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Evolution in karst massifs: Cryptic diversity among bent-toed geckos along the Truong Son Range with descriptions of three new species and one new country record from Laos

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Abstract

Species designated as 'cryptic' share a similar morphotype, and are often only clearly separable by molecular data. *Cyrtodactylus*, the most diverse gecko genus of the family Gekkonidae, is a prime example, because many morphologically similar taxa have only recently been identified as new species as a result of available genetic evidence. However, while cryptic diversity of *Cyrtodactylus* is already well documented on the Vietnamese side of the Truong Son range, only scarce data is available from central Laos. In this study, we address this issue by means of an integrative approach, which employs morphological, molecular, and ecological data to distinguish cryptic species of the *Cyrtodacylus phongnhakebangensis* species group primarily distributed along the northern Truong Son Range. Our analyses based on 12 selected morphological characters, a partial mitochondrial gene (COI), and five ecological parameters revealed three undescribed cryptic *Cyrtodactylus* species from Hin Nam No National Protected Area, which are described as *Cyrtodactylus calamei* **sp. nov.**, *Cyrtodactylus hinnamnoensis* **sp. nov.**, and *Cyrtodactylus sommerladi* **sp. nov.** A fourth discovered *Cyrtodactylus* population in Hin Nam No proved to be the first country record of *C. cryptus* for Laos. Our results highlight the importance of applying an integrative approach to resolving the taxonomy of complex and cryptic species groups, and the role of the Truong Son Range in maintaining the high level of biodiversity over time.

Key words: Cryptic species, karst forest, morphology, new species, Truong Son Range, phylogeny, taxonomy

Introduction

The species-rich clade of Bent-toed Geckos (*Cyrtodactylus*) has recently become a model group for studies of divergent evolution and adaptation of ecomorphologies among lizards, due to a variety of colorful body patterns and characteristic body shapes, sizes, scalation, and life histories found among many extant representatives (Grismer *et al*. 2015). Recent evidence suggests that a single lineage of the genus *Cyrtodactylus*, entering Southeast Asia in the early Oligocene about 35 mya, gave rise to all present-day species (Agarwal *et al.* 2014). However, the evolution and diversification of *Cyrtodacylus* in this region is still poorly understood, especially considering the ever increasing rate of new species descriptions (e.g., Luu *et al*. 2014a; Nazarov *et al*. 2014). In particular, recent findings of cryptic species in Southeast Asian *Cyrtodactylus*, i.e., species that are morphologically similar, but distinguishable genetically (e.g., Ziegler *et al.* 2010), seems counterintuitive in respect to the well-described divergent evolution of ecomorphologies in this group (Luu *et al*. 2015a; Luu *et al*. 2016a,b).

A common assumption is that cryptic species arose so recently that differentiating morphological traits have not yet evolved (Bickford *et al.* 2007). This hypothesis can be resolved by a time-calibrated phylogeny. Molecular clock estimates suggest that the major lineages of *Cyrtodactylus* in South East Asia split up between 25 to 15 mya (Agarwal *et al.* 2014); the cryptic species then should be significantly younger. Recent studies indicate, however, that certain environments and/or life histories might promote the evolution of cryptic diversity (Bickford *et al*. 2007). Evidence for the former hypothesis is provided by new discoveries of a group of cryptic frog species in the central highlands of Vietnam (Rowley *et al.* 2015). These highlands belong to the Truong Son Range (or Annamite Mountains) where Luu *et al.* (2014b, 2015b) recently also uncovered cases of multiple cryptic diversity in the genus *Gekko.*

The Truong Son Range stretches approximately 1,200 km in length and 50–75 km in width, starting from northwest to southeast along the entire length of the Laos–Vietnam border, running through the inland of Vietnam to northeastern Cambodia, with elevations between 500 and 2,000 m a.s.l. (Ziegler & Vu 2009; Bain & Hurley 2011). The Truong Son Range is characterized by its extensive limestone karst formations, which are known to bear high levels of biodiversity and endemism (Clements *et al*. 2006).

Hin Nam No National Protected Area (NPA) in Laos and Phong Nha-Ke Bang National Park (NP) in Vietnam are located on opposite sides of the Truong Son Range in one of the largest areas of contiguous limestone karst systems in Indochina (Sterling *et al*. 2006). Today it is the transitional region between the subtropical plant communities of the North and the tropical ones of the South (Groves & Schaller 2000; Sterling *et al*. 2006). New vertebrate species are still being discovered here, such as two larger mammalian species, *Pseudoryx nghetinhensis* and *Muntiacus truongsonensis* (Vu *et al.* 1993; Pham *et al.* 1998) and a rodent genus, the Laotian Rock Rat, *Laonastes aenigmamus* (Jenkins *et al*. 2005; Aplin & Lunde 2008), suggesting that the Truong Son Range acted as a refugium for the survival of species since the mid Miocene (Sterling *et al*. 2006; Le *et al*. 2015). However, changing environmental conditions during the Pleistocene likely caused longitudinal and altitudinal contractions and expansions in the distribution of lizards (Sterling *et al.* 2006; Corlett 2014), as evidenced in other vertebrate groups (Li *et al.* 2002). In this study, we provide evidence that the pattern of species radiation and the extant distribution of cryptic species did not occur randomly across Southeast Asia, but rather was aggregated in certain areas, such as today's Hin Nam No NPA and Phong Nha-Ke Bang NP, located opposite on the western and eastern sides of the Truong Son Range, viz. in Laos and Vietnam, respectively.

Whereas cryptic diversity of *Cyrtodactylus* is already well documented in the Vietnamese side of that range (e.g., Ziegler *et al.* 2010), only limited data is available from Laos (e.g., Nazarov *et al*. 2014; Luu *et al*. 2015a; Luu *et al*. 2016a,b). Luu *et al*. (2013) reported the first record of *C. phongnhakebangensis* in Laos, a species formerly only known from Phong Nha-Ke Bang NP in Vietnam. Here we provide more detailed morphological analysis in combination with molecular and ecological comparisons to show that the Laotian population in fact represents an undescribed cryptic species. This population is described together with two further new cryptic *Cyrtodactylus* species from Hin Nam No NPA, which are closely related to the phenetically similar *C. phongnhakebangensis* and *C. roesleri*, both originally described from Phong Nha-Ke Bang NP in Vietnam. The fourth discovered taxon in Hin Nam No NPA is shown to be the first country record of *C. cryptus* for Laos, a species likewise originally described from Phong Nha-Ke Bang NP. Our results indicate that certain areas of the Truong Son Range, a global biodiversity hotspot, also form centres of cryptic diversity. In addition, comparative studies on the taxonomy, phylogeny, biogeography, and evolution of cryptic and non-cryptic *Cyrtodactylus* may provide new insights into evolutionary forces that shape vertebrate communities in tropical regions.

Material and methods

Sampling. Field surveys were conducted in Hin Nam No NPA, Khammouane Province, Laos between May to July 2013, May to July 2014, and March to May 2015. Tissue samples were preserved separately in 95% ethanol and specimens were fixed in approximately 85% ethanol, then transferred to 70% ethanol for permanent storage. Specimens were subsequently deposited in the collections of the Vietnam National University of Forestry (VNUF), Hanoi, Vietnam; the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology, Hanoi, Vietnam; the National University of Laos (NUOL), Vientiane, Lao PDR and the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany.

Molecular data and phylogenetic analyses. To resolve new taxa with a high level of confidence, we included members of five different species groups, i.e. *C. irregularis*, *C. interdigitalis*, *C. phongnhakebangensis*, *C. pulchellus*, and *C. wayakonei* (Fig. 1, Table 1). The species *C. elok* Dring, 1979, was used as an outgroup.

TABLE 1. *Cyrtodactylus* samples used in the molecular analyses (for abbreviations see Material and methods).

Species	GenBank no.	Locality	Voucher number
C. badenensis	KF929505	Vietnam: Tay Ninh Province	KIZ13689
C. bansocensis	KU175573	Laos: Khammouane Province	VFU R.2015.20
C. bansocensis	KU175574	Laos: Khammouane Province	NUOL R-2015.21
C. bobrovi	KT004368	Vietnam: Hoa Binh Province	IEBR A.2015.30
C. bobrovi	KT004369	Vietnam: Hoa Binh Province	VNMN A.2015.61
Cyrtodactylus calamei **sp. nov.**	KX064043	Laos: Khammouane Province	NUOL R-2015.22
Cyrtodactylus calamei **sp. nov.**	KX064044	Laos: Khammouane Province	VNUF R.2015.28
C. cryptus	KF169971	Vietnam: Quang Binh Province	PNKB3
C. cryptus	KF169972	Vietnam: Quang Binh Province	PNKB4
C. cryptus	KX064038	Laos: Khammouane Province	VNUF R.2014.69
C. elok	HM888478	Malaysia	ZMMU RAN 1991
C. elok	HM888479	Malaysia	ZMMU RAN 1992
C. darevskii	HQ967221	Laos: Khammouane Province	ZIN FN 256
C. darevskii	HQ967223	Laos: Khammouane Province	ZIN FN 223
Cyrtodactylus hinnamnoensis **sp. nov.**	KX064045	Laos: Khammouane Province	IEBR A.2013.89
Cyrtodactylus hinnamnoensis **sp. nov.**	KX064046	Laos: Khammouane Province	IEBR A.2013.90
Cyrtodactylus hinnamnoensis **sp. nov.**	KX064047	Laos: Khammouane Province	VNUF R.2015.11
Cyrtodactylus hinnamnoensis **sp. nov.**	KX064048	Laos: Khammouane Province	VNUF R.2015.3
Cyrtodactylus hinnamnoensis **sp. nov.**	KX064049	Laos: Khammouane Province	NUOL R-2015.9
C. lomyenensis	KJ817436	Laos: Khammouane Province	IEBR KM2012.54
C. lomyenensis	KP199942	Laos: Khammouane Province	IEBR KM2012.52
C. interdigitalis	KX077901	Laos: Khammouane Province	VNUF R.2014.50

......continued on the next page

TABLE 1. (Continued)

Species	GenBank no.	Locality	Voucher number
C. jaegeri	KT004364	Laos: Khammouane Province	IEBR A.2013.55
C. jaegeri	KT004365	Laos: Khammouane Province	NUOL R.2013.1
C. jaegeri	KT004366	Laos: Khammouane Province	VFU TK914
C. cf. *jarujini*	KX077907	Laos: Bolikhamxay Province	VNUF R.2015.7
C. khammouanensis	HM888467	Laos: Khammouane Province	ZIN FN 191
C. khammouanensis	HM888469	Laos: Khammouane Province	ZIN FN 257
C. kingsadai	KF188432	Vietnam: Phu Yen Province	IEBR A.2013.3
C. cf. *martini*	KF929537	China: Yunnan	KIZ201103
C. multiporus	HM888472	Laos: Khammouane Province	ZIN FN 3
C. multiporus	HM888471	Laos: Khammouane Province	ZIN FN 2
C. otai	KT004370	Vietnam: Hoa Binh Province	IEBR A.2015.26
C. otai	KT004371	Vietnam: Hoa Binh Province	IEBR A.2015.27
C. puhuensis	KF929529	Vietnam: Thanh Hoa Province	KIZ 11665
C. pulchellus	HQ967202	Malaysia	ZMMU R-12643-3
C. pulchellus	HQ967203	Malaysia	ZMMU R-12643-4
C. pageli	KJ817431	Laos: Vientiane Province	ZFMK 91827
C. pageli	KX077902	Laos: Vientiane Province	NQT 2010.36
C. pageli	KX077903	Laos: Vientiane Province	NQT 2010.37
C. phongnhakebangensis	KF929526	Vietnam: Quang Binh Province	PNKB2011.30
C. phongnhakebangensis	KF929527	Vietnam: Quang Binh Province	PNKB2011.32
C. pseudoquadrivirgatus	KF169963	Vietnam: Hue Province	ITBCZ3001
C. cf. *pseudoquadrivirgatus*	KP199949	Vietnam	ZMMU R-13095-2
C. quadrivirgatus	HM888465	Malaysia	ZMMU RAN 1989
C. quadrivirgatus	HM888466	Malaysia	ZMMU RAN 1990
C. roesleri	KF929532	Vietnam: Quang Binh Province	PNKB2011.34
C. roesleri	KF929531	Vietnam: Quang Binh Province	PNKB2011.3
C. rufford	KU175572	Laos: Khammouane Province	VFU R.2015.14
Cyrtodactylus sommerladi **sp. nov.**	KX064039	Laos: Khammouane Province	IEBR A.2015.37
Cyrtodactylus sommerladi **sp. nov.**	KX064040	Laos: Khammouane Province	VNUF R.2013.22
Cyrtodactylus sommerladi **sp. nov.**	KX064041	Laos: Khammouane Province	VNUF R.2013.87
Cyrtodactylus sommerladi **sp. nov.**	KX064042	Laos: Khammouane Province	IEBR A.2015.39
C. spelaeus	KP199947	Laos: Vientiane Province	ZMMU R-13980-3
C. spelaeus	KP199948	Laos: Vientiane Province	ZMMU R-13980-1
C. soudthichaki	KX077904	Laos: Khammouane Province	NUOL R-2015.5
C. soudthichaki	KX077905	Laos: Khammouane Province	VFU R.2015.18
C. soudthichaki	KX077906	Laos: Khammouane Province	IEBR A.2015.34
C. teyniei	KJ817430	Laos: Khammouane Province	IEBR KM2012.77
C. teyniei	KP199945	Laos: Khammouane Province	IEBR KM2012.77
C. vilaphongi	KJ817434	Laos: Luang Prabang	NUOL R-2013.5
C. vilaphongi	KJ817435	Laos: Luang Prabang	IEBR A.2013.103
C. wayakonei	KJ817438	Laos: Luang Nam Tha Province	ZFMK 91016
C. wayakonei	KP199950	Laos: Luang Nam Tha Province	ZMMU R-13981-1

We used the protocols of Le *et al*. (2006) for DNA extraction, amplification, and sequencing. A fragment of the mitochondrial gene, cytochrome c oxidase subunit 1 (COI), was amplified using the primer pair VF1-d and VR1-d (Ivanova *et al*. 2006). After sequences were aligned by Clustal X v2 (Thompson *et al*. 1997), data were analyzed using maximum parsimony (MP) and maximum likelihood (ML) as implemented in PAUP*4.0b10 (Swofford 2001) and Bayesian inference (BA) as implemented in MrBayes v3.2 (Ronquist *et al*. 2012). Settings for these analyses followed Le *et al*. (2006), except that the number of generations in the Bayesian analysis was increased to 1×10^7. The optimal model for nucleotide evolution was set to TrN+I+G for ML and combined Bayesian analyses as selected by Modeltest v3.7 (Posada & Crandall 1998). The cutoff point for the burn-in function was set to 11 in the Bayesian analysis, as -ln*L* scores reached stationarity after 11,000 generations in both runs. Nodal support was evaluated using Bootstrap replication (BP) as estimated in PAUP and posterior probability (PP) in MrBayes v3.2. Uncorrected pairwise divergences were calculated in PAUP*4.0b10 (Table 2).

TABLE 2. Uncorrected ("p") distance matrix showing percentage pairwise genetic divergence (COI) between new and closely related species.

Species name	1	2	3	4	5
1. *Cyrtodactylus calamei* **sp. nov.** (KX064043 & 4)	-				
2. *C. darevskii* (HQ967221 & 3)	**5.2–5.3**	-			
3. *Cyrtodactylus hinnamnoensis* **sp. nov.** (KX064045-9)	**5.1–5.4**	**4.0–4.1**	-		
4. *C.* cf. *jarujini* (KX077907)	**16.2–16.3**	16.3	**16.0–16.5**	-	
5. *C. lomyenensis* (KJ817436/KP199942)	**14.2–14.5**	13.6–13.7	**14.2–14.7**	15.1–15.4	-
6. *C. multiporus* (HM888471 & 2)	**15.1–15.3**	15.6	**14.7–15.4**	9.6	14.7–15.1
7. *C. pageli* (KJ817431/KX077902 & 3)	**16.5–17.5**	18.3–18.8	**18.6–19.4**	17.1–17.8	17.1–18.3
8. *C. phongnhakebangensis* (KF929526 & 7)	**7.9**	9.7	**8.6–9.3**	17.0	14.5–14.6
9. *C. roesleri* (KF929531 & 2)	**15.5**	17.3	**16.9–17.1**	17.2–17.3	17.4–17.6
10. *Cyrtodactylus sommerladi* **sp. nov.** (KX064039-42)	**14.2–14.6**	**15.4–15.5**	**16.0–17.0**	**17.5–17.8**	**17.3–17.9**
11. *C. teyniei* (KJ817430/KP199945)	**13.9–14.1**	15.4–15.5	**14.4–15.3**	9.1–9.3	14.3–14.7

continued.

Species name	6	7	8	9	10	11
1. *Cyrtodactylus calamei* **sp. nov.** (KX064043 & 4)						
2. *C. darevskii* (HQ967221 & 3)						
3. *Cyrtodactylus hinnamnoensis* **sp. nov.** (KX064045-9)						
4. *C.* cf. *jarujini* (KX077907)						
5. *C. lomyenensis* (KJ817436/KP199942)						
6. *C. multiporus* (HM888471 & 2)	-					
7. *C. pageli* (KJ817431/KX077902 & 3)	16.4–17.3	-				
8. *C. phongnhakebangensis* (KF929526 & 7)	15.3	17.7–17.8	-			
9. *C. roesleri* (KF929531 & 2)	16.9–17.1	16.1–17.5	15.3	-		
10. *Cyrtodactylus sommerladi* **sp. nov.** (KX064039-42)	16.9–17.0	15.0–16.6	16.2–16.3	5.9–6.2	-	
11. *C. teyniei* (KJ817430/KP199945)	6.6–7.0	17.1–18.0	15.3	17.5–17.7	**17.6–17.9**	-

Morphological characters. Measurements were taken with a digital caliper to the nearest 0.1 mm. Abbreviations are as follows: snout-vent length (SVL), from tip of snout to anterior margin of cloaca; tail length (TaL), from posterior margin of cloaca to tip of tail; trunk length (TrunkL), from posterior edge of forelimb insertion to anterior edge of hind limb insertion; maximum head height (HH), from occiput to underside of jaws; head length (HL), from tip of snout to the posterior margin of the retroarticular; maximum head width (HW); greatest diameter of orbit (OD); snout to eye distance (SE), from tip of snout to anterior corner of eye; eye to ear distance (EyeEar), from anterior edge of ear opening to posterior corner of eye; ear length (EarL), maximum diameter of ear; maximum rostral width (RW); maximum rostral height (RH); maximum mental width (MW); maximum mental length (ML); forearm length (ForeaL), from base of palm to elbow; femur length (FemurL); crus length (CrusL), from base of heel to knee; length of finger IV (LD4A); length of toe IV (LD4P).

Scale counts were taken as follows: supralabials (SL); infralabials (IL); nasal scales surrounding nare, from rostral to labial (except rostral and labial), i.e. nasorostral, supranasal, postnasals (N); postrostrals or internasals (IN); postmentals (PM); dorsal tubercle rows (DTR) counted transversely across the center of the dorsum from one ventrolateral fold to the other; granular scales surrounding dorsal tubercles (GST); ventral scales in longitudinal rows at midbody (V) counted transversely across the center of the abdomen from one ventrolateral fold to the other; number of scales along midbody from mental to anterior edge of cloaca (SLB); number of scale rows around midbody (SR); femoral pores (FP); precloacal pores (PP); postcloacal tubercles (PAT); subdigital lamellae on fourth finger (LD4); subdigital lamellae on fourth toe (LT4). Bilateral scale counts were given as left/right. Femoral and precloacal pores were counted with a digital microscope (Keyence VHX-500F).

