

**The taxonomy, zoogeography and ecology of
amphibians and reptiles of Hin Nam No National
Protected Area (Laos) in comparison with data
from Phong Nha – Ke Bang National Park
(Vietnam)**

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1. Introduction

The Truong Son Range is situated along Laos' border with Vietnam. It is known to Laotians as Saiphou Louang, and in Vietnamese as Truong Son. To the rest of the world, it is known as the Annamite Mountain Range. The northern part of the Range contains a large series of contiguous limestone karst formations (Sterling *et al.* 2006). Today, it is a unique transitional region between the subtropical plant communities of the North and the tropical South in Indochina (Groves & Schaller 2000; Sterling *et al.* 2006). It is considered a region of global importance in terms of biodiversity (Myers *et al.* 2000). A complex history of geological uplifting and folding created a sequence of large limestone and granite formations in this region. The overlap of Sino-Himalayan and Indo-Malayan biotic influences as well as both climatic and historical factors have contributed to high levels of diversity and endemism in the Truong Son (Clements *et al.* 2006; Sterling *et al.* 2006; Bain & Hurley 2011). In the last two decades, several new distinct species of mammals have been discovered from the forests in this region, e.g., *Pseudoryx nghetinhensis* (Vu *et al.* 1993), *Muntiacus vuquangensis* (Do *et al.* 1994), *M. truongsongensis* (Pham *et al.* 1998), *Nesolagus timminsi* (Averianov *et al.* 2000), and *Laonastes aenigmamus* (Jenkins *et al.* 2005; Aplin & Lunde 2008).

In terms of herpetofaunal diversity, the knowledge on the species richness of amphibians and reptiles in Vietnam and Laos has dramatically increased in recent decades. In Vietnam, the species number of amphibians and reptiles increased from 458 species (162 amphibian and 296 reptile species) reported by Nguyen *et al.* (2005), to 566 species (181 amphibian and 385 reptile species) by Ziegler & Nguyen 2010. Additionally, 44 amphibian and 16 reptile species have been discovered from Vietnam since 2010 (Uetz & Hošek 2015; Forst 2016). From Laos only 95 amphibian and 89 reptile species were known in 2005 (e.g., Teynié *et al.* 2004; Stuart 2005; Uetz & Hošek 2015; Forst 2016). These numbers have rapidly increased to 103 species of amphibians and 180 species of reptiles in 2010 (Teynié & David 2010; Uetz & Hošek 2015; Frost 2016). Despite four new species of amphibians and 15 new species of reptiles that have been discovered in the last five years from Laos, resulting in a total of currently 107 amphibian and 198 reptile species (Uetz & Hošek 2015; Forst 2016), the known species-richness still appears severely underestimated in comparison to the much better studied Vietnam (Fig. 1.1).

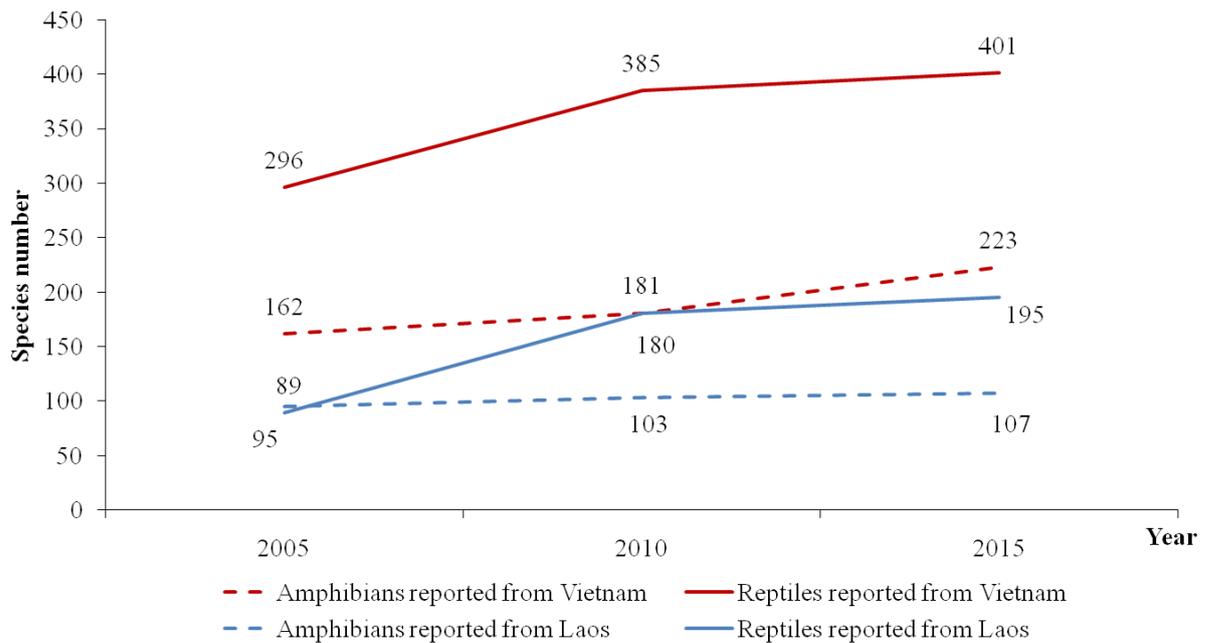


FIGURE 1.1. Comparison of the known species numbers of amphibians and reptiles between Laos and Vietnam (2005-2015)

Despite the numerous new discoveries and records which have been documented from mainland Southeast Asia in recent years (Uetz & Hošek 2015; Forst 2016), biodiversity in tropical countries like Vietnam and Laos is facing a sharp decline (Myers *et al.* 2000). The current extinction rate is estimated approximately 1000 times higher than that in historic times, which may cause an alarming decline of the functioning of ecosystems (Böhm *et al.* 2013; Pimm *et al.* 2014). The primary threats attributed to the increase of species extinction rates include timber logging and deforestation for agriculture, mining and construction activities, pollution, exploitation and unsustainable use of plants and animals, introduction of invasive species, and global climate change (Gibbons *et al.* 2000; Cox & Temple 2009). The Truong Son Range has a particularly high rate of deforestation and limestone quarrying, driving population declines and extinctions among animal taxa (Sterling & Hurley 2005; Clements *et al.* 2006). Because amphibians and reptiles are poikilothermic animals and have lower activity ranges than other vertebrates (Gibbons *et al.* 2000), they are highly at risk. On a world wide scale for instance, roughly 200 extinct species of frogs have been documented and hundreds more are expected to disappear within the next century (Alroy 2015). Twenty three reptile species have already disappeared and 164 species of the world's reptiles are estimated to be under the threat of extinction (Kumar *et al.* 2014). Therefore, effective conservation

measures are mandatory and require integrated studies on morphological and ecological traits, evolutionary history, and biogeography (Moritz *et al.* 2000; Böhm *et al.* 2013).

The Hin Nam No National Protected Area (NPA), in central Laos, and the Phong Nha - Ke Bang National Park (NP), in central Vietnam are located on opposite sides of the Truong Son Range. The herpetofauna is regarded as a significant portion of the biodiversity in these regions, with 532 recorded species of amphibians and reptiles (Bain & Hurley 2011). The herpetofaunal diversity in the Truong Son Range has been investigated since before the last century (e.g., White 1842; Mouhot 1864; Morice 1875; Tirant, 1885). Smith presented a series of studies during the 1920s (e.g., Smith 1920, 1921a-b, 1922a-b, 1923, 1924a-c), among them the first surveys on amphibian and reptile diversity (Smith 1920). Seventy years later, between 1998 and 1999, again numerous herpetofaunal surveys were conducted on the Vietnamese side of the northern Truong Son Range, e.g. Huong Son Forest Enterprises (Ha Tinh Province), Ke Bo (Nghe An Province) and Cha Lo (Quang Binh Province), revealing a total of 71 species of herpetofauna (35 amphibians and 36 reptiles) (Bain & Nguyen 2001a; Bain & Nguyen 2001b; Chou *et al.* 2001). Subsequently, intensive herpetodiversity surveys were conducted in Phong Nha - Ke Bang NP for another 10 years (e.g., Ziegler & Herrmann 2000; Ziegler *et al.* 2006; Ziegler *et al.* 2007; Hendrix *et al.* 2008; Ziegler & Vu 2009; Ziegler *et al.* 2010). At least 12 new amphibian and reptile taxa have been described in the area. Recently, Luu *et al.* (2013) published a list of 11 new records of amphibian and reptile species and subspecies, thus updating and increasing the total number of herpetofauna known from Phong Nha - Ke Bang to 151 species. Despite this progress, big gaps still remain in our knowledge on the herpetofaunal diversity and its distribution in the Truong Son Range (Ziegler & Vu 2009). Hin Nam No NPA and its surrounding areas in Khammouane Province, Laos, is an example, from where the amphibian and reptile fauna is virtually unknown. The report by Walston & Vinton (1999) is the only study that catalogued amphibian and reptile species from the area, but the given total number of 49 herpetofaunal representatives is likely a severe underestimate of the actual species richness. This region certainly yields a distinctly higher number of species, including so far undescribed taxa when compared to the comprehensive data available from Phong Nha - Ke Bang NP on the opposite side of Truong Son Range.

Herpetodiversity research and taxonomic action face multiple challenges in the Truong Son (Bain & Hurley 2011). Taxonomists with detailed knowledge on Indochina's herpetofauna are

rare. In many cases, identification to species level is difficult, because taxonomic monographs for the region are lacking, and taxonomy is based on many isolated publications. Species descriptions are of different quality but usually rely on morphological characters. However, systematics based on the morphospecies concept often results in lower species counts than systematics based on molecular data (Ohler & Delorme 2006; Stuart *et al.* 2006). Species complexes composed of species with apparently similar morphology but significant genetic differences, so-called cryptic species, can lead to wrong taxonomic assignments if they are not backed up by molecular genetic studies (e.g., Vogel & David 2006; Ohler 2007; Bain *et al.* 2009). In fact, a number of cryptic species have been reported recently from Indochina, suggesting that their formerly assigned distribution ranges are geographically much more limited (Bickford *et al.* 2007). This has important consequences for species conservation and alpha-taxonomy. DNA barcoding has become a crucial tool for detecting and differentiating species complexes in amphibians and reptiles (Vences *et al.* 2005; Stuart *et al.* 2006; Angulo & Icochea 2010; Blair *et al.* 2013; Mrinalini *et al.* 2015). Therefore, an integrative approach that combines morphological, genetic, and ecological data to delineate species boundaries and to detect cryptic species has considerably increased the recognized species richness within the Truong Son Range (e.g., Bain *et al.* 2003; Stuart *et al.* 2006; Stuart & Bain 2008; Nazarov *et al.* 2012; Nguyen *et al.* 2013).

Never before have so many surveys been conducted in one area of Vietnam as in the Truong Son Range (e.g., Inger & Kottelat 1998; Inger *et al.* 1999; Teynié *et al.* 2004; Heidrich *et al.* 2007; Teynié & David 2010; Nguyen *et al.* 2013). As a result, the species distributions may be misleading as many newly described species have only been recorded from their type localities. These species may feature endemism or restricted distributions, or there may be a discrepancy between their described ranges and their actual ranges (Bain & Hurley 2011).

Ecological studies on amphibians and reptiles of the region are also not extensive, since ecological information is mainly based on observations made during field surveys. Ecological studies of the herpetofauna on the western, Laotian side of the Truong Son Range are far fewer in comparison with those on the opposite side in central Vietnam (Ziegler & Weitkus 1999a-b; Ziegler 2002; Loos *et al.* 2012). Sampling limitations are problematic because species may only be recorded when they leave the water, emerge from underground, or come down from the trees. This observation bias is likely responsible for the lack of ecological data.

In order to fill some of the remaining gaps of knowledge on the herpetodiversity of the Truong Son Range, my aim was to investigate the composition of amphibian and reptile communities of the largely still unexplored natural habitats in karst forests with a focus on the western, Laotian side along the northern Truong Son Range. Here, a number of hypotheses arise. (1) The Truong Son Range acted as a biogeographic barrier for the distribution of amphibians and reptiles. (2) If this allopatric speciation was a recent event in evolution, we expect to find morphologically still similar, but genetically different (i.e. cryptic) species on the western side of the range in Laos when compared to the eastern side in Vietnam. (3) If allopatric speciation was related to the life-history of a taxonomic group (e.g. geckos adapted to rocky surfaces) then these specific taxonomic groups should contain higher levels of endemism and cryptic diversity than others. (4) If, however, shifts in ancient climate and subsequent range expansions and contractions of natural habitats led to allopatric speciation, all taxa adapted to a specific habitat would be separated and we expect to find spatially distinct centres of endemism and cryptic diversity in very different taxonomic groups of the herpetofauna. (5) We expect a similar diversity in Laos as on the opposite side of the range in Vietnam. (6) Since karst forests provide a number of special and clearly defined habitats, we expect similar ecological niches to be occupied within Vietnam and Laos, but the actual species filling the niches might differ within a genus. (7) The species' distribution patterns can be explained against the background of zoogeography. To answer these hypotheses, profound taxonomic descriptions are an ultimate prerequisite, which means that taxonomic problems have to be resolved first. To achieve this goal, an integrative taxonomic approach is needed, which combines morphological, molecular, and ecological data. Secondly, the species' distribution patterns and at least their relative abundances, basic habitat preferences, and ecological requirements have to be investigated in order to assign the spatial boundaries of the species, and their potential conservation status. Furthermore, a high proportion of herpetofauna from Laos, as well as along the Truong Son Range, are threatened with extinction due to increasing human populations and loss of natural habitats. Therefore, the database obtained from our morphological and molecular analyses is an extremely useful prerequisite if combined with subsequent ecological data. These can be used to define specific conservation measures such as the definition of new protected regions or the improvement of already existing conservation areas.

In brief, this study aims (1) to investigate the species richness, basic ecology, and distribution pattern of amphibians and reptiles on the western side of the Truong Son Range in Laos; (2)

to elucidate the speciation of the family Gekkonidae (*Cyrtodactylus*, *Gekko*), a species rich, but poorly known group of reptiles on both sides of Truong Son Range; (3) to address the central hypothesis that Truong Son Range represents as a biogeographic barrier to the herpetofauna and the hypotheses derived from it; and (4) to provide implications for conservation measures.

2. Material and Methods

2.1 Study site

The Truong Son Range is approximately 1,200 km in length and 50–75 km wide, running from northwest to southeast along the entire length of the Laos–Vietnam border, through the inland of Vietnam to northeastern Cambodia, with elevations between 500 and 2,000 m above sea level (a.s.l.) (Sterling *et al.* 2006; Ziegler & Vu 2009; Bain & Hurley 2011). The Truong Son Range is divided into three regions: 1) northern Truong Son, composed of ancient sea basins, which were uplifted and now are heavily eroded to form the characteristic sharp karst ridges and peaks with extensive systems of caves, tunnels, and underground rivers and streams; 2) central Truong Son, dominated by the Kon Tum Massif which consist of an enormous granite formation, being among the oldest uncovered rocks in Southeast Asia; and 3) southern Truong Son, including Dac Lac, Da Lat and Di Linh Plateaus, a series of eroded granite and basalt plateaus dotted with isolated peaks (Ziegler & Vu 2009; Bain & Hurley 2011). Central Laos' Truong Son Range is a transitional region between the subtropical communities of the north and the tropical ones from the south, and harbours many endemic species, such as a spectacular endemic mammal fauna (Groves & Schaller 2000; Herrmann *et al.* 2002).

In the northern Truong Son Range, we have selected the Hin Nam No National Protected Area (NPA) and its surrounding areas in Khammouane Province, Laos as focal study region because it is directly opposite of the well-studied Phong Nha - Ke Bang NP in Vietnam. Hin Nam No NPA and Phong Nha - Ke Bang NP are situated within one of the most extensive limestone karst formations in Asia. 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 semi-humid climate on 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).

Hin Nam No NPA is located in the Bualapha District, Khammouane Province in central Laos. The total area of protected land is about 82,000 ha and extends over a large dissected karst plateau (17°15' – 17°40' N and 105°43' – 105°09' E) (Phimmavong 2014). The highest peak is the Phou Chuang, at an elevation of 1,492 m a.s.l.. The land cover of Hin Nam No NPA is characterized by a mosaic of different types of lowland, hill and mountainous forest.

Evergreen forests are multi-storied with broad-leaved species of Podocarpaceae, Myataceae and Fagaceae. Mixed deciduous forests are classified as consisting of more than 5% but less than 70% of deciduous species with a lower density than the evergreen forests. They are dominated by Dipterocarpaceae and Lyrthaceae. Bamboo forests can be found partly along the southeastern border of the area, consisting mainly of *Bambusa arundinaceae*. The sparsely forested vegetation on the limestone surface in karst areas is primarily dominated by relatively dwarfed and drought-resistant species which are adapted to the low water ability (Rundel 1999; Averyanov *et al.* 2003) such as Agavaceae and Arecaceae (Meijboom & Ho 2002) (Fig. 1.2).

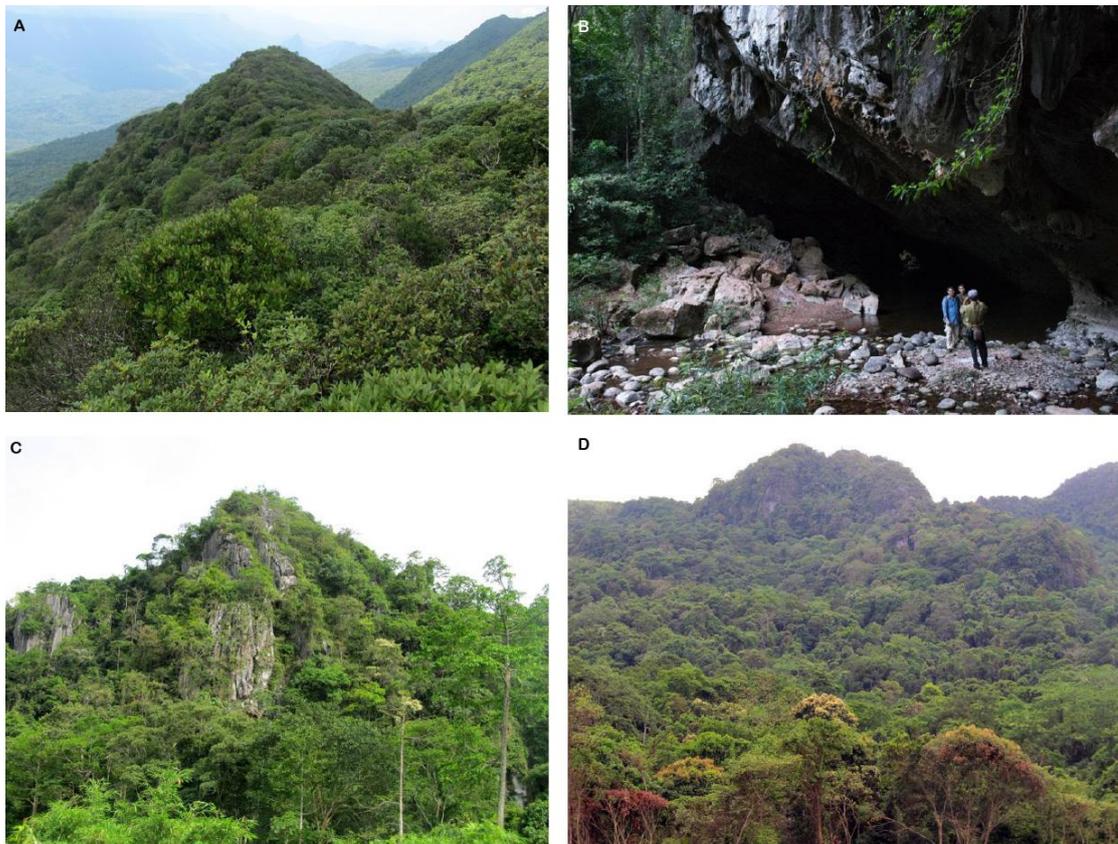


FIGURE 1.2. Main habitat types in Hin Nam No NPA: A) granite forest in the highest Mountain, Phou Chuang; B) a limestone cave in Thong Xam Village; C) karst forest in Ban Cha Lou; D) karst forest in Noong Ma Village.

2.2 Sampling

Field work was undertaken during a period of four years between 2013–2016 within Hin Nam No NPA and its surrounding areas of Bualapha District, and extended surveys into isolated karst mountains of Gnommalath, Mahaxay, Thakhek, and Hinboun districts in Khammouane

Province. In Hin Nam No NPA and its surrounding areas of Bualapha District, field surveys covered all three parts within the protected area, including forest areas of Noong Bua, Dou, Vangmano, Thong Xam (Thong Xam trail) villages and Phou Chuang mountain in the northern part; Cha Lou (Khun Kaan region) and Noong Ping (Xe Bang Fai cave region) villages in the central part; and Noong Ma Village (Hang Toi and Pa Rang regions) in the southern part as well as and surrounding areas Bualapha District (Ban Soc, Noong Nieu, Mayvangnguoc villages, Bualapha and Lang Khang towns). For the extended surveys into isolated karst mountains in Khammouane Province, we focused on the isolated karst mountains of Bualapha District (Ban Soc, Noong Nieu, May Vang Nguoc villages, Bualapha and Lang Khang towns); Gnommalath District (Nang Log cave, Hang Kan and Na Bo villages); Mahaxay District (Na Kham and Na Ngua villages); Thakhek District (Budda cave); Hinboun District (Phon Du and Ha villages, and the Khun Don cave area within Phou Hin Poun NPA) (Fig. 1.3).

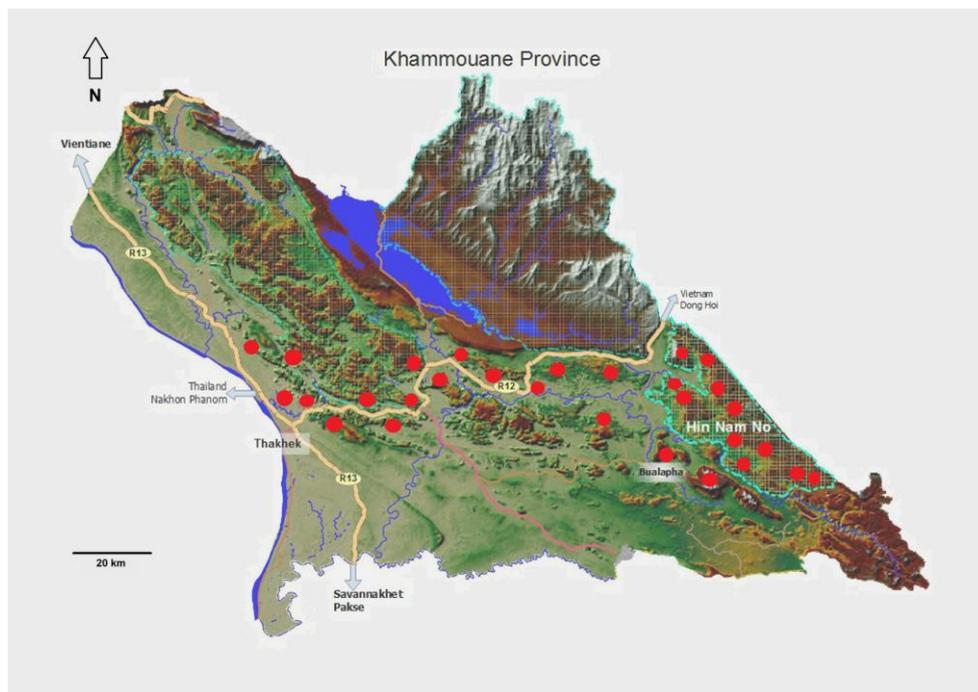


FIGURE 1.3. Map showing the survey sites (marked with red dots) in Hin Nam No NPA and surrounding areas (map source: M. de Koning & R. Dobbelsteijn).

