, no support for ML and MP analyses).

Phylogenetic relationships within the remaining members of the *C. irregularis* species group remain largely unresolved (see Fig. 2). Six subclades joining several mtDNA lineages received high node support: (1) subclade joining *C. bugiamapensis* and *C. ziegleri* (1.0/100) from north-western edges of the Langbian Plateau; (2) subclade joining *C. bidoupimontis* and *C. irregularis sensu stricto* (1.0/99) from central and eastern highlands of the Langbian Plateau; (3) clade joining *C. cucdongensis* and *C. yangbayensis* (1.0/98) from coastal areas in Khanh Hoa Province; (4) clade joining *C. dati* and *C. huynhi* (1.0/100) from lowland forests in southern Vietnam; (5) clade joining taxa from central highlands of Vietnam (Tay Nguyen Plateau): *C. pseudoquadrivirgatus*, *C. taynguyenensis* and *Cyrtodactylus* sp. 2 from Quang Tri Province (1.0/87); (6) clade joining taxa from central and southern Vietnam: *C. cryptus*, *C. kingsadai* and *Cyrtodactylus* sp. 1 from Da Nang City (0.97/64). Phylogenetic positions of *C. caovansungi* and *C. takouensis* within this group remain unclear.

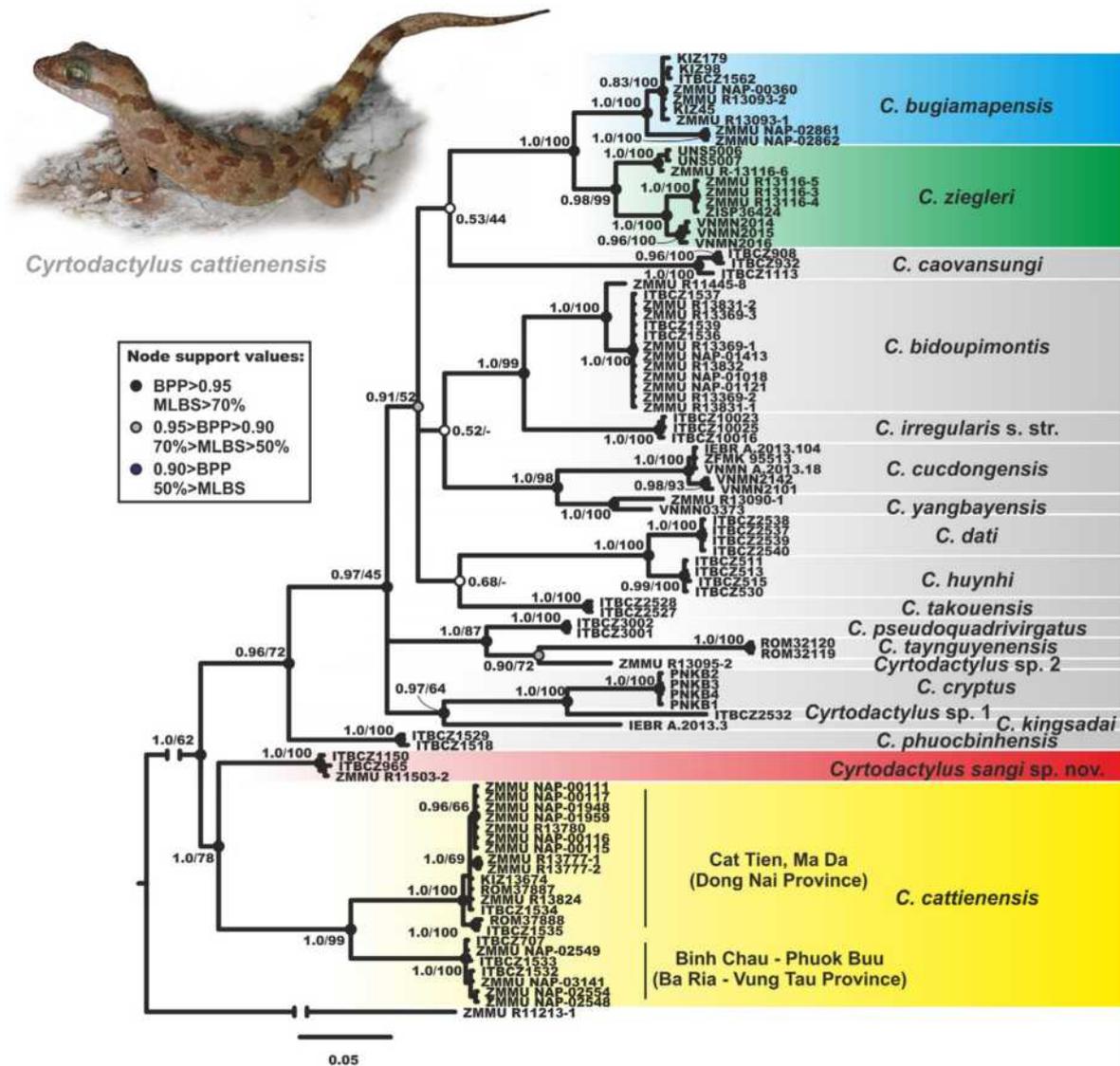


FIGURE 2. Bayesian inference tree resulting from analysis of the gene cytochrome oxidase submit I (*COI*) of the studied samples of *Cyrtodactylus irregularis* complex. For the major cladogenetic events BI/ML posterior probabilities and bootstrap support values are given.

