A New Species of *Cyrtodactylus* (Squamata: Gekkonidae) from the Karst Forests of Daweishan National Nature Reserve, Yunnan, China

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Abstract Cyrtodact ylus geckos are one of the most speciose and diverse groups of extant lizards known, distributed throughout the Asian and Pacific realms. Using molecular phylogenetic methods and supporting morphological data, we describe a new species of Cyrtodact ylus in Daweishan National Nature Reserve, Yunnan Province, China. Cyrtodact ylus hekouensis sp. nov. can be morphologically distinguished from its nearby congeners by the following characters: maximum SVL 92.3 mm and TL 98.5 mm; 11-12 supralabials; 11-12 infralabials; 36-57 scale rows between the fifth supralabials; 10-13 dorsal tubercles rows; 3 postnasals on blunt and smooth front snout; precloacalfemoral pores in a continuous series of 33-39 (females with pitted scales) located under vent/cloaca and thighs in both sexes; precloacal groove absent; 3/3 postcloacal tubercles; subdigital lamellae under the fourth finger 21 or 22, under the fourth toe 20-23; smooth midbody with smooth venter and tuberculate dorsal scale rows, tubercles from head to tail base; dorsal transverse patterns are generally large, bilaterally symmetrical. The results of the phylogenetic analysis recover specimens of this new species as sister to a clade containing C. wayakonei and C. martini. Uncorrected pairwise intraspecific distances were < 1%, and distances between our new species and other Cyrtodactylus species from nearby countries ranged from 14.2% to 26.8%.

Keywords China-Vietnam border, Yunnan Province, *Cyrtodactylus hekouensis* **sp. nov.**, Gekkonidae, molecular phylogeny, systematics, taxonomy

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1. Introduction

As one of the most diverse genera in the Gekkonidae, Cyrtodactylus contains almost 300 recognized species (Uetz et al., 2020). New species are continuously being described each year through fieldwork in underexplored localities and the development of molecular techniques, especially DNA barcoding (Hebert et al., 2003). A significant number of Cyrtodact ylus have been described from tropical karst forests in regions of Southeast Asia, including Myanmar, Malaysia, Laos, Vietnam, Thailand, Cambodia, Indonesia, Singapore, Timor Leste, Philippines, Brunei and China (e.g., Pauwels et al., 2016; Sitthivong et al., 2019; Grismer et al., 2020). Four species of Cyrtodact ylus are currently recognized in China (Wang et al., 2020) including C. cayuensis (Li, 2007; Agarwal et al., 2018), C. tibetanus (Boulenger, 1905), C. zhaoermii (Shi and Zhao, 2010) and C. wayakonei (Nguyen et al., 2010). All of these species are in the Indo-Burma species group (Agarwal et al., 2014), with the exception of C. wayakonei (Nguyen et al., 2010). The Indo-Burma species group, including three of the four Chinese species, may represent a radiation of Himalayan species; the diversity of species from Yunnan, China in the Southeast Asian group (Brennan et al., 2017; Nazarov et al., 2018). Cyrtodact ylus wayakonei has only been recorded from Xishuangbanna (Yuan and Rao, 2011), a biodiversity hotspot area in the Yunnan Province border area of China. Excluding this record, the knowledge of Cyrtodact ylus in Yunnan is lacking, despite the abundance of suitable limestone karst forests habitats along the country's border.

The China Vietnam border area is a well-known biodiversity hotspot, harboring a striking diversity of species and endemism (Myers *et al.*, 2000). However, a majority of

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this region is understudied, especially low latitudes, tropical evergreen forests, and broadleaved forests in southern Yunnan. Recently, several field expeditions were conducted by Chinese scholars, and several subsequent descriptions of new species or new country records were published, such as Paramesotriton deloustali (Zhang et al., 2017), Tylototriton ziegleri (Jiang et al., 2017), Amolops wenshanensis (Yuan et al., 2018) and Nidirana chapaensis (Yuan et al., 2019). It is likely that candidate new species might be found around the China-Vietnam border area. For example, the Daweishan National Nature Reserve in Hekou, China, near the border of Vietnam, contains well-preserved tropical forests, where herpetological research has been limited. In the past few years, we collected several specimens of Cyrtodactylus whose morphological characters were distinct from their congeners. We used molecular (COI) data and made a detailed morphological assessment to compare the Hekou specimens to described Cyrtodact ylus species, especially species from nearby countries. Our results demonstrate that this species has a distinct morphology and high interspecific distances from its congeners; we describe this new species of Cyrtodactylus herein. Additionally, we use molecular data to taxonomically identify Cyrtodact ylus from Xishuangbanna, Yunnan.

2. Materials and Methods

2.1. Sampling Fieldwork was conducted with permits in a karst limestone forest area of Daweishan National Nature Reserve, Yunnan Province, China, by Yinpeng Zhang, Xiaolong Liu, Jian Wang and Zhiyong Yuan in from 2016 to 2018. Thirteen specimens (3 males, 10 females) were collected. Specimens were fixed with 10% formalin solution and subsequently stored in 75% ethanol for voucher preservation. Prior to fixing, liver tissues were dissected out from the specimens and stored in 95% ethanol. All specimens were preserved in Southwest Forestry University, Kunming, Yunnan, China.

2.2. Morphology Measurements were taken by using a slide caliper from five well preserved samples (to the nearest 0.1 mm) due to 8 specimens were preserved in poor condition with some critical scalations missing, following the protocols of Nguyen *et al.*, (2010). Eight specimens were not measured, as multiple scalation characters were missing due to poor preservation quality. Abbreviations are as follows: snout-vent length (SVL); tail length (TL); maximum head length (HL); maximum head width (HW); maximum head height (HH), from top of skull to underside of jaws; greatest diameter of orbits (OD); snout to eye distance (SE), from tip of snout to anterior corner of eye; eye to ear distance (EE), from anterior edge of ear opening to posterior corner of eye; axilla to groin distance (AG).

The following scale characters were counted: supralabials (SL); infralabials (IL); nasal scales surrounding nare, from rostral

to labial (excluding the rostral and labials), i.e. nasorostral, supranasal, postnasals (N); granular scales surrounding dorsal tubercles (GST); number of ventral scales within longitudinal rows at midbody (V); number of tubercles at dorsum of midbody (DTR); scales around midbody (MS); number of ocular scales around ocular area (OS); scale rows between fifth supralabials (SR5); numbers of continuous precloacal-femoral pores (females with pitted scales) (PP); postcloacal tubercles (PAT); subdigital lamellae under the fourth finger (LF4); subdigital lamellae under the fourth toe (LT4). Bilateral scale counts were given as left/right. Femoral and precloacal pores were counted with a digital microscope (Nikon SMZ800N).