Survey transects were set up along streams, pools, small ponds or along forest paths, particularly in remote sites. As lizards and snakes usually inhabit rock crevices, leaf litter or tree branches, we also searched in forests near cave entrances and cliffs. Coordinates were determined by GPS. Field trips were organized between January and June each year in the dry season with low water levels, which is important for field site access, and which is the best

season to inventory amphibians and reptiles. Search effort was restricted to the night time from 19:00h to approximately 24:00h, when most of amphibian and reptile species are most active

For voucher specimens, most of animals were captured by hand. Venomous snakes were collected with a snake hook or a snake tong, and some lizards were collected with forceps. Collected specimens were kept in cloth bags. After taking photographs, common species were released. Some individuals of other species were collected for taxonomic identification in the laboratory, with a particular attention to potential cryptic species. The selected animals were anaesthetized and euthanized in a closed vessel with a piece of cotton wool, containing ethyl-acetate within 24 hours after collecting. Each specimen was labelled directly with a field tag providing information on the locality and a coded identification number. Specimens were fixed in 80-85% ethanol and subsequently transferred to 70% ethanol for permanent storage. For molecular analysis, tissue samples of muscle (e.g., frogs, lizards) and liver (snakes) were preserved in 95% ethanol (Simmons 2002). All voucher specimens were collected selectively according to appropriate permissions (e.g., CITES, Animal Welfare Law, Forest Protection regulations of Laos).

For all collected individuals information on habitat, time, air temperature and humidity, and perch height above the ground were recorded, as well as case-dependent additional observations. Geographic coordinates and elevation (a.s.l.) were tracked with a GPS (Garmin GPSMap 62st) using the geodetic datum WGS84. Air temperature and humidity were measured with a digital compact thermo-hygro-barometer (Atech, model: KW307-CSJ, accuracy 0.1% for temperature, 1% for relative humidity).

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; Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany; and the Museum für Naturkunde, Berlin (ZMB), Germany.

2.3 Data Analysis

2.3.1 Specimen examination

Taxonomic decisions were based on morphological examination of 279 collected amphibian and reptile specimens (Table 1.1) in comparison with data taken of 99 comparative specimens from Laos and bordering countries such as Cambodia, China, Thailand, and Vietnam deposited in the museum collections in Vietnam, Germany, and France. Morphological characters of specimens from Laos were also compared with data from the literature, such as species descriptions, identification keys and reviews (e.g., Boulenger 1893; Bourret 1935; Smith 1943; Taylor 1962; Zielger *et al.* 2007; Nguyen *et al.* 2011a; Rösler *et al.* 2011). A list of examined specimens from museums is listed in the Material and Methods, and Appendix in each publication.

TABLE 1.1. Number of collected and examined specimens.

Family		Laos	Bordering countries	Subtotal
AMPHIBIA	Megophryidae	32	17	49
	Bufonidae	5	0	5
	Microhylidae	15	10	25
	Dicroglossidae	27	5	32
	Ranidae	29	7	36
	Rhacophoridae	25	23	48
REPTILIA	Gekkonidae	50	11	61
	Agamidae	25	14	39
	Scincidae	25	0	25
	Colubridae	24	7	31
	Elapidae	1	0	1
	Viperidae	21	5	26
Total		279	99	378

2.3.2 Morphological analysis

The morphological examination was carried out in the laboratory of the Department of Terrestrial Ecology at the University of Cologne. External morphological characters were inspected by eye or with a stereomicroscope (Stemi 2000; Zeiss). Morphometric measurements were taken with a digital calliper to the nearest 0.1 mm (except body and tail lengths of snakes). Terminology of morphological characters followed Nguyen *et al.* (2012) for amphibians and anuran webbing formula followed Glaw & Vences (2007) (except for forearm length, FAL = from axilla to elbow and hand length, HAL = from base of outer palmar tubercle to tip of finger III), Phung & Ziegler (2011); Nguyen *et al.* (2011) for lizards, and Vogel *et al.* (2009); David *et al.* (2012) for snakes, ventral scale count followed Dowling (1951). Bilateral scale counts were given as left/right. Femoral and preloacal pores of gekkonids were counted on photographs taken with a digital microscope (Keyence VHX-500F). The following abbreviations were used:

a) Reptile specimens:

Measurements: AG = distance between axilla and groin; HL = maximum head length (Gekkonidae: from tip of snout to posterior margin of auricular opening; Viperidae: from tip of snout to posterior part of lower jaw; in Scincidae: from tip of snout to margin of parietal); HW = maximum head width (at widest point of temporal region), HH = maximum head height (measured at the deepest point at temporal region); SE = distance from snout tip to anterior corner of eye; OD = greatest diameter of orbit, TD = maximum tympanum diameter; EyeEar = orbit to ear distance (from anterior edge of ear opening to posterior corner of orbit); EarL = ear length (maximum diameter of ear); ForeaL = forearm length (from base of palm to elbow); FemurL = femur length/crus length (from base of heel to knee); LD4A = length of finger IV; LD4P = length of toe IV; RW = maximum rostral width; RH = maximum rostral height; MW = maximum mental width; ML = maximum mental length; SVL = snout-vent length (from tip of snout to anterior margin of cloaca); TaL = tail length (from posterior margin of cloaca to tip of tail); TrunkL = Trunk length; TL = Total length (SVL+TaL).

Scalation: CS = ciliary spines; N = nasals (nasorostrals, supranasals, postnasals), I = intersupranasals (scales between supranasals, in contact with rostral); SPL = supralabials (number of scales from below the middle of eye to the rostral scale); IFL = infralabials (number of scales from below the middle of eye to the mental scale); IO = interorbitals (number of scales in a line between anterior corners of eyes); PO = preorbitals (number of

scales in a line from nostril to anterior corner of the eye); PM = postmentals; GP = gulars bordering the postmentals; DTR = dorsal tubercle rows at midbody; GSDT = granules surrounding dorsal tubercles; SMC = scales in a line from mental to the front of cloacal slit; SR = scale rows at midbody (including ventral scales); V = ventral scale rows at midbody; LF1 = subdigital lamellae under whole first finger; LF4 = subdigital lamellae under whole fourth finger; LT1 = subdigital lamellae under whole first toe; LT4 = subdigital lamellae under whole fourth toe; PP = precloacal pores; PAT = postcloacal tubercles. For the snake specimens: DSR = formula of dorsal scale rows: ASR (at one head length behind head) = number of dorsal scale rows at neck; MSR (at number of VEN/2) = number of dorsal scales at midbody; PSR (at one head length before the vent) and number of dorsal scale rows before the vent; SL = supralabials (counted on upper lips); IL = infralabials (counted on lower lips); Lor = loreal scales; Loreal scale touching the orbit (yes or no); PreOc = preocular scales; PosOc = postocular scales; Temp = temporals (counted immediately behind posoculars and between posterior SL and parietals). Keel = keeled dorsal scale rows; PreVEN = preventral scales; VEN notched (present or absent): VEN keeled (present or absent); SC = subcaudal scales; numbers of pattern–units (like crossbars or vertebral blotches) are provided as number on body + numbers on tail.

b) Amphibian specimens:

Abbreviations were used as follows: SVL = snout-vent length; HL = head length (from the back of mandible to the tip of snout); HW = head width (across angle of jaws); MN = distance from the back of mandible to the nostril; MFE = distance from the back of mandible to the front of eye; MBE = distance from the back of mandible to the back of eye; IFE = distance between the front of eyes; IBE = distance between the back of eyes; IN = internasal distance; EN = distance from the front of eye to the nostril; EL = horizontal eye diameter; NS = distance from nostril to the tip of snout; SL = distance from the front of eye to the tip of snout; TYD = greatest tympanum diameter; TYE = distance from tympanum to the back of eye; IUE = minimum distance between upper eyelids; UEW = maximum width of upper eyelid. Forelimb: HAL = hand length (from the base of outer palmar tubercle to the tip of fourth toe); FLL = forelimb length (from the elbow to the base of outer tubercle); TFL = third finger length (from the base of the first subarticular tubercle to the tip of third toe); fd1-4 = width of discs of fingers I-IV; fw1-4 = width of fingers I-IV (measured at the narrowest point of the distant phalanx). Hindlimb: FL = femur length (from vent to knee); TL = tibia length; TW = tibia width; FOL = foot length (from the base of inner metatarsal tubercle to the tip of fourth

toe); FTL = fourth toe length (from the base of the first subarticular tubercle to the tip of fourth toe); TFOL = distance from the base of tarsus to the tip of fourth toe; IMT = length of the inner metatarsal tubercle; ITL = inner toe length; td1-4 = width of discs of toes I-IV; fw1-4 = width of toes I-IV (measured at the narrowest point of the distant phalanx). Webbing: MTTF = distance from the distal edge of metatarsal tubercle to the maximum incurvation of web between third and fourth toes; TFTF = distance from the maximum incurvation of web between third and fourth toes to the tip of fourth toe; MTFF = distance from the distal edge of metatarsal tubercle to the maximum incurvation of web between fourth and fifth toes; FFTF = distance from the maximum incurvation of the web between fourth and fifth to the tip of fourth toe. Webbing formula according to Glaw & Vences (2007).

2.3.3 Molecular and phylogenetic analyses

For the identification of potentially undescribed or cryptic species, a phylogenetic approach was employed to investigate the population genetics of species/populations of uncertain identity and the closest relative species/populations. This work was conducted in collaboration with Dr. Minh Le, molecular biologist from the Vietnam National University, Hanoi, Vietnam.

We sequenced a fragment of the following mitochondrial genes: cytochrome c oxidase subunit (COI) for samples of *Cyrtodactylus* and *Trimeresurus*, cytochrome b for samples of *Lycodon*, NADH dehydrogenase subunit 2 (ND2) gene for samples of *Gekko*, and the 16S ribosomal RNA gene for samples of *Gracixalus* and comparable sequences of potential undescribed species within sister groups. These mitochondrial genes have been applied successfully to resolve phylogenetic relationships at different taxonomic levels of lizards, snakes, and frogs (e.g., Nguyen *et al.* 2008; Rösler *et al.* 2011; Siler *et al.* 2012). DNA extraction, amplification, and sequencing followed the standard protocols of Le *et al.* (2006). DNA was extracted using the DNeasy kit following the manufacturer's instructions for animal tissues (QIAGEN Inc., Valencia, CA, USA). The primer pair L4437b (Macey *et al.* 1997) and ND2r102 (Greenbaum *et al.* 2007) and a pair of newly designed primers, GF1 and GR1 were used to amplify a section of the mitochondrial gene (ND2) of the *Gekko* samples. The primer pair VF1-d and VR1-d (Ivanova *et al.* 2006) were used to amplify a fragment of the mitochondrial gene, and cytochrome c oxidase subunit 1 (COI) of the *Cyrtodactylus* and *Trimeresurus* samples. The primer pair 16Sar + 16Sbr (Palumbi *et al.* 1991) were used to amplify a fragment of the 16S gene of the *Gracixalus* samples. All primer sequences are

given in the respective publications. The PCR cycling followed Le *et al.* (2006). Successful amplifications were purified to eliminate PCR components using the GeneJET™ PCR Purification kit (Fermentas, Canada). Purified PCR products were sent to Macrogen Inc. (Seoul, South Korea) or FirstBase (Malaysia) for sequencing.

After sequences were aligned using 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 analysis (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 to resolve more highly converged trees. The optimal model for nucleotide evolution was set to the matrix as selected by Modeltest v3.7 (Posada & Crandall 1998). The cutoff point for the burn-in function was set in the Bayesian analysis, when -lnL scores reached stationarity in both runs. Nodal support was evaluated using Bootstrap replication (BP) as calculated in PAUP and posterior probability (PP) in MrBayes v3.2. Uncorrected pairwise divergences were calculated in PAUP*4.0b10.

2.3.4 Integrative approach

We used an integrative taxonomic approach by incorporating morphological, molecular, and ecological data to resolve the taxonomy of cryptic species complexes. This interdisciplinary approach is superior to traditional morphological descriptions (Dayrat 2005; Padial *et al.* 2010; Schlick-Steiner *et al.* 2010). Statistical analyses were performed in PAST Statistics software version 3.17 (Hammer *et al.* 2001). Multivariate Analyses were utilized to determine interspecific differences between new species and their relatives from Laos and Vietnam. Twenty two (genus *Gekko*) and 12 (genus *Cyrtodactylus*) of the 28 morphological characters were selected for correspondence analysis (CA) and cluster analysis with 1000 bootstrap replicates. Cluster analysis was based on the average linkage method. In addition, ecological data collected from each specimen in the field were provided to support for the niche segregation of each species. Genetic differences between undescribed taxa and described species were determined by phylogeny using uncorrected pairwise genetic distances. From all available lines of evidence, we drew conclusions as to which taxa should be described as new species.

2.3.5 Identification of priority areas for conservation.

Criteria for a hot spot determination include: 1) species richness, 2) number of rare and/or threatened species, 3) forest area and habitat quality, and 4) human disturbance. In each criterion, a higher number shows a better score (ranking score from 1 to 5). High rank areas were identified as priorities for conservation.

3. Publications of the dissertation

Publication 1

**No end in sight? Further new records of amphibians and reptiles from
Phong Nha-Ke Bang National Park, Quang Binh Province, Vietnam**

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Truong Quang Nguyen

Cuong The Pham

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Biodiversity Journal, 4 (2): 285-300.

Biodiversity Journal, 2013, 4 (2): 285-300

No end in sight? Further new records of amphibians and reptiles from Phong Nha – Ke Bang National Park, Quang Binh Province, Vietnam

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ABSTRACT

We report 11 new records of amphibian and reptile species and subspecies on the basis of newly collected specimens from the UNESCO World Heritage Site Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam: *Ingerophrynus macrotis*, *Limnonectes gyldenstolpei*, *Babina chapaensis*, *Theloderma corticale*, *T. stellatum*, *Scincella rufocaudata*, *Oligodon cinereus pallidocinctus*, *Parahelicops annamensis*, *Rhynchophis boulengeri*, *Sinomicrurus maccllellandii* and *Protobothrops mucrosquamatus*. The record of *T. corticale* from Phong Nha - Ke Bang National Park is the southernmost record generally known, that of *T. stellatum* the northernmost record within Vietnam, and, most remarkably, the finding of *Limnonectes gyldenstolpei* represents the first country record for Vietnam. In addition, we report the second known specimen and the first adult male of *Sphenomorphus tetradactylus*, a species recently described based on a single female only. At time, 151 species of amphibians and reptiles are known from Phong Nha - Ke Bang National Park, including 50 species of amphibians, 12 species of turtles, 31 species of lizards, and 58 species of snakes. In addition, an updated list of the local herpetofauna is provided, including recent taxonomic or nomenclatural changes.

KEY WORDS

herpetofauna; taxonomy; distribution; limestone habitat; Truong Son Mountain Range.

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INTRODUCTION

Phong Nha - Ke Bang National Park in the Truong Son Mountain Range in central Vietnam is known as one of the country's most famous protected areas in terms of herpetofaunal diversity. Ziegler & Herrmann (2000) published a first,

preliminary list of the karst forest area's herpetodiversity, based on own fieldwork, collection-based research and first Vietnamese reports, comprising 96 amphibian and reptile species. Four years later, the total number of amphibian and reptilian species known from the area as a result of further field work was increased to 128 species (Ziegler et al., 2004).

In a third updated herpetofaunal list for the area, Ziegler et al. (2006) reported of 140 amphibian and reptilian species, demonstrating a still ongoing increase in new species records. Ziegler et al. (2007) published a comprehensive review of the snake diversity of Phong Nha - Ke Bang including nine formerly not yet recorded species, thus increasing the total number of snakes known from Phong Nha - Ke Bang to 59 species. Hendrix et al. (2008) provided an updated anuran list comprising 47 taxa recorded for the Phong Nha - Ke Bang National Park, in which five species were recorded for the first time from that karst forest area. Recently, Ziegler & Vu (2009) published an updated checklist of the amphibians and reptiles from Phong Nha - Ke Bang National Park with a total of 138 species, including 45 species of amphibians and 93 species of reptiles. The total number of recorded amphibians and reptiles has decreased in this overview, because several doubtful or unconfirmed records, e.g., mentioned in Ziegler et al. (2007) and Hendrix et al. (2008), were removed from the list provided by Ziegler & Vu (2009), viz. *Bombina maxima* (Boulenger, 1905), *Eutropis chapaensis* (Bourret, 1937), *Scincella rupicola* (Smith, 1916), *Sphenomorphus buenloicus* (Darevsky et Nguyen, 1983), and *Malayemys subtrijuga* (Schlegel et Müller, 1844). In the years 2010 and 2011, additional herpetological field surveys were conducted in Phong Nha - Ke Bang National Park and extension area which revealed the existence of a number of so far not reported amphibian and reptile species. In addition to the eleven new herpetofaunal records for Phong Nha - Ke Bang National Park we provide an updated list of amphibians and reptiles occurring in this area.

MATERIALS AND METHODS

Field surveys were conducted in the Phong Nha - Ke Bang National Park area by Thomas Ziegler, Thanh Ngoc Vu, Kien Ngoc Dang, and Sladjana Miskovic (TZ and others) from June to July 2010, as well as from 12th July to 2nd August, and from 12th September to 1st October 2011 by Truong Quang Nguyen, Cuong The Pham, Dai Van Nguyen, Hang Thi An, and Kien Ngoc Dang (TQN and others) (Figs. 1, 2). After taking photographs, specimens were anaesthetized, fixed in 40-70% ethanol (am-



Figure 1. Map showing the location of Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam.

phibians) or 80-85% ethanol (reptiles) and subsequently stored in 70% ethanol. Measurements were taken with a digital calliper to the nearest 0.1 mm.

ABBREVIATIONS. a.s.l. = above sea level; SVL (snout-vent length) = from tip of snout to anterior margin of cloacal; TaL = tail length, from posterior margin of cloacal to tip of tail; terminology of morphological characters followed Nguyen et al. (2012) for amphibians and anuran webbing formula followed Glaw & Vences (2007) (except for forearm length, FAL = from axilla to elbow and hand length, HAL = from base of outer palmar tubercle to tip of finger III), Phung & Ziegler (2011) for lizards, and David et al. (2012) for snakes. Specimens were deposited in the collections of the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology Hanoi, Vietnam, Phong Nha - Ke Bang National Park (PNKB), Quang Binh Province, Vietnam, and the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany.

RESULTS

BUFONIDAE

Ingerophrynus macrotis (Boulenger, 1887)
Big-eyed Toad / Coc tai to (Fig. 3)

EXAMINED MATERIAL. One juvenile ZFMK 94263 collected by TZ and others during night time in June 2010 in the leaf litter of karst forest near Tam Co Cave, Tan Trach Commune, Bo Trach District and one adult female IEBR A.2013.7 (SVL: 58.7 mm) collected on 15 July 2011 by TQN and others in Da Lat forest, Thuong Hoa Commune, Minh Hoa District (17°40.124'N, 105°55.031'E, at an elevation of 312 m a.s.l.).

MORPHOLOGICAL CHARACTERS. SVL of adult female 58.7 mm; head wider than long (HW 20.3 mm, HL 18.7 mm); snout truncate, protruding, longer than horizontal diameter of eye (SL 6.6 mm, ED 5.9 mm); canthus rostralis rounded, loreal region concave; interorbital distance wider than internarial distance (IOD 4.7 mm, IND 4.1 mm); nostril closer to the tip of snout than to the eye (SN 1.7 mm; EN 3.6 mm); pupil rounded; tympanum distinct (TD 3.2 mm); parotoid gland 11.1 mm; vomerine teeth absent; tongue rounded posteriorly. Forelimbs: FAL 15.4 mm, HAL 30.1 mm; fingers free of webbing, relative length of fingers: II<IV<I<III; tips of fingers rounded, without discs; dermal fringe along outer finger absent; palmar tubercles distinct. Hindlimbs: femur longer than tibia and foot length (FML 26.0 mm, TBL 24.4 mm, FTL 23.2 mm); toes long and thin, relative length of toes: I<II<V<III<IV; tips of toes rounded; webbing basal; tarsal fold absent, dermal fringe along outer toe absent; subarticular tubercles present; inner metatarsal tubercle present (IMT 2.4 mm), outer metatarsal tubercle small (OMT 1.8 mm). Dorsal skin of body covered with tubercles or warts in different sizes, those on head smallest, few enlarged tubercles around vent.

Coloration in preservative: dorsal skin greyish brown with some symmetrical darker markings on snout and interorbital region; a V-shaped conversely mark in front of shoulder and dark spots near middle of back; dorsal tubercles on body, limbs grey to yellow; tympanum dark grey; upper lip with yellow and grey flecks. Ventral skin and concealed parts of limbs dirty greyish-yellow (determination after Inger et al., 1999).

DISTRIBUTION. In Vietnam, *I. macrotis* has been recorded from Thanh Hoa, Ha Tinh, Thua Thien-Hue, Da Nang, Quang Nam, Dak Lak, Lam Dong, and Dong Nai provinces. Our finding represents the first record for Phong Nha - Ke Bang National Park and for Quang Binh Province. Elsewhere, this species is known from northeastern India, Myanmar, Laos, Thailand, Cambodia, and Malaysia (Nguyen et al., 2009; Frost, 2013).

DICROGLOSSIDAE

Limnonectes gyldenstolpei (Andersson, 1916)
Gyldenstolpe's Frog / Ech gin-den-x-ton-pi (Fig. 4)

EXAMINED MATERIAL. One adult male IEBR A.2013.8 collected on 14 September 2011 in the evergreen forest, Hoa Son Commune, Minh Hoa District (17°42.166'N, 105°47.957'E, at an elevation of 449 m a.s.l.).