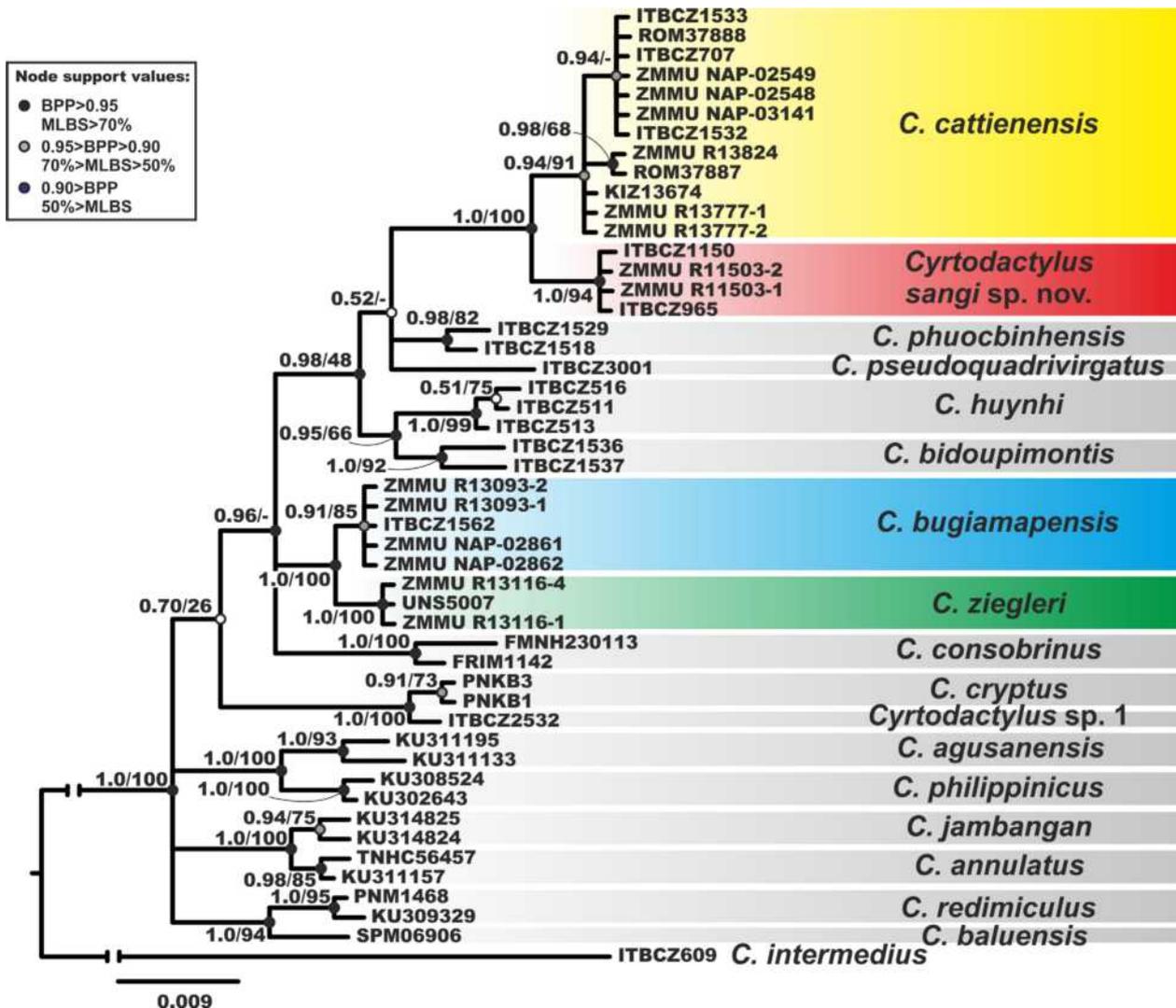


FIGURE 3. Bayesian inference tree resulting from analysis of the nuclear gene RPL35 of the studied samples of *Cyrtodactylus irregularis* complex. For the major cladogenetic events BI/ML posterior probabilities and bootstrap support values are given.

Phylogenetic relationships as inferred from nuDNA marker. Phylogenetic relationships among examined *Cyrtodactylus* taxa accessed through analyses of the RPL35 fragment are shown in Figure 3. Both BI and ML trees have much lower phylogenetic resolution compared to the matrilineal genealogy obtained from the analyses of COI mtDNA gene. Phylogenetic relationships between the accessed taxa are poorly resolved with major basal nodes in the tree having low or insignificant levels of support (BPP<0.95; BS<75%). However, we achieved higher resolution of phylogenetic relationships among *Cyrtodactylus* taxa at species level.

The Nui Chua Mt. population of *Cyrtodactylus* sp. is clearly reconstructed as a sister lineage with respect to *C. cattienensis* (see Fig. 3). Certain incongruence is observed between matrilineal (mtDNA) and phylogenetic (nuDNA) differentiation patterns in some taxa. Monophyly of the *C. irregularis* species was not supported in the RPL35 analysis. Moreover, despite certain genetic variation in RPL35 observed within *C. cattienensis*, it does not correspond to the two lineages pattern as uncovered by COI (Binh Chau—Phuoc Buu and Dong Nai mtDNA lineages). *C. cattienensis*, *Cyrtodactylus* sp. from Nui Chua Mt., *C. phuocbinhensis*, *C. pseudoquadrivirgatus*, *C. huynhi*, *C. bidoupimontis* form a monophyletic group (0.98/48). Sister-clade relationships of *C. bugiamapensis* and *C. ziegleri* are also supported (1.0/100).

Genetic distances. The uncorrected genetic *p*-distances among and within the COI gene fragment of the studied *Cyrtodactylus* species are shown in Table 4, the uncorrected genetic distances for the RPL35 nuDNA marker are given in Table 5.

TABLE 3. Meristic and morphometric (in mm) data for the type series of *Cyrtodactylus sangi* sp. nov. Paired measurements taken on the right side; paired meristic characters are given left/right.

	R-14995, Holotype	R-11503, Paratype
Sex	Male	Female
SVL	49.9	56.3
ForeaL	7.4	7.7
TibiaL	9.0	9.5
TailL	>40.8 (original but tip missing; broken)	47.9 (only first 15.1 mm original; broken)
AG	19.5	22.1
HeadL	15.6	16.6
HeadW	9.4	10.8
HeadH	6.5	7.5
OrbD	3.2	3.6
OrbEar	4.6	5.2
SnOrb	5.7	6.4
NosOrb	4.3	4.5
EarL	0.4	0.4
RH	1.4	1.5
RW	2.5	2.6
ML	1.6	1.7
MW	2.1	2.3
DorTub	19	21
ParaTub	27	29
PreclPo/PreclPi	7 PreclPo	4 PreclPi
FemPi/FemPo	0	0
EnlFemSc	4/?	4/4
Ven	37	37
SL	12/12	11/11
IL	10/10	9/9
InterorbSc	19	19

The observed interspecific distances in the COI gene within the *C. irregularis* species group varied from $p=4.5\%$ (between *C. huynhi* and *C. dati*) to $p=19.0\%$ (between *C. irregularis sensu stricto* and *C. cattienensis*) (see Table 4). These values slightly overlapped with interspecific comparisons between *C. irregularis* species group members and the outgroup *C. intermedius* ($18.5\% < p < 23.2\%$). The observed intraspecific distances in our analysis varied from $p=0\%$ to $p=4.6\%$, the last value corresponding to the genetic differentiation between mtDNA lineages of *C. cattienensis* from Ba Ria—Vung Tau and Dong Nai provinces, respectively (see Table 4). Since this differentiation is slightly higher than the minimal recorded interspecific genetic distance between *C. dati* and *C. huynhi*, such high intraspecific distances might reflect the insufficient taxonomy of the group; further studies, also including examination of additional mtDNA and nuDNA phylogenetic markers, are needed to clarify the taxonomic status of these lineages.

Genetic differentiation in examined RPL35 sequences (see Table 5) varies from $p=0.2\%$ (between *C. cryptus* and *Cyrtodactylus* sp. 1 from Da Nang City) or $p=0.6\%$ (between *C. bugiamapensis* and *C. zieglerei*) to $p=4.5\%$ (between *C. agusanensis* and *C. cryptus*). Intraspecific genetic differentiation in RPL25 fragment varied from $p=0\%$ to $p=1.1\%$ (within *C. bidoupimontis*); genetic differentiation within *C. cattienensis sensu lato* was minimal with $p=0.1\%$ (see Table 5).