2.3. Molecular analyses Four specimens of the gecko species with unique morphology were used for molecular analyses, and one sample of Cyrtodact ylus collected from Xishuangbanna was also used to identify its taxonomic affilitation (Table 1). We sequenced a ~650 bp fragment of mitochondrial cytochrome c oxidase subunit 1 (COI) to assess if the Cyrtodact ylus specimens from Daweishan National Nature Reserve are distinct from other known species in the genus. This approach has been successfully used before in delimiting Cyrtodact ylus geckos (Brennan et al., 2017). The primers used were Chmf4: 5-TYT CWA CWA AYC AYA AAG AYA TCG G-3 and Chmr4: 5-ACY TCR GGR TGR CCR AAR AAT CA-3 (Che et al. 2012). Amplification of 25 µL polymerase chain reactions (PCR) were executed on an Eppendorf Master cycler gradient thermocycler. Amplification of genomic DNA began with an initial denaturation for 2 min at 95 °C followed by 95 °C for 35 s, annealing at 50 °C for 35 s, and extension at 72 °C for 150 s with 4 s added to the extension per cycle for 32 cycles for COI. Amplified products were sequenced using an ABI 3730 automated sequencer.

Considering our samples were collected near Vietnam and Laos, 40 COI sequences of Cyrtodact ylus species (and one sequence of Cyrtopodion for our outgroup) from previous studies (Nguyen et al., 2013, 2014, 2015, 2017; Ziegler et al., 2013; Schendier et al., 2014; Le et al., 2016; Luu et al., 2016a, 2016b; Brennan et al., 2017; Connette et al., 2017; Nazarov et al., 2018; Pauwels, 2018) from Southeast Asian specimens were downloaded from Genbank (National Center for Biotechnology Information) to explore the relationships with other known species (Table 1). All 46 COI sequences were initially aligned by using Geneious Basic (Kearse et al., 2012), and then optimized by MEGA X (Kumar et al., 2018). Mean uncorrected genetic distances (p distances) between tested Cyrtodact ylus species were calculated by MEGA X (Kumar et al., 2018). Phylogenetic trees were inferred by Maximum Likelihood (ML) and Bayesian inference (BI). JModelTest 2 (Guindon and Gascuel, 2003; Darriba et al., 2012) was used to build the model of sequence evolution that best fit each partition. The model TrN+I+G was selected as the best fit

No. 3

model to the data. Metropolis coupled Markov Chain Monte Carlo (MCMCMC) analyses were run with 1 cold chain and 3 heated chains for 3 000 000 generations and sampled every 1 000 generations. Four independent MCMCMC runs were performed as result and 1 500 trees were discarded as burnin. The potential scale reduction factor (PSRF > 1) and the average standard deviation of split frequencies (ASDSF < 0.01) statistics generated by MrBayes were used to evaluate topological and branch-length convergence, respectively. Confidence of tree topology was assessed by posterior probability (PPr) (Huelsenbeck and Ronquist, 2001). Maximum Likelihood analyses were conducted through RAxML NG v0.9.0. (Kozlov *et al.*, 2019) under a GTR+GAMMA model, the recommended model from RAxML authors. Branch supports (bootstrap

Table 1 Specimens used in the study, with respective voucher numbers, localities, and GenBank accession numbers for COI. "/" mean the locality is unknown.

No.	Species	Genbank No.	Locality	Voucher No.
1	C. badenensis	KF929505	Tay Ninh Province, Vietnam	KIZ13689
2	C. bichnganae	KT004372	Son La Town, Son La Province, Vietnam	TBU PAT.250
3	C. bobrovi	KT004369	Ngoc Son-Ngo Luong, Hoa Binh Province, Vietnam:	VNMN:A.2015.61
4	C. chanquangensis	MF957261	/	NA2016.1
5	C. cryptus	KX064038	Khammuane Province, Laos	VNUF R.2014.69
6	C. elok	MF169914	/ (Captive Specimen)	JB 14
7	C. houaphanensis	KJ817428	Houaphan Province, Laos	IEBR A.2013.109
8	Cyrtodactylus hekouensis sp. nov.	MW067125	Hekou, Hong He, Yunnan, China	SWFU 002507
9	Cyrtodactylus hekouensis sp. nov.	MW067126	Hekou, Hong He, Yunnan, China	SWFU 002879
10	Cyrtodactylus hekouensis sp. nov.	MW067127	Hekou, Hong He, Yunnan, China	SWFU 002880
11	Cyrtodactylus hekouensis sp. nov.	MW067128	Hekou, Hong He, Yunnan, China	SWFU 002881
12	C. hontreensis	MF169917	Hon Tre Island, Kien Giang, Vietnam	LSUHC 8583
13	C. huongsonensis	KX430034	/	IEBR A.2011.3A
14	C. hinnamnoensis	KX064048	Khammuane Province, Laos	VNUF R.2015.3
15	C. interdigitalis	KX077901	Khammuane Province, Laos	VNUF R.2014.50
16	C. jaegeri	KT004365	Khammuane Province, Laos	NUOL-R.2013.1
17	C. khammounensis	HM888467	Khammuane Province, Laos	ZIN FN 191
18	C. khasiensis	KP199948	Kasi, Laos	ZMMU_R-13980-1
19	C. kingsadai	KF188432	Phu Yen Province, Vietnam	IEBR-A-2013.3
20	C. lenya	KY041659	Tanintharyi, Proposed Lenya National Park Extension, Myanmar	CAS:HERP:260233
21	C. lomyenensis	KJ817436	Khammuane Province, Laos	IEBR KM2012.54
22	C. loriae	MF169925	Mt. Simpson, Milne Bay, Papua New Guinea	FK 7709
23	C. martini	MF169929	Lai Chau Province, Vietnam	UNS 0471
24	C. oldhami	MF169932	/ (Captive Specimen)	JB 126
25	C. otai	MF957262	Na Bai Village, Son La Province, Vietnam	TBU 2017.2
26	C. pageli	KJ817431	Vientiane Province, Laos	ZFMK 91827
27	C. payarhtanensis	KY041664	Tanintharyi Region, Myanmar	USNM 587409
28	C. phongnhakebangensis	KF929526	Quang Binh Province, Vietnam	PNKB2011.30
29	C. puhuensis	KF929529	Thanh Hoa Province, Vietnam	KIZ11665
30	C. pulchellus	HQ967202	Malaysia	ZMMU R-12643-3
31	C. pseudoquadrivirgatus	KF169963	Hue Province, Vietnam	ITBCZ3001
32	C. quadrivirgatus	HM888466	Malaysia	ZMMU-RAN1989
33	C. rufford	KU175572	Khammuane Province, Laos	NUOL-R.2013.1
34	C. sommerladi	KX064041	Khammuane Province, Laos	VNUF R.2013.87
35	C. sonlaensis	MF957265	Son La Town, Son La Province, Vietnam	IEBR A.2017.2
36	C. soudthichaki	KX077904	Khammuane Province, Laos	NUOL-R.2015.5
37	C. sp. Xishuangbanna, China	MW067129	Xishuangbanna, Yunnan, China	SWFU 002882
38	C. sp. LuangPrabang, Laos	KJ817432	Luang Prabang Province, Laos	MDL 2014 LPB 62
39	C. sworderi	MF169946	Endau-Rompin, Johor, Malaysia	LSUHC 7700
40	C. taybacensis	MH997990	Dien Bien Province, Vietnam	IEBR 4379
41	C. teyniei	KJ817430	Khammuane Province, Laos	IEBR KM2012.77
42	C. thathomensis	MG791873	Xiangkhonang Province, Laos	ZMMU R-14919-1
43	C. tigroides	MF169948	Sai-Yok District, Kanchanaburi, Thailand	IRSNB 2380
44	C. triedrus	MF169951	Yakkunehela, Sri Lanka	Anslem de Silva 35 A
45	C. vilaphongi	KJ817435	Luang Prabang Province, Laos	IEBR A.2013.103
46	C. wayakonei	KJ817438	Luang Nam Tha Province, Laos	ZFMK 91016