MORPHOLOGICAL CHARACTERS. SVL 69.6 mm; head longer than wide (HL 35.2 mm, HW 34.4 mm); snout longer than horizontal diameter of eye (SL 12.7 mm; ED 7.2 mm); canthus rostralis rounded; nostril directed laterally; loreal region concave; interorbital distance broader than internarial distance (IOD 8.5 mm, IND 7.3 mm); nostril closer to the tip of snout than to the eye (EN 7.1 mm; SN 4.7 mm); tympanum rounded, longer than tympanum-eye distance (TD 7.4 mm, TEY 6.4 mm); vomerine teeth present; tongue notched posteriorly; vocal sac indistinct in males. Forelimbs: FAL 13 mm, HAL 32 mm; fingers free of webbing, relative length of fingers: II<IV<I<III; tips of fingers rounded, without discs; dermal fringe along outer finger absent; palmar tubercles present; nuptial pad present in males. Hindlimbs: femur shorter than tibia and foot length (FML 32.7 mm, TBL 36.7 mm, FTL 34.7 mm); toes long and thin, relative length of toes: I<II<V<III<IV; tips of toes rounded; webbing formula: Io(0)-(1)iIIo(0)-(1)iiiIo(1/2)-(1)iIVo(2)-(0) iV; dermal fringe along outer toe absent; subarticular tubercles present; inner metatarsal tubercle present (IMT 4.3 mm), outer metatarsal tubercle indistinct. Dorsal skin of head smooth with a swollen flap (10.6 mm length and 10.2 mm width); dorsal surface of forelimbs, thigh and tarsus smooth; supratympanic fold distinct, from eye to shoulder; ventral surface smooth.

Coloration in preservative: head grey with a cream broad stripe between eyes; dorsum brown; dark dorsolateral spots; dark bars present on upper surface of forelimbs, tibia and thigh; venter cream with dark spots on throat (determination after Taylor, 1962; Ohler & Dubois, 1999).

DISTRIBUTION. The specimen from Phong Nha - Ke Bang National Park represents the first country record of *Limnonectes gyldenstolpei* for Vietnam. Elsewhere, this species is known from Laos, Cambodia, and Thailand (Frost, 2013).

REMARKS. The male specimen differs from the juvenile female in the description of Ohler & Dubois (1999) by having the tibia longer than femur (TBL 36.7 mm, FML 32.7 mm versus TBL 11.6 mm, FML 11.7 mm).

RANIDAE

Babina chapaensis (Bourret, 1937)

Chapa Frog / Chang sa pa (Fig. 5)

EXAMINED MATERIAL. Two adult males IEBR A.2013.9 and ZFMK 94258, one adult female IEBR A.2013.10 collected on 14 September 2011 and one adult male ZFMK 94259 collected by TQN and others on 16 September 2011 in the forest near Cha Lo Village, Hoa Son Commune, Minh Hoa District (17°42.213'N, 105°47.748'E, at an elevation of 570 m a.s.l.).

MORPHOLOGICAL CHARACTERS. SVL 43.0-46.0 mm in males (mean \pm SE 44.2 \pm 1.6, N = 3), 56.9 mm in the female; head longer than wide (HL 17.3-20.4 mm, HW 14.9-18.0 mm); snout longer than horizontal diameter of eye (SL 6.9-7.8 mm; ED 4.7-5.6 mm); canthus rostralis rounded; nostril directed laterally; loreal region concave; interorbital distance narrower than internarial distance (IOD 3.3-4.5 mm, IND 5.1-6.3 mm); nostril closer to the eye than to the tip of snout (EN 2.9-4.0 mm; SN 3.5-4.2 mm); tympanum rounded, longer than tympanum-eye distance (TD 3.9-4.2 mm, TEY 0.3-1.4 mm); vomerine teeth present; tongue notched posteriorly; vocal sac present in males. Forelimbs: FAL 8.8-10.3 mm, HAL 20.2-23.7 mm; fingers free of webbing, relative length of fingers: II<I=IV<III; tips of fingers rounded, without discs; dermal fringe along outer finger absent; palmar tubercles distinct; nup-

tial pad present in males. Hindlimbs: femur shorter than tibia and foot length (FML 21.4-25.2 mm, TBL 24.5-29.5 mm, FTL 24.1-29.2 mm); toes long and thin, relative length of toes: I<II<V<III<IV; tips of toes rounded; webbing formula: Io(1)-(1)iIIo(1/2)-(2)iIIIo(1)-(2)iIVo(2)-(1/2)iV; dermal fringe along outer toe absent; subarticular tubercles present; inner metatarsal tubercle present (IMT 2.2-2.5 mm), outer metatarsal tubercle indistinct.

Dorsal surface of head and dorsum smooth; dorsolateral fold distinct; lateral sides smooth; a small fold present along arm; ventral surface smooth. Coloration in preservative: head and dorsum light brown with a cream vertebral stripe, edged in dark brown, running from behind the eye to vent; posterior part of dorsum with some dark spots; upper jaw with a cream stripe, from below the nostril to axilla; dorsolateral fold yellowish brown, edged in black laterally; upper surface of tibia and thigh with some dark bars; venter cream (determination after Bourret, 1942; Chuaynkern et al., 2010).

DISTRIBUTION. In Vietnam, *B. chapaensis* has been recorded from Lao Cai, Bac Giang, Ha Tinh, Kon Tum, Gia Lai, and Dak Lak provinces (Nguyen et al., 2009). This is the first record of this species from Phong Nha - Ke Bang National Park as well as from Quang Binh Province. Elsewhere, this species is known from Laos and Thailand (Nguyen et al., 2009).

RHACOPHORIDAE

Theلودerma corticale (Boulenger, 1903)

Tonkin Bug-eyed Frog / Ech cay san bac bo (Fig. 6)

EXAMINED MATERIAL. Three adult males IEBR A.2013.11, ZFMK 94262 collected on 21 July 2011 by TQN and others in Da Lat forest, Thuong Hoa Commune, Minh Hoa District (17°39.032'N, 105°54.774'E, at an elevation of 516 m a.s.l.) and PN-KB 2011.204 collected by TQN and others on 28 July 2011 in Cha Noi forest, Xuan Trach Commune, Bo Trach District (17°37.758'N, 106°05.893'E, at an elevation of 470 m a.s.l.).

MORPHOLOGICAL CHARACTERS. SVL of males 61.3-69.7 mm; head wider than long (HL 24.1-27.5 mm, HW 26.3-28.6 mm); snout longer than horizontal diameter of eye (SL 9.0-10.0 mm; ED 6.2 mm); canthus rostralis rounded; loreal region concave; interorbital distance wider than internarial dis-



Figure 2. Karst forest in Thung Hoa Commune, extension area of Phong Nha - Ke Bang National Park. Figure 3. Big-eyed Toad, *Ingerophrynus macrotis*. Figure 4. Gyldenstolpe's Frog, *Limnonectes gyldenstolpei*. Figure 5. Chapa Frog *Babina chapaensis*. Figure 6. Tonkin Bug-eyed Frog, *Theلودerma corticale*. Figure 7. Taylor's Bug-eyed Frog, *Theلودerma stellularum*. Photos: T. Q. Nguyen & T. Ziegler.

tance (IOD 6.1-6.5 mm, IND 3.7-4.4 mm); nostril closer to tip of snout than to eye (SN 2.5 mm; EN 7.1-8.3 mm); vocal sac absent; tympanum oval, greater than tympanum-eye distance (TD 4.0-4.9 mm, TEY 3.3-3.9 mm); vomerine teeth present; tongue notched posteriorly. Forelimbs: FAL 12.2-14.8 mm, HAL 33.2-34.7 mm; relative length of fingers: I<II<IV<III; tips of fingers and toes enlarged into round discs; webbing present at base of fingers III and IV; dermal fringe along outer finger present; palmar tubercles distinct; nuptial pad present. Hindlimbs: tibia longer than femur and foot length (TBL 31.8-34.0 mm, FML 25.5-32.2 mm, FTL 27.8-30.5 mm); relative length of toes: I<II<III<V<IV; webbing formula: Io(0)-(0)iIo(0)-(0)iIIo(0)-(1)iIVo(1)-(0)iV; dermal fringe along outer toe absent; subarticular tubercles present; inner metatarsal tubercle present (IMT 3.1-4.9 mm); outer metatarsal tubercle absent.

Dorsal surface of body covered with tubercles or warts of different sizes, those on head and back biggest; ventral skin with small tubercles. Coloration in preservative: dorsal colour olive-green marbled with red-brown spots; dark brown bars present on upper surface of fore and hind limbs; ventral surface greyish yellow (determination after Inger et al., 1999; Orlov et al., 2006).

DISTRIBUTION. *T. corticale* is currently known only from northern Vietnam: Ha Giang, Tuyen Quang, Cao Bang, Lang Son, Vinh Phuc, and Son La provinces (Nguyen et al., 2009; Frost, 2013). This is a new record for Phong Nha - Ke Bang National Park and for Quang Binh Province as well as the southernmost known record of the species.

***Theloderma stellatum* Taylor, 1962**

Taylor's Bug-eyed Frog / Ech cay san tay-lo (Fig. 7)

EXAMINED MATERIAL. One adult female ZFMK 94261 collected by TZ and others during night time on a tree trunk nearby a forest stream and one adult male IEBR A.2013.12 collected by TQN and others on 28 July 2011 in Cha Noi forest, Xuan Trach Commune, Bo Trach District (17°37.649'N, 106°05.806'E, at an elevation of 517 m a.s.l.).

MORPHOLOGICAL CHARACTERS. SVL 32.7-35.0 mm; head as long as wide (HL 13.5-13.9 mm, HW 13.6-14.0 mm); snout longer than horizontal diameter of eye (SL 5.3-5.4 mm; ED 4.5-4.7 mm); canthus rostralis rounded; loreal region concave;

interorbital distance wider than internarial distance (IOD 3.6-3.9 mm, IND 2.0-2.1 mm); nostril closer to tip of snout than to eye (SN 1.6-1.7 mm; EN 3.2-4.0 mm); tympanum rounded, greater than tympanum-eye distance (TD 2.2-2.9 mm, TEY 1.0 mm); vomerine teeth present; tongue notched posteriorly. Forelimbs: FAL 7.9-8.4 mm, HAL 17.5-17.9 mm; relative length of fingers: I<II<IV<III; tip of fingers and toes enlarged into large discs; webbing basal; dermal fringe along outer finger absent; palmar tubercles indistinct; nuptial pad present. Hindlimbs: tibia longer than femur and foot length (TBL 17.6-18.3 mm, FML 16.6-16.9 mm, FTL 15.6-16.0 mm); relative length of toes: I<II<III=V<IV; webbing formula: Io(1)-(1)iIo(1/2)-(2)iIIo(1)-(2)iIVo(2)-(1/2)iV; dermal fringe along outer toe absent; subarticular tubercles present; inner metatarsal tubercle present (IMT 1.3-1.5 mm).

Dorsal skin of head and body, upper surface of fore-arm, tibia, and tarsus, with tubercles covered in whitish granular asperities; ventral skin smooth. Coloration in preservative: dorsal head and body brownish with cream speckles; black spots present on snout and black marking present between shoulders; upper surface of thigh, tibia, tarsus, and foot with transverse dark bars; discs pinkish; chin and venter dark brown with light flecks (determination after Taylor, 1962; Inger et al., 1999; Orlov et al., 2006; Nguyen & Nguyen, 2008).

DISTRIBUTION. In Vietnam, *T. stellatum* has been recorded from Kon Tum, Gia Lai, Dak Lak, Dong Nai, and Kien Giang provinces (Nguyen et al., 2009). This is the first record of the species from Phong Nha - Ke Bang National Park as well as from Quang Binh Province, which at the same time is the northernmost country record. Elsewhere, this species is known from Thailand, southern Laos and Cambodia (Nguyen et al., 2009).

SCINCIDAE

***Scincella rufocaudata* (Darevsky et Nguyen, 1983)**

Red-tailed ground skink / Than lan phe-no duoi do (Fig. 8)

EXAMINED MATERIAL. One adult male IEBR A.2013.13 collected on 21 July 2011 by TQN and others in Da Lat forest, Thuong Hoa Commune, Minh Hoa District (17°39.665'N, 105°55.800'E, at

an elevation of 448 m a.s.l.), 2 adult females IEBR A.2013.14 collected on 29 July 2011 by TQN and others in Khe Ma forest, Thuong Hoa Commune, Minh Hoa District (17°39.410'N, 106°03.592'E, at an elevation of 300 m a.s.l.), and ZFMK 94256 collected on 20 July 2011 by TQN and others in Hoa Son Commune, Minh Hoa District (17°39.120'N, 105°59.678'E, at an elevation of 250 m a.s.l.) and one juvenile ZFMK 94257 collected on 18 July 2011 by TQN and others in Thuong Hoa Commune, Minh Hoa District (17°40.057'N, 105°56.049'E, at an elevation of 513 m a.s.l.).

MORPHOLOGICAL CHARACTERS. SVL 45.5 mm in the male, 45.9-47.2 mm in females; TaL 51.0 mm in one female, regenerated or lost in others; snout obtuse; rostral wider than long, nostril in the nasal; frontonasal large; prefrontals separated from each other; frontal longer than frontoparietal; parietals large, in contact posteriorly; nuchals absent; supraoculars 4; supraciliaries 8; loreals 2; supralabials 7; temporals 2 + 2, upper overlapped by lower one; infralabials 6; ear-opening oval; lower eyelid with a transparent window; midbody scales in 30-34 rows, smooth; paravertebral scales 67-69; ventral scales 61-66; enlarged preloacals 2; limbs pentadactyl; subdigital lamellae under fourth toe 15-20.

Coloration in preservative: dorsal head and body brown with a row of dark vertebral spots, a black stripe present on upper part of the side; upper surface of tail reddish; venter cream (determination after Stuart & Emmett, 2006; Nguyen et al., 2011a).

DISTRIBUTION. In Vietnam, *S. rufocaudata* is known from Thua Thien - Hue, Quang Nam, Kon Tum, Gia Lai, Dak Lak, and Ba Ria - Vung Tau provinces (Nguyen et al., 2009). Records of this species in northern Vietnam (Bac Kan, Thai Nguyen and Vinh Phuc provinces) were reidentified as *S. tonkinensis* by Nguyen et al. (2011a). Elsewhere, this species is recorded from Laos and Cambodia (Nguyen et al., 2009).

REMARKS. The red-tailed ground skink was transferred from the genus *Sphenomorphus* to *Scincella* by Nguyen et al. (2011a).

Sphenomorphus tetradactylus (Darevsky et Orlov, 2005)

Four-fingered skink / Than lan phe-no bon ngon (Fig. 9)

EXAMINED MATERIAL. One adult male IEBR A.2013.15 collected on 17 July 2011 by TQN and others in Thuong Hoa Commune, Minh Hoa District (17°40.057'N, 105°56.049'E, at an elevation of 513 m a.s.l.).

MORPHOLOGICAL CHARACTERS. Size small, SVL 36 mm, TaL 49.9 mm, tail tip lost; rostral wider than high, in contact with frontonasal; frontonasal broader than long; prefrontals small, separated from frontal; supraoculars 4/4, first two in contact with frontal on each side; loreal single; lower eyelid scaly; external ear openings hidden with slightly recessed auricular depression; supraciliaries 7/7, first in contact with frontal; supralabials 6/6, third to fifth



8



9

Figure 8. Red-tailed Ground Skink *Scincella rufocaudata*. Figure 9. Four-fingered Skink *Sphenomorphus tetradactylus*. Photos: K. N. Dang & T. Q. Nguyen.

below the eye; infralabials 7/7; nuchals 2/3; mid-body scale rows 20; paravertebral scales 48; ventral scales 51; enlarged preloacals 2; limbs very short, forelimb tetradactyl, first shortest; hind limbs pentadactyl; subdigital lamellae under fourth toe 9/10.

Coloration in preservative: dorsal head and body brown with longitudinal dark stripes along dorsum; venter cream with brown spots; legs dark above with indistinct black marks; free margins of upper and lower eyelids not edged in white (determination after Darevsky & Orlov, 2005; Nguyen et al., 2011a).

DISTRIBUTION. *S. tetradactylus* is currently known only from Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam (Nguyen et al., 2011a).

REMARKS. *S. tetradactylus* was originally described by Darevsky & Orlov (2005) as a member of the genus *Leptoseps* based on the holotype collected from Phong Nha - Ke Bang National Park. However, Nguyen et al. (2011a) removed this species from the genus *Leptoseps* to the genus *Sphenomorphus*. This is the second known specimen and the first reported adult male of the species.

COLUBRIDAE

Oligodon cinereus pallidocinctus (Bourret, 1934)
Guenther's Kukri Snake / Ran khiem xam (Fig. 10)

EXAMINED MATERIAL. One male, PNKB S.0154, collected by K.D. Ngoc in 2009.

MORPHOLOGICAL CHARACTERS. SVL 495 mm; TaL 90 mm; maxillary teeth 16/16; loreal 1/1; supralabials 8/8, fourth and fifth entering orbit; infralabials 8/8; preoculars 2; postoculars 2; temporals 1/2+2; dorsal scale rows 17 : 17 : 15, smooth; cloacal entire; ventral scales 3 + 167, subcaudals 42, divided.

Coloration in preservative: dorsal head with a grey chevron; dorsal surface of body yellowish brown with 38 grey, black-edged bands on body, 6 bands on tail; ventral surface cream with dark spots (identification after Bourret, 1936; Smith, 1943).

DISTRIBUTION. In Vietnam, this subspecies is known from Thua Thien - Hue, Ba Ria - Vung Tau, and Ho Chi Minh City ("Form IV" in Smith, 1943). This is the first record of *O. cinereus pallidocinctus* from Phong Nha - Ke Bang National Park, Quang Binh Province.

REMARKS. The male specimen differs from the description of Smith (1943) in having more light

bands on body (38 versus 27-34) and more bands on tail (6 versus 3-4).

Parahelicops annamensis Bourret, 1934
Annam Keelback / Ran binh mui trung bo (Fig. 11)

EXAMINED MATERIAL. Two males IEBR A.2013.16-A.2013.17 collected on 23 July 2011 by TQN and others in Hoa Son Commune, Minh Hoa District (17°42.612'N, 105°52.571'E, at an elevation of 537 m a.s.l.) and one female ZFMK 94255 collected on 16 September 2011 in Hoa Son Commune, Minh Hoa District (17°42.208'N, 105°46.970'E, at an elevation of 641 m a.s.l.).

MORPHOLOGICAL CHARACTERS. SVL 358-430 mm in males, 455 mm in the female; TaL 165-177 mm in males, 102 mm in the female; head distinct from neck; maxillary teeth 21/21; rostral flat, broader than high; nostril in the nasal; internasals narrowed anteriorly; prefrontals 2/2, slightly broader than long; frontal narrowed posteriorly, about half the length of the parietals; loreal single, elongated; preoculars 2/2, upper larger; postoculars 2/2; temporals 1 + 1; supralabials 8 or 9; fourth to sixth (in one male) or fifth and sixth bordering orbit; infralabials 10, first to fifth in contact with first chin shield; first pair of chin shield shorter than second pair, second pair divided by an elongated scale posteriorly; body scales rows 19 : 17 : 17, median rows strongly keeled posteriorly; dorsal scales on tail strongly keeled, eight longitudinal keel rows at base, decreasing to four rows distally; ventrals 167-169; cloacal divided; subcaudals divided, 95 and 121 in two males, 51 in the female.

Coloration in preservative: dorsal head with irregular brown markings; a yellow stripe present from posterior margin of eye to neck, continuing onto body as broken dorsolateral stripe, being less distinct posteriorly; tail iridescent yellowish-brown; ventral and subcaudal surface cream, outer margin of ventrals dark brown (determination after Bourret, 1936; Stuart, 2006; Ziegler et al., 2007).

DISTRIBUTION. In Vietnam, the species is only known from Da Nang and Kon Tum provinces (see Stuart, 2006; Nguyen et al., 2009). This is the first record from Phong Nha - Ke Bang National Park as well as from Quang Binh Province. Elsewhere, this species is reported from Laos (Xe Kong) (Nguyen et al., 2009).

REMARKS. *P. annamensis* was previously listed as *Amphiesma* sp. by Ziegler & Vu (2009).

Rhynchophis boulengeri Mocquard, 1897
Rhinoceros snake / Ran voi (Fig. 12)

EXAMINED MATERIAL. Two males deposited in PNKB.

MORPHOLOGICAL CHARACTERS. SVL 940-950 mm; TaL 350-360 mm; presence of a long pointed nasal appendage covered with small scales; inter-nasals much smaller than the prefrontals; frontal narrowed posteriorly; loreal single, longer than wide; preocular single; postoculars 2; temporals 2+3; supralabials 8 or 10, fourth to fifth or fifth to seventh in contact with the eye; infralabials 11; midbody scale rows 19, slightly keeled dorsally; ventral scales 1 + 211 or 1 + 208; subcaudal scales 122 or 126, divided; cloacal plate divided.

Coloration in preservative: dorsum green, venter paler; thin black stripe behind eye; interstitial skin on the sides of the body bluish-black and white; light stripes on subcaudal fold (determination after Smith, 1943; Nguyen et al., 2011b).

DISTRIBUTION. In Vietnam, *R. boulengeri* has been recorded from the provinces of Son La, Thai Nguyen, Vinh Phuc, Ha Noi, Quang Ninh, Hai Phong, and Ha Tinh (Nguyen et al., 2009; Nguyen et al., 2011b). This is a new record for Phong Nha - Ke Bang National Park as well as for Quang Binh Province. Elsewhere, this species is known only from China (Nguyen et al., 2009).

ELAPIDAE

Sinomicrurus maccllellandii (Reinhardt, 1844)
MacClelland's Coral Snake/ Ran la kho thuong (Figs. 13-14)

MORPHOLOGICAL CHARACTERS. Morphological characters based on photographic record: vertebral scales not larger than adjacent scales; subcaudals divided; dorsal surface reddish brown with 31 black cross-bands from behind head to tip of tail; head black with a wide, white cross-band behind eyes; ventral surface cream with black bands and black squarish marks (determination after Ziegler et al., 2007).

DISTRIBUTION. In Vietnam, this species is known from Lao Cai and Cao Bang provinces in the North southwards to Lam Dong and Dong Nai provinces (Nguyen et al., 2009). This is the first confirmed record for Phong Nha - Ke Bang National Park. Elsewhere, this species is reported

from India, Nepal, Myanmar, Thailand, China, Japan, Taiwan (Nguyen et al., 2009).

REMARKS. *S. maccllellandii* was mentioned as unconfirmed record for Phong Nha - Ke Bang by Ziegler et al. (2007) and thus was subsequently removed from the herpetofaunal list of Phong Nha -Ke Bang by Ziegler & Vu (2009).