TABLE 4. Uncorrected *p*-distance (percentage) between COI sequences of *Cyrtodactylus* species included in phylogenetic analyses (below the diagonal), and standard error estimates (above the diagonal). The ingroup mean uncorrected *p*-distances are shown on the diagonal and shaded with grey.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 <i>C. bidoupimontis</i>	0.3	1.6	1.6	1.5	1.6	1.6	1.6	1.6	1.2	1.6	1.5	1.6	1.5	1.7	1.7	1.7	1.5	1.6	1.8	1.8
2 <i>C. bugiamapensis</i>	14.2	1.3	1.4	1.4	1.5	1.3	1.5	1.4	1.5	1.3	1.2	1.4	1.4	1.6	1.0	1.6	1.4	1.5	1.6	1.8
3 <i>C. caovamsungi</i>	15.6	14.6	1.0	1.5	1.6	1.6	1.5	1.5	1.7	1.5	1.5	1.6	1.4	1.6	1.5	1.6	1.6	1.5	1.8	1.9
4 <i>C. cattienensis</i>	17.4	16.6	17.5	4.6	1.5	1.7	1.6	1.4	1.4	1.4	1.3	1.4	1.5	1.5	1.4	1.3	1.7	1.6	1.8	1.9
5 <i>C. cryptus</i>	15.8	16.1	15.2	18.2	0.0	1.6	1.6	1.6	1.5	1.6	1.7	1.4	1.6	1.6	1.4	1.6	1.6	1.3	1.8	2.0
6 <i>C. cucdongensis</i>	14.6	13.7	15.2	18.3	15.5	0.1	1.7	1.6	1.6	1.7	1.5	1.6	1.4	1.7	1.4	1.7	1.3	1.6	1.9	1.9
7 <i>C. dati</i>	14.8	15.1	17.0	18.9	16.0	16.7	0.0	0.8	1.4	1.6	1.6	1.5	1.5	1.7	1.5	1.7	1.6	1.6	2.0	2.0
8 <i>C. huynhi</i>	14.3	14.9	16.5	18.4	16.0	16.3	4.5	0.1	1.4	1.5	1.5	1.4	1.4	1.7	1.4	1.6	1.4	1.5	1.9	1.8
9 <i>C. irregularis</i>	9.9	15.6	17.1	19.0	15.7	15.0	14.7	15.0	0.1	1.5	1.4	1.4	1.4	1.5	1.6	1.7	1.4	1.6	1.8	1.9
10 <i>C. kingsadai</i>	16.0	14.4	15.2	18.1	12.5	15.5	15.4	15.4	16.3	—	1.5	1.4	1.4	1.6	1.2	1.6	1.5	1.3	1.8	1.7
11 <i>C. phuocbinhensis</i>	15.2	14.4	15.3	15.6	14.6	14.2	15.5	16.2	13.9	13.6	0.4	1.4	1.5	1.6	1.3	1.5	1.5	1.6	1.6	1.9
12 <i>C. pseudoquadrivirgatus</i>	14.2	12.8	14.8	14.9	13.5	14.1	14.3	14.3	13.5	13.9	13.2	0.0	1.5	1.3	1.4	1.4	1.6	1.5	1.2	1.8
13 <i>C. takotensis</i>	12.3	12.1	13.7	17.2	14.6	11.3	13.9	12.6	12.5	12.8	13.8	12.6	0.2	1.6	1.4	1.4	1.4	1.5	1.7	1.9
14 <i>C. taynguyenensis</i>	16.1	16.9	15.4	17.7	14.8	18.2	18.0	17.9	16.1	16.2	14.6	12.3	15.9	0.0	1.5	1.7	1.6	1.6	1.4	2.0
15 <i>C. ziegleri</i>	15.1	7.8	14.4	17.0	14.6	15.2	15.2	14.7	15.3	13.8	14.3	14.0	12.7	15.6	3.0	1.5	1.4	1.4	1.6	1.8
16 <i>Cyrtodactylus sangi</i> sp. nov.	16.4	15.1	17.5	14.0	15.6	15.7	17.9	17.3	17.1	15.9	12.9	14.0	14.6	17.0	15.9	0.3	1.7	1.6	1.7	1.9
17 <i>C. yangbayensis</i>	13.5	13.1	15.4	17.9	15.4	9.6	16.0	14.8	13.5	14.4	13.6	13.9	11.0	15.3	13.0	16.7	3.7	1.6	1.8	1.8
18 <i>Cyrtodactylus</i> sp. 1	16.0	15.0	14.7	18.9	9.6	16.1	16.0	15.3	15.3	14.1	14.9	15.0	13.8	16.0	13.7	16.4	14.9	—	1.7	1.7
19 <i>Cyrtodactylus</i> sp. 2	13.7	14.8	16.2	16.4	15.8	16.1	15.8	15.0	13.9	15.6	13.1	8.2	12.6	10.4	14.7	14.8	14.3	13.4	—	2.3
20 <i>C. intermedius</i>	20.8	22.1	23.2	20.5	22.4	21.5	20.8	20.2	22.2	19.3	18.5	20.6	21.5	21.7	22.2	19.3	21.8	20.2	21.1	—

TABLE 5. Uncorrected *p*-distance (percentage) between RPL35 sequences of *Cyrtodactylus* species included in phylogenetic analyses (below the diagonal), and standard error estimates (above the diagonal). The in-group mean uncorrected *p*-distances are shown on the diagonal and shaded with grey.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1 <i>C. agusanensis</i>	0.9	0.8	0.8	0.7	0.7	0.7	0.8	0.8	0.8	0.8	0.5	0.7	0.8	0.8	0.7	0.8	0.8	1.1
2 <i>C. annulatus</i>	3.6	0.2	0.8	0.8	0.7	0.8	0.8	0.9	0.3	0.8	0.7	0.7	0.7	0.8	0.7	0.8	0.8	1.2
3 <i>C. batuensis</i>	3.9	3.1	—	0.7	0.6	0.7	0.8	0.7	0.8	0.7	0.7	0.7	0.7	0.5	0.6	0.7	0.7	1.3
4 <i>C. bidoupimontis</i>	4.3	3.5	3.4	1.1	0.5	0.6	0.7	0.6	0.8	0.4	0.7	0.5	0.6	0.8	0.6	0.6	0.6	1.1
5 <i>C. bugiamapensis</i>	3.1	2.8	2.7	2.3	0.0	0.6	0.6	0.7	0.6	0.4	0.6	0.4	0.6	0.7	0.3	0.6	0.7	1.1
6 <i>C. cattiensis</i>	4.1	3.4	3.3	2.5	2.1	0.1	0.7	0.8	0.8	0.6	0.7	0.5	0.6	0.7	0.6	0.4	0.8	1.1
7 <i>C. consobrinus</i>	3.8	3.4	3.7	3.3	2.6	3.2	0.9	0.8	0.8	0.7	0.8	0.6	0.8	0.8	0.7	0.7	0.8	1.2
8 <i>C. cryptus</i>	4.5	3.7	3.6	2.8	2.8	3.4	3.9	0.0	0.8	0.6	0.8	0.6	0.6	0.8	0.7	0.8	0.2	1.2
9 <i>C. jambangan</i>	3.7	0.7	3.2	3.6	2.8	3.4	3.5	3.8	0.4	0.8	0.7	0.7	0.8	0.8	0.7	0.8	0.8	1.2
10 <i>C. huynhi</i>	4.0	3.2	3.1	1.8	1.6	2.4	3.0	2.9	3.3	0.1	0.7	0.4	0.6	0.8	0.5	0.7	0.6	1.1
11 <i>C. philippinicus</i>	1.7	3.2	3.5	3.9	2.8	3.7	4.2	4.1	3.3	3.6	0.2	0.7	0.7	0.7	0.6	0.8	0.8	1.1
12 <i>C. phuocbinhensis</i>	3.3	2.6	2.7	1.7	1.5	1.9	2.5	2.9	2.6	1.5	3.2	0.4	0.6	0.7	0.5	0.5	0.6	1.1
13 <i>C. pseudoquadrivirgatus</i>	3.9	2.8	3.0	2.7	2.3	2.9	3.3	2.9	3.2	2.3	3.5	2.0	—	0.8	0.6	0.7	0.6	1.1
14 <i>C. redimiculus</i>	3.8	3.0	1.4	3.7	2.9	3.5	4.0	3.9	3.1	3.4	3.4	3.0	3.3	0.2	0.7	0.7	0.8	1.2
15 <i>C. ziegleri</i>	3.3	2.9	2.8	2.5	0.6	2.3	2.8	3.0	3.0	1.8	2.9	1.7	2.1	3.1	0.0	0.6	0.7	1.1
16 <i>Cyrtodactylus sangi sp. nov.</i>	3.7	3.3	3.2	2.5	2.1	0.8	2.8	3.4	3.4	2.3	3.7	1.7	2.9	3.5	2.3	0.0	0.8	1.1
17 <i>Cyrtodactylus</i> sp. 1	4.3	3.5	3.4	2.7	2.7	3.3	3.7	0.2	3.6	2.7	3.9	2.7	2.7	3.7	2.8	3.2	—	1.2
18 <i>C. intermedius</i>	9.0	9.2	9.5	8.9	8.5	9.3	8.9	8.7	9.3	9.2	9.0	8.7	8.7	8.8	8.7	8.9	8.9	—

Systematics. In concordance with previously published research (Nazarov *et al.* 2012; Nguyen *et al.* 2013, 2014), genetic analysis of mtDNA and nuDNA genetic markers helped to clarify the taxonomic status of two populations of within the *Cyrtodactylus irregularis* species complex from southern Vietnam.

The population of *Cyrtodactylus* sp. from Nui Chua Mt. was found to be the sister lineage of a lowland-dwelling species *C. cattienensis* in the analyses of mtDNA (see Fig. 2) and nuDNA (see Fig. 3). This population was found to be phylogenetically distinct from its sister species *C. cattienensis sensu lato* at both mtDNA and nuDNA markers. Divergence values of this lineage ($p=14.0\%$ for COI; $p=0.8\%$ for RPL25) are also higher than the values observed between several recognized species of *Cyrtodactylus* (see Tables 4 and 5). The concordant phylogenetic signal of mtDNA and nuDNA strongly suggests that the population of *Cyrtodactylus* sp. from Nui Chua Mt. represents a distinct evolutionary lineage and warrants a status of distinct species. This result is concordant with profound morphological differences revealed between the specimens of *Cyrtodactylus* sp. from Nui Chua Mt. and other members of the *C. irregularis* species complex (see below).