supports [BS]) were determined based on 1000 bootstrap replicates. We consider relationships with PPr \ge 0.95 and BS \ge 70 to be strongly supported.

3. Results

Genetic Differentiation

Five new generated COI sequences of Cyrtodact ylus including four specimens from Daweishan National Nature Reserve and one unknown Cyrtodact ylus collected from Xishuangbanna, Yunnan, China were obtained (GenBank ID: MW067125, MW067126, MW067127, MW067128, MW067129). The final alignments of the examined mtDNA COI gene fragment consisted of ~650 sites without any gaps. The ML and BI analyses recovered similar topologies at strongly supported species relationship; conflicting topologies were found between relationships that received low support (BS < 70%, PPr < 0.95). Some clades in both trees were recovered with low support by both analyses, which is most likely due to COI having fewer informative sites than other mitochondrial genes, such as the commonly used NADH dehydrogenase 2 (ND2; Brennen et al., 2017). More relationships in the BI analysis were recovered with strong support than in the ML analysis, and both analyses strongly recover the same sister relationships between species or pairs of species (Figure 1). Our sample collected from Xishuangbanna was sister to C. martini from Vietnam, with an uncorrected pairwise distance of 2.8%. The new samples from Hekou form a strongly supported clade with an uncertain phylogenetic placement with regards to the C. wayakonei and C. pulchellus groups (BI analysis). In the ML analysis, the Hekou specimens are recovered as reciprocally monophyletic to the clade containing C. wayakonei + C. sp. Xishuangbanna + C. martini with poor support. Uncorrected pairwise distance between the new samples from Hekou and other Cyrtodactylus species ranged from 14.2% (with C. martini) to 26.8% (with C. badenensis) (Table S1). However, though we find support of the new species as a distinct clade, the relationships of these species in the analyses are poorly supported and require more data.

Cyrtodact ylus hekouensis **sp. nov.**

Hekou Bent-Toed Gecko (Figures 2–5)

Holotype: SWFU002507, adult male, collected by Yinpeng ZHANG, 07/24/2018, from Daweishan National Nature Reserve, Hekou County, Honghe Autonomous Prefecture, Yunnan Province, China. (N 22.673459°, E 103.943534°, ~160 m). Paratypes: SWFU001578, adult male collected by Zhiyong YUAN; SWFU002879, SWFU002880, SWFU002881, all gravid female adults collected by Zhiyong YUAN and Yinpeng ZHANG, 07.24.2018. Collected from Daweishan National Nature Reserve, Honghe Autonomous Prefecture, Yunnan Province, China (N 22.673459°, E 103.943534°, ~160 m).

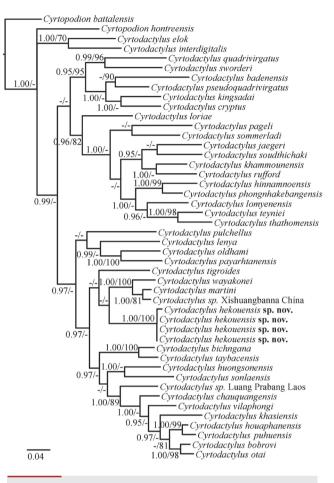


Figure 1 Bayesian phylogenetic tree of *Cyrtodactylus* inferred from mitochondrial COI. Numbers above and below branches indicate bootstrap support values (BS \ge 70%) and Bayesian posterior probabilities (PPr \ge 95%), respectively; low support values are denoted by "–".

Diagnosis

A moderate sized *Cyrtodact ylus*, with a slender trunk and bent toes, *C. hekouensis* is distinguished from other described *Cyrtodact ylus* species by the combined characteristics: maximum SVL 92.3 mm and TL 98.5 mm; 11–12 supralabials; 11–12 infralabials; 36–57 scale rows between the fifth supralabials; 10–13 dorsal tubercles rows; 3 postnasals on blunt and smooth front snout; precloacal-femoral pores in a continuous series of 33–39 (females with pitted scales) located under vent/cloaca and each side of thigh in both sexes; precloacal groove absent; 3/3 postcloacal tubercles; subdigital lamellae under the fourth finger 21 or 22, under the fourth toe 20–23; smooth midbody with smooth venter and tuberculate dorsal scale rows, tubercles from head to tail base; dorsal transverse patterns are generally large, bilaterally symmetrical.