VIPERIDAE

Protobothrops mucrosquamatus (Cantor, 1839)
Chinese Habu / Ran luc cuom (Fig. 15)

EXAMINED MATERIAL. One specimen was found at night of 27 October 2009 by TZ and others in the vegetation nearby a forest path in the Cha Noi region and one male IEBR A.2013.18 (PN-KB 2011.51), collected on 16 July 2011 by TQN and others in Thuong Hoa Commune, Minh Hoa District (17°40.405'N, 105°56.656'E, at an elevation of 260 m a.s.l.).

MORPHOLOGICAL CHARACTERS. SVL 950 mm; TaL 225 mm; head long, narrow; single loreal pit; supralabials 10; gular scales smooth; mental bordering infralabial posteriorly; elongated subocular scales, divided from supralabials; dorsal scales strongly keeled, midbody scale rows 27; ventral scales 3 + 216; subcaudals 98; cloacal undivided.

Coloration in preservative: dorsal head brown, paler below; dorsum greyish brown, with a series of large brown, dark-edged spots; ventral surface cream, with light brown, light areas appearing as squarish spots; dorsal tail light brown, with a series of conspicuous black spots (determination after Smith, 1943; Ziegler et al., 2007; Nguyen et al., 2011b).

DISTRIBUTION. In Vietnam, *P. mucrosquamatus* has been recorded from Lao Cai, Ha Giang, Cao Bang, Bac Kan, Lang Son, Thai Nguyen, Vinh Phuc, Quang Ninh, Hai Phong, Hai Duong, Ha Noi, Ninh Binh, Nghe An, Ha Tinh, Quang Tri, Thua Thien-Hue, Kon Tum, and Gia Lai provinces (Nguyen et al., 2009). This is the first record of the species for Phong Nha - Ke Bang National Park and for Quang Binh Province. Elsewhere, this species is known from India, Bangladesh, China, Taiwan, and Myanmar (Nguyen et al., 2009).

REMARKS. The male specimen differs from the description of Smith (1943) in having more subcaudals (98 versus 76-91).



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Figure 10. Guenther's Kukri Snake, *Oligodon cinereus pallidocinctus*. Figure 11. Annam Keelback, *Parahelicops annamensis*. Photos: K. N. Dang & T. Q. Nguyen. Figure 12. Rhinoceros Snake, *Rhynchophis boulengeri*. Figures 13-14. MacClelland's Coral Snake, *Sinomicrurus macclellandii*. Figure 15. Chinese Habu, *Protobothrops mucrosquamatus*. Photos: K. N. Dang, T. Q. Nguyen & T. Ziegler.

Check-list of amphibians and reptiles recorded from Phong Nha - Ke Bang

Current check-list of amphibians and reptiles recorded from Phong Nha - Ke Bang after Ziegler & Vu (2009), including the herein listed new records (*), additions (**), according to Ziegler et al. (2010), Nguyen et al. (2011a), Hoang et al. (2012), and taxonomic reassignments (***) according to Blanck et al. (2006), Stuart & Fritz (2008), Fritz et al. (2008, 2010), Inger & Stuart (2010), McLeod (2010), Yu et al. (2010), David et al. (2011), Nguyen et al. (2011b,), Ohler et al. (2011), Rösler et al. (2011), Kuraishi et al. (2012), Uetz (2013), Frost (2013), Siler et al. (2013), and Patrick David (pers. comm. to replace *Amphiesma khasiense* in central Vietnam with *A. boulengeri*); snake species which have been previously listed but could not be confirmed as occurring in Phong Nha - Ke Bang by Ziegler et al. (2007) are excluded from the list: *Typhlops diardi* Schlegel, 1839, *Calamaria pavementata* Duméril, Bibron et Duméril, 1854, *C. septentrionalis* Boulenger, 1890, *Dendrelaphis pictus* (Gmelin, 1789), *Lycodon septentrionalis* (Günther, 1875), *Orthriophis moellendorffi* (Boettger, 1886), and *Sibynophis collaris* (Gray, 1853).

AMPHIBIA

ANURA

MEGOPHRYIDAE

Brachytarsophrys intermedia (Smith, 1921)
Leptobrachium chapaense (Bourret, 1937)
Leptotalax aereus Rowley, Stuart, Richards, Phimmachak et Sivongxay, 2010 (***)
Ophryophryne hanshi Ohler, 2003
Xenophrys major (Boulenger, 1908)

BUFONIDAE

Duttaphrynus melanostictus (Schneider, 1799)
Ingerophrynus galeatus (Günther, 1864)
Ingerophrynus macrotis (Boulenger, 1887) (*)

HYLIDAE

Hyla simplex Boettger, 1901

MICROHYLIDAE

Kalophrynus interlineatus (Blyth, 1854)

Kaloula pulchra Gray, 1831
Microhyla berdmorei (Blyth, 1856)
Microhyla butleri Boulenger, 1900
Microhyla fissipes Boulenger, 1884
Microhyla heymonsi Vogt, 1911
Microhyla inornata (Boulenger, 1890)
Microhyla marmorata Bain et Nguyen, 2004
Microhyla pulchra (Hallowell, 1861)

DICROGLOSSIDAE

Fejervarya limnocharis (Gravenhorst, 1829)
Hoplobatrachus rugulosus (Wiegmann, 1834) (***)
Limnonectes bannaensis Je, Fei et Jiang, 2007 (***)
Limnonectes gyldenstolpei (Andersson, 1916) (*)
Limnonectes limborgi (Sclater, 1892) (***)
Limnonectes poilani (Bourret, 1942)
Occidozyga lima (Gravenhorst, 1829)
Occidozyga martensii (Peters, 1867)

RANIDAE

Amolops cremnobatus Inger et Kottelat, 1998
Babina chapaensis (Bourret, 1937) (*)
Hylarana attigua (Inger, Orlov et Darevsky, 1999)
Hylarana guentheri (Boulenger, 1882)
Hylarana maosonensis Bourret, 1937
Hylarana nigrovittata (Blyth, 1856)
Odorrana chloronota (Günther, 1876)
Odorrana tiannanensis (Yang et Li, 1980)
Rana johnsi Smith, 1921

RHACOPHORIDAE

Chiromantis vittatus (Boulenger, 1887)
Gracixalus quyeti (Nguyen, Hendrix, Böhme, Vu, et Ziegler, 2008)
Kurixalus banaensis (Bourret, 1939)
Kurixalus bisacculus (Taylor, 1962) (***)
Polypedates megacephalus Hallowell, 1861 (***)
Polypedates mutus (Smith, 1940)
Rhacophorus annamensis Smith, 1924
Rhacophorus dennysi Blanford, 1881
Rhacophorus exechopygus Inger, Orlov et Darevsky, 1999
Rhacophorus kio Ohler et Delorme, 2006
Rhacophorus orlovi Ziegler et Köhler, 2001
Rhacophorus rhodopus Liu et Hu, 1960
Theloderma asperum (Boulenger, 1886)
Theloderma corticale (Boulenger, 1903) (*)
Theloderma stellatum Taylor, 1962 (*)

REPTILIA

TESTUDINES

PLATYSTERNIDAE

Platysternon megacephalum Gray, 1831

GEOEMYDIDAE

Cuora cyclornata Blanck, McCord et Le, 2006 (***)

Cuora galbinifrons Bourret, 1939

Cuora mouhotii (Gray, 1862)

Cyclemys oldhamii Gray, 1863 (***)

Heosemys grandis (Gray, 1860)

Mauremys mutica (Cantor, 1842)

Ocadia sinensis (Gray, 1834)

Sacalia quadriocellata (Siebenrock, 1903)

TESTUDINIDAE

Manouria impressa (Günther, 1882)

TRIONYCHIDAE

Palea steindachneri (Siebenrock, 1906)

Pelodiscus cf. *parviformis* Tang, 1997 (***)

SQUAMATA: SAURIA

GEKKONIDAE

Cyrtodactylus cryptus Heidrich, Rösler, Vu, Böhme et Ziegler, 2007

Cyrtodactylus phongnhakebangensis Ziegler, Rösler, Herrmann et Vu, 2003

Cyrtodactylus roesleri Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh et Schmitz, 2010 (**)

Gehyra mutilata (Wiegmann, 1834)

Gekko palmatus Boulenger, 1907

Gekko reevesii Gray, 1831 (***)

Gekko scientiadventura Rösler, Ziegler, Vu, Herrmann et Böhme, 2004

Hemidactylus frenatus Duméril et Bibron, 1836

Ptychozoon lionotum Annandale, 1905 (**)

AGAMIDAE

Acanthosaura lepidogaster (Cuvier, 1829)

Calotes emma Gray, 1845

Calotes versicolor (Daudin, 1802)

Physignathus cocincinus Cuvier, 1829

ANGUIDAE

Dopasia gracilis Gray, 1845 (**)

VARANIDAE

Varanus salvator (Laurenti, 1768)

LACERTIDAE

Takydromus hani Chou, Nguyen et Pauwels, 2001

Takydromus kuehnei van Denburgh, 1909

Takydromus sexlineatus Daudin, 1802

SCINCIDAE

Eutropis longicaudata (Hallowell, 1856)

Eutropis macularia (Blyth, 1853)

Eutropis multifasciata (Kuhl, 1820)

Lygosoma boehmei Ziegler, Schmitz, Heidrich, Vu et Nguyen, 2007

Lygosoma quadrupes (Linnaeus, 1766)

Plestiodon elegans (Boulenger, 1887)

Plestiodon quadrilineatus Blyth, 1853

Scincella melanosticta (Boulenger, 1887)

Scincella rufocaudata (Darevsky et Nguyen, 1983) (*)

Sphenomorphus indicus (Gray, 1853)

Sphenomorphus tetradactylus (Darevsky et Orlov, 2005) (***)

Tropidophorus cocincinensis Duméril et Bibron, 1839

Tropidophorus noggei Ziegler, Vu et Bui, 2005

SQUAMATA: SERPENTES

TYPHLOPIDAE

Ramphotyphlops braminus (Daudin, 1803)

XENOPELTIDAE

Xenopeltis hainanensis Hu et Zhao, 1972

Xenopeltis unicolor Boie, 1827

BOIDAE

Brogammerus reticulatus (Schneider, 1801) (***)

Python molurus (Linnaeus, 1758)

XENODERMATIDAE

Fimbrios smithi Ziegler, David, Miralles, Doan et Nguyen, 2008

COLUBRIDAE

- Ahaetulla prasina* (Boie, 1827)
Amphiesma andreae Ziegler et Le, 2006
Amphiesma boulengeri (Gressitt, 1937) (***)
Amphiesma leucomystax David, Bain, Nguyen, Orlov, Vogel, Vu et Ziegler, 2007
Amphiesma stolatum (Linnaeus, 1758)
Boiga bourreti Tillack, Ziegler et Le, 2004
Boiga guangxiensis Wen, 1998
Boiga multomaculata (Boie, 1827)
Calamaria thanhi Ziegler & Le, 2005
Chrysopelea ornata (Shaw, 1802)
Coelognathus radiatus (Boie, 1827)
Cyclophiops major (Günther, 1858)
Cyclophiops multicinctus (Roux, 1907)
Dendrelaphis ngansonensis (Bourret, 1935)
Dryocalamus davisonii (Blanford, 1878)
Enhydryis plumbea (Boie, 1827)
Liopeltis frenatus (Günther, 1858)
Lycodon fasciatus (Anderson, 1897)
Lycodon futsingensis (Pope, 1928)
Lycodon paucifasciatus Rendahl, 1943
Lycodon cf. rufozonatum Cantor, 1842 (***)
Lycodon ruhstrati (Fischer, 1886)
Oligodon chinensis (Günther, 1888)
Oligodon cinereus pallidocinctus (Bourret, 1934) (*)
Oreocryptophis porphyraceus (Cantor, 1839)
Orthriophis taeniurus Cope, 1861
Parahelicops annamensis Bourret, 1934 (*)
Pareas carinatus Wagler, 1830
Pareas hamptoni (Boulenger, 1905)
Pareas macularius Blyth, 1868
Pareas margaritophorus (Jan, 1866)
Psammodynastes pulverulentus (Boie, 1827)
Pseudoxenodon macrops (Blyth, 1854)
Ptyas korros (Schlegel, 1837)
Ptyas mucosa (Linnaeus, 1758)
Rhabdophis chrysargos (Schlegel, 1837)
Rhabdophis subminiatus (Schlegel, 1837)
Rhadinophis prasinus (Blyth, 1854) (***)
Rhynchophis boulengeri Mocquard, 1897 (*)
Sinonatrix percarinata (Boulenger, 1899)
Xenochrophis flavipunctatus (Hallowell, 1860)

ELAPIDAE

- Bungarus candidus* (Linnaeus, 1758)
Bungarus fasciatus (Schneider, 1801)
Naja cf. atra Cantor, 1842

- Ophiophagus hannah* (Cantor, 1836)
Sinomicrurus maccllellandii (Reinhardt, 1844) (*)

VIPERIDAE

- Protobothrops cornutus* (Smith, 1930)
Protobothrops mucrosquamatus (Cantor, 1839) (*)
Protobothrops sieversorum (Ziegler, Herrmann, David, Orlov et Pauwels, 2000)
Trimeresurus albolabris (Gray, 1842) (***)
Trimeresurus truongsongensis (Orlov, Ryabov, Bui et Ho, 2004) (***)
Trimeresurus vogeli (David, Vidal et Pauwels, 2001) (***)

DISCUSSION

This study brings the confirmed species number of amphibians and reptiles recorded from Phong Nha - Ke Bang National Park to 151, including 50 species of amphibians (5 Megophryidae, 3 Bufonidae, 1 Hylidae, 9 Microhylidae, 8 Dicroglossidae, 9 Ranidae, 15 Rhacophoridae), 12 species of turtles (1 Platysternidae, 8 Geoemydidae, 1 Testudinidae, 2 Trionychidae), 31 species of lizards (9 Gekkonidae, 4 Agamidae, 1 Anguidae, 1 Varanidae, 3 Lacertidae, 13 Scincidae), and 58 species of snakes (1 Typhlopidae, 2 Xenopeltidae, 2 Boidae, 1 Xenodermatidae, 41 Colubridae, 5 Elapidae, 6 Viperidae), see also fig. 16. An updated list, including recent taxonomic/nomenclatural changes since the last review by Ziegler & Vu (2009), is provided. The research history of the herpetofauna of Phong Nha - Ke Bang clearly shows that even after more than a decade of very intensive herpetological surveys, additional species can be recorded or even discovered as new to science. Since the description of the first herpetological discovery from Phong Nha - Ke Bang, *Cyrtodactylus phongnhakebangensis* by Ziegler et al. (2002), a series of new species descriptions took place to date, amongst others eight snake and four gecko taxa, to mention only the most outstanding examples (see overview in Ziegler & Vu, 2009). And we are aware of further new discoveries to be described from the region in the near future. This does not only underline the importance of Phong Nha - Ke Bang National Park in a regional scale and the Truong Son Mountain Range along the border between Vietnam and Laos

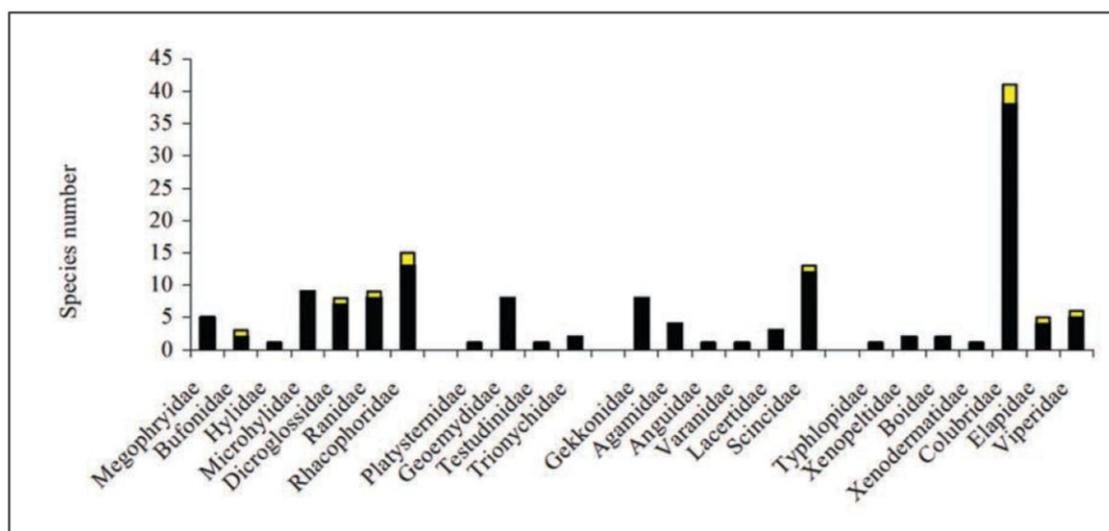


Figure 16. Species richness of amphibian and reptile families from Phong Nha – Ke Bang National Park (new records are marked by open rectangles).

in a wider geographical scale as centres of biodiversity and endemism, but also shows that longterm biodiversity research is crucial for covering the total species richness in tropical environment, which is prerequisite for appropriate evaluation of the conservation status and application of adequate protection measures.

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Publication 2

New country records of reptiles from Laos

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Taxonomic paper

New country records of reptiles from Laos

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Abstract

Four species of reptiles, of which one is represented by one of its subspecies, are recorded for the first time from Laos: *Cyrtodactylus phongnhakebangensis*, *Lycodon futsingensis*, and *L. ruhstrati*, as *L. ruhstrati abditus*, from limestone forests in Khammouane Province and *Cyrtodactylus pseudoquadrivirgatus* from hill evergreen forest in Salavan Province. These discoveries of lizards and snakes bring the total species number of reptiles to 189 in Laos.

Keywords

Colubridae, Gekkonidae, distribution, taxonomy, Khammouane Province, Salavan Province

Introduction

The knowledge on the diversity of the reptile fauna of Laos has strikingly increased during the recent decades. Stuart (1999) provided the first checklist of 109 reptile species from Laos. Teynié et al. (2004) published an updated checklist of reptiles from southern Laos with a total of 89 recognized species. Four years later, Stuart and Heatwole (2008) recorded 13 additional species of colubrid and viperid snakes from the country. The species number of reptiles from Laos was 180 in 2010 (Teynié and David 2010). Since 2010, six new species of reptiles have been described from Laos comprising *Cyrtodactylus wayakonei* Nguyen, Kingsada, Rösler, Auer & Ziegler, 2010, *C. lomyenensis* Ngo & Pauwels, 2010, *C. teyniei* David, Nguyen, Schneider & Ziegler, 2011, *C. pageli* Schneider, Nguyen, Schmitz, Kingsada, Auer & Ziegler, 2011, *Lycodon davidi* Vogel, Nguyen, Kingsada & Ziegler, 2012, and *Oligodon nagao* David, Nguyen, Nguyen, Jiang, Chen, Teynié & Ziegler, 2012 (Nguyen et al. 2010, Ngo and Pauwels 2010, David et al. 2011, Schneider et al. 2011, Vogel et al. 2012, David et al. 2012). In 2012 and 2013, additional field surveys were conducted in the hill evergreen forest within Xe Sap National Protected Area, Salavan Province, and limestone forests within Hin Nam No National Protected Area, Khammouane Province. Examination of voucher specimens from aforementioned sites revealed the existence of a number of reptile species that have not been known from Laos so far. We herein report four new records of reptiles from the country, comprising two species of Gekkonidae, and one species and one subspecies of Colubridae.

Materials and methods

Field surveys were conducted by T. Calame in Xe Sap National Protected Area (NPA), Salavan Province in May 2012 and by V. Q. Luu in Hin Nam No NPA, Khammouane Province from April to July 2013 (Figs 1, 2). Specimens were collected by hand or snake hook between 19:00-23:00. After taking photographs, specimens were anaesthetized, fixed in 80-85% ethanol and subsequently stored in 70% ethanol. Voucher specimens are deposited in the collections of the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam; the National University of Laos (NUOL), Vientiane, Laos; the Vietnam Forestry University (VFU), Hanoi, Vietnam; and the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany.



Figure 1.

Map of survey sites in Khammouane and Salavan provinces, Laos.



Figure 2.

Limestone karst forest in Hin Nam No National Protected Area, Khammouane Province and evergreen forest in Xe Sap National Protected Area, Salavan Province, Laos. Photos: V. Q. Luu and T. Calame.

a: Forest in Hin Nam No NPA

b: Forest in Xe Sap NPA

Measurements of specimens were taken with a digital caliper to the nearest 0.1 mm. Abbreviation are as follows: SVL (snout-vent length): from tip of snout to anterior margin of cloaca; TaL (Tail length): from posterior margin of cloaca to tip of tail; TL (total length): SVL

+TaL. Terminology of morphological characters follows Rösler et al. (2008) for lizards and Vogel et al. (2009) for snakes. Bilateral scale counts were given as left/right.

Taxon treatments

Cyrtodactylus phongnhakebangensis Ziegler, Rösler, Herrmann & Vu, 2002

Material

- a. country: Laos; stateProvince: Khammouane; verbatimLocality: Hin Nam No National Protected Area; verbatimElevation: 180-580 m; verbatimLatitude: 17°15'-17°40'N; verbatimLongitude: 105°43'-106°09'E; eventDate: 2013-05-07/2013-06-30; individualCount: 9; sex: 4 males, 5 females; recordedBy: V. Q. Luu; institutionCode: IEBR, VFU, NUOL, ZFMK

Description

(Fig. 3)

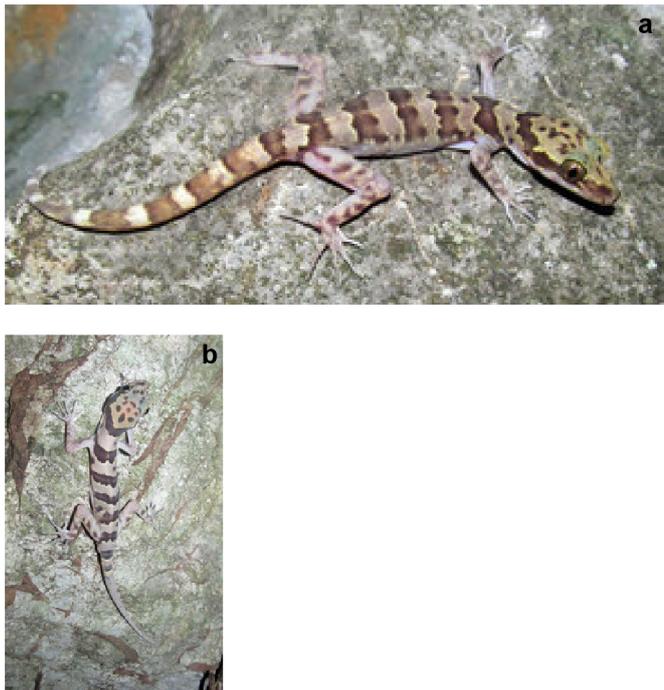


Figure 3.