On the contrary, despite profound differentiation in mtDNA (see Fig. 2), the Binh Chau—Phuoc Buu population of *Cyrtodactylus* was found to be indistinguishable from the rest of examined *C. cattienensis* populations in nuDNA-marker both in the tree and in genetic distances (see Fig. 3 and Table 5). A thorough morphological analysis (see below) failed to reveal any significant morphological differences between this population and *C. cattienensis, sensu stricto* from the type locality, primarily due to high variation of both meristic, morphometric and chromatical characters in the latter species. This suggests that the Binh Chau—Phuoc Buu population is likely conspecific with *C. cattienensis* and further detailed studies of its geographic variation including additional nuDNA markers are required to clarify its taxonomic status.

Below we examine diagnostic morphological and chromatical characters in order to clarify the taxonomic status of these two populations.

Status of the Nui Chua population. Based on its phylogenetic distinctiveness assessed both from mtDNA and nuDNA markers (see above), as well as on its morphological and chromatical distinctiveness from all other populations in the *Cyrtodactylus irregularis* complex (see diagnosis and comparisons), we describe it here as a new species:

***Cyrtodactylus sangi* sp. nov.**

(Figs. 4–6)

Chresonymy:

This population has been referred to as follows in the literature:

Cyrtodactylus irregularis: Bobrov & Semenov 2008 (*partim*: easternmost locality on map p. 118).

Cyrtodactylus sp2: Nazarov *et al.* 2012.

Cyrtodactylus sp2: Nguyen *et al.* 2013.

Cyrtodactylus sp2: Nguyen *et al.* 2014.

Cyrtodactylus sp.: Nguyen *et al.* 2017.

Holotype. ZMMU R-14995 adult male from Nui Chua National Park (11°42'06,5" N, 109°08'50,4" E; alt. ca. 230 m asl), Ninh Thuan Province, southern Vietnam. Collected by V.V. Bobrov on 11–12 Oct. 2003.

Paratype. ZMMU R-11503; adult female, bearing the same locality and collecting date as the holotype.

Diagnosis. *Cyrtodactylus sangi* sp. nov. can be distinguished from all other congeners by its small size (maximal known SVL of 56.3 mm); dorsal tubercles in 19–21 irregular rows at midbody; 37 midbody scale rows across belly between ventrolateral skin folds; presence of a continuous angular series of seven pore-bearing (male) or four pitted (female) enlarged precloacal scales, separated by a diastema of undifferentiated scales from four poreless and pitless enlarged femoral scales on each side; absence of precloacal groove; absence of transversely enlarged median subcaudal scales; and a highly irregular banded dorsal pattern.

Description of holotype (Figs. 4, 5a, 6). Adult male. SVL 49.9 mm. TailL >40.8 mm (tail original, but broken and tip missing). Head relatively long (HeadL 15.6; HeadL/SVL 0.31) and wide (HeadW 9.4; HeadW/HeadL 0.60), not markedly depressed (HeadH 6.5), distinct from neck. Loreal region inflated, canthus rostralis slightly prominent. Snout elongate (SnOrb/HeadL 0.37), rounded, longer than orbit diameter (OrbD/SnOrb 0.56). Scales on snout small, rounded to oval, granular to weakly conical, mostly homogeneous, larger than those on crown,

interorbital and occipital regions (Fig. 6b). Orbit of moderate size (OrbD/HeadL 0.21); pupil vertical with crenelated margins; supraciliaries short, forming conical spines, larger anteriorly. Ear opening vertically oval, small (EarL/HeadL 0.03); orbit to ear distance longer than orbit diameter (OrbEar/Orb D 1.44). Rostral much wider (2.5 mm) than deep (1.4 mm); rostral crease straight, starting from the upper middle of the rostral, going down less than half the rostral height. Two enlarged supranasals separated from one another anteriorly by one internasal, posteriorly by two. Rostral contacting first supralabial on each side, nostrils, two supranasals and one internasal. Nostrils oval, more or less laterally directed, each surrounded by supranasal, rostral, first supralabial and three postnasals. Three or four rows of small scales separate orbit from supralabials. Mental triangular, wider (2.1 mm) than deep (1.6 mm). A single pair of greatly enlarged postmentals in broad contact behind mental, each bordered anteromedially by mental, anterolaterally by first infralabial, posterolaterally by an enlarged lateral chinshield, and posteriorly by one (left) and two (right) granules (in total two granules contact the postmentals) (Fig. 6a). Supralabials to mid-orbital position 9/9, enlarged supralabials to angle of jaws 12/12. Infralabials 10/10. Interorbital scale rows across narrowest point of frontal bone 19.

Body moderately slender, relatively short (AG/SVL 0.39) with poorly defined, non-denticulate, ventrolateral skin folds. Dorsal scales weakly heterogeneous, domed to conical; irregularly distributed tubercles (five to six times size of adjacent dorsal scales) extending from neck onto tail base, smaller tubercles on postocular region, crown and occiput; most tubercles bearing a strong keel, tubercles on posterior trunk and sacral region most prominent; tubercles on lower flanks without keel. Dorsal tubercles in about 19 irregular rows at midbody, typically separated from one another by two dorsal granules. Paravertebral tubercles 27. Ventral scales larger than dorsals, smooth, oval and subimbricate, largest on posterior abdomen and in precloacal region. Midbody scale rows across belly between ventrolateral folds 37. Gular region with homogeneous, smooth, juxtaposed granular scales. A triangular patch of enlarged precloacal scales at the top of which lies an angular, continuous series of seven pore-bearing scales (three on the left side, one at the summit and three on the right side), separated by a diastema of 14/14 undifferentiated scales from a continuous series of 4/? enlarged femoral scales (small piece of skin missing on the right side) (Fig. 6c). Enlarged femoral scales poreless and pitless, two-three times the size of the scales of the adjacent anterior scale row. No precloacal groove. Hemipeneal bulges evident. Postcloacal spurs each bearing two much enlarged conical scales (Fig. 6c).



FIGURE 4. Live holotype of *Cyrtodactylus sangi* sp. nov. *in situ* in Nui Chua National Park, Vietnam. Photograph by V.V. Bobrov.



FIGURE 5. Preserved type series of *Cyrtodactylus sangi* sp. nov., a—holotype (ZMMU R-14995), b—paratype (ZMMU R-11503).

Scales on palm and sole smooth, rounded to oval or hexagonal, slightly domed. Scalation on dorsal surfaces of fore- and hind limbs similar to body dorsum with enlarged tubercles interspersed among smaller scales. Fore- and hind limbs moderately long (ForeaL/SVL 0.15, TibiaL/SVL 0.18), moderately slender. Digits long, slender, inflected at interphalangeal joints, all bearing robust, slightly recurved claws. Basal subdigital lamellae broad, oval to rectangular, without scansorial surfaces (5-5-6-6-5 right manus, 6-7-7-7-8 right pes); narrow lamellae distal to digital inflection and not including ventral claw sheath: 6-6-9-10-9 (right manus), 8-8-11-11-9 (right pes). Subcaudals scales larger than supracaudal scales, but not forming enlarged transverse plates nor well-defined rows or pairs (Fig. 6e).

Coloration in preservative (Figs. 5a, 6). Dorsal ground color of head, neck, body, limbs and tail beige. Dorsal surface of head with irregular brown markings, skin grayish-bluish above orbits. Supralabials each showing a light beige part and a brown part, poorly contrasting. On each side a poorly marked preocular stripe. On each side a postocular stripe reaching the nape but not meeting the one of the opposite side (i.e., a discontinuous nuchal collar). The upper surface of limbs shows irregular brown marks. The dorsum shows five irregularly-shaped transversal bands, with additional irregular smaller blotches. Seven dark brown irregular bands on tail nearly or completely encircling the tail (tail tip missing, probably two or three additional distal bands were present on the original tail); additional irregular spots between the bands on tail sides and on the undersurface of tail. The undersurfaces of the head, throat, venter and members are uniformly beige.