Holotype Description

Male collected from Daweishan National Nature Reserve, Honghe Autonomous Prefecture, Yunnan Province, China, with total length 149.8 mm (SVL 77.0 mm, TL 72.8 mm with

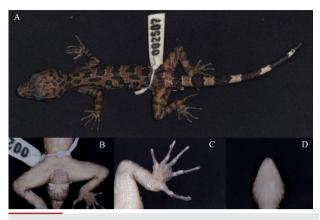


Figure 2 Holotype of *Cyrtodactylus hekouensis* **sp. nov.** (SFU002507): Dorsum (A); precloacal region (B); subdigital lamellae under left hindfeet toes (C); pair of chin-shields under dentary (D). Photo credit: Yinpeng ZHANG.



Figure 3 Dorsal color variations of *Cyrtodactylus hekouensis* **sp. nov.** Photo credit: Xiaolong LIU.

tail tip regenerated), slender, elongate trunk.

Head with short and smooth snout, some tuberculate scales start to regularly distribute into scales rows behind end of ocular scale to the tail base; nasal surrounded by 3 postnasals and connected with one large rectangular front lip scale; 11 supralabials; 12 infralabials; 43 scale rows behind fifth supralabials; 1st infralabials connect with a large pair of chin shields; elongated supralabials reach to the end of ocular, 5th and 6th supralabials enlarged in middle; a narrow row of scales separating the supralabials from the infraoculars; always one wide dark brown band with yellow granular scales starts from nasal and crosses eye; external ears located below the dark brown band behind eyes.

Dorsal scales from head to tail base, flat and smooth, with irregularly located tuberculate scales around trunk of body and above venter mostly around black dorsum patterns; the greatest diameter of the orbits is 12.2 mm; 129 scales around the midbody; wrinkles slightly developed until the gular scale; lateral skin fold with no tubercles; 10 rows of dorsum tubercles; 9 granular scales surrounding dorsal tubercles; 71 ventral scale rows, smooth, subimbricated round, larger than dorsal scales; three rows of enlarged scales presented in front of region of precloacal pores; 37 precloacal femoral pores series located in enlarged precloacal scales (9 precloacal pores plus in 14+14 femoral pores on each side under thighs), continuous; precloacal groove absent.

Fore and hind limbs stout and slender; small scales covered dorsum; small scales covered dorsum fore and hind limbs, with some tubercles; scales on ventral fore and hind limbs rectangular; fingers and toes with no webbing; subdigital lamellae: finger I with 15, finger II with 18, finger III with 19, finger IV with 21, and finger V with 21 subdigital scales (left measured); toe I with 16, toe II with 18, toe III with 18, toe IV with 22, and toe V with 22 subdigital scales covered (left measured); relative length of fingers (right and left) is IV > III > V > II > I; relative length of toes (right and left) is IV > V > III > II > I.

Tail regenerated at tip; 3 postcloacal tubercles on each side of the tail base; tubercles concentrated in dorsum tail base in 6–8 scale rows; 5 dark dorsum tail bands.

Holotype, fixed with 10% formalin solution and transferred to 75% ethanol, light brown dorsally and dark gray ventrally. Coloration in live animals can be described as follows: light, yellow brown coloration with large blotches on dorsal surface of head, neck, dorsal, extremities and tail, head color slightly lighter; wide dark brown band starts from nasal and crosses eye; five irregular bands on dorsal, patterns on dorsal are generally large, and bilaterally symmetrical; some small irregular dorsal patterns present in between those bands, closed to belly; light whitish pink belly; five dark brown irregular transversal bands on tail completely encircled, with regenerated tail tip; light whitish gray tail venter.

Variation

Paratypes are similar to the holotype in morphological characteristics. For measurements and scalations variations see Table 2. Individuals show variation in color and blotch pattern at dorsal tail bases, dorsal limb surfaces, and midbody dorsal surfaces. The dark dorsal tail bands vary in numbers but are lost in the regenerated tails of the type specimens. Dark blotches on midbody dorsal surfaces less or more symmetrical and meet near spine (Figure 3). Dark blotches on dorsal head surfaces variable in position and size, with blotch size variable between and within specimens. Background coloration of specimens ranges from light tan to a moderate to dark brown, with darker blotches. The number of precloacal femoral pores show variation between different specimens, ranging from 33 to 39. For measurements and scalations, see Table 2.

Distribution

C. hekouensis only known from the type locality, Daweishan National Nature Reserve, Honghe Autonomous Prefecture,

Yunnan Province, China.

Etymology

The species is named after the county of the type locality ("Hekou"= $\overline{m}\square$ in Chinese).

Natural history

All specimens were found and collected in a karst (i.e., limestone) river valley with low density of vegetation near a stream at night from 20: 00 to 24: 00. Specifically, all *C. hekouensis* in this study were found on karst edges near a road side of Daweishan National Nature Reserve, about 1.0–1.5 m height from the ground (Figure 5). Geckos were observed on the cliff sides or limestone burrow edges within high moisture. All collected females were gravid with two large, developed eggs, both ~10 mm in length and 7–8 mm in diameter.

The specimens of *C. hekouensis* were collected from a tropical broadleaf evergreen forest. The locality is located next to the Nanxi River (part of the Red River system), close to the China-Vietnam border. Day time temperatures generally rises in the range of 34–41 degrees centigrade in one day and the limestone

surfaces are typically dry during the daytime from June to August; night temperatures drops to around 28–30 degrees centigrade, on average. Limestone surfaces show moisture by condensation of water vapor from groundwater, the Nanxi River, plant transpiration and other sources.

Comparisons

Species of *Cyrtodactylus* endemic to tropical karst forest are often limited to small areas. Thus, rather than compare *C. hekouensis* with all species of *Cyrtodactylus*, we mainly focused on species from north and central regions of Laos, Vietnam, and Myanmar, which distribute geographically near China, as this is where *C. hekouensis* been found.

C. hekouensis **sp. nov.** can be differentiated from *C. huongsonensis* (Luu, Nguyen, Do and Ziegler, 2011) by having more ventral scale rows (68–72 vs. 41–48), and having more continuous precloacal-femoral pores (continuous 33–39 vs. 6–8 precloacal plus in 15–17 femoral pores in separate).