Cyrtodactylus phongnhakebangensis (female and male) from Hin Nam No National Protected Area, Khammouane Province, Laos. Photos: V. Q. Luu.

a: Female

b: Male

Specimens examined (n = 9): Four adult males and five adult females, all collected by V. Q. Luu in Hin Nam No NPA, Khammouane Province: IEBR A.2013.89, adult male, 7 May 2013, from Hang Toi region, Noong Ma Commune (17°17.766'N, 106°08.803'E, elevation 580 m a.s.l.); VFU A.2013.1 and NUOL R-2013.2, adult males, 9 June 2013, from Vang Ma No Commune (17°30.778'N, 105°49.259'E, elevation 180 m a.s.l.); IEBR A.2013.90, adult male, 11 June 2013, from Ban Dou Commune (17°30.385'N, 105°49.160'E, elevation 183 m a.s.l.); ZFMK 95235, adult female, 8 May 2013, from Hang Toi region, Noong Ma Commune (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 Commune (17°20.248'N, 105°56.693'E, elevation 252 m a.s.l.); VFU A.2013.2-A.2013.3, adult females, 9 June 2013, from Vang Ma No Commune (17°30.778'N, 105°49.259'E, elevation 180 m a.s.l.); NUOL R-2013.3, adult female, 11 June 2013, from Ban Dou Commune (17°31.545'N, 105°49.086'E, elevation 197 m a.s.l.).

Morphological characters: SVL males 83.6-92.5 mm (mean \pm SD 87.9 \pm 4.9 mm), females 95-100.6 mm (mean \pm SD 93.8 \pm 5.0 mm); tail length (TaL) 101.6 mm in males, 108.3 mm in females; head depressed (HL/HW 1.6 in males, 1.5 in females), distinct from neck; snout longer than diameter of ocular (SE/OD 2 in males, 1.9 in females); snout scales small, homogeneous, granular, larger than those in frontal and parietal regions; rostral wider than high with a Y-shape in the middle; supranasals in contact; rostral bordered by first supralabial and nostril on each side; nares oval, surrounded by supranasal, rostral, first supralabial, and two enlarged postnasals; ear oval-shaped; mental triangular; postmental two, enlarged, in broad contact posteriorly; supralabials 9-12; infralabials 8-10; dorsal scales granular to flattened; dorsal tubercles triangular, conical, present on occiput, back and tail base, each surrounded by 8-9 granular scales, in 14-19 irregular longitudinal rows at midbody; ventral scales smooth, medial scales 2-3 times larger than dorsal scales, round, in 35-48 longitudinal rows at midbody; ventrolateral folds present; gular region with homogeneous smooth scales; precloacal groove absent; enlarged femoral scales present; femoral and precloacal pores 36-44 in males, pitted scales 0-28 in females; postcloacal tubercles 4-6; subcaudals enlarged; dorsal surface of fore and hind limbs with small tubercles; fingers and toes without distinct webbing; lamellae under fourth finger 16-21, under fourth toe 19-22. Coloration in preservative: Ground coloration of dorsal head and back greyish brown with dark spots; nuchal loop distinct, in U-shape, from posterior corner of eye through tympanum to the neck, dark brown, edged in white; body bands between limb insertions four to five, somewhat irregular, dark brown, edged in white; dorsal surface of fore and hind limbs with dark bars; tail brown dorsally with seven to eight light brown bands, edged in white; chin, throat, and belly cream; upper and lower lips with dark brown bars; tail ventrally grey with light dots (determination after Ziegler et al. 2002).

Distribution

C. phongnhakebangensis has been known from Phong Nha - Ke Bang National Park, Quang Binh Province, central Vietnam (Nguyen et al. 2009). This is the first record of the species from Laos.

Ecology

Specimens were found between 19:00 and 22:00 on karst walls, ca. 0.5-3 m above the ground, near cave entrances in limestone forests, at elevations from 180 to 580 m a.s.l.

Notes

The Laotian specimens differ from the original description of Ziegler et al. (2002) by having somewhat higher femoral and precloacal pore counts in males (36-44 versus 32-42).

Cyrtodactylus pseudoquadrivirgatus Rösler, Nguyen, Vu, Ngo & Ziegler, 2008

Material

- a. country: Laos; stateProvince: Salavan; verbatimLocality: Xe Sap National Protected Area; verbatimElevation: 960 m; verbatimLatitude: 16°09.400'N; verbatimLongitude: 106°49.567'E; eventDate: 2012-05-20; individualCount: 2; sex: 2 females; recordedBy: T. Calame; institutionCode: IEBR, NUOL

Description

(Fig. 4)



Figure 4.

Cyrtodactylus pseudoquadrivirgatus from Xe Sap National Protected Area, Salavan Province, Laos. Photo: T. Calame.

Specimens examined (n = 2). Two adult females (IEBR A.2013.91 & NUOL R-2013.4), collected by T. Calame on 20 May 2012 from Xe Sap NPA, Salavan Province (16°09.400'N, 106°49.567'E, elevation ca. 960 m a.s.l.).

Morphological characters. SVL 70.7-83.8 mm, tail regenerated (TaL 72.1-72.6 mm); head depressed (HL/HD 1.6), distinguished from neck; loreal region inflated; snout longer than diameter of orbit (SE/OD 1.9); snout scales small, homogeneous, granular, larger than those in frontal and parietal regions; rostral wider than high with a median suture; supranasals separated from each other posteriorly by a pentagonal internasal; rostral bordered by first supralabial and nostril on each side; nares oval, surrounded by supranasal, rostral, first supralabial, and three enlarged postnasals; eyelid fringe with tiny spines posteriorly; ear oval-shaped, somewhat angular; mental triangular, slightly wider than rostral; postmentals in one pair, enlarged, in broad contact posteriorly, bordered by mental anteriorly, first two infralabials laterally, and one pair of distinctly enlarged gular scales posteriorly, which is separated from each other by two small gular scales; supralabials 8-10; infralabials 7-10; dorsal scales granular to flattened; dorsal tubercles triangular, conical, present on occiput, back and tail base, each surrounded by 10-11 granular scales, in 17-18 irregular longitudinal rows at midbody; ventral scales smooth, medial scales 2-3 times larger than dorsal scales, round, subimbricate, in 39-40 longitudinal rows at midbody; ventrolateral folds with interspersed tubercles; gular region with homogeneous smooth scales; precloacal groove absent; enlarged femoral scales and femoral pores absent; precloacal pores 7-9; postcloacal tubercles 2-3; subcaudals slightly enlarged; dorsal surface of fore and hind limbs with tubercles; fingers and toes without distinct webbing; lamellae under fourth finger 16-19, under fourth toe 17-20. Coloration in preservative: Ground coloration of dorsal head and back blackish brown; a narrow curved black stripe from posterior corner of eye, running above tympanum to the neck, interrupted posteriorly; shoulders, dorsal body blotched, irregular from oval to elongate, dark brown; fore and hind limbs with dark bars; dorsal tail grey with dark brown bands; chin, throat, chest and belly brown; ventral tail marked with light and dark bands; upper and lower lips dark brown (determination after Rösler et al. 2008).

Distribution

This species was previously known in Central Vietnam from Quang Tri province southwards to Kon Tum Province (Rösler et al. 2008). Therefore, our record of *C. pseudoquadrivirgatus* from Salavan Province is the first country record for Laos.

Ecology

Specimens were found between 19:40 and 20:10 on a small bush stem ca. 40 cm above the ground, approximately 3 m away from a rocky stream. The surrounding habitat was hill evergreen forest at an elevation of 960 m a.s.l. Within the hill evergreen forest in western Xe Sap NPA the canopy is characterized, in many areas, by the conspicuous presence of emergents of the restricted range conifer *Pinus dalatensis*.

Lycodon futsingensis* (Pope, 1928)*Material**

- a. country: Laos; stateProvince: Khammouane; verbatimLocality: Hin Nam No National Protected Area; verbatimElevation: 581 m; verbatimLatitude: 17°17.499'N; verbatimLongitude: 106°10.606'E; eventDate: 2013-05-14; individualCount: 1; sex: female; recordedBy: V. Q. Luu; institutionCode: VFU

Description

(Fig. 5)



Figure 5.

Lycodon futsingensis from Hin Nam No National Protected Area, Khammouane Province, Laos.
Photos: V. Q. Luu.

a: Dorsal view

b: Ventral view

Specimen examined (n = 1). VFU A.2013.4, adult female, collected by V. Q. Luu on 14 May 2013 from Noong Ma Commune, Boualapha District, Khammouane Province (17°17.499'N, 106°10.606'E, elevation 581 m a.s.l.), within Hin Nam No NPA.

Morphological characters. Total length (TL) 760 mm (SVL 603mm, TaL 157 mm); body subcylindrical; head moderately distinguished from neck, rather flattened; snout elongate, projecting anteriorly beyond lower jaw; pupil vertically elliptic; maxillary teeth 12/12; rostral distinctly broader than high, partly visible from above; internasals as wide as long, not in contact with loreal; prefrontal less than half length of frontal; frontal hexagonal; parietals longer than wide; nasal paired; loreal 1/1, not in contact with orbit; supralabials 8/8, third to fifth touching the eye, seventh largest; infralabials 9/9, first to fifth bordering chin shields; preocular 1/1; postoculars 2/2, bordering anterior temporals; anterior temporals 2/2, posterior temporals 2/2; dorsal scale rows 17-17-15, smooth; ventrals 209; subcaudals 79, paired; cloacal undivided. Coloration in preservative: Dorsal surface greyish-black with 19-21 grey rings on body and 9 cross-bands on tail; belly cream, anterior part uniform, speckled posteriorly, under tail dark (determination after Vogel et al. 2009, Vogel and David 2010).

Distribution

Lycodon futsingensis has been reported from southern China and northern Vietnam (Vogel et al. 2009). This is a new record of the species from Laos and it is approximately about 20 km far from the nearest record of this species in Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam.

Ecology

The adult female was collected at ca. 21:30 while moving on the forest floor, near a slow running stream. The surrounding habitat was karst forest at elevation of 581 m a.s.l.

***Lycodon ruhstrati abditus* Vogel, David, Pauwels, Sumontha, Norval, Hendrix, Vu & Ziegler, 2009**

Material

- a. country: Laos; stateProvince: Khammouane; verbatimLocality: Hin Nam No National Protected Area; verbatimElevation: 556 m; verbatimLatitude: 17°17.648'N; verbatimLongitude: 106°10.053'E; eventDate: 2013-05-14; individualCount: 1; sex: male; recordedBy: V. Q. Luu; institutionCode: VFU

Description

(Fig. 6)

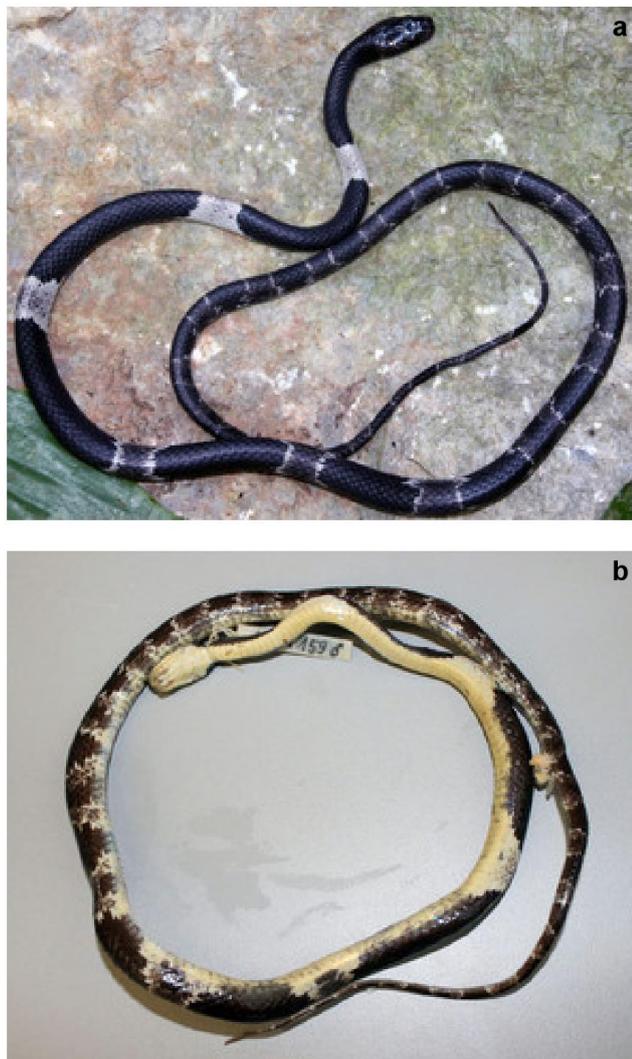


Figure 6.

Lycodon ruhstrati abditus from Hin Nam No National Protected Area, Khammouane Province, Laos. Photos: V. Q. Luu.

a: Dorsal view

b: Ventral view

Specimen examined (n = 1). VFU A.2013.5, adult male, collected by V. Q. Luu on 14 May 2013 from Pa Rang region, Noong Ma Commune, Boualapha District, Khammouane Province (17°17.648'N, 106°10.053'E, elevation 556 m a.s.l.), within Hin Nam No NPA.

Morphological characters. Total length (TL) 665 mm (SVL 520 mm, TaL 145 mm); body elongate; head moderately distinct from neck, rather flattened; snout projecting anteriorly beyond lower jaw; pupil vertically oval; tail tapered and thin; maxillary teeth 12/12; snout scale broad; rostral distinctly broader than high, partly visible from above; internasals large, pentagonal, not in contact with loreal; prefrontal more than half length of internasal, subrectangular, wider than long, not entering orbit; frontal hexagonal, narrowed posteriorly; parietals longer than wide; nasal paired; loreal 1/1, small, pentagonal, not bordering the eye; supralabials 8/8, third to fifth in contact with the eye, sixth largest; infralabials 10/10, first to fifth bordering chin shields; preocular 1/1; postoculars 2/2, bordering anterior temporal; anterior temporals 2/2; posterior temporals 3/3; dorsal scale rows 17-17-15; five middorsal scales keeled, the outer rows usually smooth; ventrals 224; subcaudals 96, paired; cloacal single. Coloration in preservative: Dorsal surface greyish or blackish, with white and cream cross-bars, 17 on the body, increasing the size at the bottom of each light cross-bands, best marked anteriorly, and becoming dim posteriorly; belly cream, progressively but not extensively speckled with dark grey on the posterior edges of the ventral scales; upper tail as the posterior body, tail rings cream and extending towards the under part of the tail (determination after Vogel et al. 2009, Ziegler et al. 2007).

Distribution

Lycodon ruhstrati has been known from Taiwan, China and northern Vietnam: *L. r. ruhstrati* is endemic to Taiwan and the range of *L. r. abditus* is widespread in the mainland of China and Vietnam (see Vogel et al. 2009). Our finding represents the first record of the species as well as the subspecies, *L. r. abditus*, from Laos and it is approximately about 20 km far from the type locality of the subspecies in Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam.

Ecology

The specimen of *L. ruhstrati abditus* was found at 11:00 while moving through a forest path. The surrounding habitat was karst forest at the elevation of 556 m a.s.l.

Notes

The specimen from Laos differs from the description of Vogel et al. (2009) in having fewer cross-bands on the body (17 versus 19-43).

Discussion

The recent discoveries of *Cyrtodactylus phongnhakebangensis* and *C. pseudoquadrivirgatus* in Laos bring the species number of the genus *Cyrtodactylus* known from that country to ten. This is still a low number compared with the *Cyrtodactylus*

diversity from neighbouring Vietnam (which currently comprises 29 species, see Ziegler et al. 2013). In central Vietnam's Phong Nha – Ke Bang National Park two other bent-toed geckos, *C. cryptus* Heidrich, Rösler, Vu, Böhme & Ziegler, 2007 (Heidrich et al. 2007) and *C. roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz, 2010 (Ziegler et al. 2010), are known to occur sympatrically with *C. phongnhakebangensis* (Loos et al. 2012). In Hin Nam No NPA, our observation also supports the finding of Loos et al. (2012) about niche segregation of *Cyrtodactylus* species. Both *C. roesleri* and *C. phongnhakebangensis* were found on karst cliffs in the same habitat (Fig. 7). In Laos, *C. roesleri* was previously recorded from Phou Hin Boun in Khammouane Province by Teynié and David (2010). This is the first record of the species from Hin Nam No NPA. The new records of *Lycodon futsingensis*, and *L. ruhstrati abditus* from Khammouane Province increase the species number of snakes in Laos to 107. However, the diversity of reptiles in Laos is still poorly studied, particular in Hin Nam No NPA. In the bordering Phong Nha – Ke Bang National Park in Vietnam, Luu et al. (2013) recently provided a list of 101 reptile species including 15 new species and one new subspecies that have been described only from this site since 2000. Therefore, further field research is required to explore the actual herpetofaunal diversity of the largest karst formation in central Laos.

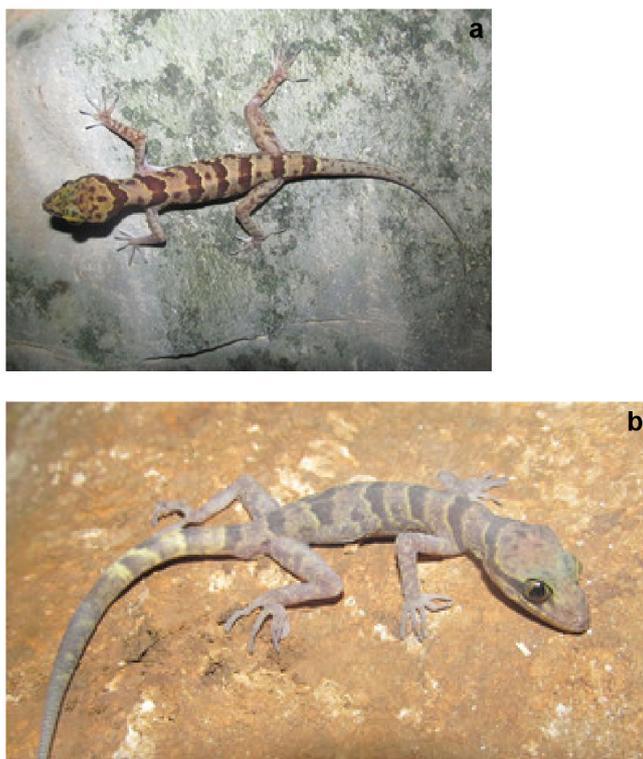


Figure 7.

Two sympatric species, *Cyrtodactylus phongnhakebangensis* and *C. roesleri*, in situ on limestone walls in Hin Nam No National Protected Area, Khammouane Province, Laos. Photos: V. Q. Luu.

a: *Cyrtodactylus phongnhakebangensis*

b: *Cyrtodactylus roesleri*

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Publication 3

**First records of *Gracixalus supercornutus* (Orlov, Ho & Nguyen, 2004) and
Rhacophorus maximus Günther, 1858 from Laos**

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Herpetology Notes, 7: 419-423.

First records of *Gracixalus supercornutus* (Orlov, Ho and Nguyen, 2004) and *Rhacophorus maximus* Günther, 1858 from Laos

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Abstract. Two rhacophorid anurans are recorded for the first time from Laos: *Gracixalus supercornutus* from hill evergreen forest of Salavan Province and *Rhacophorus maximus* from limestone forest of Khammouane Province. These discoveries bring the total species number of amphibians to 103 in Laos.

Keywords. Rhacophoridae, distribution, new records, Khammouane Province, Salavan Province.

Introduction

The knowledge on the species diversity of amphibians in Laos has remarkably increased during the last decade. Stuart (1999) reported the first checklist of amphibians from Laos with a total of 58 recognized species. At present, the number of amphibian species from Laos has almost doubled up to 101 species (Frost, 2014). Ranidae and Rhacophoridae are the two most species-rich families of amphibians in Laos with 28 and 23 recorded species, respectively, followed by Megophryidae (19 species), Microhylidae (14 species), Dicroglossidae (10 species), Bufonidae (4 species), Salamandridae and

Ichthyophiidae (2 species each) as well as Hylidae (1 species) (Frost, 2014).

In 2012 and 2013, further field surveys were conducted in the hill evergreen forest within Xe Sap National Protected Area, Salavan Province, and



Figure 1. Map showing survey sites (black circles) in Khammouane and Salavan provinces, Laos.

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Figure 2. a. Evergreen forest in Xe Sap National Protected Area, Salavan Province, Laos; b. Limestone karst forest in Hin Nam No National Protected Area, Khammouane Province, Laos. Photographs by Thomas Calame and Vinh Quang Luu.

limestone forest within Hin Nam No National Protected Area, Khammouane Province. Examination of voucher specimens from aforementioned sites revealed the existence of two rhacophorid amphibian species that have been not reported from Laos so far. We herein report the occurrence of *Gracixalus supercornutus* and *Rhacophorus maximus* for the first time from the country.

Materials and methods

Field surveys were conducted by T. Calame in Xe Sap National Protected Area (NPA), Salavan Province in May 2012 and by V. Q. Luu and N. V. Ha in Hin Nam No NPA, Khammouane Province from April to July 2013 (Figs. 1, 2). Specimens were collected by hand between 19:00 and 23:00. After taking photographs, specimens were anaesthetized, fixed in 80–85% ethanol and subsequently transferred into 70% ethanol for permanent storage. Voucher specimens were deposited

in the collections of the National University of Laos (NUOL), Vientiane, Laos and the Vietnam Forestry University (VFU), Hanoi, Vietnam.

Measurements were taken with a digital calliper to the nearest 0.1 mm. Abbreviations are as follows: a.s.l.: above sea level; SVL, snout-vent length; HW, head width at the greatest cranial width; HL, head length from the rear of the lower jaw to the tip of the snout; UEW, upper eyelid width: greatest width of upper eyelids; IOD, interorbital distance; ED, horizontal diameter of eye; TD, horizontal diameter of tympanum; SL, tip of snout-eye distance; TED, tympanum-eye distance from anterior edge of tympanum to posterior corner of the eye; IND, internarial distance: distance between nostrils; END, eye to nostril distance: distance from anterior corner of eye to nostril. FLL, length of forelimb from axilla to elbow; HAL, hand length from elbow to the tip of third finger; NPL, nuptial pad length. HLL, length of hindlimb from tip of disk of toe IV to groin; FL, femur length; TL, tibia length; FOL, length of hindlimb from tip of disk of toe IV to posterior edge of tibia; MTTi, length of inner metatarsal tubercle. Terminology of morphological characters followed Orlov *et al.* (2010); Nguyen *et al.* (2013) and anuran webbing formula followed Glaw and Vences (2007).