Variation. Morphometric and meristic values for the type series are provided in Table 3. Morphological and coloration characters of the paratype agree in most respects with those of the holotype, differing only in minor details (see Table 3 and remarks hereafter). In the female paratype postmentals bordered posteriorly by three (left) and one (right) granules (in total three granules contact the postmentals); supralabials to mid-orbital position 8/8; four pitted precloacal scales (one on the left side, one on the top, two on the right side) in a continuous series, separated by a diastema of 10/12 undifferentiated scales from a continuous series of 4/4 enlarged femoral scales; postcloacal spurs each bearing a single, slightly enlarged rounded prominent scale. In the female paratype, 5-5-5-6-4 basal subdigital lamellae on right manus, 7-6-7-7-7 on right pes; distal narrow lamellae 6-7-9-8-8 on right manus, 8-9-10-11-10 on right pes. Subcaudals on original part of tail same as in male; subcaudals in regenerated part of tail very irregular, smaller than on original part of tail, but still larger than supracaudals. The original part of the paratype's tail shows three brown bands; the upper and lower surfaces of the regenerated part are marbled with beige and light brown. The photograph of a live adult individual was presented by Nguyen *et al.* (2014: 56: Fig. 3;

under *C. sp2*); its colors are slightly darker and more contrasted than in preserved specimens, especially on the tail, which is complete and shows 11 dark brown bands.

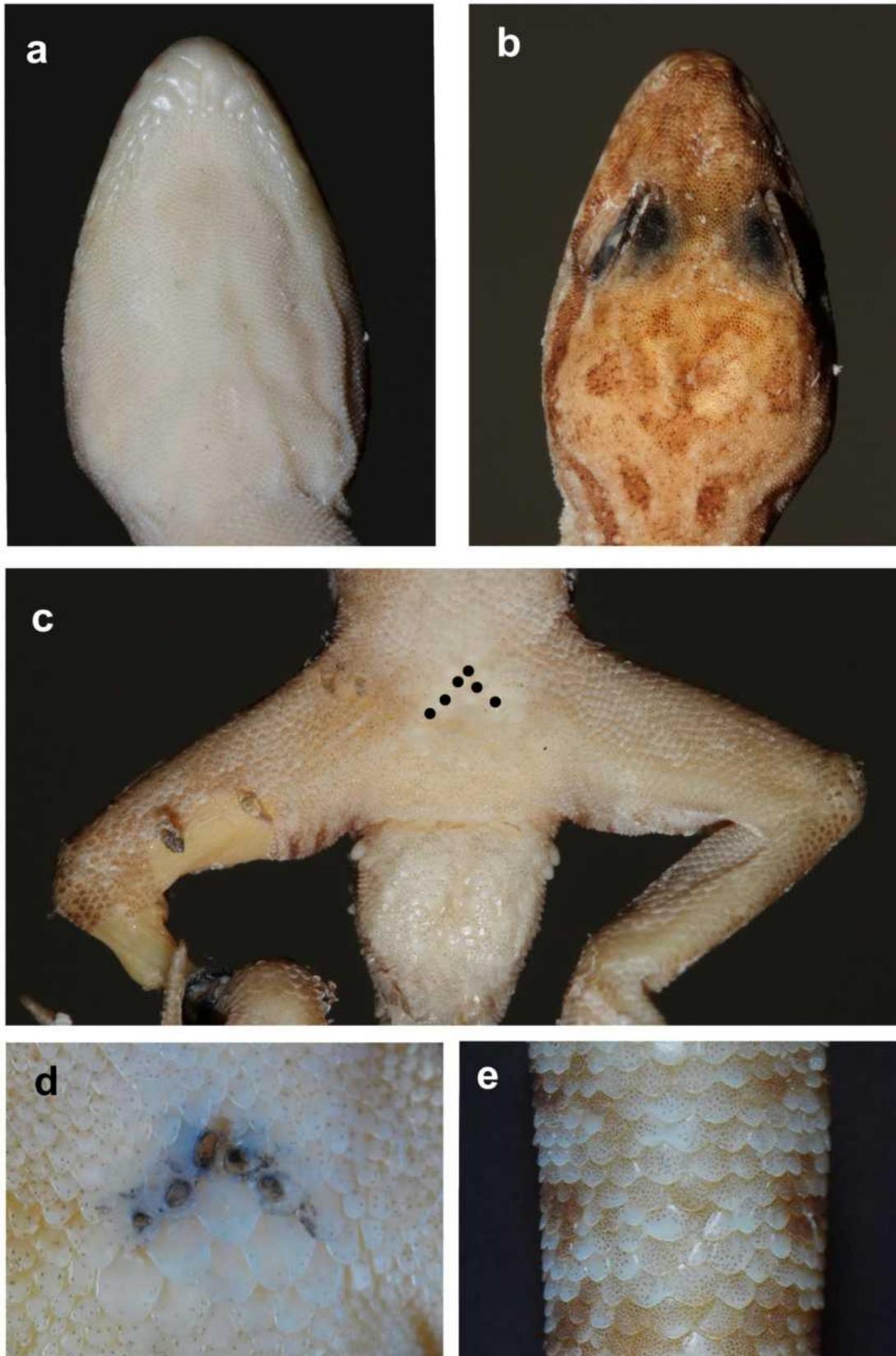


FIGURE 6. Morphological characters of the preserved male holotype of *Cyrtodactylus sangi* **sp. nov.** *a*—ventral view of the head; *b*—dorsal view of the head; *c*—cloacal region, showing the position of precloacal pores (black dots) and the postcloacal spurs; *d*—precloacal pores and surrounding scales; *e*—subcaudal scalation.



FIGURE 7. Live *Cyrtodactylus cattienensis* in situ in Binh Chau—Phuoc Buu National Park, Vietnam.

Comparison with other species. Based on molecular data, *Cyrtodactylus sangi* **sp. nov.** is the sister species to a clade containing *C. cattienensis sensu stricto* + Binh Chau—Phuoc Buu N.R. population (Fig. 7). Among the species of the *Cyrtodactylus irregularis* group, *Cyrtodactylus sangi* **sp. nov.** differs from Binh Chau—Phuoc Buu N.R. population by its smaller SVL (56.3 vs. 63.7 mm), its higher Ven (37 vs. 30–33), a lower number of interorbital scales (19 vs. 20–24), its irregular (vs. regular) nuchal collar, and its highly irregular dark tail bands (vs. regular) with band length much shorter than intervals (vs. subequal). It differs from *C. bidoupimontis* by its much smaller SVL (maximal known SVL 56.3 vs. 86.3 mm), lower Ven (37 vs. 38–43), higher number of precloacal pores in males (7 vs. 4–6), lower number of enlarged femoral scales on each side (4 vs. 8–10), highly irregular (vs. regular), medially interrupted (vs. uninterrupted), nuchal collar, without (vs. with) white bordering, higher number of dark tail bands (11 vs. 7–9), and highly irregular (vs. regular) dark tail bands with band length much shorter (vs. longer) than intervals. It differs from *C. bugiamapensis* by its much smaller size (maximal known SVL 56.3 vs. 76.8 mm), lower number of enlarged femoral scales on each side (4 vs. 6–8), generally lower DorTub (19–21 vs. 20–24) and generally lower Ven (37 vs. 36–46), highly irregular, medially interrupted, nuchal collar, without white bordering (vs. regular and with white bordering), dorsum with highly irregular thin bands (vs. irregular spots), and highly irregular (vs. regular) dark tail bands with band length much shorter (vs. longer) than intervals. It is distinguished from *C. cattienensis sensu stricto* by its smaller size (maximal known SVL 56.3 vs. 64.8 mm), highly irregular dark tail bands (vs. regular) with band length much shorter than intervals (vs. subequal), its medially interrupted, irregular (vs. regular) nuchal collar, and its much more irregular dorsal bands. From *C. cryptus*, it differs by its much smaller size (maximal known SVL 56.3 vs. 90.8 mm), its smaller Ven (37 vs. 47–50), its smaller number of precloacal pores (7 vs. 9–11), its lower numbers of subdigital lamellae on the 4th toe (18 vs. 20–23) and the 4th finger (16 vs. 18–19), its medially interrupted (vs. uninterrupted), irregular (vs. regular) nuchal collar without (vs. with) yellowish bordering, and dark tail bands much shorter (vs. longer) than band-interspace. It can be separated from *C. cucdongensis* by its smaller size (maximal known SVL 56.3 vs. 65.9 mm), generally higher DorTub (19–21 vs. 16–19), its lower Ven (37 vs. 41–44), its higher number of precloacal pores in males (7 vs. 5–6), and its lower number of enlarged femoral scales on each side (4 vs. 5–9). It differs from *C. dati* by its smaller size