Multivariate analysis was applied for examining interspecific differences between the new species and their *Cyrtodactylus* relatives from Laos and Vietnam. We selected 12 of the 28 morphological characters from the Material and methods, that were used to perform the cluster analysis of paired group method with 1000 bootstrap replicates and correspondence analysis to assess the degree of similarity between species. Statistical analysis was computed using PAST Statistics software version 3.06 (Hammer *et al.* 2001).

Results

Molecular data, phylogenetic analysis. The final matrix consisted of 668 aligned characters, of which 267 are parsimony informative. The alignment contained no gap. MP analysis of the dataset recovered 39 most parsimonious trees with 1710 steps (CI = 0.31; RI = 0.76). The topology derived from the Bayesian analysis (Fig. 1) is similar to those in Nguyen *et al.* (2015) and Luu *et al*. (2016a,b), but *Cyrtodactylus pageli* is supported as the sister taxon to *C. roesleri* + *Cyrtodactylus sommerladi* **sp. nov.** in our analyses with low statistical values. The statistical support for all nodes in the phylogeny is generally higher than that shown in previous studies. The monophyly of five species groups is strongly corroborated by all three analyses, i.e., ML, MP, and Bayesian inferences, except *C. irregularis*, which did not receive strong support from MP and ML analyses (Fig. 1).

The new samples were placed in two species groups, the *C. irregularis* and the *C. phongnhakebangensis* species complexes (see Nazarov *et al.* 2012, 2014). Genetically, the sample in the *C. irregularis* complex is almost identical to that of *C. cryptus* (only 0.2% of genetic divergence). Other new samples in the *C. phongnhakebangensis* species group are clustered in three genetically distinct populations. One of them is recovered as the sister taxon to *C. roesleri*, while two others are closely related to *C. darevskii*. The former taxon is about 6% genetically divergent from *C. roesleri*, while the other taxa are 4% and 5%, respectively, from *C. darevskii*, the most closely related taxon to them. The latter two species are about 8% to 9% divergent from *C. phongnhakebangensis* (Table 2).

Integrative approach. Integrative taxonomy, i.e., using multiple lines of evidence to delineate species boundaries, has become an increasingly common approach in taxonomic research (Dayrat 2005; Padial *et al*. 2010; Schlick-Steiner *et al*. 2010). The approach can take advantage from diverse disciplines, e.g., morphology, population biology, molecular evolution, and ecology, by utilizing strength from different types of data to address problems related to taxonomy. To decipher the *Cyrtodactylus* species complex in Hin Nam No, we used an integrative taxonomic method by incorporating morphological, molecular, and ecological evidence. Morphological distinctness (concerning measurement, scalation, colour pattern, ratios) of the new taxa is shown in Figs. 2–5 & Table 3 which is documented in details in the following section. Cluster and correspondence analyses were conducted to compare inter-specific morphological variation using all 22 *Cyrtodactylus* species from Laos and one (*C. phongnhakebangensis*) from Vietnam based on selected 12 of 28 morphological characters (see Figs. 2–3).

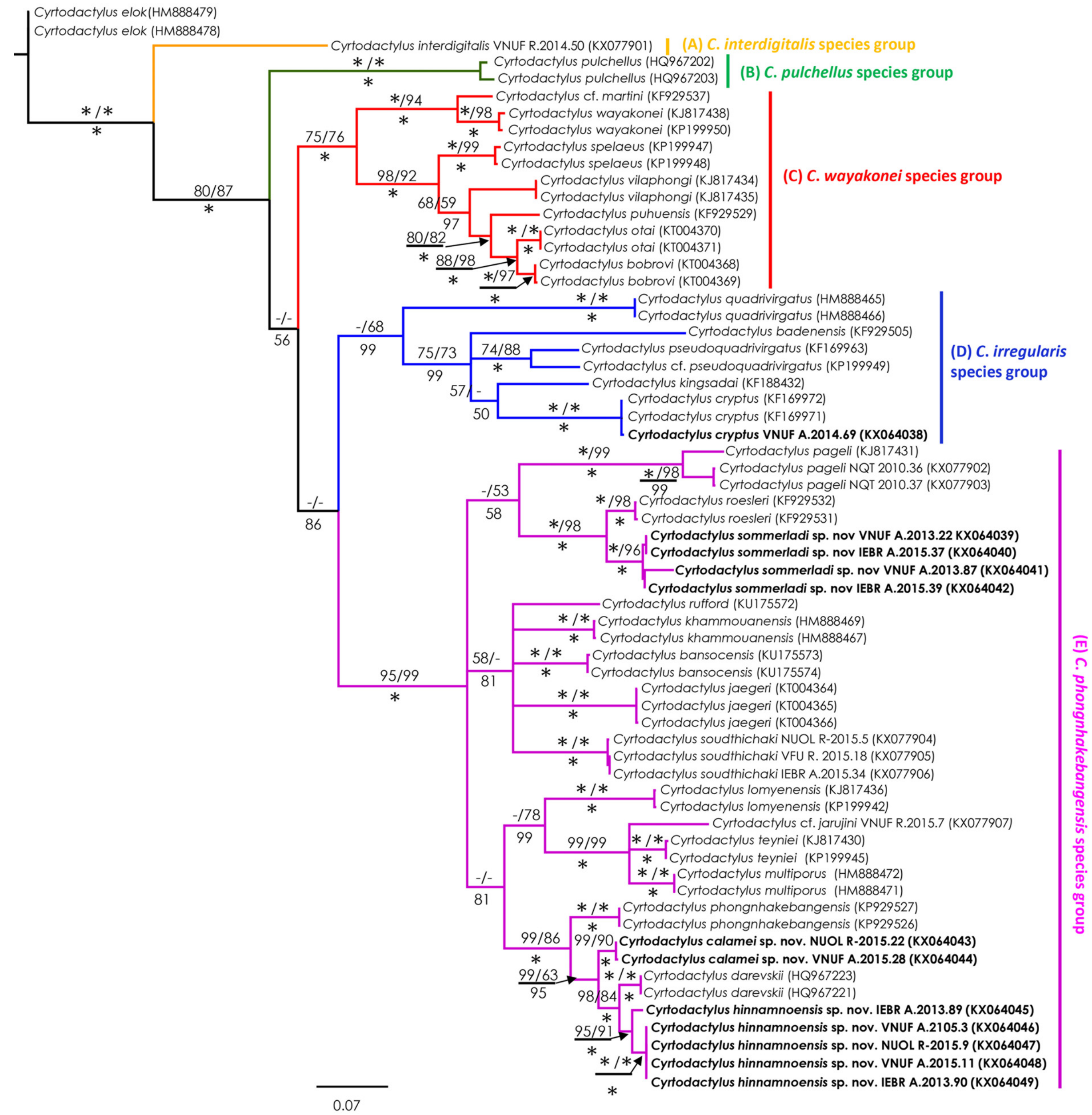

FIGURE 1. Phylogram based on the Bayesian analysis. Number above and below branches are MP/ML bootstrap values and Bayesian posterior probabilities (>50%), respectively. Asterisk denotes 100% value. Hyphen indicates the statistical support value lower than 50%. Scale shows the number of expected substitutions per position as calculated in MrBayes v3.2. New species and records marked in bold.

We also carried out a correspondence analysis to differentiate four sibling species by using morphometric characters of all adult male specimens, which could be observed (Fig. 4). Principal components analysis shows evidence of two cryptic species based on two qualitative characters: head width and head height (Fig. 5). In addition, first ecological data collected from each specimen in the field were included. Although these records were not analyzed quantitatively, our own data suggest sympatric pattern in the area. Genetic distinction between the newly recognized taxa and described species exceeds or is equivalent to molecular divergence among the species, for example *C. bobrovi versus C. otai* (Nguyen *et al*. 2015) and *C. dati versu*s *C. huynhi* (Nguyen *et al*. 2014). From all available lines of evidence, we come to the conclusion that the taxa cannot be considered conspecific and that separation through evolutionary processes already has began at different levels, and thus are described in the following.

TABLE 3. Morphological comparisons between *Cyrtodactylus calamei* **sp. nov.**, *Cyrtodactylus hinnamnoensis* **sp. nov.**, *Cyrtodactylus sommerladi* **sp. nov.**, and their congeners from Laos and neighbouring countries in the Indochina region (compiled after Luu *et al*. 2014; Nazarov *et al*. 2014; Nguyen *et al*. 2014; Panitvong *et al*. 2014; Pauwels *et al*. 2014; Pauwels & Sumontha 2014; Schneider *et al*. 2014; Sumontha *et al*. 2015; Nguyen *et al*. 2015; Luu *et al*. 2015; Luu *et al*. 2016a,b). Abbreviations are as follows: – = characters unobtainable from literature; * = tail regenerated; SVL = snout–vent length; TaL = tail length; V = ventral scales; EFS = enlarged femoral scales; FP = femoral pores; PP = precloacal pores; LD4 = subdigital lamellae on fourth finger; TL4 = subdigital lamellae on fourth toe; FPl = femoral pores in the left side; FPr = femoral pores in the right side.

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
Cyrtodactylus calamei **sp. nov.**	**75.0–89.3**	**86.1–107.5**	**39–42**	**present**	**present**	**35–39 (FP+PP)**	**38 (FP+PP)**	**16–18**	**18–20**	**banded**	**present**
Cyrtodactylus hinnamnoensis **sp. nov.**	**83.6–100.6**	**76.1–108.3***	**35–48**	**present**	**present**	**36–44 (FP+PP)**	**0–28 (FP+PP)**	**16–21**	**19–22**	**banded**	**present**
Cyrtodactylus sommerladi **sp. nov.**	**58.8–80.3**	**58.8*–89.4**	**31–39**	**present**	**present**	**20–26 (FP+PP)**	**17–21 (FP+PP)**	**16–19**	**17–24**	**banded**	**present**
C. bansocensis	71.0–74.0	98.5–103.5	34–35	present	present	34 (FP+PP)	unknown	16–19	18–21	banded	present
C. rufford	68.3–72.5	94.5–96.8	27–29	present	present (in males)	42–43 (FP+PP)	unknown	19–20	18–19	banded	present
C. soudthichaki	69.2–70.0	95.1*–95.2	32–33	present	present (in males)	29 (FP+PP)	absent	16-18	18	banded	present
C. angularis	80.0–92.0	92–95.2	40–45	present	absent	3	3	18–19	18–19	banded	present
C. astrum	46.4–108.3	99.0*–109.0*	31–46	–	present	31–38 (FP+PP)	–	–	20–24	banded	present
C. auribalteatus	82.8–98.1	106.5–138.7	38–40	5–7	4–5 (in males)	6	absent	–	18–21	banded	present
C. badenensis	59.3–74.1	58.6–82.4	25–29	absent	absent	0	0	–	18–22	banded	present
C. bichnganae	95.3–99.9	96.3–115.6	30–31	11–13	18	10	8	18–20	16–20	banded	present
C. bidoupimontis	74.0–86.3	75.0–86.0	38–43	6–8	absent	4–6	0	15–20	18–23	banded	absent
C. bobrovi	75.2–96.4	80.8–90.3	40–45	0	0	5	0	19–21	21–22	banded	absent
C. brevipalmatus	64.0–72.0	77.0	35–44	present	present	6+9+7 (FPl+PP+FPr)	6+9+7 (FPl+PP+FPr)	–	–	blotched	present
C. bugiamapensis	58.6–76.8	65.3–83.0	36–46	6–10	absent	7–8	0–7	15–17	17–20	blotched	absent
C. buchardi	60.0–65.0	46.0–54.0	30	absent	absent	9	0	14	12	blotched	absent
C. caovansungi	90.4–94.0	120.0	38–44	8	6	9	0	22	23–25	banded	present
C. cattienensis	43.5– 69.0	51.0–64.7	28–42	3–8	absent	6–8	0	12–16	14–19	banded	absent
C. chanhomeae	69.9–78.8	74.4–74.7	36–38	present	present	32 (FP+PP)	34 (FP+PP)	18–20	21–23	banded	present
C. chauquangensis	90.9–99.3	97.0–108.3	36–38	absent	absent	6	7	16–18	19–23	banded	present

……*continued on the next page*

TABLE 3. (Continued)

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
C. cryptus	62.5–90.8	63.5–88.4	47–50	absent	absent	9–11	0	18–19	20–23	banded	absent
C. cucdongensis	55.8–65.9	22.1–27.8	35–44	present	absent	5–6	4–6	8–11	15–20	banded	absent
C. cucphuongensis	96.0	79.3*	42	14	absent	0	–	21	24	banded	present
C. darevskii	84.6–100.0	95.0–113.0	38–46	present	present	38–44 (FP+PP)	24–34	17–20	18–22	banded	present
C. dumnuii	76.2–84.2	100.2*	40	present	present in males/absent in females	6+5–6+6–7 (FPl+PP+FPr)	0–7	16	19	banded	present
C. eisenmanae	76.8–89.2	91.0–103.8	44–45	4–6	absent	0	0	18–20	17–18	banded	present
C. erythrops	78.4	83.0*	28	present	present	10+9+9 (FPl+PP+FPr)	–	16	20	blotched	present
C. grismeri	68.3–95.0	111.3–115.1	33–38	absent	–	0	0	16–18	16–19	banded	present
C. huongsonensis	73.4–89.8	90.5	41–48	7–9	15–17	6	8	17–19	20–23	banded	present
C. huynhi	54.8–79.8	61.5–78.6	43–46	3–5	3–8	7–9	0–8	14–17	17–21	banded	absent
C. interdigitalis	59.0–80.0	71.0–90.0	37–42	present	16–18	14	0	17–22	16–20	banded	absent
C. intermedius	61.0–85.0	80.0–110.0	40–50	6–10	–	8–10	–	20	22	banded	present
C. irregularis	72.0–86.0	66.0–74.0	38–45	7–8	–	5–7	0–6	15–16	18–19	blotched	absent
C. jaegeri	60.0–68.5	82.4–83.4	31–32	17–19	present	44 (FP+PP)	21	17–19	20–23	banded	present
C. jarujini	85.0–90.0	105.0–116.0	32–38	present	present	52-54 (PP+FP)	0	15–17	18–19	blotched	present
C. khammouanensis	70.8–73	83.0–95.0	32–38	present	present	40–44 (PP+FP)	0-17	18–20	20–23	banded	present
C. khelangensis	72.8–95.3	max. 96.0*	32–35	present	present	6+2–5+6–7 (FPl+PP+FPr)	2+6+1 (FPl+PP+FPr)	18	22	banded	present
C. kingsadai	83.0–94.0	max. 117.0	39–46	9–12	0–7	7–9	4–8	19–21	21–25	banded	present
C. lekaguli	80.5–103.5	115.0–125.0	31–43	present	present	30–36 (PP+FP)	0	–	20–25	banded	present
C. lomyenensis	57.7–71.2	72.2–86.1	35–36	17–18	present	39–40 (PP+FP)	32 (PP+FP)	16–19	19–23	banded	present
C. martini	64.4–96.2	76.0–101.2	39–43	14–18	absent	4	0	19–23	22–24	banded	present
C. multiporus	81.0–98.0	97.0–105.0	30–38	present	present	58–60 (PP+FP)	0	18–20	18–22	banded	present
C. nigriocularis	82.7–107.5	70.6–121	42–49	absent	absent	0–2	0	–	17–21	uniformly brown	present

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TABLE 3. (Continued)

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
C. oldhami	63.0–68.0	69*–70*	34–38	present	absent	1–4	–	–	–	striped and spotted	present
C. otai	85.2–90.6	89.7–97.6	38–43	absent	absent	7–8	0	16–19	19–22	banded	absent
C. pageli	76.2–81.8	85.4*–113.2*	41–44	absent	absent	4	4	19–23	19–23	banded	present
C. paradoxus	52.0–84.0	80.8–111.0	32–40	present	absent	0–4	0	15–18	17–23	banded	present
C. phongnhakebangensis	78.5–96.3	98.0–110.0	32–42	present	present	32–42 (PP + FP)	0–41 (PP + FP)	15–20	18–26	banded	present
C. phuocbinhensis	46.0–60.4	76.1	43–47	5	absent	7	0	16–21	17–19	blotched	absent
C. pseudoquadrivirgatus	48.6–83.3	55.7–82.3	41–57	absent	absent	5–9	5–10	15–21	16–25	blotched	absent
C. puhuensis	79.2	82.59	36	present	absent	5	–	18	23	banded	present
C. quadrivirgatus	39.0–67.0	77.0	40	present	absent	4	4	–	–	striped	absent
C. ranongensis	56.9–59.6	66.0–67.1	35–40	present	0	0	0	17	18	blotched	absent
C. roesleri	51.1–75.3	63.4–101.0	34–40	7–10	present	20–28 (PP + FP)	17–22 (PP + FP)	17–19	17–21	banded	present
C. saiyok	56.7–61.0	66.7–67.5	23–24	present	absent	5	–	–	16–17	banded	present
C. samroiyot	63.2–66.9	78.8–87.5	33–34	present	absent	7	6	18	19	banded	present
C. sanook	72.9–79.5	104.2	27–28	present	absent	3–4	absent	–	19–20	banded	present
C. spelaeus	88.9–91.0	max. 83*	36–39	absent	absent	8–9	0	19–20	22–24	banded	present
C. sumonthai	61.5–70.7	89.9–94.0	33–36	absent	absent	2	0	16	18	banded	present
C. takouensis	74.7–81.1	77.7–91.0	39–40	3–5	0–2	3–4	0	16–17	18–20	banded	present
C. taynguyenensis	60–85	66–94	42–49	absent	absent	6	0	13–18	17–21	blotched	absent
C. teyniei	89.9	ca. 110.0	38	23	absent	unknown	13	17–18	19–20	blotched	present
C. thuongae	57.3–77.6	max. 78.1	29–44	2–5	0–3	0–1	0	14–17	14–20	blotched	absent
C. wayakonei	72.0–86.8	76.8–89.0	31–35	absent	absent	6–8	7	17–18	19–20	banded	present
C. thirakhupti	72.0–79.6	99.1	37–40	present	absent	absent	absent	16	20	banded	present
C. tigroides	74.3–83.2	108.5–117.0	34	present	present	6+8+7 (FPl+PP+FPr)	5+9+7 (FPl+PP+FPr)	18–19	20–22	banded	present
C. vilaphongi	60.9–86.1	61.2–68.1	34–36	0	–	–	0	18–19	18–20	banded	absent
C. yangbayensis	78.5–92.3	91.3–109.1	39–46	5–16	0–2	6–8	0	16–19	15–17	banded	present
C. ziegleri	84.6–93.0	95.0–107.0	33–39	8–10	0–6	5–8	0–8	16–19	18–21	banded	absent