Results

Gracixalus supercornutus

(Orlov, Ho and Nguyen, 2004) (Fig. 3)

Specimen examined (n = 1). VFU A.2014.20, subadult, collected by T. Calame on 01 March 2012 in Xe Sap NPA, Salavan Province (16°03.917'N, 106°48.850'E, elevation ca. 1,120 m a.s.l.).



Figure 3. *Gracixalus supercornutus* from Xe Sap National Protected Area, Salavan Province, Laos. Photograph by Thomas Calame.

Morphological characters. SVL 19.0 mm; head longer than wide (HL 7.4 mm, HW 6.6 mm); snout pointed, longer than horizontal diameter of eye (SL 2.7 mm; ED 2.1 mm); canthus rostralis angular; loreal region concave; interorbital distance wider than internarial distance and upper eyelid (IOD 2.4 mm, IND 1.6 mm, UEW 1.1 mm); nostrils in lateral direction, closer to the tip of snout than to eye (SN 0.9 mm; END 1.7 mm); tympanum oval, smaller than tympanum-eye distance (TD 0.7 mm, TED 1.2 mm); supratympanic fold indistinct; vomerine teeth absent; tongue notched posteriorly. Forelimbs: FLL 4.3 mm, HAL 9.1 mm; relative length of fingers: I<II<IV<III; tip of fingers enlarged into large discs; finger free of webbing; subarticular tubercles distinct, rounded, formula 1, 1, 2, 2; dermal fringe along outer finger present; palmar tubercles visible. Hind limbs: foot length longer than tibia and femur (FOL 12.3 mm, TL 10.1 mm, FL 10.0 mm); relative length of toes: I<II<III=V<IV; discs of toes smaller than those of fingers; webbing formula: Io(1)–(1½)iIIo(½)–(2)iIIIo(1)–(2½)iIVo(2)–(1)iV; subarticular tubercles rounded, formula 1, 1, 2, 3, 2; dermal fringe along outer tarsus distinct; inner metatarsal tubercle present; outer metatarsal tubercle absent. Dorsal surface of head, body, and limbs covered by small tubercles; dermal fringes, area surrounding vent, and upper eyelids with tiny horned spines; ventral skin of throat, chest, belly and thigh granular. Coloration in life: Dorsal surface yellowish green with brown dots in different sizes; a brown marking, in T-shape present in interorbital region; under the eye and tympanum with white patches; dorsal surface of fingers and toes with dark bars; ventral surface yellowish white with white granules (determination after Orlov et al., 2004).

Distribution. *G. supercornutus* has been recorded from Central Vietnam: Da Nang, Thua Thien-Hue, Quang Nam, and Kon Tum provinces (Nguyen et al., 2009; Rowley et al., 2011). This is the first record of the species for Laos. It is noted that the Xe Sap NPA is contiguous to the Bach Ma National Park in Vietnam and the newly recorded locality of *G. supercornutus* in Laos is approximately 30 km in the west of the type locality of this species.

Natural history. The specimen was found in the evening (20:30) on a leaf, about 1.5 m above the ground, near a small stream. The main habitat was hill evergreen forest at an elevation of 1,120 m a.s.l., with some patches of open conifer forest.

***Rhacophorus maximus* Günther, 1858 (Fig. 4)**

Specimens examined (n = 2). VFU A.2014.21, adult male and NUOL A–2014.3, adult female, collected from Hin Nam No NPA, in the area of Noong Ma Commune, Boulapha District, Khammouane Province on 11 May 2013 (17°16.981'N, 106°09.900'E, elevation 539 m a.s.l.).

Morphological characters. SVL 74.2 mm in the male, 93.5 mm in the female; head wider than long (HW 27.6–36.7 mm, HL 27.3–33.7 mm); snout rounded, longer than horizontal diameter of eye (SL 11.8–14.3 mm; ED 7.7–8.4 mm); canthus rostralis angular; loreal region concave; interorbital distance wider than internarial distance and upper eyelid (IOD 8.9–11.8 mm, IND 8.0–9.7 mm, UEW 6.2–7.4 mm); nostril in lateral direction, equidistant from snout and from eye (SN 5.5–6.9 mm; END 5.8–6.8 mm); tympanum rounded, distinctly greater than tympanum-eye distance (TD 4.4–4.8 mm, TED 2.2–2.8 mm), supratympanic

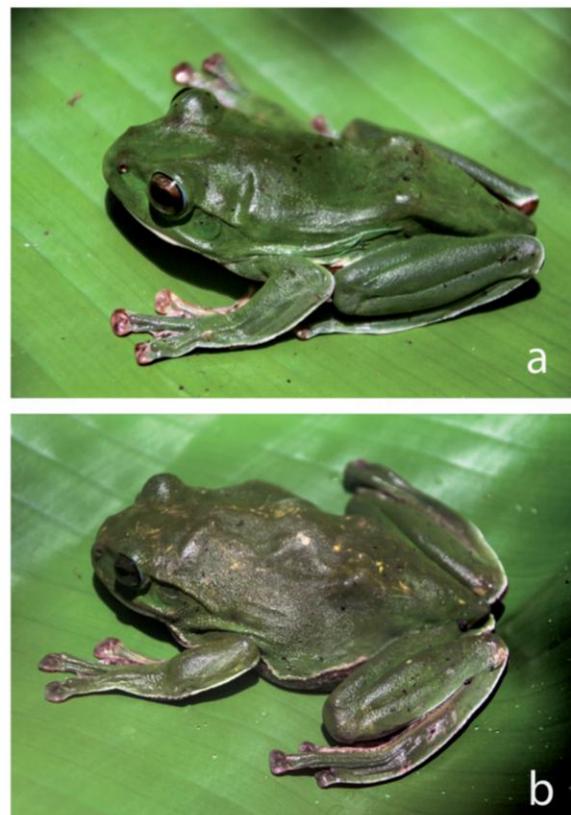


Figure 4. *Rhacophorus maximus* (a. Male; b. Female) from Hin Nam No National Protected Area, Khammouane Province, Laos. Photograph by Vinh Quang Luu.

fold visible; vomerine teeth present; tongue cordate; internal vocal sac present in the male. Forelimbs: FLL 13.0–14.1 mm, HAL 36.7–50.4 mm; relative length of fingers: I<II<IV<III; tip of fingers enlarged into large discs, webbing formula: Io(1)–(1)iIlo(0)–(1)iIIIo(0)–(0)iIV; subarticular tubercles prominent, formula 1, 1, 2, 2; dermal fringe along outer finger present; palmar tubercles distinct; nuptial pad present in the male (NPL 6.2 mm). Hind limbs: foot length longer than tibia and femur (FOL 49.1–67.1 mm, TL 36.2–46.7 mm, FL 33.6–40.8 mm); relative length of toes: I<II<III=V<IV; toes fully webbed; dermal fringe along outer toe weakly developed; subarticular tubercles prominent, formula 1, 1, 2, 3, 2; inner metatarsal tubercle present (MTTi 2.9–4.8 mm); outer metatarsal tubercle absent. Dorsal skin of head, shoulder, thigh and tibia smooth with some granules in the female; dorsal skin of the male smooth; ventral skin granular, especially on throat, belly and under thighs. Coloration in life: Dorsal surface green with some yellow dots; a light stripe from the margin of the lower jaw to the groin; webbing and the tips of fingers and toes violet; ventral surface cream or violet isolated from the green part by a white line on flanks; lateral parts of body and femur with some reddish brown dots (determination after Anders and Rai, 2002).

Distribution. This species has been reported from northeastern India, Nepal, western Thailand, southern China and northern Vietnam (Nguyen *et al.*, 2009). Our finding represents the first record of the species from Laos.

Natural history. Both specimens of *R. maximus* were collected in the evening (19:45) on a leaf, near a slowly flowing stream at an elevation of 539 m. They were found after a heavy rain, the temperature was 26°C and the humidity was 81%. Wildenhues *et al.* (2010) provided the first description of larval and juvenile stages of this species from Vietnam.

Remarks. Granules on dorsal surface of head, shoulder, thigh, and tibia are more distinct in the female than in the male, which is in contrast with the description of Anders and Rai (2002). Moreover, further studies are needed to clarify the phylogenetic relationship among populations of *R. maximus* because the widespread distribution of the species in different biogeographic subregions in Asia suggests that this species might include cryptic taxa.

Discussion

As mentioned above, although the species number of amphibians in Laos has increased twice between 1999 and 2013, the actual diversity of the amphibian fauna of this country is still underestimated. Since 2000, a total of 19 new species have been described from Laos, comprising seven species of Ranidae, six species of Megophryidae, three species of Rhacophoridae, two species of Salamandridae, and one species of Microhylidae (Stuart and Papenfuss, 2002; Ohler, 2003; Teynié *et al.*, 2004; Ohler *et al.*, 2004; Stuart and Heatwole, 2004; Stuart and Bain 2005; Stuart and Chan-ard, 2005; Stuart *et al.*, 2005; Bain *et al.*, 2006; Ohler and Delorme, 2006; Orlov *et al.*, 2010; Rowley *et al.*, 2010; Stuart *et al.*, 2010a; Stuart *et al.*, 2010b; Ohler *et al.*, 2011; Stuart *et al.*, 2012; Chan *et al.*, 2013; Matsui, 2013). According to Bain and Hurley (2011), the newly recorded locality of *R. maximus* in Khammouane is located in the Northern Annamites subregion whereas the new recorded locality of *G. supercornutus* in Salavan Province belongs to the Central Annamites subregion. Both subregions harbour a high level of species diversity (63 and 77 recorded species, respectively) and of endemism (19 and 36 endemic species, respectively) (Bain and Hurley, 2011). It is noted that many species that occur in neighboring countries (i.e. Cambodia, China, Thailand, and Vietnam), are expected to be found in Laos as well (see Frost, 2014). Therefore, further studies are required to fill the knowledge gap on the diversity and distribution of reptiles and amphibians in Laos, particularly in the remote montane forests in upland areas.

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Publication 4

**A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from
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A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from Khammouane Province, Laos

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Abstract

We describe a new species of the genus *Cyrtodactylus* based on two adult specimens from Khammouane Province, Laos. *Cyrtodactylus jaegeri* **sp. nov.** is distinguished from the remaining Indochinese bent-toed geckos by a combination of the following characters: a moderately sized *Cyrtodactylus* with a maximum SVL reaching 68.5 mm; dorsal pattern consisting of a dark nuchal loop and four narrow brown body bands between limb insertions; dorsal tubercles in 15–17 irregular rows; ventrals in 31–32 longitudinal rows at midbody; lateral skin folds present with interspersed tubercles; precloacal–femoral pores 44 in the male, in a continuous series; enlarged femoral scales and precloacal scales present; postcloacal tubercles 3–6; subcaudals transversely enlarged. *Cyrtodactylus jaegeri* **sp. nov.** is the ninth species of *Cyrtodactylus* known from Laos.

Key words: *Cyrtodactylus jaegeri* **sp. nov.**, Indochina, karst forest, morphology, taxonomy

Introduction

Cyrtodactylus is known as the most diverse genus of gekkonids to date with a total of 172 currently recognized species (e.g., Uetz *et al.* 2013; Nguyen *et al.* 2013; Ziegler *et al.* 2013). This genus has a widespread distribution throughout tropical South Asia, Indochina, the Philippines, the Indo–Australian Archipelago, and the Solomon Islands in the East (Bauer & Henle 1994). In Laos, eight species of *Cyrtodactylus* have been recorded so far and five of them have been described during last three years: *C. buchardi* David, Teynié & Ohler, 2004 from Champasak Province, *C. interdigitalis* Ulber, 1993 from Vientiane Province, *C. jarujini* Ulber, 1993 from Borikhamxay Province, *C. lomyenensis* Ngo & Pauwels, 2010 from Khammouane Province, *C. wayakonei* Nguyen, Kingsada, Rösler, Auer & Ziegler, 2010 from Luang Nam Tha Province, *C. roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz, 2010 from Khammouane Province (Teynié & David 2010), *C. teyniei* David, Nguyen, Schneider & Ziegler, 2011 from Borikhamxay Province, and *C. pageli* Schneider, Nguyen, Schmitz, Kingsada, Auer & Ziegler, 2011 from Vientiane Province. Our recent field research in Laos led to the discovery of another new population of *Cyrtodactylus*. Based on morphological examination of two adult specimens, we herein describe a new species from Khammouane, Laos.

Material and methods

Sampling. A field survey was conducted in a mixed secondary forest near Thakhek Town, Khammouane Province, Laos, by Thomas Calame and Peter Jäger in April 2012. Specimens were anaesthetized and fixed in approximately 85% ethanol, then later transferred to 70% ethanol for permanent storage. Specimens were subsequently deposited in the collections of the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology, Hanoi, Vietnam and the National University of Laos (NUOL), Vientiane, Lao PDR.

Morphological characters. Measurements were taken with a digital calliper 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 hindlimb 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; 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 counting rostral and labial), i.e. nasorostral, supranasal, postnasals (N); postrostrals or internasals (IN); postmentals (PM); dorsal tubercle rows (DTR), granular scales surrounding dorsal tubercles (GST); ventral scales in longitudinal rows at midbody (V); number of scales along the midbody from mental to anterior edge of cloaca (SLB); enlarged femoral scales (EFS); 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).

Results

Cyrtodactylus jaegeri sp. nov.

(Figs. 1–3)

Holotype. IEBR A.2013.55, adult male, collected on 29 April 2012 by Thomas Calame and Peter Jäger on a karst wall of a karstic massif, ca. 1.5 m above the forest floor, in a mixed secondary forest of hardwoods and shrubs near Thakhek Town (17°27.44'N, 104°55.44'E), Khammouane Province, Laos, at an elevation of 170 m a.s.l.

Paratype. NUOL R–2013.1, adult female, the same collection data as the holotype.

Diagnosis. A moderately sized *Cyrtodactylus* with a maximum SVL reaching 68.5 mm, distinguished from its congeners by a combination of the following characters: 1) dorsal pattern consisting of a dark nuchal loop and four narrow brown body bands between limb insertions; 3) dorsal tubercles in 15–17 irregular rows; 4) ventrals in 31–32 longitudinal rows at midbody; 5) lateral skin folds present with interspersed tubercles; 6) precloacal–femoral pores 44 in the male, in a continuous series; 7) enlarged femoral scales and precloacal scales present; 8) postcloacal tubercles 3–6; and 9) subcaudals transversely enlarged.

Description of the holotype. Adult male, SVL 60 mm, body slender (TrunkL/SVL 0.41); head elongate (HL/SVL 0.31), relatively narrow (HW/HL 0.61), depressed (HH/HL 0.4), distinguished from neck; loreal region inflated, frontonasal and posterior nasal regions concave; snout long (SE/HL 0.39), pointed, longer than diameter of orbit (OD/SE 0.65); snout scales small, rounded, homogeneous, granular, larger than those on frontal and parietal regions; eye large (OD/HL 0.26) with dark blue colour, pupils vertical; eyelid fringe with tiny spines posteriorly; ear in oval shape, small (EarL/HL 0.1); rostral wider than high (RW 2.9 mm, RH 1.3 mm, RW/RH 2.23) with a median suture; supranasals separated by a hexagonal internasal; rostral bordered by first supralabial and nostril on each side; nares oval, surrounded by supranasal, rostral, first supralabial, and two enlarged postnasals; mental triangular, slightly wider than rostral; postmentals in one pair, enlarged, longer than wide, in broad contact posteriorly, bordered by mental anteriorly, first two infralabials laterally, and one pair of distinctly enlarged gular scales posteriorly, which separated from each other by three small gular scales; supralabials 10/10; infralabials 9/9.

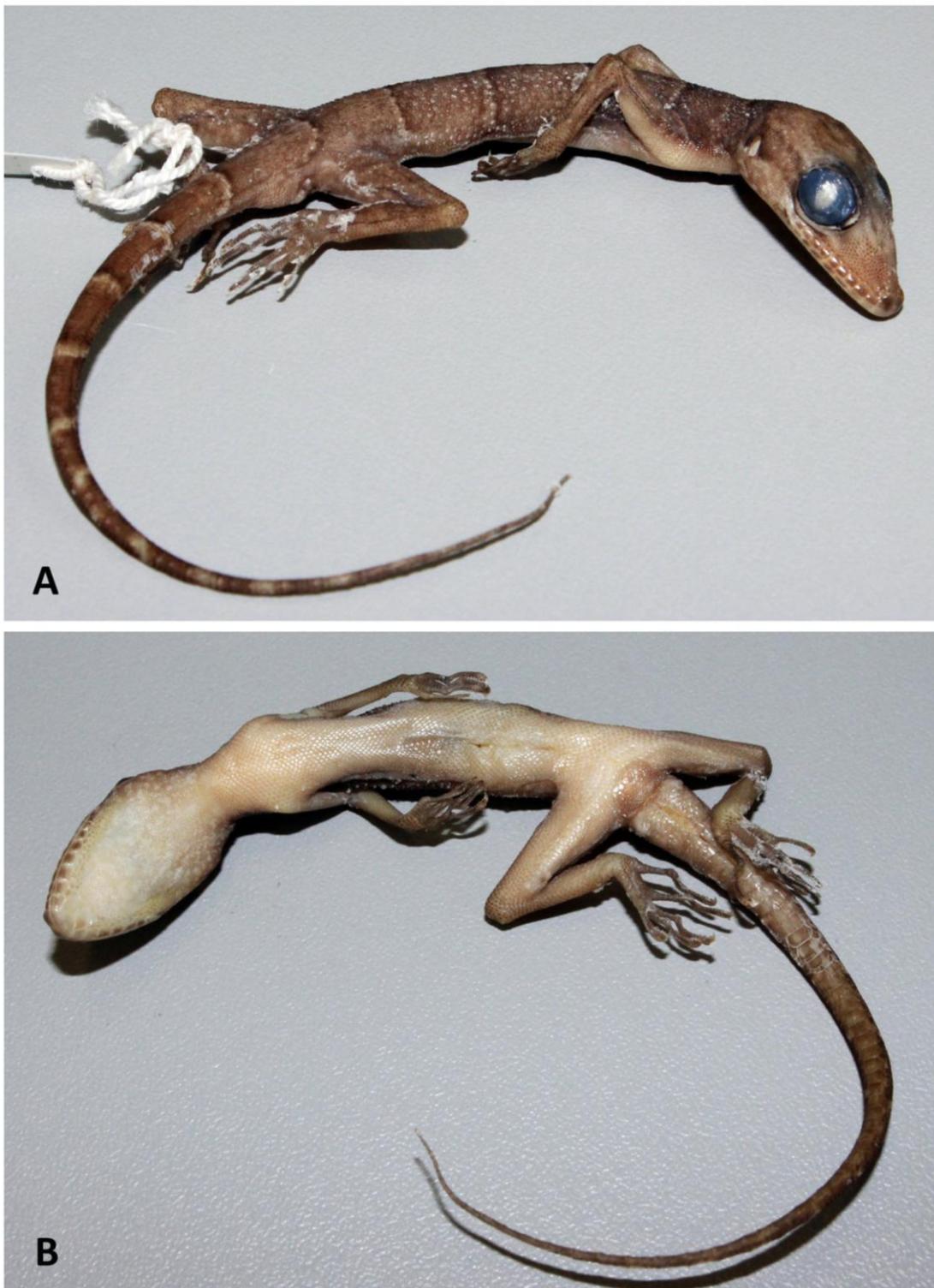


FIGURE 1. Adult male holotype of *Cyrtodactylus jaegeri* sp. nov. (IEBR A.2013.55) in preserved state: A) dorsolateral view and B) ventral view. Photos V. Q. Luu



FIGURE 2. Adult female paratype (NUOL R-2013.1) of *Cyrtodactylus jaegeri* sp. nov. in life. Photo T. Calame.

Dorsal scales granular to flattened; dorsal tubercles round, conical, present on occipital region, back and tail base, surrounded by 9–10 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 31 longitudinal rows at midbody; ventrolateral folds present with interspersed tubercles; gular region with homogeneous smooth scales; preloacal groove absent; a series of distinctly enlarged femoral scales present; femoral and preloacal pores 44, in a continuous series.

Fore and hind limbs moderately slender (ForeL/SVL 0.17, CrusL/SVL 0.21); dorsal forelimbs with slightly developed tubercles; dorsal hindlimb covered by distinctly developed tubercles; fingers and toes without distinct webbing; lamellae under fourth finger 18/17, under fourth toe 19/19.

Tail longer than snout–vent length (TaL 82.4 mm, TaL/SVL 1.37); postloacal tubercles 5/6; dorsal tail bearing distinct tubercles at base; subcaudals distinctly transversely enlarged, flat, smooth.

Coloration in ethanol. Ground coloration of dorsal head and back light brown; nuchal loop distinct, in U-shape, from posterior corner of eye, running partly above tympanum to the neck, dark brown, edged in white posteriorly; body bands between limb insertions four and another one at the tail base, all thin, dark brown, edged in white posteriorly; dorsal tail brown with four dark brown bands in the anterior part, edged in white posteriorly, the bands indistinct in the posterior part; chin, throat, and belly cream; ventral tail dark brown; upper and lower lips with dark brown bars. For coloration in life see Fig. 2.

Sexual dimorphism. The female paratype differs from the male holotype in having a larger size (SVL 68.5 mm vs. 60.0 mm), 21 femoral and preloacal-pitted scales in a continuous series, and the absence of an internasal scale as well as hemipenial swellings at the tail base (see Table 1).

Comparisons. We compare 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 obtained from the literature (Table 2).

Cyrtodactylus jaegeri sp. nov. has enlarged subcaudals, which are absent in *C. bidoupimontis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, 2012, *C. buchardi* David, Teynié & Ohler, 2004, *C. bugiamapensis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, 2012, *C. cattienensis* Geissler, Nazarov, Orlov, Böhme, Phung, Nguyen & Ziegler, 2009, *C. cryptus* Heidrich, Rösler, Vu, Böhme & Ziegler, 2007, *C. huynhi* Ngo & Bauer, 2008, *C. irregularis* (Smith, 1921), *C. phuocbinhensis* Nguyen, Le, Tran, Orlov, Lathrop,

TABLE 1. Selected measurements (in mm) and morphological characters of the type series of *Cyrtodactylus jaegeri* **sp. nov.** (m = male, f = female, measurements in mm, * = regenerated or broken tail; for other abbreviations see material and methods).