(maximal known SVL 56.3 vs. 70.1 mm), smaller number of paravertebral tubercles (27–29 vs. 34–35), smaller Ven (37 vs. 42–48), and higher number of precloacal pores in males (7 vs. 5 or 6). It differs from *C. gialaiensis* by its smaller size (maximal known SVL 56.3 vs. 62.8 mm), smaller Ven (37 vs. 38–45), lower number of precloacal pores in males (7 vs. 9 or 10), and its medially interrupted (vs. uninterrupted) nuchal collar. It is distinguishable from *C. huynhi* by its smaller size (maximal known SVL 56.3 vs. 79.8 mm), its higher DorTub (19–21 vs. 16–18), its lower Ven (37 vs. 43–46), a medially interrupted (vs. uninterrupted), irregular (vs. regular) nuchal collar, and dark tail bands much shorter (vs. longer) than inter-band spaces. From *C. irregularis*, it differs by its smooth (vs. pitted) enlarged femoral scales, by lacking (vs. having) light margins around the dark marks on the back, and by lacking (vs. having) enlarged spurs on the whorls of the tail base. It can be separated from *C. phuocbinhensis* based on its smaller size (maximal known SVL 56.3 vs. 60.4 mm), lower number of enlarged femoral scales on each side (4 vs. 5), lower Ven (37 vs. 43–47), higher number of dark tail bands (11 vs. 10) and its transversal (vs. longitudinal) dorsal colour pattern. It differs from *C. pseudoquadrivirgatus* by its much smaller size (maximal known SVL 56.3 vs. 83.3 mm), its lower Ven (37 vs. 41–58), and the presence (vs. absence) of enlarged femoral scales. From *C. taynguyenensis* it differs by its much smaller size (maximal known SVL 56.3 vs. 85 mm), the presence (vs. absence) of enlarged femoral scales, its higher number of precloacal pores in males (7 vs. 6), its lower Ven (37 vs. 42–49), its medially interrupted (vs. uninterrupted), irregular (vs. regular) nuchal collar, and dark tail bands much shorter (vs. subequal or longer) than inter-band spaces. It can be distinguished from *C. ziegleri* by its much smaller size (maximal known SVL 56.3 vs. 93 mm), its lower number of enlarged femoral scales on each side (4 vs. 8–10), the absence (vs. presence) of femoral pores in males, its much narrower dorsal bands, and its highly irregular (vs. regular) dark tail bands with band length much shorter than intervals (vs. subequal).

Distribution and natural history. The species is still known only from its type locality. The individuals were collected at night on a large tree trunk in forest at an elevation of approximately 230 m a.s.l.

Etymology. The specific epithet honors our colleague Nguyen Ngoc Sang (Institute of Tropical Biology, Ho Chi Minh City) for his contributions to the herpetology of Vietnam and his benchmark works on taxonomy and diversity of the genus *Cyrtodactylus* in Vietnam (Nguyen *et al.* 2013, 2014). We suggest the following common names: Nui Chua Bent-toed Gecko (English), *Nuichuakromvingergekko* (Dutch), *Cyrtodactyle de Nui Chua* (French), Нюйтюинский кривопалый геккон [transliterated as *Nuityuynskiy krivopalyi gekkon*] (Russian) and *Thằn lằn chân ngón Núi Chúa* (Vietnamese).

Status of the Binh Chau-Phuoc Buu Nature Reserve population

This population has been referred to as follows in the literature:

Cyrtodactylus irregularis complex: Nazarov *et al.* 2008: 142 (map's locality 19).

Cyrtodactylus cattienensis: Geissler *et al.* 2009: 29 (*partim*; locality not shown on map p. 28).

Cyrtodactylus cf. *cattienensis*: Nazarov *et al.* 2012: 3 (map's localities 23 & 24).

Cyrtodactylus cattienensis: Nguyen *et al.* 2013: 401: Fig. 1 (*partim*); 402 (Tab. 1, *partim*); 405: Fig. 2 (*partim*).

Material examined. ZMMU R-11937-1–4, Binh Chau—Phuoc Buu N.R., Ba Ria—Vung Tau Province, southern Vietnam; collected by V.V. Bobrov on 26 June 2004. ZMMU R-14508 (NAP-02549, NAP-02558, NAP-02559), Binh Chau sector of Binh Chau—Phuoc Buu N.R., Ba Ria—Vung Tau Province, southern Vietnam on 20, 22 and 22 Nov. 2011 respectively; ZMMU R-14509 (NAP-03141) from the same locality but on 9 Jul. 2012; collected by N.A. Poyarkov and A.B. Vassilieva.

Morphological description. Morphometric and meristic values are provided in Table 6. SVL 47.6–63.7 mm. Head relatively long (HeadL/SVL 0.29–0.33) and wide (HeadW/HeadL 0.60–0.65), not markedly depressed, distinct from neck. Loreal region inflated, canthus rostralis slightly prominent. Snout elongate (SnOrb/HeadL 0.35–0.40), rounded, longer than orbit diameter (OrbD/SnOrb 0.58–0.73). Scales on snout small, rounded to oval, granular to weakly conical, mostly homogeneous, larger than those on crown, interorbital and occipital regions. Orbit of moderate size (OrbD/HeadL 0.23–0.26); pupil vertical with crenelated margins; supraciliaries short, forming conical spines, larger anteriorly. Ear opening oval, small (EarL/HeadL 0.03–0.07); orbit to ear distance longer than orbit diameter (OrbEar/Orb D 1.07–1.26). Rostral much wider than deep; rostral crease an inverted Y, starting from the upper middle of the rostral, going down half the rostral height. Two enlarged supranasals separated from one another anteriorly by one internasal. Rostral contacting first supralabial on each side, nostrils,

TABLE 6. Meristic and morphometric data for the Binh Chau - Phuoc Buu Nature Reserve population. Morphometric data (in mm) are given for the right side except otherwise noted. Paired meristic characters are given left/right.

Sex	ZMMU R-11937-3	ZMMU R-11937-4	ZMMU R-11937-1	ZMMU R-14509 (NAP-03141)	ZMMU R-11937-2	ZMMU R-14508 (NAP-02549)	ZMMU R14508 (NAP-02559)	ZMMU R-14508 (NAP-02558)
	M	M	M	M	F	F	FF	FF
SVL	47.6	55.7	53.4	57.3	49.1	49.8	63.7	62.3
ForeaL	7.2	8.0	7.2	9.2	7.7	7.6	8.7	8.6
TibialL	8.6	10.4	9.3	10.4	9.3	9.3	11.0	11.2
TailL	>47.2 (tail original but tip missing)	41.7 (only first 8.3 original)	57.9	36.2 (only first 5.5 original)	43.8	55.1	33.0 (only first 6.3 original)	63.3
AG	18.3	23.5	21.8	27.4	20.0	22.0	30.0	25.0
HeadL	14.9	18.1	15.9	17.8	15.8	15.2	18.3	18.5
HeadW	9.6	10.8	9.6	11.2	10.0	9.9	11.5	11.1
HeadH	7.1	7.1	6.3	7.7	6.6	6.1	7.0	6.9
OrbD	3.5	4.6	4.1	4.7	4.0	3.8	4.3	4.6
OrbEar	4.4	4.9	4.9*	5.2	4.4	4.6	5.4	5.2
SnOrb	6.0	6.5	6.1	6.4	5.5	5.8	6.9	6.4
EarL	0.7	0.7	0.7*	0.8	0.5	0.7	1.2	0.6
RH	1.4	1.5	1.4	1.8	1.2	1.2	1.8	1.6
RW	2.5	2.7	2.4	2.6	2.2	2.5	2.7	2.9
ML	1.4	1.8	1.6	1.7	1.5	1.7	1.9	1.9
MW	1.8	2.4	2.1	2.3	2.0	2.3	2.8	2.6
DorTub	21	19	20	20	19	20	20	19
ParaTub	28	27	29	30	28	29	30	29
PrecIPo/PrecIPi	6 PrecIPi	6 PrecIPo	6 PrecIPi**	0	1 PrecIPi***	0	6 PrecIPi	6 PrecIPi
FemPi/FemPo	0	0	0	0	0	0	0	0
EnlFemSc	4/2	4/4	4/4	4/4	4/4	5/5	5/5	5/5
Ven	33	33	30	32	31	32	30	31
SL	11/11	11/11	11/11	12/11	12/11	11/11	12/11	9/12
IL	9/9	9/9	10/10	10/10	10/10	10/10	9/9	9/9
InterorbSc	24	21	23	23	20	21	23	23