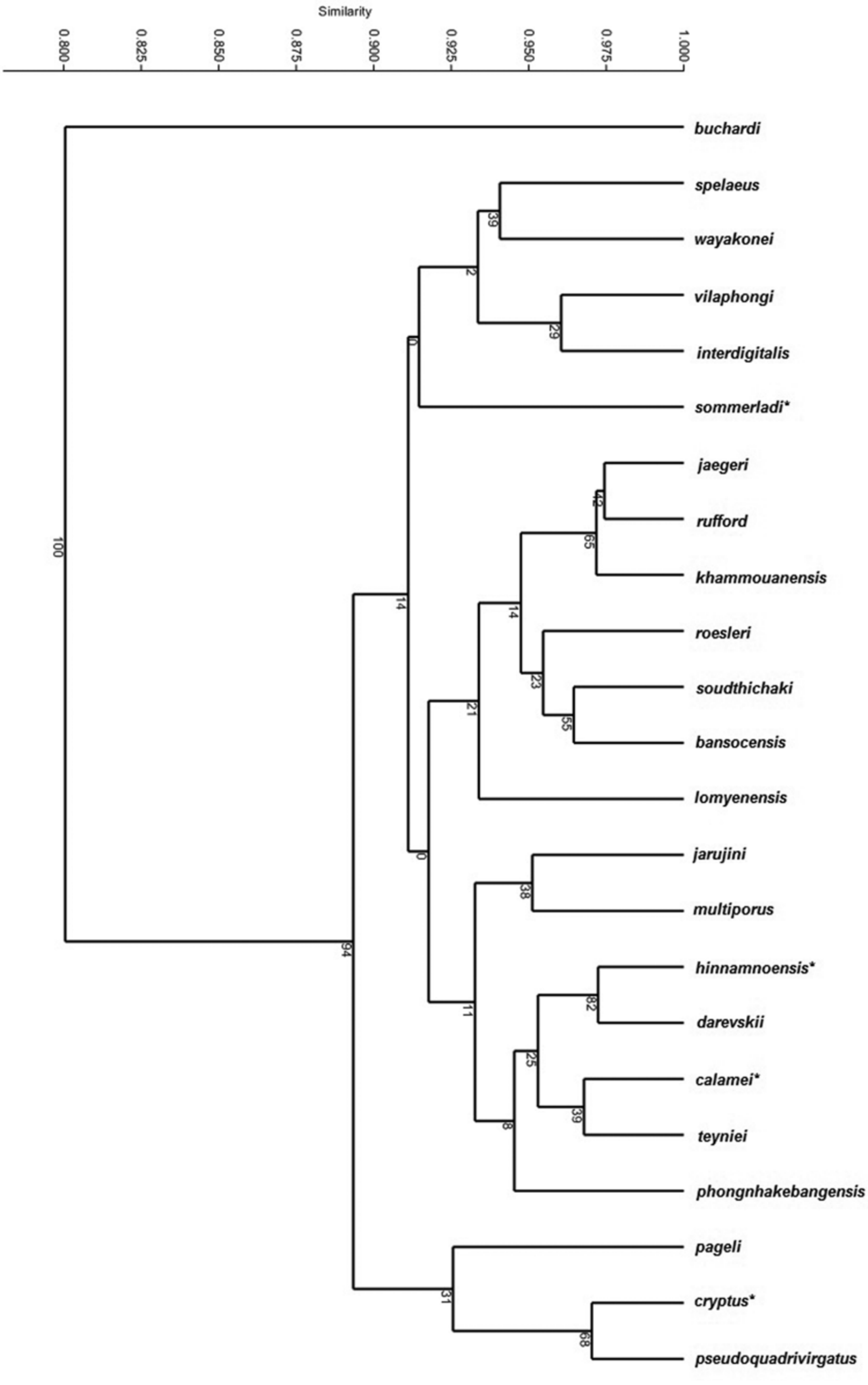

FIGURE 2. Cluster analysis showing species correlation of the *Cyrtodactylus* species based on morphological comparisons (1000 bootstrap replicates).

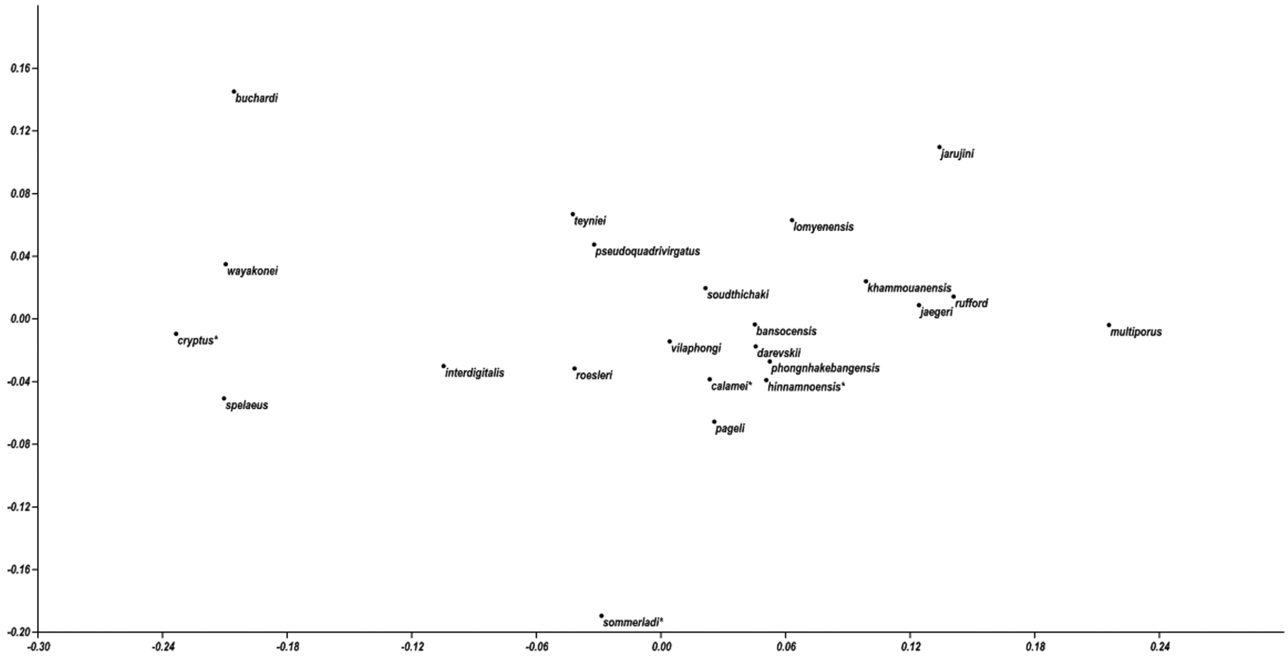

FIGURE 3. Correspondence analysis showing species association of *Cyrtodactylus* from Laos (except for *Cyrtodactylus phongnhakebangensis* and *C. roesleri* which are from Vietnam) based on morphological comparisons.

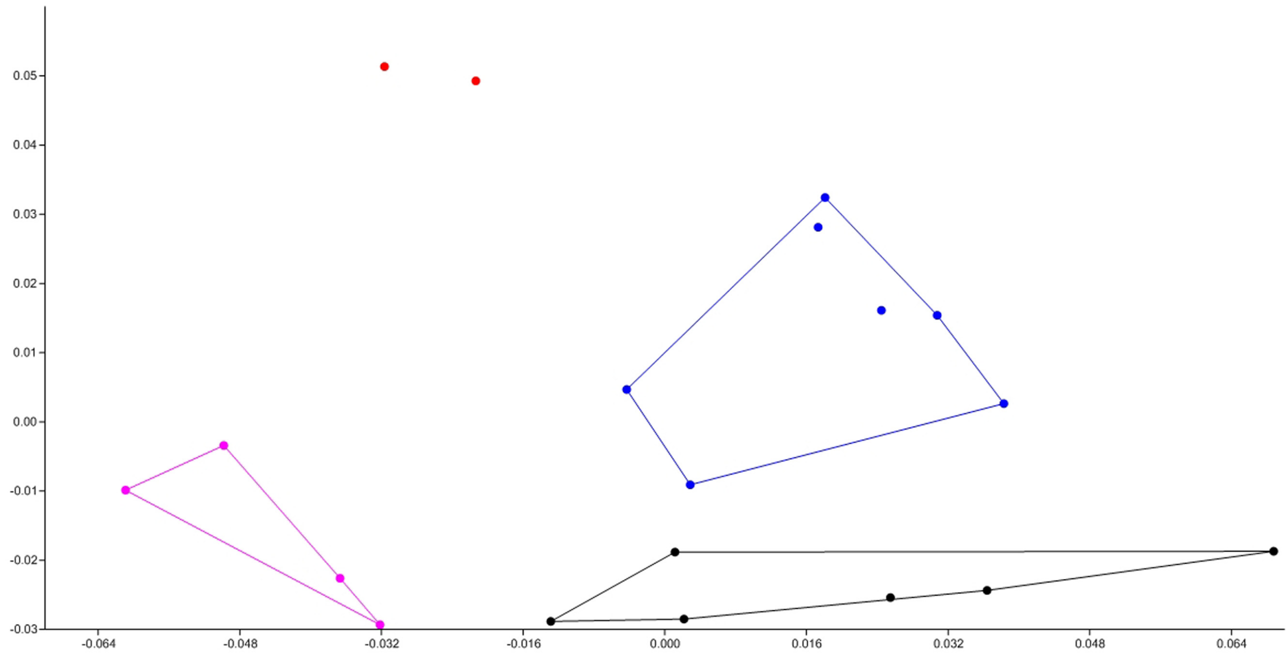

FIGURE 4. Correspondence analysis comparing all adult male measurements of four *Cyrtodactylus* sibling species: *Cyrtodactylus hinnamnoensis* **sp. nov**. (blue dots); *Cyrtodactylus darevskii* (pink dots); *Cyrtodactylus calamei* **sp. nov.** (red dots); and *Cyrtodactylus phongnhakebangensis* (black dots).

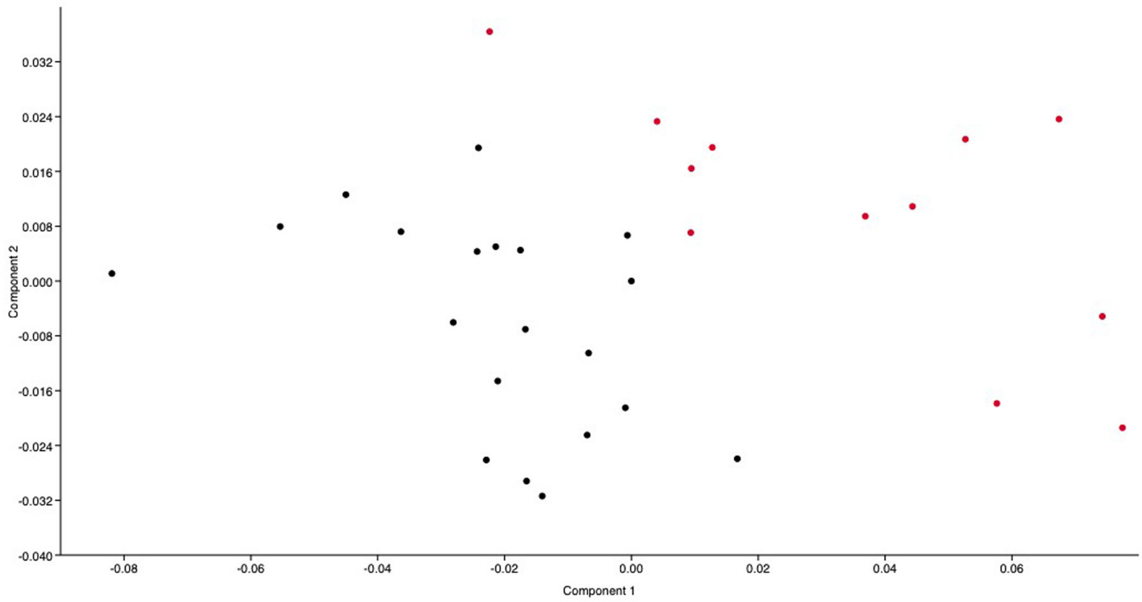

FIGURE 5. Principal components analysis comparing head shape of *Cyrtodactylus sommerladi* **sp. nov.** (red dots) and *Cyrtodactylus roesleri* (black dots) based on relative head width and head height.

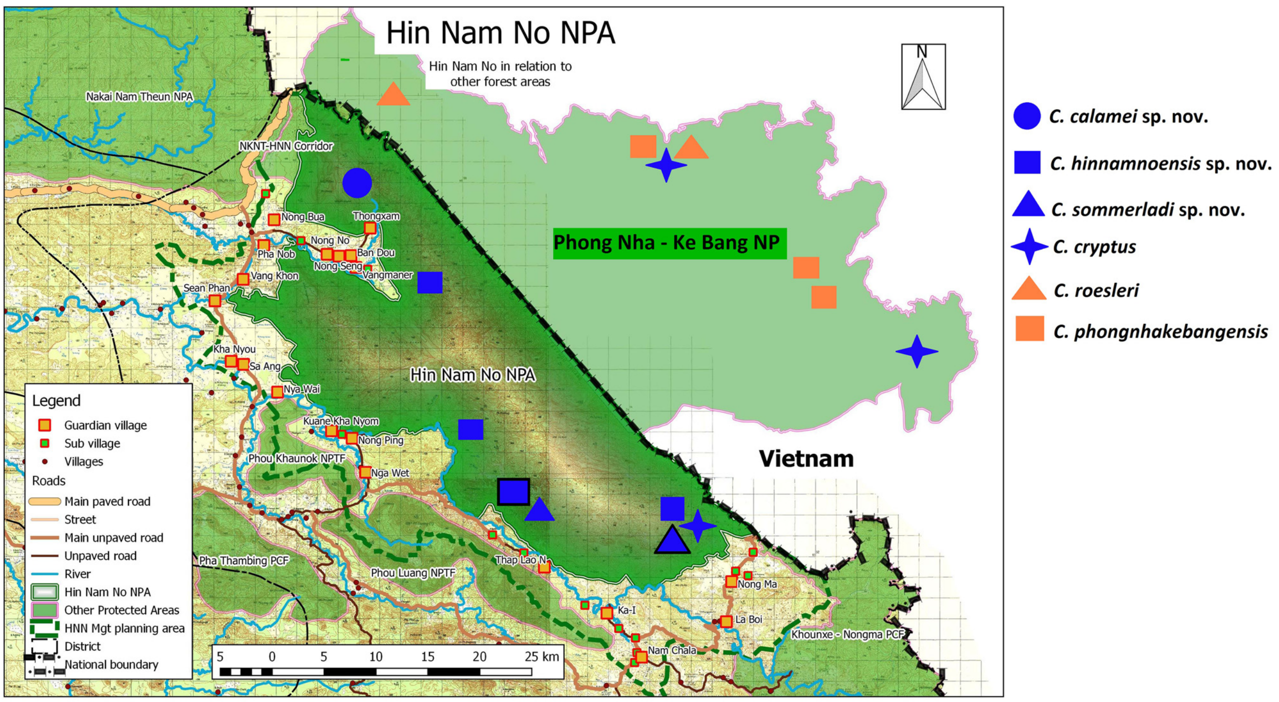

FIGURE 6. Map showing the localities (blue) of the three new *Cyrtodactylus* species (type localities are encircled with black line) and the new *Cyrtodactylus* country record from Khammouane Province, central Laos.

Taxonomic accounts

Cyrtodactylus calamei sp. nov.
(Fig. 7)

Holotype. VNUF R.2015.28, adult male, in the karst forest, Tham Nok Aen region, Thong Xam Village (17°34.179’N, 105°50.329’E, elevation 210 m a.s.l.) within Hin Nam No NPA, Khammouane Province, central Laos, was collected on 25 March 2015 by V. Q. Luu, T. Calame, and K. Thanabuaosy.

Paratypes. IEBR A. 2015.36, adult male; NUOL R-2015.22, subadult male; VNUF R.2015.27, adult female, the same data as the holotype.

Diagnosis. *Cyrtodactylus calamei* **sp. nov.** can be distinguished from its congeners by a unique combination of the following characters: Adult SVL 80.0 ± 8.0 mm (mean ± SD); head dorsally with grey small scattered spots; nuchal loop present with indentations, not enlarged posteriorly, extending from each postnasal cross orbit and contacting on nape; four greyish brown, wide transverse bands between limbs, sometimes irregular; dorsal surface with homogenous, low, round, weakly keeled scales; 39–42 ventral scales at midbody; ventrolateral skin folds well-defined; 183–197 ventral scale rows from mental to cloacal slit; 101–114 scale rows at midbody; 35–39 precloacal-femoral pores in males, 38 in the female; enlarged femoral and precloacal scales present; four postcloacal tubercles; subcaudal scales transversely enlarged.

Description of holotype. Adult male, medium sized, SVL 75.8 mm; body long (TrunkL/SVL 0.44); head moderate (HL/SVL 0.29), narrow (HW/HL 0.77), somewhat depressed (HH/HL 0.42), differentiated from neck; prefrontal and postnasal regions concave; snout elongate (SE/HL 0.45), obtuse; snout scales small, homogeneous, granular, about two times larger than those in frontal and parietal regions; eye large (OD/HL 0.29), pupils vertical; supraciliaries with tiny spines posteriorly; ear opening oval, obliquely directed, small in size (EarL/HL 0.10); rostral subrectangular, wider than high (RH/RW 0.61), medially deep furrow, vertical suture, bordered by nasorostral, nare and first supralabial laterally; nares oval, surrounded by rostral anteriorly, supranasal, first supralabial laterally, and posteriorly by two enlarged postnasals; intersupranasal scale single; mental subtriangular, nearly as wide as rostral (MW/RW 0.94), bordered by two postmentals and first infralabial laterally; supralabials nine; infralabials eight. Dorsal scales granular to flattened; dorsal tubercles round, weakly keeled, extending from postocciput to base of tail; ventrolateral folds distinct; ventral scales smooth, medial scales about two times larger than dorsal scales, imbricate, 40 rows at midbody between folds; midbody scale rows 104; ventral scales from mental to cloacal slit 183; enlarged femoral-precloacal scales present; precloacal-femoral pores 39, in a continued row; precloacal groove absent.

Fore and hind limbs moderately long (ForeL/SVL 0.18, CrusL/SVL 0.2); tubercles on dorsum of fore limbs absent; dorsal surface of hind limbs interspersed with tubercles; interdigital webbing weakly developed; subdigital lamellae on fourth fingers 16/16 and on fourth toes 19/18.

Tail tapering to a point (TaL/SVL 1.42); four postcloacal tubercles laterally; subcaudals distinctly enlarged.

Coloration in life. Ground color of dorsal head, back, limbs, and tail yellowish brown; dorsal head with small spread spots and a heart-shaped marking on postocciput; nuchal loop present, in U-shape, from posterior corner of nare crossing eye and tympanum, extending to nape, dark brown, bolder from postocular to nape, irregularly edged in yellow; four greyish brown body bands between limb insertions with indentations in mid-dorsal region, edged in yellow; dorsal surface of fore and hind limbs with grey reticulations; tail with narrow light bands; ventral surface greyish cream.

Sexual dimorphism. The single adult female differs from two adult males by its larger size (maximum SVL 89.3 mm *versus* 75.8 mm in the males) and lacking of hemipenial swellings at the base of tail (see Table 4 & Fig. 6).