C. hekouensis **sp. nov.** can be distinguished from *C. sonlaensis* (Nguyen, Pham, Ziegler, Ngo and Le, 2017) by having

Table 2 Morphological measurements and scalation from holotype and paratypes of *Cyrtodactylus hekouensis* **sp. nov.** specimens. Only the maximum value was given for continuous data (i.e., distances). M: males; F: females; *: regenerated or broken tails; **: snout broken, no scales of sufficient quality to measure or count; m: mean; min: minimum; max: maximum; s: standard deviation.

	SWFU002507	SWFU001578	SWFU002879	SWFU002880	SWFU002881	min-max (m \pm s)
SEX	М	М	F	F	F	
SVL (mm)	77	84.3	80.8	92.3	91.8	max. 92.3
TL	72.8	98.6	80.9	99.2*	75.9*	max. 99.2
HL	26.4	24.5	24.9	28.4	28.6	max. 28.6
HW	15.5	14.7	14.2	17.6	17.3	max. 17.6
HH	8.7	8.6	9.7	10.7	10.8	max. 10.8
OD	12.2	11.9	11.7	15.8	17	max. 17.0
SE	6.5	8.4	7.2	8.2	8.5	max. 8.5
EE	6.2	6.6	5.6	6.7	7.2	max. 7.2
AG	42.5	47.6	44.5	54.5	50.3	max. 54.5
SL	11	10	11	12	11	11–12 (10.9 ± 0.7)
IL	12	11	12	11	11	11–12 (11.4 ± 0.5)
Ν	3	3	/**	3	3	3
V	71	70	72	69	68	68–72 (70.4 ± 1.6)
OS	33	32	24	29	33	24-33 (28 ± 3.8)
SR5	43	52	36	57	50	36-57 (46.4 ± 8.2)
GST	9	9	9	10	9	9-10 (9.2 ± 0.4)
MS	129	125	132	153	137	125–153 (134.9 ± 10.9)
DTR	10	12	13	12	13	10–13 (11.9 ± 1.2)
РР	37	35	33	35	39	33-39 (35.2 ± 2.3)
PAT	3/3	3/3	3/3	3/3	3/3	3/3
LF4	21	22	22	21	22	21–22 (21.4 ± 0.5)
LT4	22	23	20	23	22	20-23 (21.3 ± 1.2)



Figure 4 Dorsal view of live *C. hekouensis* **sp. nov.** from Yunnan, China. Photo credit: Zhiyong YUAN.



Figure 5 Type locality of *Cyrtodactylus hekouensis* **sp. nov**, Daweishan National Nature Reserve, Hekou County, Honghe Autonomous Prefecture, Yunnan Province, China. Photo credit: Yinpeng ZHANG.

presenting precloacal-femoral pores in females (absent in *C. sonlaensis*).

C. hekouensis **sp. nov.** can be distinguished from *C. otai* (Nguyen, Le, Pham, Ngo, Hoang, Pham and Ziegler, 2015) by having presenting femoral pores (absent in *C. otai*).

C. hekouensis **sp. nov.** can be distinguished from *C. bobrovi* (Nguyen, Le, Pham, Ngo, Hoang, Pham and Ziegler, 2015) by having more precloacal-femoral pores (33-39 vs. 5 in males and absent in females), and numbers of postcloacal tubercles (3/3 vs. 1/1+2/3).

C. hekouensis **sp. nov.** can be differentiated from *C. jaegeri* (Luu, Calame, Bonkowski, Nguen and Ziegler, 2014) by having fewer postcloacal tubercles (3/3 vs. male 5/6), and dorsal patterns (bilaterally symmetrical patterns vs. wide bands).

C. hekouensis **sp. nov.** can be differentiated from *C. puhuensis* (Nguyen, Yang, Le, Nguyen, Orlov, Hoang, Nguyen, Jin, Rao, Hoang, Che, Murphy and Zhang, 2014) by having more ventral scale rows (68–72 vs. 36), and having femoral pores (absent in *C. puhuensis*).

C. hekouensis **sp. nov.** can be differentiated from *C. soudthichaki* (Luu, Calame, Nguyen, Bonkowski and Ziegler, 2015) by having fewer postcloacal tubercles (3/3 vs. 4/4–5/5);

more precloacal-femoral pores (33–39 vs. 29); and dorsal body patterns (bilaterally symmetrical patterns vs. 5 transverse bands).

C. hekouensis **sp. nov.** can be distinguished from *C. soni* (Le, Nguyen, Le and Ziegler, 2016) by different formations of precloacal-femoral pores (continuous 33–39 vs. males 6/7 precloacal+6–8 femoral, separate).

C. hekouensis **sp. nov.** can be distinguished from *C. taybacensis* (Pham, Le, Ngo, Ziegler and Nguyen, 2019) by having more ventral scale rows (68–72 vs. 30–38), and more precloacal-femoral pores (33–39 vs. males 11–13+females 5/15 pitted+femoral absent).

C. hekouensis **sp. nov.** can be differentiated from *C. houaphanensis* (Schneider, Luu, Sitthivong, Teynié, Le, Nguyen and Ziegler, 2020) by having more ventral scale rows (68–72 vs. 35); more precloacal-femoral pores (33–39 vs. 6+femoral absent); and more postcloacal tubercles (3/3 vs. 2/2).

C. hekouensis **sp. nov.** can be differentiated from *C. ngoiensis* (Schneider, Luu, Sitthivong, Teynié, Le, Nguyen and Ziegler, 2020) by having more precloacal-femoral pores (33–39 vs. males 7 precloacal+14 femoral+female absent).

C. hekouensis **sp. nov.** can be distinguished from *C. vilaphongi* (Schneider, Nguyen, Le, Nophaseud, Bonkowski and Ziegler, 2014) by having more ventral scale rows (68–72 vs. 34–36); more postcloacal tubercles (3/3 vs. 2/2); existence of precloacal-femoral pores (continuous pores 33–39 vs. precloacal pore unknown in male and absent in female).

C. hekouensis **sp. nov.** can be distinguished from *C. martini* (Tri, 2011) by having more postcloacal tubercles (3/3 vs. 2/2); more ventral scale rows (68–72 vs. 39–43); and more precloacal-femoral pores (continuous pores 33–39 vs. 4 precloacal pores and femoral absent).