* = data for the left side, right side damaged. ** = in ZMMU R-11937-1 the two lowest preclacal pits are much deeper and open and could be regarded as pores. *** = in ZMMU R-11937-2 the single pitted scale is at the top of the patch of enlarged preclacal scales.

two supranasals and one internasal. Nostrils oval, more or less laterally directed. Each nostril surrounded by supranasal, rostral, first supralabial and four small postnasals (except in ZMMU R-11937-1;4), where each nostril is posteriorly in contact with three small postnasals, and in ZMMU R-14508 (NAP-02558) where nostrils are in contact with 4/3 small postnasals). Three or four rows of small scales separate orbit from supralabials. Mental triangular, wider than deep. A single pair of greatly enlarged postmentals in broad contact behind mental, each bordered anteromedially by mental, anterolaterally by first infralabial, posterolaterally by an enlarged lateral chinshield, and posteriorly by two (left and right) granules (in total three granules contact the postmentals, middle one contacts both), except in ZMMU R-11937-1; ZMMU R-14508 (NAP-02558 and NAP-02559) where postmentals are bordered posteriorly by 3 (left) and 2 (right) granules, and in ZMMU R-14509 (NAP-03141) by 2/1. Supralabials to mid-orbital position 7–11, generally 8/8, enlarged supralabials to angle of jaws 9–12. Infralabials 9 or 10. Interorbital scale rows across narrowest point of frontal bone 20–24.

Body moderately slender, relatively short (AG/SVL 0.38–0.48) with poorly defined, non-denticulate, ventrolateral skin folds. Dorsal scales weakly heterogeneous, domed to conical; irregularly distributed tubercles (three to six times size of adjacent dorsal scales) extending from shoulder region onto tail base, smaller tubercles on postocular region, crown, occiput and nape; most tubercles bearing a strong keel, tubercles on posterior trunk and sacral region most prominent. Dorsal tubercles in 19–21 irregular rows at midbody, typically separated from one another by two to four dorsal granules. Paravertebral tubercles 27–30. Ventral scales larger than dorsals, smooth, oval and subimbricate, largest on posterior abdomen and in precloacal region. Midbody scale rows across belly between ventrolateral folds 30–33. Gular region with homogeneous, smooth, juxtaposed granular scales. A triangular patch of enlarged precloacal scales at the top of which lies an angular, continuous series of at most six pitted or pore-bearing scales (three on each side), separated by a diastema of undifferentiated scales from a continuous series of 4 or 5 (rarely 2) enlarged femoral scales on each side. Enlarged femoral scales poreless and pitless, three to six times the size of the scales of the adjacent anterior scale row. No precloacal groove. In all specimens, postcloacal spurs each bearing two enlarged conical scales, except in ZMMU R-11937-1 where postcloacal spurs bear two/one enlarged conical scales, and in ZMMU R-14509 (NAP-03141) and ZMMU R-14508 (NAP-02549) where they bear one/one enlarged conical scale.

Scales on palm and sole smooth, rounded to oval or hexagonal, slightly domed. Scallation on dorsal surfaces of fore- and hind limbs similar to body dorsum with enlarged tubercles interspersed among smaller scales. Fore- and hind limbs moderately long (ForeaL/SVL 0.13–0.16, TibiaL/SVL 0.17–0.19), moderately slender. Digits long, slender, inflected at interphalangeal joints, all bearing robust, slightly recurved claws. Basal subdigital lamellae broad, oval to rectangular, without scansorial surfaces. Basal subdigital lamellae in ZMMU R-11937-3 – 6-6-7-5-6 right manus, 6-5-7-8-7 right pes; in ZMMU R-14509 (NAP-03141) 6-6-6-6-6 on right manus, 6-6-7-9-8 on right pes; in ZMMU R-14508 (NAP-02559) 6-6-6-6-6 on right manus, 6-6-8-9-9 on right pes. Narrow lamellae distal to digital inflection and not including ventral claw sheath: in ZMMU R-11937-3 – 8-8-11-10-8 (right manus), 7-10-12-11-11 (right pes); in ZMMU R-14509 (NAP-03141) 6-8-10-10-9 on right manus, 9-10-12-12-11 on right pes; in ZMMU R-14508 (NAP-02559) 7-8-10-10-9 on right manus, 8-11-11-11-10 on right pes (lamellae not counted in the other specimens). Subcaudals scales larger than supracaudal scales, but not forming enlarged transverse plates nor well defined rows or pairs. In ZMMU R-11937-4 subcaudals of the regenerated part of tail larger than supracaudals and more irregular than in the original part of tail.

Coloration in life. Dorsal ground color of head, neck, body, limbs and tail beige. Dorsal surface of head with irregular light brown markings, skin grayish-bluish above orbits. On each side a poorly marked preocular stripe. On each side a postocular stripe reaching the nape and meeting the one of the opposite side (i.e., forming a continuous nuchal collar, except in ZMMU R-11937-2 where it is briefly posteromedially interrupted). The upper surface of limbs shows irregular brown marks. Behind the nuchal collar, the neck shows a band which is generally medially interrupted; the dorsum shows five irregular bands between the limb insertions. ZMMU R-11937-3 shows eight dark brown bands on tail completely encircling the tail, although they show a lighter color on the undersurface of tail (tail tip missing, probably one or two additional distal bands were present on the original tail). The complete tails of ZMMU R-11937-1;2 show 11 dark rings; the one of ZMMU R-14508 (NAP-02558) shows nine. The undersurfaces of the head, throat, venter and members are uniformly beige.

Comparison with other species. The Binh Chau—Phuoc Buu N.R. and Nui Chua N.P. populations both belong to the *C. irregularis* species group, morphologically defined as follows by Nguyen *et al.* (2013: 408): possessing an irregular dorsal color pattern, enlarged femoral scales if present separated from precloacal scales, and