Comparisons. We compared *Cyrtodactylus calamei* **sp. nov.** with other *Cyrtodactylus* species known from Laos and neighbouring countries in the mainland Indochina region, including Vietnam, Cambodia, and Thailand based on examination of specimens (see Appendix) and data provided from taxonomic publications (Luu *et al*. 2014a; Nazarov *et al*. 2014; Nguyen *et al*. 2014; Panitvong *et al*. 2014; Pauwels *et al*. 2014; Pauwels & Sumontha 2014; Schneider *et al*. 2014; Sumontha *et al*. 2015; Nguyen *et al*. 2015; Luu *et al*. 2015a; Luu *et al*. 2016a,b) (see Table 3). The cluster and correspondence analyses indicated that *Cyrtodactylus calamei* **sp. nov.** is nested in the same clade with *C. darevskii* and the species to be described in the following (Figs. 2–3). Molecular phylogenetic analyses also strongly supported the sister relationship between the new species and afore mentioned taxa (see Fig. 1).

Morphologically, *Cyrtodactylus calamei* **sp. nov.** closely resembles the other karst forest species, *C. darevskii* and *C. phongnhakebangensis*, in dorsal colour pattern. However, the new species can be distinguished from *C. darevskii* by its smaller size (maximum SVL 89.3 mm *versus* 100 mm), having fewer dorsal tubercle rows (10–16 *versus* 16–20), fewer femoral and precloacal pores in males (35–39 *versus* 38–44), more femoral and precloacal pores in females (38 *versus* 24–34), the presence of heart-shaped marking on postocciput (*versus* absent), four greyish brown regular transverse body bands as wide as nearly two times of nuchal band (*versus* four to five dark irregular transverse breaking bands as narrow as nuchal band), first body band wide, butterfly-shaped (*versus* thin, U-shaped in *C. darevskii*), tail with light rings (*versus* banded); from *C. phongnhakebangensis* by its smaller size (maximum SVL 89.3 mm *versus* 96.3 mm), more scale rows from mental to the front of cloacal slit (183–197 *versus* 161–177), nuchal loop narrow, indented, not posteriorly enlarged (*versus* wide, posteriorly enlarged), four greyish brown transverse body bands, slightly narrower light bands (*versus* three to five dark transverse body bands, twice wider than light bands), and tail with light rings (*versus* bands) (see Table 4).

TABLE 4. Morphometric measurements (in mm) and meristic characters of the type series of *Cyrtodactylus calamei* **sp. nov.** (* = regenerated or broken tail, for other abbreviations see material and methods).

Character	VNUF R.2015.28 holotype	IEBR A. 2015.36 paratype	NUOL R-2015.22 paratype	VNUF R.2015.27 paratype
Sex	male	male	subadult male	female
SVL	75.8	75.0	64.1	89.3
TaL	107.5	92.4	86.1	102.0*
HL	21.7	21.5	18.8	24.8
HW	14.1	13.9	11.9	16.6
HH	9.0	7.4	6.5	10.4
OD	6.2	5.8	4.9	6.5
SE	9.7	10.0	7.8	10.8
EyeEar	6.0	5.8	5.8	6.7
EarL	2.2	2.1	2.1	2.4
TrunkL	33.4	31.6	28.4	38.2
ForeL	13.6	13.4	11.2	14.2
FemurL	17.8	16.3	14.7	18.6
CrusL	15.5	16.0	13.4	17.9
LD4A	9.0	8.8	7.6	9.1
LD4P	10.7	9.6	8.9	11.3
RW	3.3	3.3	2.8	3.8
RH	2.0	1.8	1.7	2.0
MW	3.1	3.4	2.6	3.7
ML	2.3	2.2	2.0	2.7
SL	9/9	11/11	10/10	10/10
IL	8/8	10/11	8/8	9/10
N	3/3	3/3	3/3	3/3
IN	1	1	0	1
PM	2	2	2	2
DTR	16	16	10	14
GST	8	9	8	9
V	40	39	40	42
SLB	183	193	187	197
SR	104	107	101	114
FP+PP	39	38	35	38
PAT	4/4	4/4	4/4	4/4
LD4	16/16	17/18	18/18	18/17
LT4	19/18	18/19	21/20	18/18

Distribution. *Cyrtodactylus calamei* is currently known only from the type locality in Tham Nok En area, Hin Nam No NPA, Khammouane Province, central Laos (Fig. 6).

Etymology. The new species is named in honour of our friend and colleague, Mr. Thomas Calame, from WWF Greater Mekong, Vientiane, Laos, who participated in our field research in Hin Nam No NPA, Khammouane Province between 2014 and 2015. As common names, we suggest Calame's Bent-toed Gecko (English), Ki Chiem Calame (Laotian).

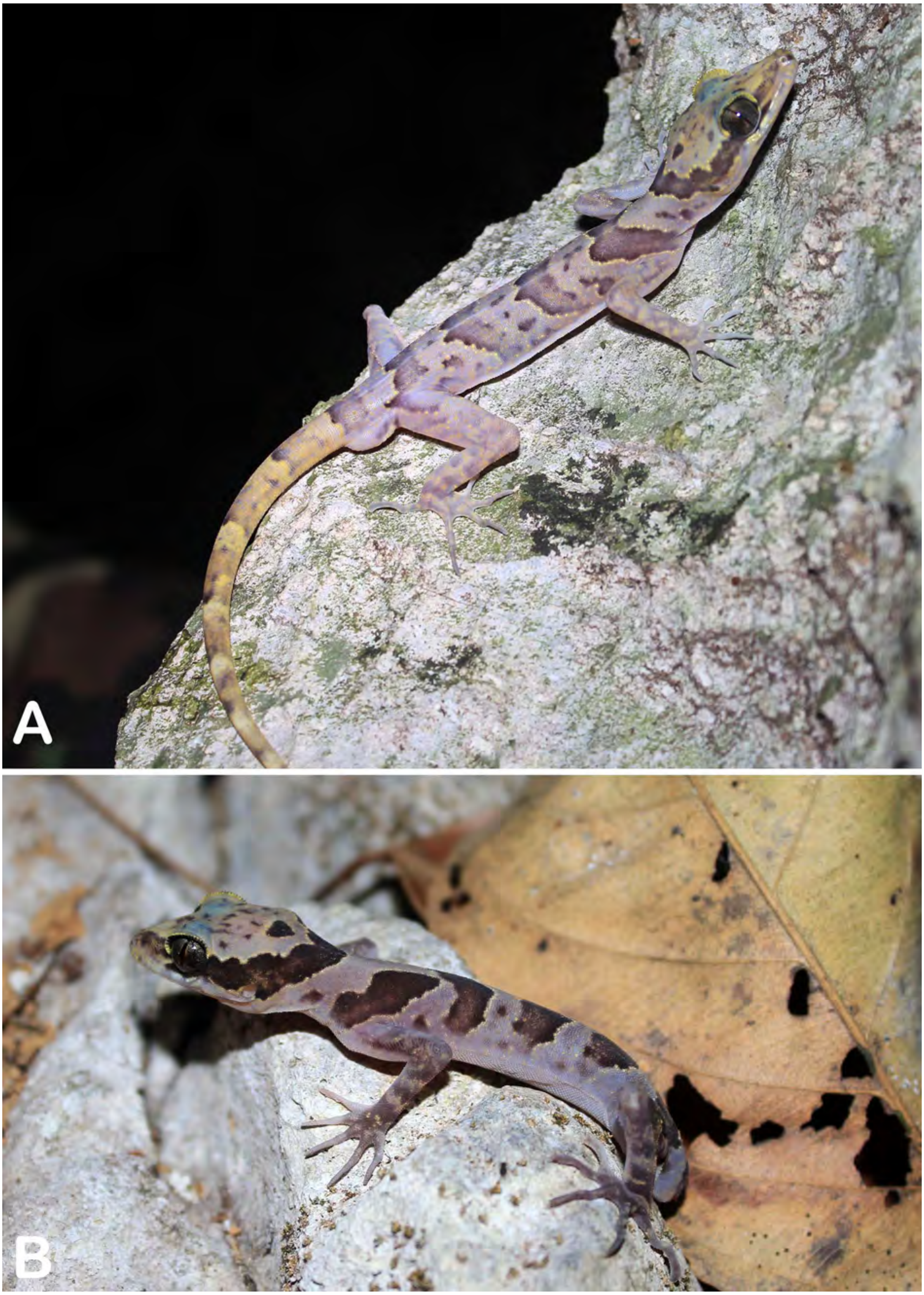

FIGURE 7. A) Dorsolateral view of the holotype (VNUF R.2015.28); B) lateral view of the paratype (NUOL R.2015.22) of *Cyrtodactylus calamei* **sp. nov.** in life. Photos: V. Q. Luu.

Natural history. Specimens were found at night between 19:30 and 21:08h, on limestone outcrops, at elevations between 190 and 260 m a.s.l. The surrounding habitat was karst forest. The relative humidity was 80% and the air temperature ranged from 23 to 26ºC (see Table 5).

TABLE 5. Ecological details for the type series of *Cyrtodactylus calamei* **sp. nov.** from Hin Nam No NPA. central Laos. Abbreviations are as follows: m.= male; f.= female; sub. m. = subadult male).

Nr.	Museum No.	Type	Date	Locality	Sex	Time
Cyrtodactylus calamei **sp. nov.**						
1	VNUF R.2015.28	Holotype	25 March 2015	Thong xam	m.	20:54
2	IEBR A. 2015.36	Paratype	25 March 2015	Thong xam	m.	19:30
3	NUOL R-2015.22	Paratype	24 March 2015	Thong xam	sub. m.	21:08
4	VNUF R.2015.27	Paratype	25 March 2015	Thong xam	f.	20:09

continued.

Nr.	Museum No.	Temp.	Humidity	Elevation	Microhabitat
Cyrtodactylus calamei **sp. nov.**					
1	VNUF R.2015.28	25ºC	85%	210 m	karst cliff ca. 1 m height
2	IEBR A. 2015.36	26ºC	87%	205 m	karst cliff ca. 0.5 m height
3	NUOL R-2015.22	26ºC	81%	193 m	small tree ca. 0.2 m height
4	VNUF R.2015.27	25.5ºC	86%	260 m	karst cliff ca. 0.3 m height

Cyrtodactylus hinnamnoensis sp. nov.
(Fig. 8)

Cyrtodactylus phongnhakebangensis—Luu, Nguyen, Calame, Hoang, Soudthichack, Bonkowski, Ziegler, 2013. *Biodiversity Data Journal*, e1015: 4.

Holotype. IEBR A.2013.90, adult male, from Ban Dou Village (17°30.385'N, 105°49.160'E, elevation 183 m a.s.l.) within Hin Nam No NPA, Khammouane Province, central Laos, was collected on 11 June 2013 by V. Q. Luu and N. V. Ha.

Paratypes. IEBR A.2013.89, adult male, 7 May 2013, from Hang Toi region, Noong Ma Village (17°17.766'N, 106°08.803'E, elevation 580 m a.s.l.); VNUF R.2013.1 and NUOL R-2013.2, adult males, 9 June 2013, from Vang Ma No Village (17°30.778'N, 105°49.259'E, elevation 180 m a.s.l.); VNUF R.2014.99, adult male, 27 May 2014, from Cha Lou Village (17°19.504'N, 105°57.630'E, elevation ca. 300 m a.s.l.); ZFMK 95235, adult female, 8 May 2013, from Hang Toi region, Noong Ma Village (17°17.763'N, 106°08.778'E, elevation 555 m a.s.l.); ZFMK 95236, adult female, 30 May 2013, from Noong Choong Region, Cha Lou Village (17°20.248'N, 105°56.693'E, elevation 252 m a.s.l.); NUOL R-2013.3, adult female, 11 June 2013, from Ban Dou Village (17°31.545'N, 105°49.086'E, elevation 197 m a.s.l.); VNUF R.2015.3, female, 13 March 2015, from Xebangfai cave, Noong Ping Village (17°22.459'N, 105°49.626'E, elevation 182 m a.s.l.); NUOL R-2015.9, female, 13 March 2015, from Xebangfai cave, Noong Ping Village (17°22.648'N, 105°52.931'E, elevation 182 m a.s.l.); VNUF R.2015.11, female, 14 March 2015, from Xebangfai cave, Noong Ping Village (17°22.759'N, 105°52.931'E, elevation 285 m a.s.l.). The paratypes (VNUF R.2015.3, NUOL R-2015.9, and VNUF R.2015.11) were collected by V. Q. Luu and K. Thanabuaosy in March 2015; the paratype (VNUF R.2014.99) was collected by V. Q. Luu, N. V. Ha, T. Calame, D. V. Phan and K. Thanabuaosy in May 2014, the remaining type series was collected by V. Q. Luu, N. V. Ha, and K. Thanabuaosy in May and June 2013 (V. Q. Luu *et al.*).

Diagnosis. *Cyrtodactylus hinnamnoensis* **sp. nov.** is characterized by: Adult SVL 84.1 ± 11.7 mm (mean ± SD); dorsal head with dark blotches; nuchal loop wide, distinct, posteriorly enlarged; dorsal body with four to six blackish brown bands between limb insertions; 13–19 irregular, weakly keeled dorsal tubercle rows; 35–48 ventral scale rows; ventral scale rows from mental to cloacal slit 179–201; scale rows at midbody 93–112; ventrolateral folds present, without tubercles; 36–44 precloacal-femoral pores in the males; 0–28 pores in females; enlarged femoral and precloacal scales present; 4–6 postcloacal tubercles; subcaudals enlarged.

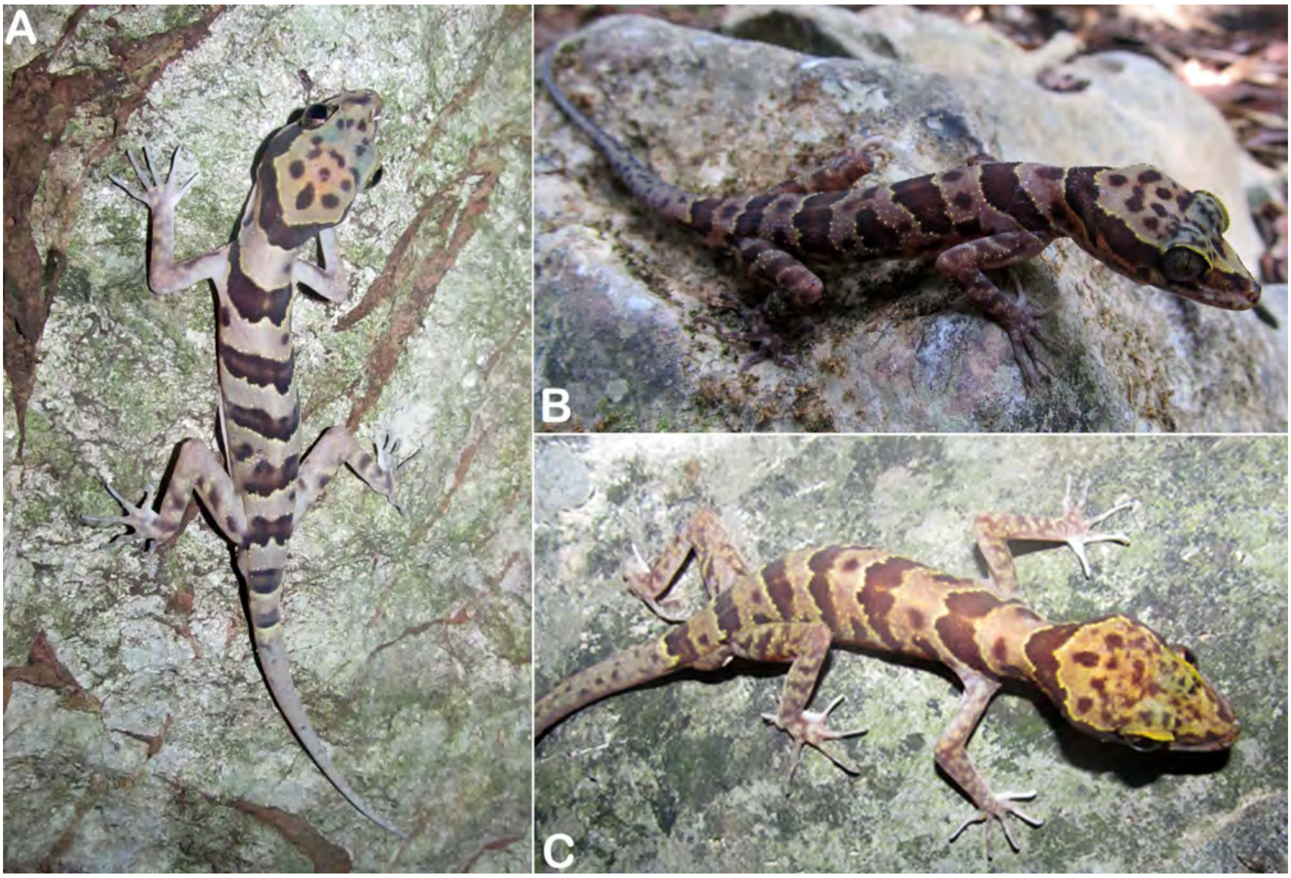

FIGURE 8. A) Dorsal view of the holotype (IEBR A.2013.90); and dorsal views of the paratypes of *Cyrtodactylus hinnamnoensis* **sp. nov.** in life B) VNUF R.2014.99; and C) VNUF R.2013.3. Photos: V. Q. Luu.

Description of holotype. Adult male, snout-vent length (SVL) 83.6 mm; body elongate (TrunkL/SVL 0.42); head elongate (HL/SVL 0.27), relatively wide (HW/HL 0.68), depressed (HH/HL 0.40), distinguished from neck; loreal region concave; snout long (SE/HL 0.43), obtuse, longer than diameter of orbit (OD/SE 0.60); snout scales small, homogeneous, granular, larger than those on frontal and parietal regions; eye large (OD/HL 0.26), pupils vertical; eyelid fringe with tiny spines posteriorly; ear oval-shaped, small (EarL/HL 0.08); rostral wider than high (RH/RW 0.60), with a median suture; supranasals in contact anteriorly and separated from each other by a small scale posteriorly; rostral in contact with first supralabial and nostril scales on each side; nares oval, surrounded by supranasal, rostral, first supralabial, and two enlarged postnasals; mental triangular, wider than high (ML/MW 0.65); two enlarged postmentals in broad contact posteriorly, bordered by mental anteriorly, first two infralabials laterally, and eight small scales posteriorly; supralabials 12/10; infralabials 10/9. Dorsal scales granular to flattened; dorsal tubercles round, weakly keeled, present on occiput, back and tail base, each surrounded by 8 granular scales, in 15 irregular longitudinal rows at midbody; ventral scales smooth, medial scales 2–3 times larger than dorsal scales, round, subimbricate, largest posteriorly, in 35 longitudinal rows between lateral folds at midbody; ventrolateral folds present, without tubercles; gular region with homogeneous smooth scales; ventral scales in a line from mental to cloacal slit 186; precloacal groove absent; enlarged femoral scales present; femoral and precloacal pores 42.

Fore and hind limbs moderately slender (ForeL/SVL 0.17, CrusL/SVL 0.21); dorsal fore limbs with slightly developed tubercles; dorsal hind limbs covered by distinctly developed tubercles; fingers and toes free of webbing; lamellae under fourth fingers 19/19, under fourth toes 20/20.

Tail regenerated, postcloacal tubercles 5/5; dorsal tail bearing tubercles at base; subcaudals distinctly enlarged, flat, smooth.