	IEBR A.2013.55 (holotype)	NUOL R-2013.1 (paratype)
Sex	m	f
SVL	60.0	68.5
TaL	82.4	83.4*
HH	7.3	7.9
HL	18.3	20.6
HW	11.2	12.7
OD	4.7	5.3
SE	7.2	8.3
EyeEar	3.8	5.0
EarL	1.8	2.1
TrunkL	24.7	27.9
ForeL	10.2	11.9
FemurL	13.8	14.7
CrusL	13.8	14.7
LD4A	5.3	6.2
LD4P	7.1	7.5
SL	10/10	11/10
IL	9/9	11/9
N	3/3	3/3
IN	1	0
PM	2	2
DTR	15	17
GST	9	9
V	31	32
SLB	164	156
EFS	17/17	17/19
FP+PP	44	21 (pitted scales)
PAT	5/6	3/3
LD4	18/17	19/19
LT4	20/20	23/23

Macculloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, 2013, *C. pseudoquadrivirgatus* Rösler, Vu, Nguyen, Ngo & Ziegler, 2008, *C. quadrivirgatus* Taylor, 1962, *C. taynguyenensis* Nguyen, Le, Tran, Orlov, Lathrop, Macculloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, 2013, and *C. ziegleri* Nazarov, Orlov, Nguyen & Ho, 2008. *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. angularis* (Smith, 1921) by having fewer ventral scale rows (31–32 versus 40–45 in *C. angularis*), the presence of femoral pores (absent in *C. angularis*), more femoral and preloacal pores in the male (44 vs. 3 in *C. angularis*). *Cyrtodactylus jaegeri* **sp. nov.** has 44 femoral and preloacal pores in the male and thus differs from *Cyrtodactylus astrum* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Ahmad, Bauer, Wangkulangkul, Grismer & Pauwels, 2012 that has only 31–38 femoral and preloacal pores. *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. auribalteatus* Sumontha, Panitvong & Deen, 2010 by having more enlarged femoral scales (18–19 vs. 5–7 in *C. auribalteatus*) and more femoral and preloacal pores in the male (44 vs. 10–11 in *C. auribalteatus*). *Cyrtodactylus jaegeri* **sp. nov.** can be distinguished from *C. badenensis* Nguyen, Orlov & Darevsky, 2006 by having enlarged femoral scales, the presence of femoral and

preloacal pores (absent in *C. badenensis*), and more ventral scale rows (31–32 vs. 25–29 in *C. badenensis*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. bichnganae* Ngo & Grismer, 2010 by having more enlarged femoral scales (18–19 vs. 11–13 in *C. bichnganae*) and more femoral and preloacal pores (44 vs. 28 in *C. bichnganae*) in males. *Cyrtodactylus jaegeri* **sp. nov.** has 44 femoral and preloacal pores in a continuous series and thus differs from *C. brevipalmatus* (Smith, 1923) and *C. dumnuii* Bauer, Kunya, Sumontha, Niyomwan, Pauwels, Chanhome & Kunya, 2010, which are separated by poreless scales (6+9+7 in *C. brevipalmatus* and 6+5–6+6–7 in *C. dumnuii*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. caovansungi* Orlov, Nguyen, Nazarov, Ananjeva & Nguyen, 2007 by its smaller size (60.0–68.5 mm vs. 90.4–94.0 mm in *C. caovansungi*), fewer ventral scale rows (31–32 vs. 38–44 in *C. caovansungi*), and more femoral and preloacal pores in the male (44 vs. 15). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. chanhomeae* Bauer, Sumontha & Pauwels, 2003 in having fewer ventral scale rows (31–32 vs. 36–38) and more femoral and preloacal pores in the male (44 vs. 32). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. chauquangensis* Hoang, Orlov, Ananjeva, Johns, Hoang & Dau, 2007 by its smaller size (SVL 60.0–68.5 mm vs. 90.9–99.3 mm), the presence of enlarged femoral scales and femoral pores (absent in *C. chauquangensis*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. cucphuongensis* Ngo & Chan, 2011 by its smaller size (SVL 60–68.5 mm vs. 96 mm), fewer ventral scale rows (31–32 vs. 42), and the presence of femoral and preloacal pores (absent in *C. cucphuongensis*). *Cyrtodactylus jaegeri* **sp. nov.** has femoral and preloacal pores in males, which are absent in *C. eisenmanae* Ngo, 2008 and *C. grismeri* Ngo, 2008. *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. erythrops* Bauer, Kunya, Sumontha, Niyomwan, Panitvong, Pauwels, Chanhome & Kunya, 2009 by having more ventral scale rows (31–32 vs. 28), 44 femoral and preloacal pores in a continuous series which are separated by poreless scales in *C. erythrops* (10+9+9). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. huongsonensis* Luu, Nguyen, Do & Ziegler, 2011 by having fewer ventral scale rows (31–32 vs. 41–48) and more femoral and preloacal pores in males (44 vs. 21–23). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. interdigitalis* Ulber, 1993 by having fewer ventral scale rows (31–32 vs. 37–42), more femoral and preloacal pores in males (44 vs. 30–32), and the presence of preloacal pitted scales in the female (absent in *C. interdigitalis*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. intermedius* (Smith, 1917) by having fewer ventral scale rows (31–32 vs. 40–50) and more enlarged femoral scales (18–19 vs. 6–10). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. jarujini* Ulber, 1993 by its smaller size (60.0–68.5 vs. 85.0–90.0 in *C. jarujini*), fewer femoral and preloacal pores in males (44 vs. 52–54 in *C. jarujini*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. kingsadai* Ziegler, Phung, Le & Nguyen, 2013 by its smaller size (60.0–68.5 vs. 83.0–94.0), fewer ventral scales (31–32 vs. 39–46), and more femoral and preloacal pores in males (44 vs. 0–16). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. lekaguli* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Ahmad, Bauer, Wangkulangkul, Grismer & Pauwels, 2012 and *C. lomyenensis* Ngo & Pauwels, 2010 in having more femoral and preloacal pores in males (44 vs. 31–44 in *C. lekaguli* and 39–40 in *C. lomyenensis*), and fewer pitted scales in females (21 vs. 33–43 in *C. lekaguli* and 32 in *C. lomyenensis*). The new species differs from *C. martini* Ngo, 2011 by having fewer ventral scale rows (31–32 vs. 39–43 in *C. martini*) and the presence of femoral pores (absent in *C. martini*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. nigriocularis* Nguyen, Orlov & Darevsky, 2006 in having smaller size (SVL 60–68.5 mm vs. 82.7–107.5 mm in *C. nigriocularis*), fewer ventral scale rows (31–32 vs. 42–49 in *C. nigriocularis*), and the presence of enlarged femoral scales and femoral pores (absent in *C. nigriocularis*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. oldhami* (Theobald, 1876) by having more femoral and preloacal pores (44 vs. 1–4 in *C. oldhami*) and the dorsal color pattern (banded vs. striped and spotted body in *C. oldhami*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. pageli* Schneider, Nguyen, Schmitz, Kingsada, Auer & Ziegler, 2011 and *C. paradoxus* (Darevsky & Szczerbak, 1997) by the presence of enlarged femoral scales and femoral pores (absent in *C. pageli* and *C. paradoxus*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. phonghakebangensis* Ziegler, Rösler, Herrmann & Vu, 2002 by its smaller size (SVL 60–68.5 mm vs. 85–96.3 mm in *C. phonghakebangensis*) and a higher number of femoral and preloacal pores in males (44 vs. 32–42 in *C. phonghakebangensis*). *Cyrtodactylus jaegeri* **sp. nov.** has 44 femoral and preloacal pores in the male and thus differs from *C. roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz, 2010 (20–28). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. sanook* Pauwels, Sumontha, Latinne & Grismer, 2013 and *C. sumonthai* Bauer, Pauwels & Chanhome, 2002 by the presence of femoral pores (absent in *C. sanook* and *C. sumonthai*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. takouensis* Ngo & Bauer, 2008 by its smaller size (SVL 60–68.5 mm vs. 74.7–81.1 mm in *C. takouensis*), fewer number of ventral scale rows (31–32 vs. 39–40), and more femoral and preloacal pores in males (44 vs. 3–6 in *C. takouensis*). *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. teynieii* David, Nguyen, Schneider & Ziegler, 2011 by its smaller size (SVL 60–68.5 mm vs. 89.9 in *C. teynieii*),

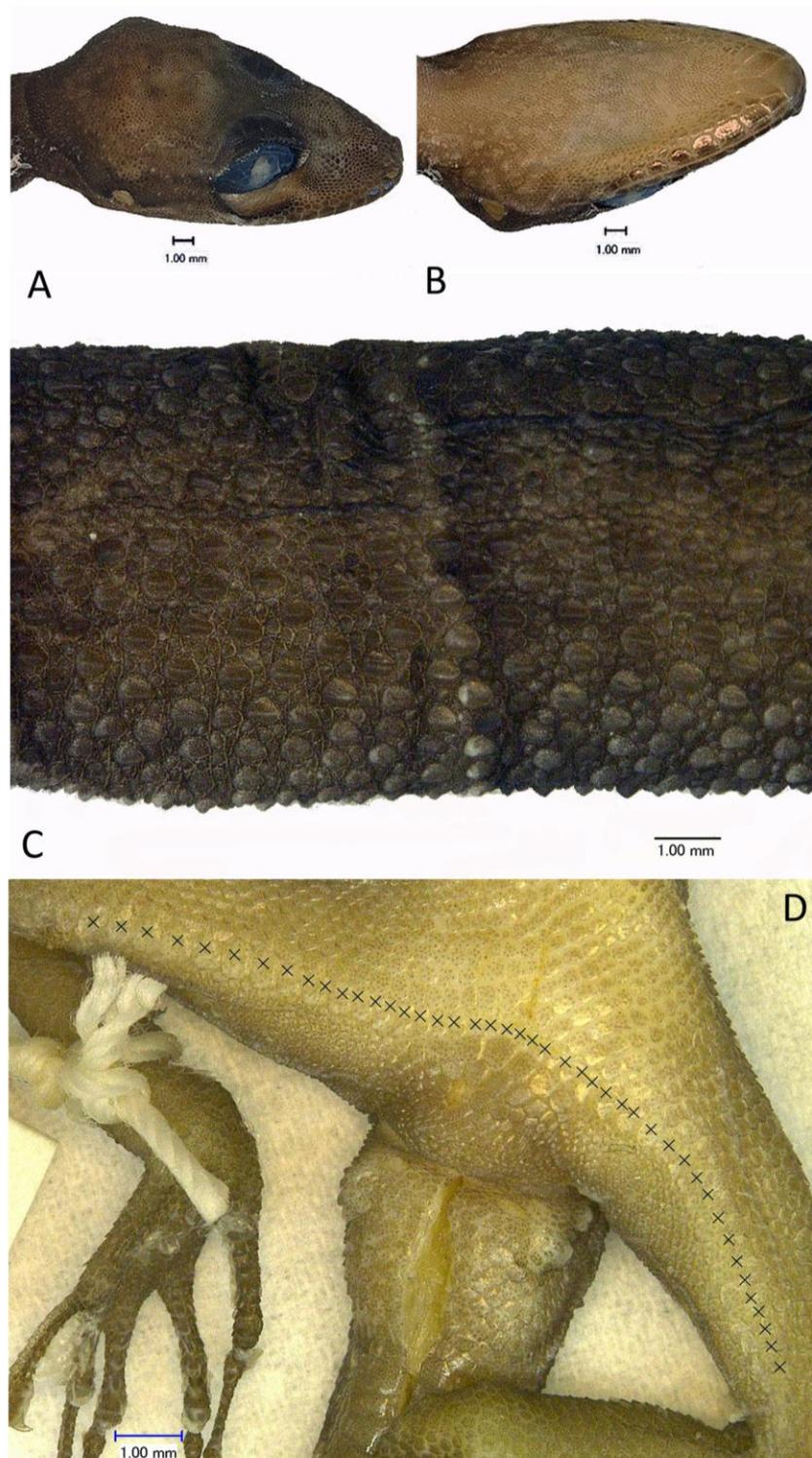


FIGURE 3. Head portraits: A) Dorsal view and B) Ventral view; C) dorsal tubercles at midbody; and D) cloacal region of the preserved holotype of *Cyrtodactylus jaegeri* **sp. nov.** (IEBR A.2013.55). Photos V. Q. Luu



FIGURE 4. Map showing the type locality (black circle) of *Cyrtodactylus jaegeri* sp. nov. in Khammouane Province, Laos.

TABLE 2. Morphological characters of *Cyrtodactylus jaegeri* sp. nov. compared with its congeners from Laos and neighbouring countries in the mainland Indochina region (compiled after Smith 1921, 1923; Taylor 1962, 1963; Ulber 1993; Bauer *et al.* 2002, 2003, 2009, 2010, David *et al.* 2004, 2011; Ngo & Pauwels 2010; Nguyen *et al.* 2010; Sumontha *et al.* 2010; Schneider *et al.* 2011; Grismer *et al.* 2012; Pauwels *et al.* 2013; Ziegler *et al.* 2013). Abbreviations are as follows: m = male; f = female; – = characters unobtainable from literature; * = tail regenerated, for other abbreviations see material and methods.

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
<i>Cyrtodactylus jaegeri</i> sp. nov.	60.0–68.5	82.4–83.4	31–32	17–19	present	44 (FP+PP)	21	17–19	20–23	banded	present
<i>C. angularis</i>	80.0–92.0	92–95.2	40–45	present	absent	3	3	18–19	18–19	banded	present
<i>C. astrum</i>	46.4–108.3	99.0*–109.0*	31–46	–	present	31–38 (FP+PP)	–	–	20–24	banded	present
<i>C. auribalteatus</i>	82.8–98.1	106.5–138.7	38–40	5–7	4–5 (in males)	6	absent	–	18–21	banded	present
<i>C. badenensis</i>	59.3–74.1	58.6–82.4	25–29	absent	absent	0	0	–	18–22	banded	present
<i>C. bichinganae</i>	95.3–99.9	96.3–115.6	30–31	11–13	18	10	8	18–20	16–20	banded	present
<i>C. bidoupimontis</i>	74.0–86.3	75.0–86.0	38–43	6–8	absent	4–6	0	15–20	18–23	banded	absent
<i>C. brevipalmatus</i>	64.0–72.0	77.0	35–44	present	present	6+9+7	6+9+7	–	–	blotched	present
<i>C. bugiamapensis</i>	58.6–76.8	65.3–83.0	36–46	6–10	absent	7–8	0–7	15–17	17–20	blotched	absent
<i>C. buchardi</i>	60.0–65.0	46.0–54.0	30	absent	absent	9	0	14	12	blotched	absent
<i>C. caovansungi</i>	90.4–94.0	120.0	38–44	8	6	9	0	22	23–25	banded	present
<i>C. cattienensis</i>	43.5–69.0	51.0–64.7	28–42	3–8	absent	6–8	0	12–16	14–19	banded	absent
<i>C. chanhomeae</i>	69.9–78.8	74.4–74.7	36–38	present	present	32 (FP+PP)	34 (FP+PP)	18–20	21–23	banded	present
<i>C. chauquangensis</i>	90.9–99.3	97.0–108.3	36–38	absent	absent	6	7	16–18	19–23	banded	present
<i>C. cryptus</i>	62.5–90.8	63.5–88.4	47–50	absent	absent	9–11	0	18–19	20–23	banded	absent
<i>C. cucphuongsensis</i>	96.0	79.3*	42	14	absent	0	–	21	24	banded	present
<i>C. dumnui</i>	76.2–84.2	100.2*	40	present	present in males/absent in females	6+5–6+6–7	0–7	16	19	banded	present
<i>C. eisenmanae</i>	76.8–89.2	91.0–103.8	44–45	4–6	absent	0	0	18–20	17–18	banded	present
<i>C. erythroops</i>	78.4	83.0*	28	present	present	10+9+9 (PP+FP)	–	16	20	blotched	present
<i>C. grismeri</i>	68.3–95.0	111.3–115.1	33–38	absent	–	0	0	16–18	16–19	banded	present
<i>C. huongsongensis</i>	73.4–89.8	90.5	41–48	7–9	15–17	6	8	17–19	20–23	banded	present
<i>C. huynhi</i>	54.8–79.8	61.5–78.6	43–46	3–5	3–8	7–9	0–8	14–17	17–21	banded	absent

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TABLE 2. (Continued)

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
<i>C. interdigitalis</i>	59.0–80.0	71.0–90.0	37–42	present	16–18	14	0	17–22	16–20	banded	present
<i>C. intermedius</i>	61.0–85.0	80.0–110.0	40–50	6–10	–	8–10	–	20	22	banded	present
<i>C. irregularis</i>	72.0–86.0	66.0–74.0	38–45	7–8	–	5–7	0–6	15–16	18–19	blotched	absent
<i>C. jarujini</i>	85.0–90.0	105.0–116.0	32–38	present	present	52–54 (PP+FP)	0	15–17	18–19	blotched	present
<i>C. kingsadai</i>	83.0–94.0	max. 117.0	39–46	9–12	0–7	7–9	4–8	19–21	21–25	banded	present
<i>C. lekaguli</i>	80.5–103.5	115.0–125.0	31–43	present	present	31–41 (PP+FP)	33–43 (PP+FP)	–	20–25	banded	present
<i>C. lompenensis</i>	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
<i>C. martini</i>	64.4–96.2	76.0–101.2	39–43	14–18	absent	4	0	19–23	22–24	banded	present
<i>C. nigriocularis</i>	82.7–107.5	70.6–121.0	42–49	absent	absent	0–2	0	–	17–21	uniformly brown	present
<i>C. oldhami</i>	63.0–68.0	69*–70*	34–38	present	absent	1–4	–	–	–	striped and spots	present
<i>C. pageli</i>	76.2–81.8	85.4*–113.2*	41–44	absent	absent	4	4	19–23	19–23	banded	present
<i>C. paradoxus</i>	52.0–84.0	80.8–111.0	32–40	present	absent	0–4	0	15–18	17–23	banded	present
<i>C. phonghakebangensis</i>	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
<i>C. phuocbinhensis</i>	46.0–60.4	76.1	43–47	5	absent	7	0	16–21	17–19	blotched	absent
<i>C. pseudoquadrivirgatus</i>	48.6–83.3	55.7–82.3	41–57	absent	absent	5–9	5–10	15–21	16–25	blotched	absent
<i>C. quadrivirgatus</i>	39.0–67.0	77.0	40	present	absent	4	4	–	–	striped	absent
<i>C. roesleri</i>	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
<i>C. sanook</i>	72.9–79.5	104.2	27–28	present	absent	3–4	absent	–	19–20	banded	present
<i>C. sumonthai</i>	61.5–70.7	89.9–94.0	33–36	absent	absent	2	0	16	18	banded	present
<i>C. takouensis</i>	74.7–81.1	77.7–91.0	39–40	3–5	0–2	3–4	0	16–17	18–20	banded	present
<i>C. taynguyenensis</i>	60.0–85.0	66.0–94.0	42–49	absent	absent	6	0	13–18	17–21	blotched	absent
<i>C. teyniei</i>	89.9	ca. 110.0	38	23	absent	unknown	13	17–18	19–20	blotched	present
<i>C. wayakonei</i>	72.0–86.8	76.8–89.0	31–35	absent	absent	6–8	7	17–18	19–20	banded	present
<i>C. thirakhupti</i>	72.0–79.6	99.1	37–40	present	absent	absent	absent	16	20	banded	present
<i>C. tigroides</i>	74.3–83.2	108.5–117.0	34	present	present	6+8+7	5+9+7	18–19	20–22	banded	present
<i>C. yangbaysensis</i>	78.5–92.3	91.3–109.1	39–46	5–16	0–2	6–8	0	16–19	15–17	banded	present
<i>C. ziegleri</i>	84.6–93.0	95.0–107.0	33–39	8–10	0–6	5–8	0–8	16–19	18–21	banded	absent

fewer number of ventral scale rows (31–32 vs. 38 in *C. teyniei*), and the presence of femoral pores (absent in *C. teyniei*). *Cyrtodactylus jaegeri* **sp. nov.** has femoral and precloacal pores which are lack in *C. thirakhupti* Pauwels, Bauer, Sumontha & Chanhome 2004. *Cyrtodactylus jaegeri* **sp. nov.** has 44 femoral and precloacal pores in a continuous series and thus differs from *C. tigroides* Bauer, Sumontha & Pauwels, 2003 which are separated by poreless scales (6+8+7 in males and 5+9+7 in females). *Cyrtodactylus jaegeri* **sp. nov.** has enlarged femoral scales and femoral pores which are absent in *C. wayakonei* Nguyen, Kingsada, Rösler, Auer & Ziegler, 2010. *Cyrtodactylus jaegeri* **sp. nov.** differs from *C. yangbayensis* Ngo & Chan, 2010 by its smaller size (SVL 60–68.5 mm vs. 78.5–92.3 mm in *C. yangbayensis*) and more femoral and precloacal pores in males (44 vs. 4–14 in *C. yangbayensis*).

Distribution. *Cyrtodactylus jaegeri* **sp. nov.** is currently known only from the type locality in Khammouane Province, Laos (Fig. 4).

Etymology. The new species is named in honour of our colleague Dr. Peter Jäger, arachnologist from the Research Institute Senckenberg, Frankfurt am Main, Germany, who collected the holotype.

Ecological notes. The type specimens were found at night, on karst cliffs ca. 1.5 m above the ground in a small belt of the secondary vegetation in front of a limestone cliff, at an elevation of 170 m a.s.l.

Discussion

The discovery of *Cyrtodactylus jaegeri* brings the species number of the genus *Cyrtodactylus* known from Laos to nine. This is also the fourth species of bent-toed geckos reported from Khammouane Province apart from *C. lomyenensis*, *C. roesleri* and *C. teyniei* (Ngo & Pauwels 2010; Teynié & David 2010; Luu et al. 2013). Morphologically, *C. jaegeri* resembles *C. lomyenensis* in its small size and dorsal color patterns. However, both can be distinguished from each other by the number of femoral and precloacal pores in males (44 vs. 39–40) and ventral scale rows (31–32 vs. 35–36) in *C. jaegeri* vs. *C. lomyenensis*, respectively. The type localities of both species are not very far from each other, approximately 30 km between Thakhek and Gnommalath. Therefore, additional molecular data might help to reveal the phylogenetic relationships between both species and with other species of *Cyrtodactylus* from Laos. The actual diversity of gekkonids from Laos is certainly underestimated. For example, in the bordering country of Vietnam, the species numbers of *Cyrtodactylus* has strikingly increased from three in 1997 to 31 in 2013 (Nguyen et al. 2013; Ziegler et al. 2013) compared to nine for the whole country of Laos.

The small size and depressed body of *C. jaegeri* maybe reflect an adaptation to hunting and shelter in the narrow rock crevices of limestone karst formations, as is seen in many *Goniurosaurus*, *Cyrtodactylus*, and *Tropidophorus* species (see Honda et al. 2006; Ziegler et al. 2007, 2008). Limestone mountains often represent island-like structures in a matrix of ancient, intensively cultivated farmland. Therefore population fragmentation may have led to species separation. The role of the Truong Son range (Annamite Mountains) as an evolutionary barrier, separating neighboring lizard communities on the eastern side in Laos and on the western side in Vietnam, potentially led to differing evolutionary trajectories. Further studies are crucially needed to elucidate the feedbacks of ecological adaptations on evolutionary process, and also to provide a better understanding of the natural history of the different lizard species.