small subcaudal scales; this combination of characters distinguishes them from all other Southeast Asian *Cyrtodactylus*. Based on molecular data (Figs. 2, 3), within the *Cyrtodactylus irregularis* complex, the Binh Chau—Phuoc Buu N.R. population is the sister lineage to *C. cattienensis sensu stricto*. Among the species of the *Cyrtodactylus irregularis* group, the Binh Chau—Phuoc Buu N.R. population differs from *C. bidoupimontis* by its smaller SVL (maximal known SVL 63.7 vs. 86.3 mm), its lower Ven (30–33 vs. 38–43), its lower number of enlarged femoral scales on each side (4–5, exceptionally 2, vs. 8–10), and generally higher number of dark bands on tail (9–11 vs. 7–9). It can be differentiated from *C. bugiamapensis* by its lower Ven (30–33 vs. 36–46), its lower number of preloacal pores (maximum 6 vs. 7–11), its lower number of enlarged femoral scales on each side (4–5, exceptionally 2, vs. 6–8). It differs from *C. cryptus* by its much smaller size (maximal known SVL 63.7 vs. 90.8 mm), its much lower Ven (30–33 vs. 47–50), and lower number of preloacal pores (maximum 6 vs. 9–11). It can be separated from *C. cucdongensis* based on its generally higher DorTub (19–21 vs. 16–19) and its lower Ven (30–33 vs. 41–44). From *C. dati*, it can be distinguished by its higher number of InterorbSc (20–24 vs. 17–19), lower Ven (30–33 vs. 42–48) and absence (vs. presence) of femoral pores in males. From *C. huynhi*, it differs by its smaller size (maximal known SVL 63.7 vs. 79.8 mm), higher DorTub (19–21 vs. 16–18), lower Ven (30–33 vs. 43–46) and lower number of preloacal pores (maximum 6 vs. 7–9). From *C. irregularis*, by its smooth (vs. pitted) enlarged femoral scales, by lacking (vs. having) light margins around the dark marks on the back, and by lacking (vs. having) enlarged spurs on the whorls of the tail base. From *C. phuocbinhensis*, by its lower Ven (30–33 vs. 43–47), lower number of preloacal pores (maximum 6 vs. 7) and its transversal (vs. longitudinal) dorsal pattern. From *C. pseudoquadrivirgatus*, by its smaller size (maximal known SVL 63.7 vs. 83.3 mm), lower Ven (30–33 vs. 41–58) and the presence (vs. absence) of enlarged femoral scales. From *C. taynguyenensis* by its smaller size (maximal known SVL 63.7 vs. 85 mm), lower Ven (30–33 vs. 42–49) and the presence (vs. absence) of enlarged femoral scales. From *C. zieglerei* by its much smaller size (maximal known SVL 63.7 vs. 107 mm), lower number of EnlFemS on each side (4–5, exceptionally 2, vs. 8–10) and the absence (vs. presence) of femoral pores in males. From the last remaining species of the complex, *C. cattienensis*, we did not find a single significant morphological or chromatical difference, since all meristic and morphometric characters widely overlap: maximal known SVL 63.7 vs. 69 mm; HeadL/SVL 0.29–0.33 vs. 0.27–0.31; HeadW/HeadL 0.60–0.65 vs. 0.61–0.74; OrbD/HeadL 0.23–0.26 vs. 0.17–0.24; OrbEar/OrbD 1.07–1.26 vs. 1.19–1.46; OrbD/SnOrb 0.58–0.73 vs. 0.44–0.66; SnOrb/HeadL 0.35–0.40 vs. 0.36–0.45; AG/SVL 0.38–0.48 vs. 0.37–0.46; SL 9–12 vs. 9–11, DorTub 19–21 vs. 17–22; tubercles present on head, body, limbs and tail; poorly defined, non-denticulate, ventrolateral skin folds; Ven 30–33 vs. 28–42; patch of enlarged preloacal scales in both sexes; preloacal pores in an angulous continuous series 0–6 vs. 0–8; preloacal groove absent; femoral pores absent; enlarged femoral scales on each side 4–5 (exceptionally 2) vs. 4–8; subdigital lamellae under 4th finger 15–16 vs. 13–16; subdigital lamellae under 4th toe 19–21 vs. 14–19; postloacal spurs 2 (rarely one) vs. 2–3; subcaudal scales small, not transversely enlarged; nuchal collar extending to the posterior margin of the eye; ca. five irregular dorsal bands between limb insertions (comparison with *C. cattienensis sensu stricto* among the type series presented by Geissler *et al.* 2009, i.e., holotype and all 14 other specimens from Cat Tien National Park only). We hence conclude that the Binh Chau—Phuoc Buu N.R. population is to be referred to *C. cattienensis*.

Distribution and natural history. ZMMU R-14508 (NAP-02549, NAP-02558, NAP-02559) and ZMMU R-14509 (NAP-03141) were collected at night on tree trunks near a pool in tropical forest. The female ZMMU R-14508 (NAP-02558) contains two eggs at an advanced development stage (respective maximal diameters 10.4 and 7.8); the female ZMMU R-14508 (NAP-02559) contains two smaller eggs and both individuals were collected at the end of November, indicating that the eggs would likely be laid during the transition between the wet and the dry season. These are the first observations on the reproduction of this species. Binh Chau—Phuoc Buu N.R. is the last remaining area to retain a significant cover of natural forest along the southern coastline of Vietnam (Anonymous, 2002); with Cat Tien National Park this is thus the second protected area from where the species is known. *Cyrtodactylus cattienensis*, endemic to Vietnam, is thus currently known from the adjacent Ba Ria—Vung Tau and Dong Nai provinces.

Discussion

Once believed to be a widespread, variable species, *Cyrtodactylus irregularis* was shown to be composed of at least

13 distinct species with very restricted geographical distributions. So far 40 *Cyrtodactylus* species have been recorded from Vietnam (Grismer *et al.* 2015, Nguyen *et al.* 2015, 2017, Le *et al.* 2016, Luu *et al.* 2017); the presently described species is thus the 41th. More than 40% of the described *Cyrtodactylus* species recorded from Vietnam thus belong to the *C. irregularis* group. To these we add two undescribed candidate species in the *Cyrtodactylus irregularis* group referred to here as *Cyrtodactylus* sp. 1 and *Cyrtodactylus* sp. 2.

DNA-barcoding techniques are now widely applied for uncovering hidden diversity in different groups of amphibians and reptiles (Smith *et al.* 2008; Solovyeva *et al.* 2011, 2014; Che *et al.* 2012; Nagy *et al.* 2012; Xia *et al.* 2012; Murphy *et al.* 2013; Hartmann *et al.* 2013; Amarasinghe *et al.*, 2017; Orlova *et al.* 2017). COI DNA-barcoding proved to be especially useful in revealing cryptic lineages within the genus *Cyrtodactylus* (Nazarov *et al.* 2012, 2014; Nguyen *et al.* 2013, 2014, 2017; Schneider *et al.* 2014). However, recent results of Nguyen *et al.* (2013, 2017), who compared data from mtDNA-based genealogy and nuclear DNA-based phylogeny (RPL35, RAG1), documented the presence of cytonuclear discordance in *Cyrtodactylus*, with highly divergent mtDNA lineages (up to K2P = 10.2%, Ta Kou Mt. population) being not distinguishable from nuclear DNA perspective, indicating free gene flow among sympatric matrilineal lineages. Our study is in concordance with the results of Nguyen *et al.* (2013, 2017): the Binh Chau—Phuoc Buu N.R. population of *C. cattienensis* shows no differentiation in nuclear genes from the Dong Nai Province populations despite significant differentiation in mtDNA (*p*-distance = 4.6%). Thus, despite DNA-barcoding being a useful and powerful tool for identifying cryptic diversity, for the genus *Cyrtodactylus* its results should be taken cautiously and verified by analyses of nuclear DNA and morphological differentiation. In the present study, morphological differentiation was concordant with nuclear phylogeny: the deeply divergent Nui Chua N.P. population is morphologically distinct from the rest of the *C. irregularis* complex members, while the Binh Chau—Phuoc Buu N.R. population appears to be morphologically indistinguishable from *C. cattienensis*.

Nui Chua N.P.'s forest is critically important for biodiversity conservation as it houses the most arid forest ecosystem in Vietnam and, probably, in Southeast Asia (Vu *et al.* 2013). Recent studies on the herpetofauna of this national park indicate that despite low rainfall, Nui Chua Mountain hosts a unique population of stream-dwelling horned toads of the genus *Ophryophryne* (see Poyarkov *et al.* 2017) and several rare reptile species. The sylvicolous *Cyrtodactylus sangi* **sp. nov.** might however be threatened by the development of human infrastructures occurring within the park, possibly similarly affecting the near-endemic *Dixonius aaronbaueri* (Squamata: Gekkonidae) Ngo & Ziegler, 2009 and a population of *Bungarus candidus* (Linnaeus) (Squamata: Elapidae) with a unique color pattern (Nguyen *et al.* 2017a). The discovery of a new species of *Cyrtodactylus*, which is most likely an endemic of Nui Chua Mountain, indicates that the herpetofaunal diversity of Nui Chua N.P. is still insufficiently studied, and reinforces the role of the park in the conservation of the Vietnamese herpetofauna.

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APPENDIX. Comparative material examined.

Cyrtodactylus bidoupimontis: type series (see Nazarov *et al.* 2012); *C. bugiamapensis*: type series (see Nazarov *et al.* 2012); *C. ziegleri*: type series (see Nazarov *et al.* 2008).