Coloration in life. Ground coloration of dorsal head greyish brown with dark blotches; nuchal loop black, in

U-shape, from posterior corner of eye through tympanum to the neck, dark brown, edged in yellow; body bands between limb insertions five, somewhat irregular, dark brown, edged in white; dorsal surface of fore and hind limbs with dark bars; tail brown dorsally with light brown rings, edged by yellowish white; chin, throat, and belly cream; upper and lower lips with dark brown bars; tail ventrally grey with light dots.

Sexual dimorphism. The females differ from the males by lacking or having fewer precloacal-femoral pores (0–28 *versus* 36–44 in the males) and the absence of hemipenial swellings at the tail base (see Table 6).

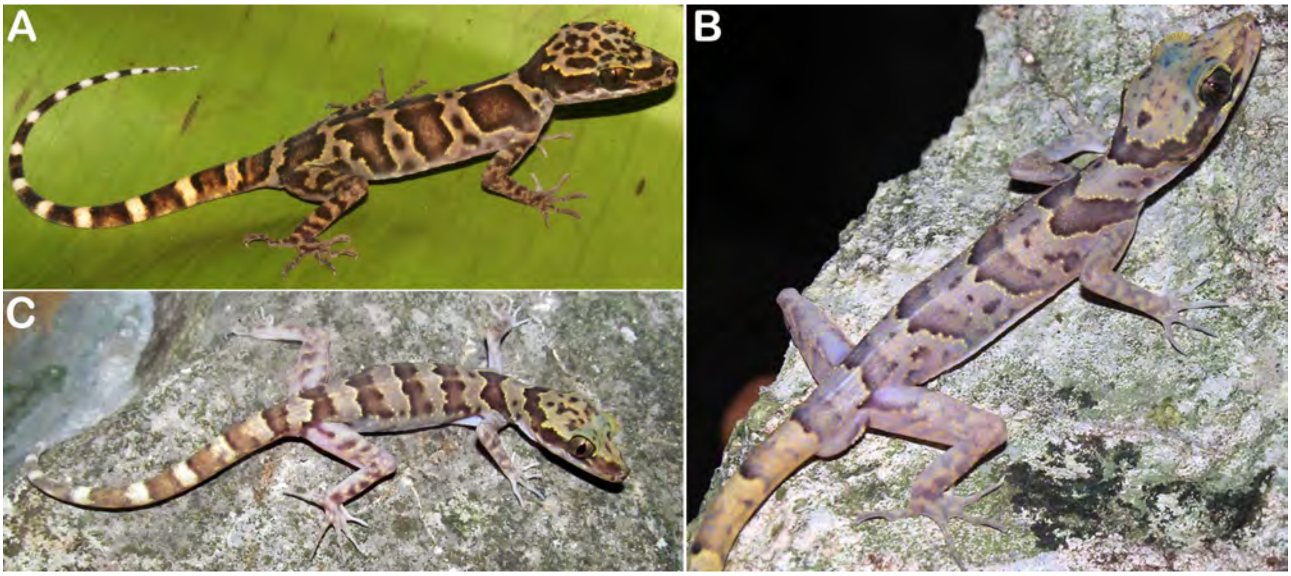

FIGURE 9. Dorsal pattern of three *Cyrtodactylus* sibling species: A) *Cyrtodactylus phongnhakebangensis* from Vietnam (Phong Nha-Ke Bang National Park); B) *Cyrtodactylus calamei* **sp. nov.**; and C) *Cyrtodactylus hinnamnoensis* **sp. nov.** (VNUF R.2013.4), from Laos. Photos: T. Ziegler & V. Q. Luu.

Comparisons. We compared the new species with its congeners from Laos and neighbouring countries in the mainland Indochina region, including Vietnam, Cambodia, and Thailand based on examination of specimens (see Appendix) and data integrated from the literature (compiled after Luu *et al*. 2014a; Nazarov *et al*. 2014; Nguyen *et al*. 2014; Panitvong *et al*. 2014; Pauwels *et al*. 2014; Pauwels & Sumontha 2014; Schneider *et al*. 2014; Sumontha *et al*. 2015; Nguyen *et al*. 2015; Luu *et al*. 2015a; Luu *et al*. 2016a,b) (see Tables 3). The cluster and correspondence analyses of morphological characters supported *Cyrtodactylus hinnamnoensis* **sp. nov.** as a sister taxon to *C. darevskii* (Figs. 2–3). Molecular phylogenetic analyses also demonstrated the close relationships between these species (see Fig. 1).

Morphologically, *Cyrtodactylus hinnamnoensis* **sp. nov.** is closely related to the *C. phongnhakebangensis* group including *C. darevskii*, *C. phongnhakebangensis*, *C. calamei* by dorsal colour pattern and the number of cloacal and femoral pores in males. However, the new species can be distinguished from *C. darevskii* by having fewer cloacal and femoral pores in females (maximum 0–28 *versus* 24–34), four to six blackish brown transverse body bands, as wide as light bands (*versus* four to five dark irregular transverse breaking body bands, 0.5 times narrower than light band), first body band wide, butterfly-shaped (*versus* thin, U-shaped in *C. darevskii*), the presence of tubercles on fore limbs (*versus* absent), and tail consisting of light rings (*versus* banded); *Cyrtodactylus hinnamnoensis* **sp. nov.** differs from *C. phongnhakebangensis* by its slightly larger size (SVL reaching 100.6 mm *versus* 96.3 mm), having fewer cloacal and femoral pores in females (0–28 *versus* 0–41), having more scale rows from mental to the front of cloacal slit (179–201 *versus* 161–177), the presence of tubercles on fore limbs (*versus* absent), a narrower nuchal loop, not enlarged posteriorly (wide, enlarged posteriorly), four to six blackish brown transverse body bands as wide as light bands (*versus* three to five dark transverse body bands as wide as double light bands, light transverse bands with small spots (*versus* with big black blotches), and tail pattern consisting of light rings (*versus* banded); *Cyrtodactylus hinnamnoensis* **sp. nov.** differs from *C. calamei* by its larger size (SVL reaching 100.6 mm *versus* 89.3 mm), fewer cloacal and femoral pores in females (0–28 *versus* 38), more postcloacal tubercles (4–6 *versus* 4), dorsal head marking with distinctly dark spots and blotches (*versus* indistinct dots), the absence of heart-shaped marking on postocciput (*versus* present), four to six blackish brown body

TABLE 6. Morphometric measurements (in mm) and meristic characters of *Cyrtodactylus hinnamnoensis* **sp. nov.** (* = regenerated or broken tail, m = mean. max. = maximum, SD = standard deviation, for other abbreviations see material and methods).

Character	IEBR A.2013.90 Holotype	IEBR A.2013.89 paratype	VNUF R.2013.1 paratype	NUOL R-2013.2 paratype	VNUF R.2014.99 paratype	m±SD	min–max
Sex	Male	male	male	male	male		
SVL	83.6	91.9	83.7	92.5	85.0	87.3±4.5	83.6–92.5
TaL	70.6*	100.9*	71.4*	101.6	loss	101.6 (n=1)	101.6 (max)
HL	22.7	26.3	23.6	26.2	23.8	24.5±1.6	22.7–26.3
HW	15.4	18.5	17.0	16.5	15.4	16.6±1.3	15.4–18.5
HH	9.0	10.5	9.6	9.1	8.2	9.3±0.8	8.2–10.5
OD	5.9	6.2	5.9	6.1	5.5	5.9±0.3	5.5–6.2
SE	9.8	11.0	10.3	10.9	9.4	10.3±0.7	9.4–11.0
EyeEar	6.2	7.2	7.7	7.3	6.6	7.0±0.6	6.2–7.7
EarL	1.8	3.0	1.9	2.1	2.1	2.2±0.5	1.8–3.0
TrunkL	34.7	39.0	36.6	38.4	38.1	37.4±1.7	34.7–39.0
ForeL	14.5	15.2	15.1	16.2	14.9	15.2±0.7	14.5–16.2
FemurL	18.1	19.4	18.9	20.4	17.3	18.8±1.2	17.3–20.4
CrusL	17.5	19.4	17.9	19.8	16.2	18.2±1.5	16.2–19.8
LD4A	8.0	9.3	9.0	8.5	8.4	8.6±0.5	8.0–9.3
LD4P	9.6	11.3	10.1	10.6	10.9	10.7±0.5	10.1–11.3
RW	3.5	4.0	3.7	4.4	3.7	3.8±0.4	3.5–4.4
RH	2.1	2.5	2.3	2.5	2.3	2.3±0.2	2.1–2.5
MW	3.4	4.0	3.7	3.7	3.7	3.7±0.2	3.4–4.0
ML	2.2	3.0	2.7	2.7	2.6	2.6±0.3	2.2–3.0
SL	12/10	10/10	10/10	11/9	9/11	10.2±0.9	9–12
IL	10/9	9/9	11/8	10/10	10/10	9.6±0.8	8–11
N	3	3	3	3	3	3.0±0.0	3–3
IN	0	0	0	0	1	0.2±0.4	0–1
PM	2	2	2	2	2	2.0±0.0	2–2
DTR	15	18	17	17	16	16.6±1.1	15–18
GST	8	7	9	9	7	8.0±1.0	7–9
V	35	44	37	36	36	37.6±3.6	35–44
SLB	186	183	189	201	188	189.4±6.9	183–201
SR	103	110	99	101	98	102.2±4.8	98–110
PP+FP	42	38	36	44	38	39.6±3.3	36–44
PAT	5/5	4/4	4/4	5/5	5/5	4.6±0.5	4–5
LD4	19/19	18/19	19/17	18/18	19/18	18.0±0.7	17–19
LT4	20/20	19/19	19/19	21/21	19/21	20.0±0.9	19–21

……*continued on the next page*

TABLE 6. (Continued)

Character	ZFMK.95235 paratype	NUOL R–2013.3 paratype	ZFMK 95236 paratype	VNUF R.2015.3 paratype	NUOL R-2015. 9 paratype	VNUF R.2015.11 paratype	m±SD	min–max
Sex	female	female	female	female	female	female		
SVL	100.6	95.0	88.7	70.0	62.1	71.8	81.4±15.5	62.1–100.6
TaL	108.3*	92.8*	82.9*	86.2	76.1	100.0	91.1±11.8	76.1–108.3
HL	29.0	26.7	25.6	19.5	19.3	20.4	23.4±4.2	19.3–29
HW	19.6	18.0	16.3	12.4	12.0	13.2	15.3±3.2	12–19.6
HH	9.2	9.4	7.8	6.0	5.5	5.5	7.2±1.8	5.5–9.4
OD	6.2	5.7	5.5	5.3	5.3	5.4	5.6±0.3	5.3–6.2
SE	11.9	11.9	10.8	8.0	8.6	8.7	10.0±1.8	8.0–11.9
EyeEar	8.4	7.8	6.7	5.3	4.6	4.6	6.2±1.6	4.6–8.4
EarL	3.6	2.8	3.1	2.3	1.8	2.0	2.6±0.7	1.8–3.6
TrunkL	43.0	38.4	37.9	32.5	25.5	30.6	34.7±6.3	25.5–43.0
ForeL	16.0	15.9	15.2	11.7	10.9	12.3	13.7±2.3	10.9–16.0
FemurL	21.3	19.6	19.6	15.3	14.2	15.9	17.7±2.9	14.2–21.3
CrusL	20.3	17.9	18.1	14.2	12.7	15.0	16.4±2.9	12.7–20.3
LD4A	9.8	8.9	9.2	7.7	7.5	8.1	8.5±0.9	7.5–9.8
LD4P	11.0	10.9	11.2	8.8	8.6	9.8	10.1±1.2	8.6–11.2
RW	4.6	4.1	3.8	2.8	2.9	3.1	3.6±0.7	2.8–4.2
RH	3.0	2.7	2.5	1.6	1.6	1.7	2.2±0.6	1.6–3.0
MW	4.2	3.7	3.8	2.9	2.8	2.9	3.4±0.6	2.8–4.2
ML	3.3	2.5	3.1	2.3	2.0	2.2	2.6±0.5	2.0–3.3
SL	10/10	10/10	9/11	9/9	9/10	11/10	9.8±0.7	9.0–11.0
IL	9/9.	9/9.	9/9.	7/7.	7/8.	9/8.	8.3±0.9	7–9
N	3	3	3	3	3	3	3.0±0.0	3–3
IN	1	1	1	0	1	0	0.7±0.5	0–1
PM	2	2	2	2	2	2	2.0±0.0	2–2
DTR	19	17	16	13	16	15	16.0±2.0	13–19
GST	10	9	10	9	9	8	9.2±0.8	8–10
V	43	48	38	42	39	40	41.7±3.6	38–48
SLB	179	197	199	188	182	199	190.7±8.9	179–199
SR	112	105	110	93	108	106	105.7±6.7	93–112
PP+FP	28	0	24	13	19	14	16.3±9.9	0–28
PAT	6/6	4/4	5/5	4/4	4/4	4/4	4.5±0.8	4–6
LD4	16/19	18/18	20/20	19/19	18/17	21/20	18.8±1.4	16–21
LT4	20/20	21/19	22/22	20/21	17/19	21/21	20.3±1.4	17–22

TABLE 7. Comparison of *Cyrtodactylus calamei* **sp. nov.** and *Cyrtodactylus hinnamnoensis* **sp. nov.** with other members of the *C. phongnhakebangensis* group (data obtained from Ziegler *et al*. 2002; Nazarov *et al.* 2014; and own data). SLB = number of scales along the midbody from mental to anterior edge of cloaca opening.

Character	*Cyrtodactylus calamei* **sp. nov.**	*Cyrtodactylus hinnamnoensis* **sp. nov.**	*C. darevskii*	*C. phongnhakebangensis*
Number of specimens	4	11	7	11
Maximal SVL (mm)	89.3	100.6	100	96.3
Ventral scales	39–42	35–48	38–46	32–42
Dorsal tubercle rows	10–16	13–19	16–20	11–20
Femoral and precloacal pores (in males)	35–39	36–44	38–44	32–42
Femoral and precloacal pores (in females)	38	0–28	24–34	0–41
SLB	183–197	179–201	180–208	161–177
Tubercle on fore limbs	present	present	absent	absent
Postcloacal tubercles	4	4–6	4–5	3–5
Nuchal loop	narrow, not enlarged posteriorly	narrow, not enlarged posteriorly	thin, not enlarged posteriorly	wide, enlarged posteriorly
Dorsal pattern between limb insertions	4 greyish brown transverse bands, narrower light bands	4–6 blackish brown transverse bands, as wide as light bands	4–5 dark transverse breaking bands, as narrow as nearly half light bands	3–5 dark transverse bands, as wide as double light bands
Tail pattern	light rings	light rings	light bands	light bands

TABLE 8. Ecological details for the type series of *Cyrtodactylus hinnamnoensis* **sp. nov.** from Hin Nam No NPA, central Laos. Abbreviations are as follows: m.= male; f.= female; Temp. = temperature).

Nr.	Museum No.	Type	Date	Locality	Sex	Time	Temp.	Humidity	Elevation	Microhabitat
1	IEBR A.2013.90	Holotype	11 June 2013	Ban Dou	m.	20:50	28.3°C	81%	193 m	karst cliff, in 0.5 m height
2	IEBR A.2013.89	Paratype	7 May 2013	Noong Ma	m.	20:52	24.9°C	81%	580 m	karst cliff, in 3 m height
3	VNUF R.2013.1	Paratype	9 June 2013	Vangmano	m.	22:03	29.9°C	90%	175 m	karst cliff, in 5 m height
4	NUOL R-2013.2	Paratype	9 June 2013	Vangmano	m.	21:59	30.7°C	87%	180 m	karst cliff, in 3 m height
5	VNUF R.2014.99	Paratype	27 May 2014	Chalou	m.	21:59	30.6°C	81%	ca.300 m	tree trunk, in 1 m height
6	ZFMK95235	Paratype	8 May 2013	Noong Ma	f.	21:35	29.8°C	90%	555 m	cave entrance, karst cliff, in 2 m height
7	NUOL R-2013.3	Paratype	11 June 2013	Ban Dou	f.	20:40	28.8°C	81%	197 m	karst cliff, in 2 m height
8	ZFMK 95236	Paratype	30 May 2013	Cha Lou	f.	20:36	27.1°C	81%	252 m	in the slit of karst cliff, in 0.5 m height
9	VNUF R.2015.3	Paratype	13 March 2015	Xebangfai cave	f.	21:15	28.3°C	78%	182 m	tree trunk, near karst cliff, in 0.3 m height
10	NUOL R-2015. 9	Paratype	14 March 2015	Xebangfai cave	f.	19:41	26°C	80%	200 m	on the karst cliff, in 0.3 m height
11	VNUF R.2015.11	Paratype	13 March 2015	Xebangfai cave	f.	20:57	26.3°C	81%	285 m	on the karst cliff, in 0.3 m height

transverse bands, as wide as light bands (*versus* four greyish brown transverse bands, narrower than light bands) (for more details see Table 7, Fig. 9). The results of the correspondence analysis comparing all adult male morphological maesurements of *Cyrtodactylus hinnamnoensis* **sp. nov.** and the latter species indicated four distinct groups between these species (see Fig. 4).

Distribution. *Cyrtodactylus hinnamnoensis* **sp. nov.** is currently known only from the type locality in the karst forest of Hin Nam No NPA, Khammouane Province, central Laos (Fig. 6).

Etymology. We name this species after its type locality, Hin Nam No NPA where the new *Cyrtodactylus* species was discovered and propose the following common names: Hinnamno Bent-toed Gecko (English), Ki Chiem Hin Nam No (Laotian).

Natural history. Specimens were found at night between 19:41 and 22:03h on karst walls, ca. 0.3–5 m above the ground, near cave entrances in the limestone forest, at elevations between 175 and 580 m a.s.l. Only one male specimen VNUF R.2014.99 was collected on a tree trunk, about 1 m from the forest floor. The surrounding habitat was karst forest, dominated by species of Ebenaceae, Dracaenaceae, Arecaeae, Poaceae, Meliaceae, and Moraceae. The relative humidity ranged from 78% to 90%, and temperatures were from 24.9 to 30.7°C (see Table 8). When capturing individuals of the species, we observed an increased rate of tail autotomy and many individuals had regenerated tail, for example, seven of 11 specimens of *Cyrtodactylus hinnamnoensis* **sp. nov.** had dropped or/and regenerated tails. This suggests that these populations might be under the stress of predators (see also Grismer *et al*. 2016).

Cyrtodactylus sommerladi sp. nov.
(Fig. 10)

Holotype. VNUF R.2013.22 adult male, in karst forest, Hang Toi region, Noong Ma Village (17°17.795'N, 106°08.738'E, elevation 572 m a.s.l.) within Hin Nam No NPA, Khammouane Province, central Laos, collected on 05 May 2013 by V. Q. Luu and N. V. Ha.

Paratypes. NUOL R-2013.23, IEBR A.2015.37, ZFMK 97196, VNUF R.2013.105, VNUF R.2014.87, NUOL R-2013.14, IEBR A.2015.39, NUOL R-2013.21, IEBR A.2015.38, VNUF R.2013.104, ZFMK 97197, VNUF R.2014.89, VNUF R.2013.67 the same locality as the holotype. IEBR A.2015.40 adult female, in karst forest, Cha Lou Village (17°18.880'N, 105°57.103'E, elevation 572 m a.s.l.) within Hin Nam No NPA, Khammouane Province, central Laos, collected on 25 May 2013.