C. hekouensis **sp. nov.** can be distinguished from *C. wayakonei* (Nguyen, Kingsada, Rösler, Auer and Ziegler, 2010) by having more precloacal-femoral pores (continuous pores 33–39 vs. 6–8); more postcloacal tubercles (3/3 vs. 2/2); and by having different dorsal banded patterns (bilaterally symmetrical vs. reticulated).

4. Discussion

Cyrtodact ylus wayakonei might be misidentified in China based on our phylogeny result of a *Crytodact ylus* specimen from Xishuangbanna. However, while *C. wayakonei* in China is only known from Yunnan (Yuan and Rao, 2011), previous records of Xishuangbanna's *C. wayakonei* were established by morphological comparison only. According to our phylogenetic results, the sample from Xishuangbanna county (*C. sp.* Xishuangbanna in our gene tree) is sister to *C. martini*, and the two former specimens together are the sister group to *C. wayakonei* by ML analysis (BS > 70%), which is consistent

with the study of Brennan et al. (2017) who also identified a Cyrtodact ylus specimen from Xishuangbanna as C. aff. martini. Additionally, the uncorrected *p* distance results (Table S1) suggest that the samples from Xishuangbanna have a smaller genetic divergence from C. martini than to C. wayakonei (C. sp. Xishuangbanna and C. martini: 2.8%; C. sp. Xishuangbanna and C. wayakonei: 6.8%). This result also corresponds with a study from Nazarov et al. (2018), which acknowledged a Cyrtodact ylus specimen from Xishuangbanna as C. cf. martini. Moreover, the morphological characters identified by Yuan and Rao (2011) from four specimens (male 2011R0010; females KIZ201101, KIZ201102, KIZ201103) may be inaccurate or represent variation. For example, precloacal-femoral pores data as a sexual character of lizards (Mayerl et al., 2015) from both genders are not provided; supralabials and infralabials differed from the holotype description (males/females supralabials and infralabials 9-10 in Yuan and Rao's [2011] study vs. supralabials 7-8 and infralabials 9-10 in type specimens description). The evaluation of C. wayakonei and distribution of C. martini in China should be discussed and supplemented with further morphological data by more specimens from these localities in future studies.

The karstic habitats of southwestern China represent the world's largest karst habitat system, and harbor an extraordinary diverse endemic flora and vertebrate fauna, which are in danger to anthropogenic threats (National Bureau Statistics of China, 2011; Luo et al., 2016). Fieldwork in these areas since 2015 has discovered eight amphibians and reptiles as new species or new locality records (Böhme, 2003; Nicodemo and Bain, 2007; Wang et al., 2015; Chen et al., 2018; Ren et al., 2018; Wang et al., 2018; Zhang et al., 2018; Yuan et al., 2019). Although these recent discoveries provide a greater understanding of the reptilian biodiversity in this region, it also indicates that there is likely much biodiversity that has yet to be discovered. Most of these works were conducted in Yunnan Province of China near the international boundary with Vietnam, and there is a lack of survey and collecting work in other areas of this hotspot, such as the areas between northern Hanoi, Vietnam and Guangxi Province, China. Extensive collaboration between China and Vietnam to conduct comprehensive fieldworks on amphibians and reptiles will be crucial to discovering cryptic species and understanding the full diversity of this region, which is critical in the current time during which global extinction rates have increased (Pimm et al., 2014).

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Appendix

Table S1 Uncorrected ("p") distance matrix showing uncorrected pairwise divergences from COI fragments of *Cyrtodactylus* species used in this study. The minimum genetic diverge between *Cyrtodactylus hekouensis* **sp. nov.** and selected species ranges from 14.2% to 26.8%.