Diagnosis. *Cyrtodactylus sommerladi* **sp. nov.** is characterized by: Adult SVL 72.3 ± 3.8 mm (mean ± SD); dorsal head greyish brown without dark blotches; nuchal loop present, narrow, not enlarged posteriorly; five or six dark transverse bands between limbs; dorsal surface with homogenous, tubercle-like scales; ventral scales at midbody 31–39; ventrolateral skin folds present; ventral scale rows from mental to cloacal slit 168–192; scale rows at midbody 76–93; precloacal-femoral pores 20–26 in males, 17–21 in females; enlarged femoral and precloacal scales present; postcloacal tubercles 4–6; subcaudal scales slightly enlarged.

Description of holotype. Adult male, small sized (SVL 70.3 mm); body elongate (TrunkL/SVL 0.45); head elongate (HL/SVL 0.25), width (HW/HL 0.77), relatively depressed (HH/HL ratio 0.41), distinct from neck; loreal area concave; snout long (SE/HL ratio 0.47), obtuse, two times longer than diameter of orbit (OD/SE 0.50); snout scales small, homogeneous, granular, about one and a half times larger than those in frontal and parietal regions; eye large (OD/HL ratio 0.23), pupils vertical; eyelid fringe with tiny spines in posterior part, posterior ones more developed; ear opening oval, obliquely orientated, small (EarL/HL 0.12); rostral square-shaped, wider than high (RH/RW ratio 0.55), medially with a straight, vertical suture, in contact with nasorostral, nare and first supralabial on each side; nares oval, surrounded by rostral anteriorly, supranasal, first supralabial laterally, and two enlarged postnasals posteriorly; supranasals in contact; mental triangular, slightly narrower than rostral (RW/MW ratio 0.94), in contact with two postmentals and the first infralabial on each side, postmentals surrounded by first infralabial on each side and seven granular scales posteriorly, two outer ones enlarged; supralabials 10/10; infralabials 8/9; supralabials separated from orbit by 3 or 4 rows of granular scales. Dorsal scales homogenous, tubercle-like; dorsal tubercles indistinct; ventrolateral folds present; ventral scales smooth, medial scales 2 or 3 times larger than dorsal scales, round, and in 37 rows at midbody; midbody scale rows 87; scales between mental and cloacal slit 192; femoral scales enlarged; precloacal scales enlarged, precloacal-femoral pores 23, in a continuous row; precloacal groove absent.

FIGURE 10. A) Dorsal view of the holotype (VNUF R.2013.22); and dorsal views of the paratypes of *Cyrtodactylus sommerladi* **sp. nov.** in life B) VNUF R.2013.67; C) IEBR A.2015.39; and D) NUOL R-2013.105. Photos: V. Q. Luu.

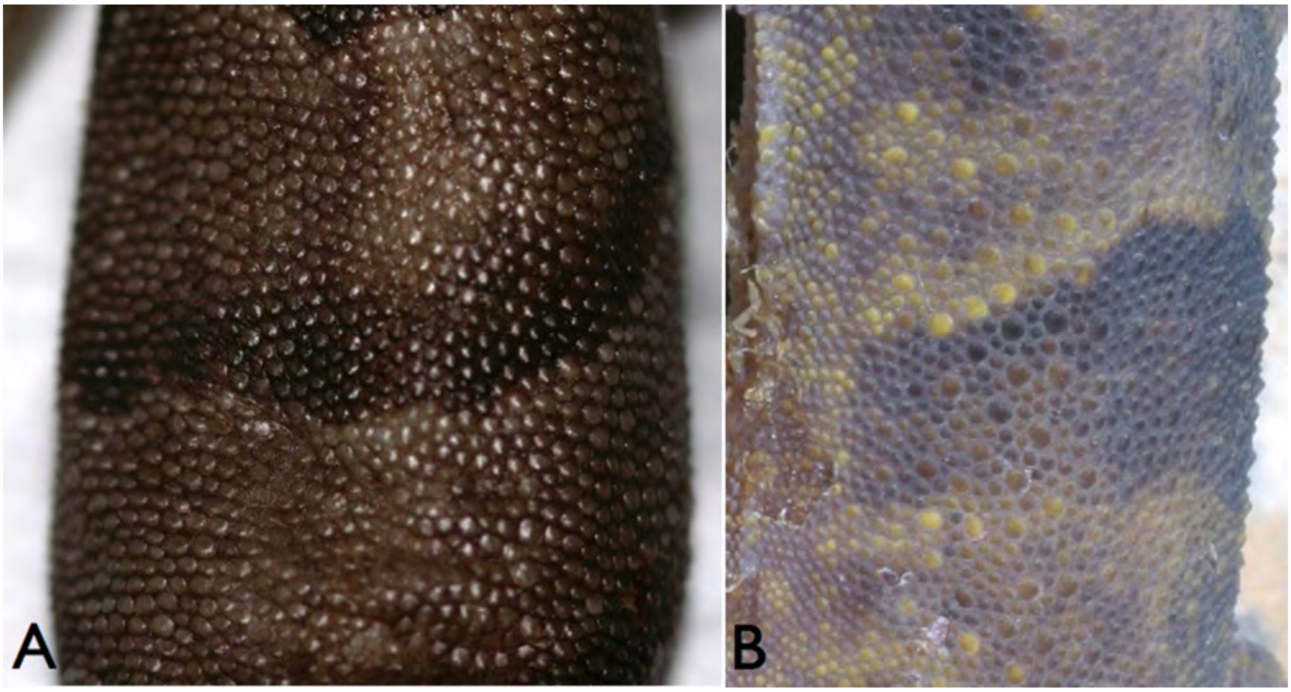

FIGURE 11. Comparison of dorsal scale structure of *Cyrtodactylus sommerladi* **sp. nov.** (A: with homogenous tubercle-like scales) and *C. roesleri* (B: with distinct dorsal tubercle rows). Photos: N. Schneider & T. Ziegler.

Fore and hind limbs moderately slender (ForeL/SVL 0.15, CrusL/SVL 0.19); dorsal surface of hind limbs with tubercles, absent on fore limbs; fingers and toes with rudimental webbing; lamellae under fourth fingers 18/18, under fourth toes 20/22.

Tail longer than snout-vent length (TaiL/SVL 1.14); postcloacal tubercles 6 on each side; subcaudals slightly enlarged.

TABLE 9. Morphometric measurements (in mm) and meristic characters of the type series of *Cyrtodactylus sommerladi* **sp. nov.** (* = regenerated or broken tail, m = mean, max. = maximum, SD = standard deviation, sub. = subadult, for other abbreviations see material and methods).

Character	VNUF R.2013.22 Holotype	IEBR A.2015.39 paratype	VNUF R.2014.87 paratype	IEBR A.2015.37 paratype	ZFMK97196 paratype	NUOL R-2013.105 paratype	m±SD	min–max
Sex	male	male	male	male	male	male		
SVL	70.3	71.3	70.2	71.0	67.3	69.6	70.0±1.4	67.3–71.3
TaL	79.8	67.9*	loss	69.7*	84.8*	89.4	84.6±6.8	79.8–89.4
HL	17.9	19.4	18.3	19.7	17.6	17.9	18.5±0.9	17.6–19.7
HW	13.7	12.3	13.5	13.8	12.9	13.3	13.3±0.6	12.3–13.8
HH	7.3	7.1	8.3	7.6	7.1	7.3	7.5±0.5	7.1–8.3
OD	4.2	4.3	4.3	4.2	3.9	4.2	4.2±0.1	3.9–4.3
SE	8.4	8.6	8.7	8.7	7.9	8.6	8.5±0.3	7.9–8.7
EyeEar	5.3	5.6	6.5	5.5	5.8	5.8	5.8±0.4	5.3–6.5
EarL	2.2	1.5	1.4	1.8	1.5	1.5	1.7±0.3	1.4–2.2
TrunkL	31.7	27.3	29.9	29.4	26	26.9	29.0±2.0	26.9–31.7
ForeaL	10.6	10.6	11.8	10.7	10.8	10.6	10.9±0.5	10.6–11.8
FemurL	14.3	15.7	14.6	15.9	12.6	14.6	14.6±1.2	12.6–15.9
CrusL	13.6	12.9	14.4	12.5	12.8	13.7	13.3±0.7	12.5–14.4
LD4A	6.4	6.4	5.6	7.0	6.0	5.4	6.1±0.6	5.4–7.0
LD4P	8.3	7.8	6.9	8.2	7.4	8.1	7.8±0.5	6.9–8.3
RW	2.9	2.5	3.4	3.0	2.8	2.9	2.9±0.3	2.5–3.4
RH	1.6	1.6	1.9	1.2	2.1	2.1	1.8±0.4	1.2–2.1
MW	3.1	2.9	3.2	3.5	3.3	2.9	3.2±0.2	2.9–3.5
ML	1.9	2.4	2.4	2.0	2.6	2.2	2.3±0.3	1.9–2.6
SL	10/10	9/10	10/11	11/10	10/9	10/10	10.0±0.6	9–11
IL	8/9	9/9	8/8	9/7	8/9	9/9	8.5±0.7	7–9
N	3	2	2	3	3	3	2.7±0.5	2–3
IN	0	0	0	0	0	0	0	0
PM	2	2	2	2	2	2	2.0±0.0	2–2
DTR	no	no	no	unclear	no	no		
GST	no	no	no	7-8	no	no		
V	37	32	31	38	39	31	34.7±3.7	31–39
SLB	192	182	177	170	185	168	179±9.2	168–192
SR	87	86	78	88	91	76	84.3±6.0	76–91
FP+PP	23	26	24	22	21	21	22.8±1.9	21–26
PAT	6/6	5/5	4/4	5/5	5/5	5/5	5.0±0.6	4–6
LD4	18/18	18/17	17/16	16/16	17/16	18/17	17.0±0.9	16–18
LT4	20/22	22/22	19/18	19/18	17/20	22/21	20.0±1.8	17–22

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TABLE 9. (Continued)

Character	NUOL R-2013.23 paratype	NUOL R-2014.90 paratype	IEBR A.2015.38 paratype	VNUF R.2013.104 paratype	ZFMK97197 paratype	IEBR A.2015.40 paratype	VNUF R.2014.89 paratype	NUOL R-2013.21 paratype	VNUF R.2013.67 paratype	m±SD	min–max
Sex	sub.. male	sub. male	female	female	female	female	female	female	female		
SVL	61.8	58.8	74.1	80.3	68.6	69.6	76.2	76.6	75.0	74.3±4.1	68.6–80.3
TaL	63.7*	58.8*	89.9	72.5*	82.8	84.3	82.2*	71.7*	78.1*	85.7±3.7	82.8–89.9
HL	15.9	16.8	19.2	20.5	19.3	17.9	18.9	18.4	20.9	19.3±1.1	17.9–20.9
HW	12.2	11.4	15.1	14.6	13.8	12.9	13.6	13.9	14.7	14.1±0.8	12.9–15.1
HH	6.6	5.9	8.0	7.8	7.2	7.8	7.2	8.1	7.3	7.6±0.4	7.2–8.1
OD	3.8	3.7	4.6	4.5	3.6	4.4	4.2	4.6	4.8	4.4±0.4	3.6–4.8
SE	7.5	7.9	8.8	10.4	8.7	8.5	8.5	8.6	9.0	8.9±0.7	8.5–10.4
EyeEar	4.5	4.7	5.9	6.8	5.8	5.6	5.9	6.4	5.8	6.0±0.4	5.6–6.8
EarL	1.4	1.2	2.4	1.5	1.5	1.5	1.4	1.7	2.0	1.7±0.4	1.4–2.4
TrunkL	25.9	20.9	29.1	34.1	26.4	27	30.6	35.2	29.9	30.9±3.3	26.4–35.2
ForeaL	9.4	9.6	11.4	12.4	10.8	10.7	11.4	11.4	11.8	11.4±0.6	10.7–12.4
FemurL	14.2	13.2	16.4	17.3	15.7	14.8	16.8	15.0	16.2	16.0±0.9	14.8–17.3
CrusL	12.4	11.9	14.9	14.6	13.8	13.3	13.9	14.3	15.3	14.3±0.7	13.3–15.3
LD4A	5.6	5.3	6.8	6.8	5.7	6.1	6.2	6.4	7.3	6.5±0.5	5.7–7.3
LD4P	5.9	7.2	7.9	7.7	7.5	7.2	7.5	8.9	9.0	8.0±0.7	7.2–9.0
RW	2.4	2.4	3.2	3.2	3.3	3.1	3.1	3.1	3.1	3.2±0.1	3.1–3.3
RH	1.8	1.6	2.0	2.3	2.0	1.9	1.9	1.8	2.0	2.0±0.2	1.8–2.3
MW	2.4	2.6	3.0	3.1	2.7	3.1	3.2	3.3	2.8	3.0±0.2	2.7–3.3
ML	2.2	2.1	2.4	1.9	2.7	2.4	1.9	2.6	2.5	2.3±0.3	1.9–2.7
SL	9/10	9/9	10/9	10/11	10/10	11/9	10/11	9/9	9/10	9.7±0.8	9–11
IL	7/8	8/9	8/8	8/8	8/8	8/8	9/9	9/8	8/7	8.1±0.6	7–9
N	3	2	3	3	3	3	3	3	3	3.0±0.0	3–3
IN	0	0	0	0	0	0	0	0	0	0	0
PM	2	2	2	2	2	2	2	2	2	2.0±0.0	2–2
DTR	no	no	no	no	no	no	no	no	4-5		
GST	no	no	no	no	no	no	no	7.00	8.00		
V	35	34	37	34	33	32	31	34	32	33.3±2.0	31–37
SLB	191	187	179	189	170	184	186	188	183	182.7±6.5	170–189
SR	87	87	87	93	78	87	78	86	88	85.3±5.5	78–93
FP+PP	23	20	19	21	18	17	21	21	20	19.6±1.6	17–21
PAT	5/5	4/5	4/4	4/4	4/4	5/5	4/5	5/6	5/5	5.0±0.6	4–6
LD4	16/17	17/18	17/17	17/17	17/16	17/16	17/17	19/20	17/18	17.2±1.0	16–20
LT4	23/21	20/20	21/20	24/24	20/19	22/19	20/19	23/23	19/19	20.9±1.8	19–24

TABLE 10. Ecological details for the type series of *Cyrtodactylus sommerladi* **sp. nov.** from Hin Nam No NPA, central Laos. Abbreviations are as follows: m.= male; f.= female; Temp. = temperature).

Nr.	Museum No.	Type	Date	Locality	Sex	Time	Temp.	Humidity	Elevation	Microhabitat
1	VNUF R.2013.22	Holotype	5 May 2013	Noong Ma	m.	20:10	25.6°C	90%	572 m	karst cliff. in 2 m height
2	NUOL R-2013.23	Paratype	5 May 2013	Noong Ma	m.	20:15	22.7°C	87%	572 m	karst cliff. in 2.5 m height
3	IEBR A.2015.39	Paratype	6 May 2013	Noong Ma	m.	19:20	24.1°C	81%	576 m	cave entrance. karst cliff. in 2 m height
4	ZFMK 97196	Paratype	6 May 2013	Noong Ma	m.	19:20	25.0°C	81%	576 m	karst cliff. in 3 m height
5	NUOL R-2013.105	Paratype	7 May 2013	Noong Ma	m.	21:37	25.6°C	90%	555 m	karst cliff. in 3 m height
6	VNUF R.2014.87	Paratype	24 May 2014	Noong Ma	m.	21:03	29.9°C	81%	580 m	karst cliff. in 1 m height
7	NUOL R-2013.14	Paratype	24 May 2014	Noong Ma	m.	20:02	29°C	80%	600 m	karst cliff. in 2 m height
8	IEBR A.2015.37	Paratype	24 May 2014	Noong Ma	m.	20:30	28.8°C	74%	614 m	karst cliff. in 1.5 m height
9	NUOL R.2013.21	Paratype	5 May 2013	Noong Ma	f.	20:30	22.7°C	87%	572 m	karst cliff. in 2 m height
10	IEBR A.2015.38	Paratype	7 May 2013	Noong Ma	f.	20:05	26.0°C	81%	561 m	tree trunk. near karst cliff. in 2 m height
11	VNUF R.2013.104	Paratype	7 May 2013	Noong Ma	f.	21:11	26.0°C	81%	ca.550 m	karst cliff. in 4.5 m height
12	ZFMK 97197	Paratype	10 May 2013	Noong Ma	f.	21:43	27.1°C	81%	546 m	tree trunk. near karst cliff. in 1 m height
13	VNUF R.2014.89	Paratype	24 May 2014	Noong Ma	f.	20:03	28.9°C	83%	580 m	karst cliff. in 1 m height
14	IEBR A.2015.40	Paratype	26 May 2013	Cha Lou	f.	19:45	29.8°C	90%	269 m	karst cliff. in 1.5 m height
15	VNUF R.2013.67	Paratype	6 May 2013	Noong Ma	m.	19:20	24.1°C	81%	576 m	cave entrance. karst cliff. in 2,5 m height

Coloration in life. Ground color of dorsal head and back greyish brown; head without dark blotches; nuchal loop present, narrow, in U-shape, not enlarged posteriorly, extending from posterior corner of eye through tympanum to the neck, dark brown, edged in yellow posteriorly; four dark brown body bands between limb insertions, edged in yellow; dorsal surface of fore and hind limbs with greyish-brown dark spots; tail dorsally brown with 12 yellow-whitish rings, edged in yellow; ventral surface bright beige.

Variation. The nuchal loop in the adult female paratype (ZFMK 97197) is interrupted in the middle. Other paratypes have some indistinct spot markings on dorsal head and somewhat irregular and breaking transverse bands.

Sexual dimorphism. The females differ from the males by having fewer precloacal-femoral pores (17–21 *versus* 20–26 in the males) and females lack hemipenial swellings at the tail base (see Table 9).

Comparisons. We compared the new species with its congeners from Laos and neighbouring countries in the mainland Indochina region, including Vietnam, Cambodia, and Thailand based on data obtained from the literature (compiled after Luu *et al*. 2014a; Nazarov *et al*. 2014; Nguyen *et al*. 2014; Panitvong *et al*. 2014; Pauwels *et al*. 2014; Pauwels & Sumontha 2014; Schneider *et al*. 2014; Sumontha *et al*. 2015; Nguyen *et al*. 2015; Luu *et al*. 2015a; Luu *et al*. 2016a,b) and based on the examination of specimens and photographs (see Appendix and Table 3). *Cyrtodactylus sommerladi* **sp. nov.** was well separated by the cluster and correspondence analyses from *C. roesleri* (Figs. 2–3). Molecular phylogenetic analyses also revealed the close relationships between these species (see Fig. 1).

The new species is most similar to *C. roesleri* from Vietnam in body size, and dorsal pattern. However, the new species can be distinguished from the latter by its larger size (maximal SVL 80.3 mm *versus* 73.5 mm), having more dark body bands: 5 or 6 (n=15) *versus* 4–5 (n=19), dorsal surface of the new species shows homogenous scales, all appear tubercle-like, with unclear dorsal tubercles (0–5) (*versus* dorsal tubercles being arranged in 13–19 rows) (Fig. 11), dorsal surface of tail without tubercles (*versus* present) (see Fig. 12A,B) and the shape of the rostral suture in the new species is just straight vertical *versus* Y-shaped in *C. roesleri*. In addition, *Cyrtodactylus sommerladi* **sp. nov.** can be distinguished from *C. roesleri* by the different head shape, the head of the new species is wider and flatter (Fig. 5).

Distribution. Currently, *Cyrtodactylus sommerladi* **sp. nov.** is known only from the type locality in the karst forest of Hin Nam No NPA, Khammouane Province, central Laos (Fig. 6).

Etymology. The specific epithet *sommerladi* refers to our colleague and good friend Ralf Sommerlad, late Regional vice chairman of the IUCN SSC Crocodile Specialist Group (CSG) for Europe, who passed away on 11 June 2015, to honor his lifework and strong commitment for reptile conservation. As common names, we suggest Sommerlad's Bent-toed Gecko (English), Ki Chiem Sommerlad (Laotian).

Natural history. Specimens were collected at night from 19:20 to 21:43h, mainly on karst walls, ca. 1–4.5 m above the ground, near cave entrances in the limestone forest, at elevations between 269 and 614 m a.s.l. Two female specimens IEBR A.2015.38 and ZFMK 97197 were found on tree trunks, about 1–2 m from the forest floor. The surrounding habitat was karst forest dominated by species of Ebenaceae, Dracaenaceae, Arecaeae, Poaceae, Meliaceae, and Moraceae. The relative humidity was between 74% and 90%, and temperatures ranged from 22.7 to 29.9ºC (see Table 10). Female specimens contained eggs in May, by contrast, no records of gravid females or hatchlings were made in March. Thus, the breeding season seems to start only in April or May. The majority of the caves, karst walls, and karst forests where *Cyrtodactylus sommerladi* **sp. nov.** have been explored had dry surfaces, without flowing streams inside (e.g., Ellis & Pauwels 2012).

First record of *Cyrtodactylus cryptus* Heidrich, Rösler, Vu, Böhme & Ziegler, 2007 from Laos
(Fig. 12–13)

Specimens examined (n = 3). Three specimens collected by V. Q. Luu, N. V. Ha, T. Calame, D. V. Phan, and K. Thanabuaosy (V. Q. Luu *et al*.) from Hin Nam No NPA, Khammouane Province, central Laos: VNUF R.2014.86, adult male, 24 May 2014, from Pa Rang region, Noong Ma Village (17º17.328'N, 106º09.909'E, elevation 575 m a.s.l.); VNUF R.2014.69, adult female and NUOL R-2014.68, juvenile, 23 May 2014, from Pa Rang region, Noong Ma Village (17º17.394'N, 106º09.980'E, elevation 592 m a.s.l.).

Morphological characters of the Laotian specimens agreed well with the description of Heidrich *et al*. (2007):

Snout-vent length (SVL) 69.6 mm in the male, 83.6 mm in the female, 46.7 mm in the juvenile; body slender (TrunkL/SVL 0.42 in the male, 0.39 in the female, 0.50 in the juvenile); head tapering (HL/SVL 0.28 in the male, 0.27 in the female, and 0.29 in the juvenile), distinct from neck; loreal region concave; snout elongate (SE/HL 0.39–0.43), round, longer than diameter of orbit (OD/SE 0.53–0.60); eye large (OD/HL 0.22–0.24); pupils vertical; ear oval-shaped, small (EarL/HL 0.07–0.08); rostral about 1.6 times broader than high (RH/RW 0.64–0.68), with a median suture coming to the middle of the rostral scale; supralabials 7 or 8; infralabials 6 or 7; nares oval, in contact with supranasal, rostral, first supralabial, and three enlarged postnasals; postnasal region flattened; supranasals separated from each other by one enlarged scale; mental triangular; postmentals two, bordering 7 or 8 gular scales posteriorly. Dorsal tubercles round, conical, present from occiput towards tail base, each surrounded by 10 granular scales, in 15–17 irregular longitudinal rows; ventral scales smooth, in 40–43 longitudinal rows at midbody; ventrolateral folds distinct; ventral scales in a line from mental to cloacal slit 211–218; scale rows at midbody 122–131; precloacal groove absent; enlarged femoral scales absent; precloacal pores 11 in the male, 8 pitted scales in the female; femoral pores absent; postcloacal tubercles 3–4; subcaudals slightly enlarged; dorsal surface of fore limbs without tubercles; dorsal surface of hind limbs with small tubercles; fingers and toes without webbing; lamellae under fourth fingers 17–19, under fourth toes 17–19 (see Table 11).

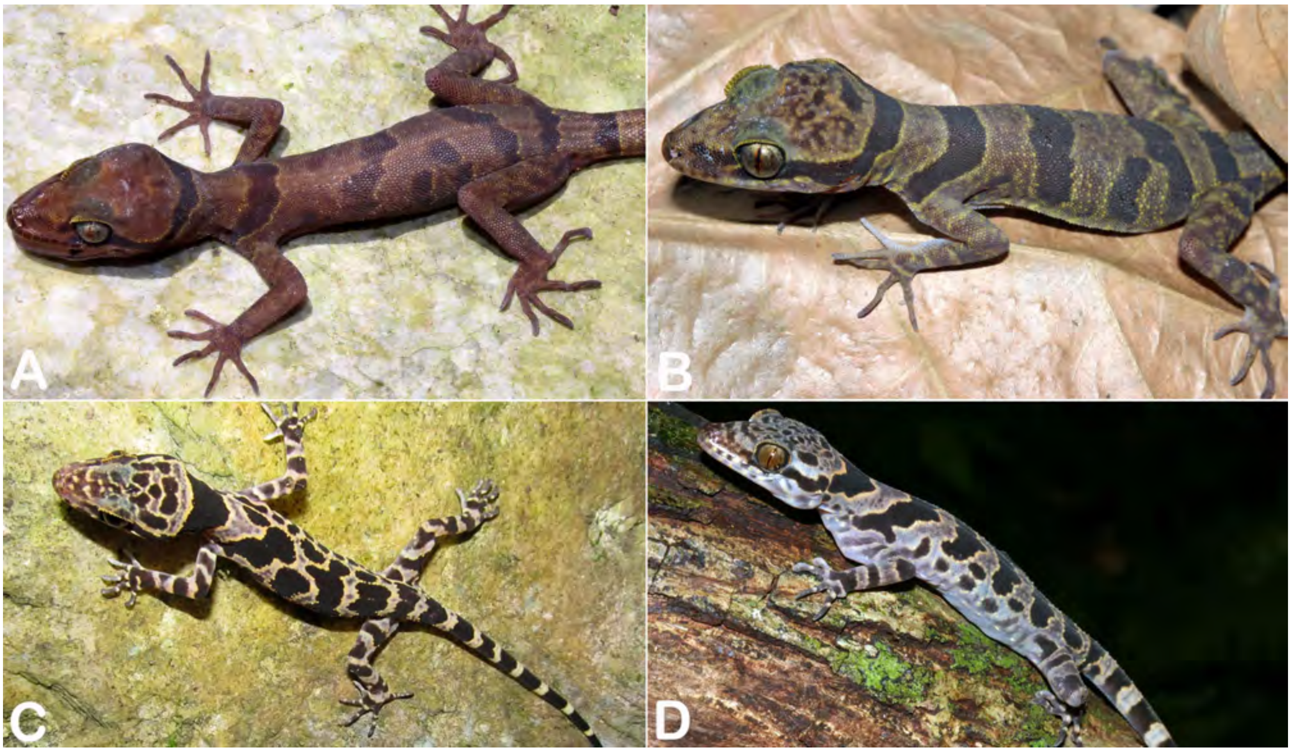

FIGURE 12. Dorsal pattern of two *Cyrtodactylus* pairs from Hin Nam No NPA (left side) and Phong Nha-Ke Bang NP (right side): A) Paratype of *Cyrtodactylus sommerladi* **sp. nov.** (NUOL R-2013.21) from Laos and B) paratype of *Cyrtodactylus roesleri* (ZFMK 86433) from Vietnam; C) *Cyrtodactylus cryptus* (VNUF R.2014.86) from Laos and D) *Cyrtodactylus cryptus* from Vietnam. Photos: V. Q. Luu & T. Ziegler.

Coloration in life. Dorsal surface brownish-gray; labials brown with yellowish gray blotches; dorsal head with black blotches dorsally; nuchal loop triangular-shaped, dark brown, edged in whitish yellow, from the outermost neck band corner to the posterior margin of each eye; dorsum with dark violet-brown blotches, irregularly shaped; lateral side of head and flanks with small to larger black oval-shaped blotches, running from posterior of ear to anterior hindlimb insertion; venter greyish-brown; dorsal surface of limbs, including fingers and toes, with yellowish brown stripes; tail with brown and dark rings.

Distribution. *C. cryptus* was originally described from Phong Nha-Ke Bang NP, Quang Binh Province, central Vietnam (Heidrich *et al*. 2007). The record of the species from Hin Nam No NPA, Laos is approximately 60 km distant from the type locality of this species in Vietnam (Fig. 6).

Remarks. The Laotian specimens differ from the original description of Heidrich *et al*. (2011) by having blotches on the dorsum (*versus* banded dorsum in the Vietnamese specimens), fewer ventral scales (40–43 *versus*

47–50 in the Vietnamese specimens), and more postcloacal tubercles (3–4 *versus* 0–3 in the Vietnamese specimens). Despite these morphological differences between the Laotian and Vietnamese populations, we herein treat them as conspecific, given the small sample size and in particular due to the strong genetic accordance (only 0.2% of genetic divergence). Once larger series is available for more thorough morphological comparisons, and if afore mentioned morphological differences are furthermore supported, this then could be reflected by a different subspecific status (species in statu nascendi) of the Laotian population (see Fig. 12C,D).

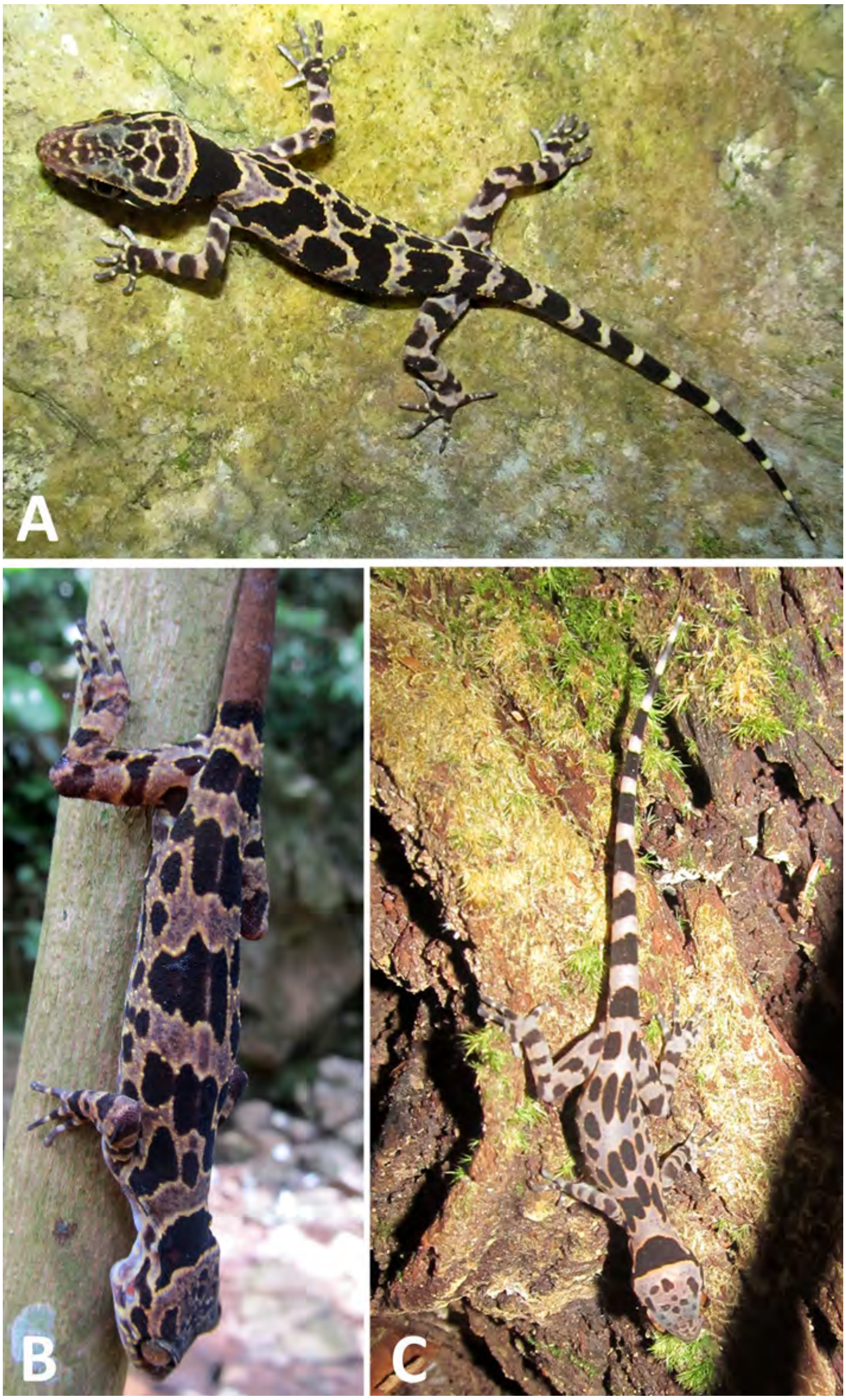

FIGURE 13. A) Adult male (VNUF R.2014.86); B) adult female (VNUF R.2014.69); and C) juvenile (VNUF R.2014.68) of *Cyrtodactylus cryptus* from Laos in life. Photos: V. Q. Luu.

TABLE 11. Morphometric measurements (in mm) and meristic characters of *Cyrtodactylus cryptus* from Laos (* = regenerated tail, for other abbreviations see material and methods).

Character	VNUF R.2014.86	VNUF R.2014.69	NUOL R-2014.68
Sex	male	female	juvenile
SVL	69.6	83.6	46.7
TaL	73.0	61.6*	44.7
HL	19.4	22.7	13.6
HW	12.2	14.0	8.7
HH	7.5	8.6	4.9
SE	7.5	9.2	5.8
OD	4.5	4.9	3.2
EyeEar	7.5	6.1	3.9
EarL	1.5	1.5	1.1
TrunkL	28.9	33.0	23.4
ForeaL	11.4	13.2	7.1
FemurL	12.7	15.7	9.4
CrusL	11.9	14.1	8.2
LD4A	6.1	7.3	3.8
LD4P	6.8	7.8	4.7
RW	3.3	3.7	2.4
RH	2.1	2.5	1.6
MW	3.2	3.4	2.4
ML	1.8	2.3	1.6
SL	7/7	7/7	8/8
IL	6/7	6/6	7/6
N	4	4	4
IN	1	1	1
PM	2	2	2
DTR	16	15	17
GST	10	10	10
V	40	43	42
SLB	211	218	212
SR	128	131	122
PP	11	8 (pitted scales)	8
FP	0	0	0
PAT	4/4	4/4	3/3
LD4	19/18	19/18	18/17
LT4	18/19	19/19	17/17

Natural history. The specimens were discovered between 20:05 and 21:30h, the juvenile was observed on a stump of a rotten tree, the female was seen on a tree trunk about 0.5 m from the juvenile, the sitting places of these individual were very close to the forest floor, at an elevation of 592 m a.s.l., temperature 27.3°C and humidity 81%. The male was found on the karst wall of an outcrop, ca. 0.3 m above the ground, at an elevation of 575 m a.s.l., with a temperature of 26.1°C and a humidity of 83% (see Table 12).

TABLE 12. Ecological details for *Cyrtodactylus cryptus* from Hin Nam No NPA, central Laos. Abbreviations are as follows: m.= male; juv. = juvenile; Temp. = temperature).

Nr.	Museum No.	Type	Date	Locality	Sex	Time
Cyrtodactylus cryptus						
1	VNUF R.2014.86		24 May 2014	Noong Ma	m.	20:05
2	VNUF R.2014.69		23 May 2014	Noong Ma	juv.	21:30
3	NUOL R-2014.68		23 May 2014	Noong Ma	juv.	21:30

continued.

Nr.	Museum No.	Temp.	Humidity	Elevation	Microhabitat
Cyrtodactylus cryptus					
1	VNUF R.2014.86	27ºC	81%	587 m	on the karst cliff ca. 0.3 m height
2	VNUF R.2014.69	27.3ºC	81%	592 m	on the trunk of a small tree, ca.0.2 m height
3	NUOL R-2014.68	27.3ºC	81%	592 m	on the stump of a big tree

Cyrtodactylus species groups in Laos

As currently recognized, 21 *Cyrtodactylus* species are known from Laos. Based on our molecular phylogeny, the molecular data presented in Nazarov *et al*. (2014), and a combination of characters including size, dorsal color pattern, scalation, and geographic distribution, we herein propose four species groups within the genus *Cyrtodactylus* occurring in Laos (see Table 13), which are defined as follows:

Cyrtodactylus phongnhakebangensis group

Species. *C. bansocensis*, *C. calamei*, *C. darevskii*, *C. hinnamnoensis*, *C. jaegeri*, *C. jarujini*, *C. khammouanensis*, *C. lomyenensis*, *C. multiporus*, *C. pageli*, *C. rufford*, *C. sommerladi*, *C. soudthichaki*, *C. teyniei*.

Characters. Adult SVL 73–100.6 mm, supranasals 0–1; dorsal tubercles 10–24 (except for *C. sommerladi*, which only has 0–5); webbing between fingers and toes absent; tubercles on fore limbs lacking (except for *C. calamei*, *C. hinnamnoensis*, *C. jaegeri*, *C. jarujini*, *C. multiporus*, and *C. soudthichaki*); tubercles on hind limbs present (except for *C. pageli*); precloacal and femoral pores in males 20–60 (except for *C. pageli* only four and for *C. teyniei* such data is lacking); postcloacal tubercles 3–8 (rarely two); subcaudals enlarged; body bearing well-defined bands 3–8 (except for *C. jarujini* and *C. teyniei*, which are blotched).

Distribution. The group is mainly distributed in the karst forest mountains of Khammouane Province in central Laos, *C. calamei*, *C. hinnamnoensis*, and *C. sommerladi* are restricted to Hin Nam No NPA in the south-eastern Khammouane Province. C. *jarujini* and *C. teyniei* are recorded from Bolikhamxay Province, while *C. pageli* is only known to occur in Vientiane Province.

Remarks. The *Cyrtodactylus phongnhakebangensis* group is very complex. Different morphological traits of the species of this group (e.g., body size, shape and number of dorsal bands, and number of precloacal and femoral pores, see Tables 7&13) were supported by other morphological and phylogenetic analyses (see Figs. 1–5). All species of the group are adapted to karst forested formations.

Cyrtodactylus irregularis group

Species. *C. buchardi*, *C. cryptus*, *C. pseudoquadrivirgatus.*

Characters. Adult SVL 65.0–83.8 mm, supranasal single; dorsal tubercle rows 15–25; webbing between fingers and toes absent; tubercles on limbs present; number of precoacal and femoral pores in males 8–11; postcloacal tubercles 2–4; tail dorsally with tubercles; without enlarged subcaudals; dorsal body blotched.