Min Brandise			e					4	4	5	:	5	:	:	3	3	5		2			5		2				\$	-	\$	5	2				ş	s	:	4	\$:
		-	7	n	•	0		•	~	2	=	7	5	<u>z</u>	9	9	-	9	N N	17	77	57	8		7	Q7 17	6		10	7					ec .		96	ē	76	6.6	ş	Cê
1 Cyrtodactylus hontreensis																																										
2 C. Ioriae	MF169925	0.218																																								
3 C. tigroides	MF169948	0.239	0.232																																							
4 C. bicluganae	KT004372	0.247	0.186	0.177																																						
5 C. wayakanei	KJ817438	0.239	0.2.08	0.158	0.165																																					
6 C. martini	MF169929	0.224	0.203	0.162	0.175 (0.072																																				
7 C. Janja	KY041659	0.223	0.227	0.214	0.202	0.188 0.1	0.190																																			
8 C. pukikellus	HQ967202	0.232	0.237	0.228	0.240 0	0.217 0.2	0.203 0.2	0.225																																		
9 C. snorderi	MF169946	0.245	0.225	0.215	0.234 0	0.202 0.2	0.201 0.2	0.245 0.235	ý,																																	
10 C. olahami	MF169932	0.243	0.2.30	0.195	0.202	0.200 0.1	0.183 0.1	0.193 0.220	0 0.249	6																																
11 C. payarhtanensis	KY041664	0.2.50	0.2.29	0.202	0.179	0.214 0.2	0.207 0.1	0.194 0.211	11 0.261	0.136	6																															
12 C. qr. Luang Prabang, Lace	x KJ817432	0.223	0.197	0.184	0.166 0	0.170 0.1	0.163 0.2	0.213 0.207	0.240	0 0.198	8 0.200	p																														
13 C. chanquangenais	MF957261	0.207	0.197	0.161	0.158 0	0.169 0.1	0.152 0.1	0.191 0.210	0 0.227	7 0.185	5 0.183	3 0.125	\$																													
14 C. vilapikon gi	KJ817435	0.218	0.207	0.179	0.177	0.179 0.1	0.164 0.1	0.185 0.234	4 0.227	7 0.181	1 0.183	3 0.142	2 0.086	¢																												
15 C. khasienais	KP199948	0.232	0.236	0.181	0.172 (0.182 0.1	0.167 0.2	0.214 0.219	9 0.231	1 0.209	9 0.192	2 0.148	8 0.125	5 0.126																												
 C. aff. cucphinongenuis 	KJ817428	0.213	0.203	0.184	0.188 0	0.194 0.1	0.174 0.1	0.188 0.229	9 0.230	0 0.181	1 0.200	0 0.144	4 0.093	3 0.087	0.116																											
17 C. otai	MF957262	0.214	0.211	0.192	0.181 0	0.207 0.1	0.178 0.2	0.206 0.225	25 0.227	7 0.186	6 0.211	1 0.144	4 0.099	9 0.101	0.119	0.065																										
18 C. bolvrovi	KT004369	0.210	0.206	0.186	0.187 (0.188 0.1	0.169 0.2	0.205 0.220	0 0.221	1 0.184	4 0.207	7 0.135	5 0.099	9 0.099	0.108	0.065	0.039																									
19 C. huongsonensis	KX430034	0.248	0.198	0.199	0.162 0	0.188 0.1	0.169 0.2	0.204 0.195	5 0.223	3 0.214	4 0.200	0 0.158	8 0.164	4 0.172	0.188	0.181	0.174	0.177																								
20 C. sonlaensis	MF957265	0.241	0.236	0.203	0.175 0	0.179 0.1	0.163 0.2	0.227 0.192	2 0.245	5 0.220	0 0.202	0.176	6 0.193	3 0.198	0.179	0.205	0.199	0.188	0.149																							
21 C. elok	MF169914	0.231	0.227	0.238	0.222	0.219 0.1	0.196 0.2	0.265 0.208	8 0.210	0 0.246	6 0.235	\$5 0.225	5 0.221	1 0.228	0.221	0.231	0.237	0.233 (0.234 0.2	0.227																						
22 C. taybacensis	066799HM	0.269	0.198	0.167	0.062	0.176 0.1	0.164 0.2	0.205 0.230	90 0.245	5 0.197	7 0.179	9 0.175	5 0.159	9 0.178	0.169	0.182	0.185	0.181_0	0.169 0.1	0.183 0.216	9																					
23 C. interdigitalis	KX077901	0.241	0.238	0.219	0.222	0.211 0.2	0.212 0.2	0.254 0.271	1 0.235	5 0.242	2 0.233	3 0.238	8 0.226	6 0.229	0.240	0.241	0.238	0.237 (0.241 0.2	0.245 0.175	5 0.212																					
24 C. khammounensis	HM88 8467	0.242	0.222	0.251	0.236 (0.237 0.2	0.234 0.2	0.259 0.241	11 0.258	8 0.249	9 0.246	6 0.222	2 0.226	6 0.256	0.258	0.257	0.243	0.235 (0.246 0.2	0.226 0.249	9 0.250	0.271																				
25 C. rufford	KU175572	0.260	0.225	0.237	0.219 (0.239 0.2	0.224 0.2	0.258 0.226	26 0.261	1 0.240	0 0.241	1 0.220	0 0.211	1 0.254	0.230	0.243	0.232	0.230	0240 02	0.234 0.264	4 0.228	0.288	0.130																			
26 C. souddichali	KX077904	0.264	0.241	0.242	0.228	0.247 0.2	0.235 0.2	0.262 0.251	51 0.278	8 0.258	8 0.252	52 0.242	2 0.238	8 0.243	0.247	0.255	0.244	0.247 (0.251 0.2	0.243 0.266	6 0.242	0.285	0.147	0.159																		
27 C. jaegeri	KT004365	0.2.57	0.2.29	0.258	0.256 (0.250 0.2	0.228 0.2	0.238 0.206	6 0.244	4 0.237	7 0.241	11 0.262	2 0.237	7 0.262	0.262	0.259	0.275	0.272 (0.264 0.2	0.265 0.243	3 0.248	0.288	0.163	0.164 (0.154																	
28 C. sommerladi	KX064041	0.241	0.221	0.258	0.243 (0.244 0.2	0.228 0.2	0.267 0.266	6 0.256	6 0.232	2 0.228	28 0.224	4 0.227	7 0.240	0.235	0.234	0.241	0.252 (0.248 0.2	0.216 0.253	3 0.238	0.254	0.189	0.196	0.174 0.	0.178																
29 C. himawwo entis	KX064048	0.2.72	0.236	0.229	0.235 (0.231 0.2	0.238 0.2	0.270 0.257	57 0.263	3 0.260	0 0.248	18 0.232	2 0.217	7 0.228	0.259	0.248	0.2.52	0.257 (0.230 0.2	0.229 0.248	8 0.232	0.268	0.186	0.216 (0.217 0.	0.205 0.1	0.185															