TABLE 13. Morphological characters and distribution of members of the genus *Cyrtodactylus* from Laos.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
***Cyrtodactylus phongnhakebangensis* species group**															
C. bansocensis	74	103.5	8–10	8	3	0	3	0	14–15	158–170	86–87	34–35	0	16–19	18–21
Cyrtodactylus calamei* sp. nov.	89.3	107.5	9–11	8–11	3	1	4	0	10–16	183–193	101–114	39–42	0	16–18	18–21
C. darevskii	100	113	10–12	9–11	3	0	4–5	1	16–20	190–216	–	38–46	0	17–20	18–22
Cyrtodactylus hinnamnoensis* sp. nov.	100.6	108.3	9–12	7–11	3	0–1	4–6	0	14–19	179–201	93–112	35–48	0	16–21	18–22
C. jaegeri	68.5	83.4	10–11	9–11	3	0–1	5	1	15–16	156–164	–	31–32	1	17–19	20–23
C. jarujini	90	116	12–16	10–12	4	1	0	0	18–20	169	–	32–38	0	15–17	18–19
C. khammouanensis	73	95	11–12	9–10	3	0	4–5	0	16–21	155–172	–	32–38	0	18–20	20–23
C. lomyenensis	71.2	86.1	13–14	11	3	0–1	4	0	20–24	–	–	35–36	0	16–19	19–23
C. multiporus	98	105	9–11	9–11	4	0	6–8	0	16–20	164–181	–	30–38	0	18–20	18–22
C. pageli	81.8	113.2	9–11	9	4	0	5	0	10–14	216–239	115–122	41–44	0	19–23	19–23
C. phongnhakebangensis	96.3	110	9–13	8–12	3	0–1	3–5	0	11–20	161–177	90–107	32–42	1	15–20	18–26
C. roesleri	73.5	101	10–12	7–10	3	0–1	4–5	1	13–19	158–187	–	34–40	0	17–19	17–20
C. rufford	72.5	96.8	11–12	9–11	3	1	4	0	14–16	153–167	74–79	27–29	0	19–20	18–19
Cyrtodactylus sommerladi* sp. nov.	80.3	89.9	9–11	8–9	2–3	0–1	5–6	0	0–5	168–192	76–93	31–39	0	16–20	17–24
C. soudthichaki	70.0	95.2	10–11	8–9	3	0–1	5	0	19–20	165–170	78–85	32–33	1	16–18	18
C. teyniei	89.9	110	10	9	4	0	0	0	19	184	108	38	0	17–18	19–20
***Cyrtodactylus irregularis* species group**															
C. buchardi	65	54	13–14	10–11	4	1	0	0	25	–	–	30	0	14	12
C. cryptus*	83.6	73	7–8	6–7	4	1	0	0	15–17	211–218	122–131	40–43	0	17–19	17–19
C. pseudoquadrivirgatus	83.8	72.6	8–10	7–10	4	1	0	0	17–18	–	–	39–40	1	16–19	17–20
***Cyrtodactylus wayakonei* species group**															
C. spelaeus	91	83	9–12	8–10	3	1	0	0	10	156–183	–	36–39	0	19–20	22–24
C. vilaphongi	86.1	68.1	9–10	7–9	3	0	5	0	15–16	161–165	106–122	34–36	1	18–19	18–20
C. wayakonei	86.8	89	7–8	9–10	4	0	0	0	17–19	151–163	85–98	31–35	1	17–18	19–20
***Cyrtodactylus interdigitalis* species group**															
C. interdigitalis	80	90	10–12	8–9	3	1	6	0	18	174	105–109	37–42	1	17–22	16–20

……*continued on the next page*

TABLE 13. (continued)

Taxon	16	17	18	19	20	21	22	23	24	25	26	27	28	29	Reference
***Cyrtodactylus phongnhakebangensis* species group**															
C. bansocensis	0	0	1	34	5–7	1	2	Greyish brown	1	0	1	0	0	Khammouane Province	Luu *et al*. 2016b
Cyrtodactylus calamei* sp. nov.	0	1	1	35–39	4	0	2	Grey	1	1	1	0	0	Khammouane Province	This paper
C. darevskii	0	0	1	38–44	4–5	0	1	Brownish grey	1	1	1	0	0	Khammouane Province	Nazarov *et. al*. 2014
Cyrtodactylus hinnamnoensis* sp.nov.	0	1	1	36–44	4–6	0	2	Yellowish brown	1	0	1	0	1	Khammouane Province	This paper
C. jaegeri	0	1	1	44	3–6	1	2	Greyish brown	0	0	1	0	0	Khammouane Province	Luu *et al*. 2014a
C. jarujini	0	1	1	52–54	4	1	2	Grey brown	1	1	0	0	1	Bolikhamxay Province	Bain & Hurley 2011
C. khammouanensis	0	0	1	40–44	5–6	0	1	Brown	0	0	1	0	1	Khammouane Province	Nazarov *et al*. 2014
C. lomyenensis	0	0	1	39–40	5	0	1	Brownish grey	1	0	1	0	0	Khammouane Province	Ngo & Pauwels 2010
C. multiporus	0	1	1	58–60	5–6	0	2	Brown	1	1	1	0	0	Khammouane Province	Nazarov *et al*. 2014
C. pageli	0	0	0	4	4	1	1	Light brown	1	0	0	0	1	Vientiane Province	Schneider *et al*. 2011
C. phongnhakebangensis	0	0	1	32–42	4–5	0	2	Dark grey	1	1	1	0	1	Invalid	Luu *et al*. 2013
C. roesleri	0	0	1	20–28	5–8	1	2	Brownish grey	0	0	1	0	1	Invalid	Teynié & David 2010
C. rufford	0	0	1	42–43	4–5	0	1	Brown-Grey	1	0	1	0	0	Khammouane Province	Luu *et al*. 2016a
Cyrtodactylus sommerladi* sp. nov.	0	0	1	20–26	4–6	0	2	Yellowish grey	0	0	1	0	0	Khammouane Province	This paper
C. soudthichaki	0	1	1	29	4–5	1	2	Greyish brown	1	0	1	0	1	Khammouane Province	Luu *et al*. 2015a
C. teyniei	0	0	1	–	3	1	1	Greyish brown	1	1	0	0	1	Borikhamxay Province	David *et al*. 2011
***Cyrtodactylus irregularis* species group**															
C. buchardi	0	1	1	9	–	1	0	Dark tan	0	1	0	1	1	Champasak Province	David *et al*. 2004
C. cryptus*	0	0	1	8–11	3–4	1	0	Brownish grey	1	1	0	0	1	Khammouane Province	This paper
C. pseudoquadrivirgatus	0	1	1	–	2–3	1	0	Blackish brown	1	1	0	0	1	Salavan Province	Luu *et al*. 2013
***Cyrtodactylus wayakonei* species group**															
C. spelaeus	0	1	1	8	2–3	0	1	Grey brown	1	1	0	0	0	Vientiane Province	Nazarov *et al*. 2014
C. vilaphongi	0	1	1	–	2	1	1	Blackish brown	1	1	1	0	0	Luang Prabang Province	Schneider *et al*. 2014
C. wayakonei	0	1	1	6–8	4	1	1	Grey-brown	1	1	1	0	0	Luang Nam Tha Province	Nguyen *et al*. 2010
***Cyrtodactylus interdigitalis* species group**															
C. interdigitalis	1	1	1	16–18	1–2	1	0	Dark brown	0	0	1	0	1	Vientiane and Khammouane provinces	Teynié & David 2010; our specimens from Khammouane Province

1—maximum snout-vent length (in mm); 2—maximal TaL; 3—number of supralabials; 4—number of infralabials; 5— number of nasals; 6—number of intersupranasals; 7—number of dark body bands between limb insertions; 8—sharp of dorsal tubercles (0=weakly keeled, 1=keeled); 9—number of dorsal tubercle rows; 10—number of scales in a line from mental to the front of cloacal slit; 11—number of scales around midbody; 12—number of ventrals; 13—lateral folds with tubercles; 14—number of subdigital lamellae under the fourth finger; 15—number of subdigital lamellae under the fourth toe; 16—toes webbed; 17—tubercles on fore limbs; 18—tubercles on hind limbs; 19—number of precloacal and femoral pores (only in males); 20—number of postcloacal tubercles; 21—tubercles on dorsal surface of tail; 22—subcaudals enlarged (0=absent, 1=median row, or slightly enlarged, 2=under surface); 23—ground coloration of dorsum; 24—marking on upper side of head; 25—back flecked or blotched; 26—banded back; 27—striped back; 28—tail pattern (0=ring, 1=band); 29—distribution.
"1" = presence of character state; "0" = absence of character state.
"*" = contribution of this study.

Distribution. The species of this group are more widespread distributed in northern and central Laos including Khammouane, Champasak, and Salavan provinces. These species have a tree-dwelling life style.

Cyrtodactylus wayakonei group

Species. *C. spelaeus*, *C. vilaphongi*, *C.wayakonei.*

Characters. Adult SVL 86.1–91.0 mm, supranasals 0–1; dorsal tubercles 10–19; webbing between fingers and toes absent; tubercles on limbs present; a low number of precoacal pores in males 6–8; postcloacal tubercles 2–4; subcaudals slightly enlarged; dorsal body blotched (except for *C. spelaeus*).

Distribution. The group is distributed in karst formations of northern Laos including Luang Nam Tha, Luang Prabang, and Vientiane provinces.

Cyrtodactylus interdigitalis group

Species. *C. interdigitalis.*

Characters. Adult SVL 80.0 mm, supranasal single; dorsal tubercle rows 18; webbing between fingers and toes present; tubercles on limbs present; number of precoacal and femoral pores in males 16–18; postcloacal tubercles 1–2; tail dorsally with tubercles; without enlarged subcaudals; dorsal body blotched or ambiguous.

Distribution. The species is known to occur in central Laos including Vientiane and Khammouane provinces. It is adapted as a tree-dweller, but in contrast to the *C. irregularis* species group that lives near the base of trees, *C. interdigitalis* is found higher on tree trunks and in tree crowns.

Discussion

The northern Truong Son Range—a hotspot of *Cyrtodactylus* speciation. As shown above, there are five endemic karst-dwelling *Cyrtodactylus* species occurring in a restricted area on opposite sides of the northern Truong Son Range. In Vietnam, there are two endemic karst-adapted species: *C. phongnhakebangensis* and *C. roesleri* as opposed to three endemic karst-adapted species in Laos: *C. calamei*, *C. hinnamnoensis*, and *C. sommerladi*. Thus, the karst forests in the northern Truong Son Range mirror a hotspot of *Cyrtodactylus* speciation. These karst formations must have played a significant role in the evolution of the biota, which needs to be emphasized in future conservation measures. Only one endemic, ground to tree-adapted species, namely *C. cryptus*, occupies both sides of the range.

In contrast to the cryptic species, the population of *C. cryptus* from Laos differed in morphology but showed only minor genetic divergence from the Vietnamese population, so that they have to be considered with our current knowledge as a single taxon occurring on both sides of the Truong Son Mountain Range. The fact that there has been no obvious or only slight influence of the Range on the split of the *C. cryptus* populations on both sides of the Truong Son Range is surprising. The life style of the species, which is a ground to tree-associated, forest dweller contrasts to the aforementioned distinctly karst adapted species pairs (see also Ziegler *et al*. 2010; Loos *et al*. 2012), can be attributed to the different evolution patterns. As the environmental conditions in karst are known to accelerate evolutionary processes (Nicolas *et al*. 2012; Le *et al.* 2015), the rapid adaptation to isolated local conditions compared with generalist ground to tree-associated taxa might offer an explanation.

The record of *C. roesleri* in Phou Hin Boun NPA, Khammouane Province, Laos by Teynié & David (2010) may be due to the misidentification of another species. This site is ca. 140 km apart and there are many river systems such as Xebangfai that separate these populations at present. In addition, we could not confirm the presence of *C. roesleri* during a three-year survey period in Hin Nam No NPA, which is only ca. 15 km distant from the locality of *C. roesleri* in Phong Nha-Ke Bang NP. Thus, there is no confirmed record of *C. roesleri* in Laos so far.

Cyrtodactylus is generally more adapted to rocky habitats than to specific forest types (Agrawal *et al*. 2014) and therefore species separation and survival in karst areas with their complex topography may have played a major role in facilitating the elevated level of speciation in this area (Qiu *et al.* 2011). A major driver of allopatric speciation was probably the complex geological and climatic history of the northern Truong Son Range. The vast Khammouane limestone formation, stretching about 150 km across central Laos to Vietnam (Sterling *et al*. 2006; Bain & Hurley 2011), was folded in the Miocene and subsequently uplifted and heavily eroded since the Pliocene about 5–3 million years ago (Rundel 1999). Clear climatic differences still exist today between the semihumid climate in the Laotian side of the Truong Son Range with 1500–2000 mm precipitation per year and four months of dry season, and the wetter Vietnamese side with more intense annual rainfall (up to 2500 mm) and a comparatively shorter dry season (Bain & Hurley 2011). Thus, geographic and climatic barriers have likely contributed to the fragmentation of *Cyrtodactylus* founder populations into separated, closely related species in these karst forest systems. Complex interactions between organisms and localized environment conditions have resulted in incongruence between morphotype and genotype, which poses a severe problem in alpha taxonomical research (Bickford *et al.* 2007). Therefore an integrative approach combining morphological, ecological, and molecular data is needed, as it is applied in this study, to adequately uncover and distinguish morphologically similar species.

Patterns of cryptic diversity. *C. roesleri* in Vietnam is phenetically similar to its sibling species *C. sommerladi* in Laos (see Fig. 12), and only our phylogenetic analyses revealed them to represent distinct taxa, with slight morphological differences in dorsal pattern and tubercle arrangement. Such ambiguous morphological characters are characteristic for initial stages of allopatric speciation, which can promote cryptic diversity (Ahmadzadeh *et al.* 2013). The fact that a pair of sibling species (*C. roesleri versus C. sommerladi*) occurs on opposite sides of the Truong Son Range (Phong Nha-Ke Bang NP *versus* Hin Nam No NPA, respectively), indicates that vicariance was a driver of cryptic speciation in the Truong Son Mountain Range.

Also *C. phongnhakebangensis* from Vietnam and *C. hinnamnoensis* from Laos are generally very similar in morphology, which is the reason they were initially considered a single taxon (Luu *et al.* 2013). However, our phylogenetic analyses show that *C. phongnhakebangensis* (Vietnam) is basal to the entire group of *Cyrtodactylus* species from Khammouane Province, Laos, including *C. calamei* and *C. darevskii,* with *C. hinnamnoensis* being the most distant relative (Fig. 1). This is an example of rapid speciation caused by the interaction between topological complexity and changing paleoclimate conditions resulting in a complicated plesiomorphic pattern in cryptic species of *Cyrtodactylus*. Stabilizing selection by extreme environmental conditions have been shown to conserve phenotypes (Nevo 2001), but currently we know too little of the mechanisms that led to the evolution of cryptic species in the Truong Son Range.

Patterns in sympatric species. Our first ecological observations revealed *C. hinnamnoensis* to be more abundant and widespread, occurring from the northern to southern parts of Hin Nam No NPA. *C. sommerladi* is recorded from the central and southern parts, and *C. cryptus* is currently known only from the southern part of Hin Nam No NPA. Remarkably, all three *Cyrtodactylus* species are known to occur sympatrically in the southern parts of Hin Nam No NPA. A similar case was first reported by Ziegler *et al.* (2010) in Phong Nha-Ke Bang NP in central Vietnam (see also Loos *et al*. 2012).

Sympatric occurrence usually leads to resource partition. We found *C. hinnamnoensis* and *C. sommerladi* often sympatric on cliff walls and at cave entrances, while *C. cryptus* was found nearby, but ground to tree-associated. The larger *C. hinnamnoensis* (mean ± SD 84.1 ± 11.7 mm SVL) generally occurred at higher perches (ca. 3–5 m height) compared to < 3 m height for the smaller *C. sommerladi* (mean ± SD 72.3 ± 3.8 mm SVL) (see tables 8&10). Larger body size in lizards is often associated with increased intraspecific competition and access to a wider range of resources (Donihue *et al*. 2015). The ground to tree-dwelling *C. cryptus* (mean ± SD 76.6 ± 9.8 mm SVL), and the non-sympatric *C. calamei* (mean ± SD 80.0 ± 8.0 mm SVL) were of intermediate size. A similar pattern was reported for *Cyrtodactylus* in Phong Nha-Ke Bang NP, where the larger *C. phongnhakebangensis* occupied higher perches on rock walls than the small *C. roesleri*, while the intermediate-sized *C. cryptus* again was ground to tree-associated (Loos *et al*. 2012).

Cryptic species diversity poses a major problem for species conservation. Unravelling the patterns and mechanisms of cryptic speciation is therefore of primary importance, especially in the light of ever increasing forest destruction in the tropics (Grace *et al*. 2014, Crowther *et al.* 2015). As cryptic speciation may be more widespread in the tropics than currently assumed (Bickford *et al*. 2007), Phong Nha-Ke Bang and Hin Nam No with their high numbers of cryptic species in herpetofauna may serve as a model to discover the ecological and evolutionary forces that lead to cryptic speciation in vertebrates.

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APPENDIX. Specimens examined for comparisons.

Cyrtodactylus bansocensis. Laos: Khammouane Province: Ban Soc: VFU R.2015.20 (Holotype), NUOL R-2015.21 (Paratype).
C. cryptus. Vietnam: Quang Binh Province: Phong Nha-Ke Bang: ZFMK 86037 (Holotype), ZFMK 86038, ZFMK 86039 (Paratypes).
C. huongsonensis. Vietnam: Hanoi: Huong Son: IEBR A.2011.3 (holotype), ZFMK 92293 (paratype).
C. jarujini. Thailand: Nong Khai Province: Bung Ban: ZMB 50648 (holotype).
C. cf. *jarujini*. Laos: Bolikhamxay Province: Tad Leuk: VNUF R.2015.7 (field number: PKK07.15).
C. pageli. Laos: Vientiane Province: Vang Vieng: IEBR A.2010.36 (holotype), IEBR A.2010.37, MTD 48025, MHNG 2723.91, NUOL 2010.3–2010.7, ZFMK 91827 (paratypes).
C. phongnhakebangensis. Vietnam: Quang Binh Province: Phong Nha-Ke Bang: ZFMK 76169 (Holotype), ZFMK 76193, ZFMK 76197, ZFMK 83671, ZFMK 80648, ZFMK80649, ZFMK86432, ZFMK80650, ZFMK 76194, ZFMK 76168 (Paratypes), TZ01, TZ02.
C. roesleri. Vietnam: Quang Binh Province: Phong Nha-Ke Bang: ZFMK 89377 (holotype), IEBR A.0932, MHNG 2713.79, VNUH 220509, ZFMK 86433, 89378 (paratypes).
C. rufford. Laos: Khammouane Province: Ban Dean: VFU R.2015.14 (Holotype), IEBR R.2015.35, NUOL R-2015.15 (Paratypes).
C. soudthichaki. Laos: Khammouane Province: Khun Don: VFU R.2015.18 (Holotype), IEBR A.2015.34, NUOL R-2015.5 (Paratypes).
C. teyniei. Laos: Borikhamxay Province: near Ban Na Hin: NEM 0095 (holotype); Khammouane Province: Ban Na Than: KM2012.14–2012.15.
C. wayakonei. Laos: Luang Nam Tha: Vieng Phoukha: IEBR A.2010.01 (holotype), ZFMK 91016, MTD 47731, NUOL 2010.1 (paratypes).