30 C. phongukakebangensis	KF929526	0.2.52	0.2.29	0.218	0.234 (0.236 0.2	0.217 0.2	0.242 0.266	6 0.252	2 0.250	0 0.238	88 0.219	9 0.220	0 0.244	0.244	0.251	0.2.59	0.258	0.258 0.2	0.229 0.245	5 0.239	0.241	0.174	0.200	0.203 0.	0.190 0.1	0.183 0.098	86														
31 C lomyenensis	KJ817436	0.246	0.233	0.238	0.239	0.246 0.2	0.244 0.2	0.242 0.247	7 0.242	2 0.244	4 0.231	1 0.236	6 0.242	2 0.249	0.273	0.248	0.261	0.261	0.242 0.5	0.246 0.260	0 0.249	0.274	0.185	0.205 (0.214 0.	0.191 0.2	0.204 0.166	66 0.164														
32 C. thathomenus	MG791873	0.254	0.226	0.220	0.250	0.249 0.2	0.239 0.2	0.242 0.264	54 0.246	6 0.248	8 0.223	3 0.257	7 0.237	7 0.229	0.276	0.259	0.257	0.253 (0.251 0.0	0.255 0.266	6 0.250	0.272	0.200	0.216 0	0.209 0.	0.205 0.1	0.195 0.190	90 0.182	0.178													
33 C. teynkei	KJ817430	0.237	0.241	0.222	0.255 (0.252 0.2	0.247 0.2	0.251 0.263	3 0.250	0 0.227	7 0.223	23 0.250	0 0.231	1 0.211	0.238	0.242	0.240	0.238 (0279 02	0.247 0.258	8 0.268	0.271	0.187	0.206	0.193 0.	0203 0.2	0.205 0.172	72 0.172	0.162	0.104												
34 C. pageli	KJ817431	0.258	0.236	0.230	0.236 (0.242 0.2	0.221 0.2	0.237 0.237	57 0.265	6 0.232	2 0.228	28 0.243	3 0.217	7 0.228	0.253	0.228	0.232	0.224 (0.241 0.5	0.229 0.250	0 0.244	0.273	0.213	0.218 (0.211 0.	0.221 0.1	0.187 0.222	22 0.204	0200	0.209	0.202											
35 C. cryptus	KX064038	0.235	0.222	0.219	0.203	0.212 0.2	0.202 0.2	0.218 0.238	88 0.222	2 0.215	5 0.206	6 0.231	1 0.228	8 0.222	0.233	0.232	0.224	0.224 (0.2.29 0.2	0.230 0.222	2 0.204	0.232	0.250	0.259 (0.267 0.	0.257 0.2	0.243 0.263	63 0.236	0.250	0.236	0.246	0.229										
36 C. kingsadai	KF188432	0.267	0.196	0.232	0.229	0.228 0.2	0.213 0.2	0.234 0.227	27 0.221	1 0.207	7 0.206	6 0.231	1 0.223	3 0.226	0.239	0.235	0.247	0.237 (0.205 0.2	0.220 0.231	1 0.224	0.244	0.235	0.243 (0.257 0.	0.219 0.2	0.232 0.243	43 0.217	0.238	0.237	0.238	0.236 (0.141									
37 C. pseudoquadrivingatus	KF1699G	0.242	0.2.19	0.244	0.220	0.207 0.2	0.206 0.2	0.204 0.249	9 0.214	4 0.216	6 0.210	0 0.255	5 0.211	1 0.215	0.227	0.206	0.211	0.212 0	0.218 0.2	0.230 0.232	2 0.203	0.248	0.243	0.269	0.262 0.	0.256 0.2	0.273 0.240	40 0.237	0.261	0.246	0.237	0.252 (0.149 0.	0.156								
38 C. badenensis	KF929505	0.271	0.267	0.252	0.227	0.241 0.2	0.236 0.2	0.228 0.226	26 0.235	5 0.241	1 0.233	3 0.261	1 0.264	4 0.255	0.280	0.257	0.270	0.260	0.241 0.2	0.276 0.261	1 0.237	0.266	0.256	0.267	0.292 0.	0.267 0.2	0.293 0.274	74 0.285	0.277	0.306	0.295	0.262	0.225 0.	0.199 0.1	0.187							
39 C. quadrivirgatus	HM88 846 6	0.270	0.237	0.224	0.205	0.236 0.2	0.235 0.2	0.254 0.248	88 0.205	6 0.233	3 0.226	26 0.240	0 0.212	2 0.234	0.234	0.240	0.226	0.229	0.242 0.2	0.241 0.230	0 0.209	0.229	0.247	0.244 (0.237 0.	0.235 0.2	0.240 0.254	54 0.247	0.260	0.264	0.256	0.263	0.218 0.	0.212 0.2	0.213 0.257	57						
40 C. pulmensis	KF929529	0.224	0.205	0.197	0.219	0.211 0.1	0.183 0.1	0.189 0.223	3 0.233	3 0.200	0 0.211	11 0.173	3 0.115	5 0.111	0.121	0.033	0.078	0.078	0.212 0.2	0.224 0.246	6 0.204	0.265	0.272	0.258 (0263 0	0.260 0.2	0.247 0.275	75 0.267	0.259	0.274	0.250	0.244 (0.237 0.	0.238 0.2	0.225 0.267	67 0.256	2					
41 C. Isekouensis sp. nov.	MW067125	5 0.252	0.217	0.172	0.171 0	0.164 0.1	0.142 0.2	0.212 0.206	6 0.238	8 0.211	1 0.199	9 0.183	3 0.190	0 0.199	0.194	0.195	0.197	0.206	0.167 0.1	0.170 0.234	4 0.186	0.246	0.231	0.229	0.237 0.	0.225 0.2	0.236 0.229	29 0.232	0.249	0.248	0.242	0.225 (0.225 0.	0.233 0.2	0.245 0.268	68 0.234	4 0.208					
42 C. hekouentis sp. nov.	MW067126	6 0.252	0.217	0.172	0.171 0	0.164 0.1	0.142 0.2	0.212 0.206	6 0.238	8 0.211	1 0.199	9 0.183	3 0.190	0 0.199	0.194	0.195	0.197	0.206	0.167 0.1	0.170 0.234	4 0.186	0.246	0.231	0.229	0.237 0.	0.225 0.2	0.236 0.229	29 0.232	0.249	0.249	0.242	0.225 (0.225 0.	0.233 0.2	0.245 0.268	68 0.234	4 0.208	0.00.0				
43 C. hekovensis sp. nov.	MW067127	7 0.255	0.217	0.172	0.171 0	0.164 0.1	0.143 0.2	0.210 0.206	6 0.236	6 0.211	1 0.200	0 0.183	3 0.190	0 0.199	0.194	0.195	0.195	0.206	0.167 0.1	0.171 0.234	4 0.186	0.244	0.231	0.229	0.237 0.	0.225 0.2	0.236 0.228	28 0.232	0.250	0.249	0.242	0.225 (0.226 0.	0.234 0.2	0.245 0.268	68 0.234	4 0.208	0.000	0.000			
44 C. hekovenús sp. nov.	MW067128	8 0.250	0.223	0.173	0.178 0	0.175 0.1	0.154 0.2	0.214 0.206	6 0.245	5 0.225	5 0.201	0.194	4 0.193	3 0.202	0.199	0.200	0.203	0.208	0.176 0.1	0.173 0.237	7 0.191	0.253	0.239	0.237 (0.248 0.	0.228 0.2	0.245 0.227	27 0.232	0.259	0.255	0.245	0.230	0.233 0.	0.229 0.2	0.246 0.266	66 0.247	7 0.211	0.008	0.008	0.008		
45 C. sp. Xishungbarma, China	im MW067129	9 0.241	0.201	0.161	0.174 0	0.068 0.0	0.028 0.1	0.195 0.212	2 0.194	4 0.195	5 0.218	8 0.166	6 0.156	6 0.176	0.166	0.171	0.181	0.175 (0.172 0.	0.164 0.203	3 0.159	0.215	0.246	0.231	0.245 0.	0.232 0.2	0.229 0.238	38 0.226	0.257	0.243	0.252	0.216	0209 0.	0.218 0.2	0.206 0.249	49 0.234	4 0.190	0.150	0.150	0.150	0.161	
						1															1									1						1	1	1				