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APPENDIX. Comparative material examined.

- Cyrtodactylus huongsonensis*. Vietnam: Hanoi: Huong Son: IEBR A.2011.3 (holotype), ZFMK 92293 (paratype).
- 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. 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. 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).

Publication 5

**A new species of the *Gekko japonicus* group (Squamata: Gekkonidae)
from central Laos**

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A new species of the *Gekko japonicus* group (Squamata: Gekkonidae) from central Laos

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Abstract

A new species of the *Gekko japonicus* group is described from Khammouane Province, central Laos, based on distinct morphological and molecular features. *Gekko thakhekensis* sp. nov. is distinguished from the remaining congeners by a combination of the following characters: size moderate (SVL 67.6–79.2 mm); nares in contact with rostral; internasals absent; postmentals enlarged; interorbital scales between anterior corners of the eyes 22–26; dorsal tubercles absent; ventral scales between mental and cloacal slit 165–174; midbody scale rows 110–116; ventral scale rows 32–40; subdigital lamellae on first toe 11–13, on fourth toe 14–15; finger and toe webbing present at base, about one fifth of length of digits; tubercles on upper surface of fore and hind limbs absent; precloacal pores 1–5 in males; postcloacal tubercles two; tubercles absent on dorsal surface of tail base; subcaudals enlarged; dorsal surface of body with greyish brown blotches. In molecular analyses, the new species is recovered as a sister taxon to *G. scientiaventura*, but the two species are separated by approximately 12% divergence as shown by the partial mitochondrial ND2 gene.

Key words: *Gekko thakhekensis* sp. nov., Khammouane Province, karst forest, morphology, molecular phylogeny

Introduction

The diversity of the genus *Gekko* in Laos is poorly studied. Only three species are currently recognized from this country, namely *Gekko gecko* (Linnaeus), *Gekko scientiaventura* Rösler, Ziegler, Vu, Hermann & Böhme (Teynié & David 2010), and *Gekko petricolus* Taylor (Bain & Hurley 2011). Another gekkonid species, *G. reevesii* (Gray), has been reported to be common in southern China and northern Vietnam (Rösler *et al.* 2011). However, the distribution of this species in Laos needs to be confirmed due to its morphological similarity to *G. gecko* (Linnaeus).

During our recent field surveys in central Laos, two gekkonid specimens were collected in the karst forests of Khammouane Province. Morphologically, these specimens can be assigned to the *Gekko japonicus* group based on the following features: size moderate; nares in contact with rostral; postcloacal tubercles present; webbing between fingers and toes weakly developed; lateral folds without tubercles; subcaudals enlarged; dorsum with large light blotches and bands (see Rösler *et al.* 2011; Nguyen *et al.* 2013). Our molecular data showed that the specimens

from Laos were clustered in the same clade with *G. scientiadventura*. However, the molecular divergence calculated using data from a fragment of the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene between these species is approximately 12%. Although only two male individuals are available, morphological differences are so distinct and in addition supported by our molecular findings that we describe it as a new species.

Material and methods

Sampling. Field surveys were conducted in mixed secondary forest near Thakhek Town, Khammouane Province, Laos, by Thomas Calame and Peter Jäger in April 2012, and by Vinh Quang Luu and Thomas Calame in June 2014. Tissue samples were preserved separately in 95% ethanol and voucher specimens were fixed in approximately 85% ethanol, then later transferred to 70% ethanol for permanent storage. Specimens were subsequently deposited in the collection of the Institute of Ecology and Biological Resources (IEBR) and Vietnam Forestry University (VFU), Hanoi, Vietnam. Other abbreviations are as follows: PNKB: Zoological Collection of the Phong Nha—Ke Bang National Park, Quang Binh Province, Vietnam; VNMN: Vietnam National Museum of Nature, Hanoi, Vietnam; ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Molecular data and phylogenetic analyses. We included samples of *Gekko scientiadventura* collected from Phong Nha—Ke Bang National Park, central Vietnam, and from Khammouane, central Laos. Additional samples of *G. adleri* Nguyen, Wang, Yang, Lehmann, Le, Ziegler & Bonkowski, *G. palmatus* Boulenger, and *G. truongi* Phung & Ziegler were sequenced. We also used all sequences available on Genbank for taxa in the *Gekko japonicus* group. Two species, *G. badenii* Shcherbak & Nekrasova and *G. grossmanni* Günther of the *G. petricolus* complex were used as outgroups. We used the protocols of Le *et al.* (2006) for DNA extraction, amplification, and sequencing. A fragment of the mitochondrial gene, the ND2, was amplified using the primer pair L4437b (Macey *et al.* 1997) and ND2r102 (Greenbaum *et al.* 2007). 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 analysis (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 to identify better converged trees. The optimal model for nucleotide evolution was set to GTR+I+G as selected by Modeltest v3.7 (Posada & Crandall 1998). The cutoff point for the burn-in function was set to 7 in the Bayesian analysis, as $-\ln L$ scores reached stationarity after 7,000 generations in both runs. Nodal support was evaluated using Bootstrap replication (BP) as calculated in PAUP and posterior probability (PP) in MrBayes v3.2. Uncorrected pairwise divergences were calculated in PAUP*4.0b10 (Table 1).

Morphological characters. Measurements were taken with digital calipers to the nearest 0.1 mm. The following abbreviations were used: Measurements: SVL = snout–vent length (from tip of snout to anterior margin of cloaca), TaL = tail length (from posterior margin of cloaca to tip of tail), AG = distance between axilla and groin, HL = maximum head length (from tip of snout to posterior margin of auricular opening), HW = maximum head width, HH = maximum head height, SE = distance from snout tip to anterior corner of eye, EE = distance between posterior margin of eye to posterior margin of ear opening, RW = maximum rostral width, RH = maximum rostral height, MW = maximum mental width, ML = maximum mental length. Scallation: CS = ciliary spines, N = nasals (nasorostrals, supranasals, postnasals), I = intersupranasals (scales between supranasals, in contact with rostral), SPL = supralabials (number of scales from below the middle of eye to the rostral scale), IFL = infralabials (number of scales from below the middle of eye to the mental scale), IO = interorbitals (number of scales in a line between anterior corners of eyes), PO = preorbitals (number of scales in a line from nostril to anterior corner of the eye), PM = postmentals, GP = gulars bordering the postmentals, DTR = dorsal tubercle rows at midbody, GSDT = granules surrounding dorsal tubercles, SMC = scales in a line from mental to the front of cloacal slit, SR = scale rows at midbody (including ventral scales), V = ventral scale rows at midbody, LF1 = subdigital lamellae under whole first finger, LF4 = subdigital lamellae under whole fourth finger, LT1 = subdigital lamellae under whole first toe, LT4 = subdigital lamellae under whole fourth toe, PP = precloacal pores (in males), PAT = postcloacal tubercles. Bilateral scale counts were given as left/right. Pictures of the species were taken with a digital microscope (Keyence VHX–500F).

Table 1. Uncorrected (“p”) distance matrix showing percentage pairwise genetic divergence (ND2) between *Gekko* species

Species name with Genbank number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. <i>G. badenii</i> (IEBR A.2012.24 (KP205398))	-																
2. <i>G. auriverrucosus</i> (JNO19062)	24.5	-															
3. <i>G. badenii</i> (JNO19065)	24.2	26.2	-														
4. <i>G. chinensis</i> (O19058)	15.7	26.4	26.4	-													
5. <i>G. grossmanni</i> (JNO19064)	29.0	32.0	25.5	30.3	-												
6. <i>G. hokouensis</i> (JNO19060)	22.6	21.2	24.6	22.6	30.3	-											
7. <i>G. japonicus</i> (JQ173424)	18.5	23.1	22.8	22.8	30.8	20.8	-										
8. <i>G. palmatus</i> (IEBR 3622 (KP205396))	23.6	25.1	15.5	15.5	30.1	21.5	27.1	-									
9. <i>G. subpalmatus</i> (JNO19063)	7.5	23.8	24.8	22.8	30.6	21.2	27.1	1.2	-								
10. <i>G. scientiadventura</i> (PKNG 2011.67 (KP205393))	24.6	20.4	25.8	22.6	30.3	21.2	21.2	23.5	23.0	-							
11. <i>G. scientiadventura</i> (IEBR 2014.7 (KP205392))	24.2	20.4	25.8	22.6	30.3	21.2	21.2	23.3	22.8	0.4	-						
12. <i>G. scientiadventura</i> (VFU 2014.1 (KP205395))	24.2	19.6	24.0	22.3	31.5	20.5	20.3	23.1	22.6	2.8	1.8	-					
13. <i>G. scientiadventura</i> (VFU 2014.2 (KP205394))	24.7	20.0	25.4	22.6	31.7	21.0	21.0	24.0	23.5	2.8	3.2	3.2	-				
14. <i>G. subpalmatus</i> (JNO19063)	23.7	18.9	24.2	24.6	31.2	22.1	22.6	24.2	23.8	19.8	19.8	19.8	19.2	-			
15. <i>G. swinhonis</i> (JNO19061)	23.7	18.9	24.0	21.0	30.1	19.2	19.4	20.6	20.3	21.0	21.0	21.0	20.6	20.3	-		
16. <i>G. thakoenensis</i> (IEBR A.2014.6, VFU R. 2014.9 (KP205396-7))	20.6-20.7	24.3	24.2-24.4	21.2-21.8	29.7-30.3	21.0-21.2	19.7-19.9	22.8-23.0	22.2-22.4	13.2	13.2	11.7	11.9	20.3	20.3	20.3	-
17. <i>G. inouei</i> (IEBR R.2011.1 (KP205395))	22.6	24.3	25.3	21.7	29.7	22.6	21.9	22.1	21.9	22.1	22.1	20.6	21.7	21.9	21.2	20.3-20.5	-

Results

Molecular phylogeny. The combined matrix contained 565 aligned characters. MP analysis of the dataset recovered a single most parsimonious tree with 883 steps (Consistency Index = 0.55; Retention Index = 0.59). One tree with a score of 4301.43 was retained in the ML analysis after 2076 rearrangements tried. The ML and BA topologies are similar to that produced by the MP analysis (Fig. 1). Overall, two clades within the *Gekko japonicus* group are strongly supported in all three analyses. The first one contains three species, *G. adleri*, *G. chinensis* Gray, and *G. palmatus*. In the second clade, the new species is strongly supported as a sister taxon to *G. scientiadventura* (BP = 100 and 99, PP = 100) (Fig. 1). It is also significantly divergent from others in terms of genetic distance with a minimum pairwise divergence of approximately 12% in the mitochondrial fragment of ND2 (see Table 1).

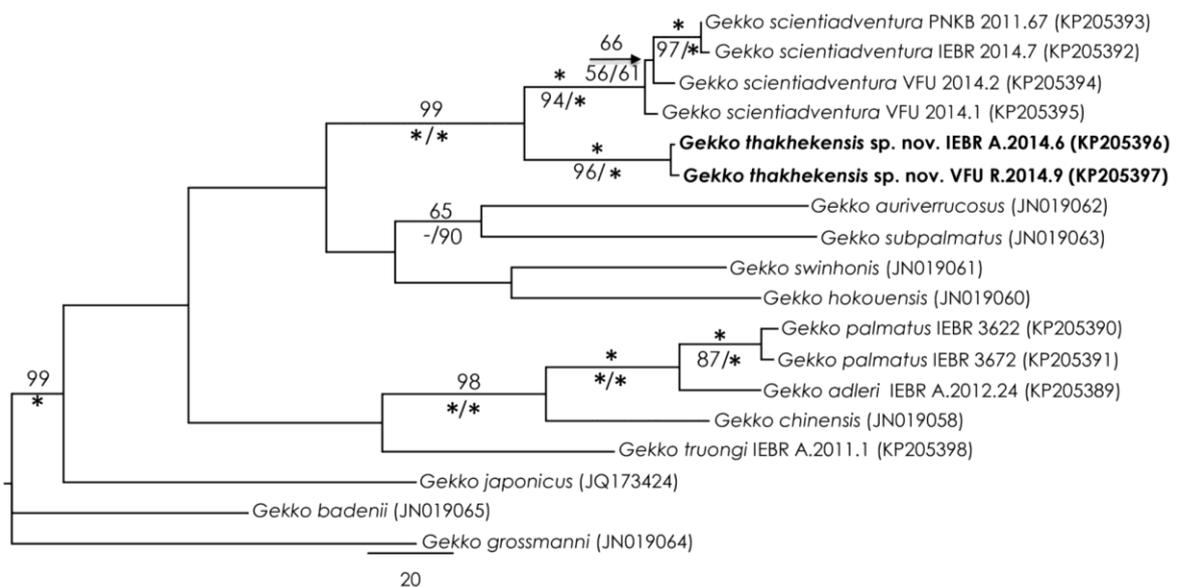


FIGURE 1. Single most parsimonious tree. Number above and below branches are MP and ML bootstrap values and Bayesian posterior probabilities (>50%), respectively. Asterisk denotes 100% value.

Gekko thakhekensis sp. nov.

(Figs. 2 and 4)

Holotype. IEBR A.2014.6, subadult male, collected on 29 April 2012 by Thomas Calame and Peter Jäger on a karst wall of a karstic massif, ca. 1.5 m above the forest floor, in a mixed secondary forest of hardwoods and shrubs near Thakhek Town (17°27.64'N, 104°55.24'E), Khammouane Province, Laos, at an elevation of 170 m a.s.l.

Paratype. VFU R.2014.9, adult male, collected on 02 June 2014 by Vinh Quang Luu and Thomas Calame on a liana near the wall of a karstic massif, ca. 2 m above the forest floor, in a mixed secondary forest of hardwoods and shrubs near Thakhek Town (17°27.707'N, 104°52.496'E), Khammouane Province, Laos, 4 km from the holotype locality at an elevation of 168 m a.s.l.

Diagnosis. The new species differs from its relatives on the basis of the following combination of characters: size moderate (SVL 67.6–79.2 mm); nares in contact with rostral; internasals absent; postmentals enlarged; interorbital scales between anterior corners of the eyes 22–26; dorsal tubercles absent; ventral scales between mental and cloacal slit 165–174; midbody scale rows 110–116; ventral scale rows 32–40; subdigital lamellae on first toe 11–13, on fourth toe 14–15; finger and toe webbing present at base, about one fifth of length of digits; tubercles on upper surface of fore and hind limbs absent; precloacal pores 1–5 in males; postcloacal tubercles two; tubercles absent on dorsal surface of tail base; subcaudals enlarged; dorsal surface of body with greyish brown blotches.

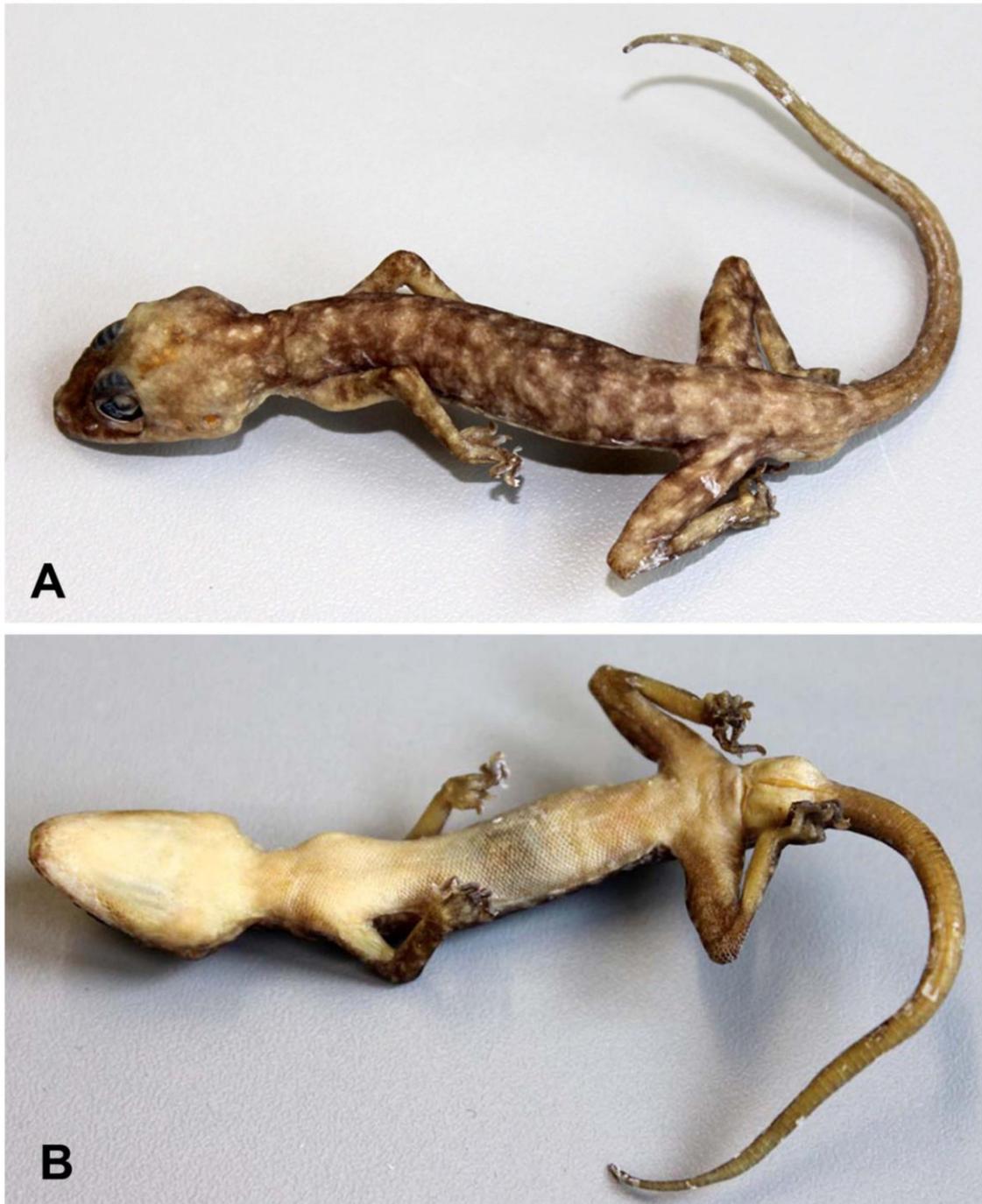


FIGURE 2. Holotype of *Gekko thakhekensis* sp. nov. (IEBR A.2014.6) in preserved state: A) dorsolateral view and B) ventral view. Photos V. Q. Luu.



FIGURE 3. Head portraits: A) dorsal view and B) ventral view; Body portraits: C) dorsal view and D) ventral view; and E) cloacal region of the preserved holotype (X mark: precloacal pore) of *Gekko thakhekensis* sp. nov. (IEBR A.2014.6). Photos V. Q. Luu.

TABLE 2. Measurements (in mm) and morphological characters of the type series of *Gekko thakhekensis* sp. nov. (* = regenerated partially; for other abbreviations see material and methods).

	IEBR A.2014.6 (holotype)	VFU R.2014.9 (paratype)
Sex	subadult male	adult male
SVL	67.6	79.2
TaL	66.7*	76.5
AG	29.3	35.7
HL	18.5	23.0
HW	14.1	16.3
HH	8.0	8.7
SE	7.7	9.4
EE	4.5	5.6
RW	3.3	3.4
RH	1.6	1.7
MW	2.2	2.2
ML	1.7	1.5
CS	3/5	3/5
N	3/3	3/3
PO	18	18
I	0	0
SPL	10/11	12/13
IFL	10/9	11/11
IO	22	26
PM	2	2
GP	5	5
DTR	0	0
GSDT	0	0
SMC	174	165
SR	110	116
V	32	40
LF1	13/13	13/10
LF4	15/15	13/13
LT1	13/13	11/12
LT4	15/15	14/14
PP	1	5
PAT	2/2	2/2

Description of holotype. Size moderate, SVL 67.6 mm, tail partially regenerated, TaL 66.7 mm, AG 29.3 mm; head longer than wide (HL 18.5 mm, HW 14.1 mm); rostral quadrangular, wider than high (RW 3.3 mm, RH 1.6 mm) and wider than mental (MW 2.2 mm), without suture; rostral in contact with first supralabial and supranasal; nostrils round, each surrounded by rostral, first supralabial, supranasal, and two enlarged nasals posteriorly; internasal absent; preorbitals 18; interorbitals 22; eye large (EE 4.5 mm, HL 18.5 mm), pupil vertical; ear opening oval, oblique, about 40% of the eye diameter (maximum tympanum diameter 1.7 mm, horizontal eye diameter 4.5 mm; mental triangular, wider than long (MW 2.2 mm, ML 1.7 mm); postmentals two, relatively trapezoidal, twice longer than wide, and longer than length of mental, in contact with mental and first infralabials anteriorly, medial suture between; postmentals longer than the length of mental; postmental in contact with 5 gular scales posteriorly, outer gular scales larger than inner scales; supralabials 10/11; infralabials 10/9; dorsal scales on body smooth,

round, granular and juxtaposed; lateral fold weakly developed; ventral scales much larger than dorsal scales, smooth, relatively hexagonal, imbricate, and largest in the middle of belly; ventrals between lateral folds 32; scales around midbody in 110 rows; ventral scales in a line between mental and cloacal slit 174; scales on upper and lower arm slightly enlarged; tubercles absent on dorsal surface of fore and hind limbs; scales on anterior and ventral parts of thigh larger than those on dorsal and posterior parts; enlarged femoral scales absent; fingers and toes basally webbed (about 1/5); subdigital lamellae under first finger 13/13, under fourth finger 15/15, under first toe 13/13, under fourth toe 15/15; precloacal pore one, precloacal scales enlarged; postcloacal tubercles 2/2, blunt; tail thickened at base, without tubercles on dorsal surface of tail base; dorsal caudal scales approximately twice the size than dorsal body scales, flat, in regular transverse rows; subcaudals flat, enlarged.



FIGURE 4. Adult male paratype (VFU R.2014.9) of *Gekko thakhekensis* **sp. nov.** in life. Photo T. Calame.

Coloration in ethanol. Dorsal surface of head, body, limbs, and tail greyish brown with irregular vertebral blotches; nuchal surface with a light-colored patch, nuchal loop absent; upper eyelids greyish black; snout and interorbital region vermiculate; some small light spots present in temporal region and on sides of neck; neck with a light grey blotch; dorsum without vertebral stripe; some light and grey spots present on dorsal surface; a row of light spots present along lateral folds; limbs with small light spots and bars; throat, venter, and precloacal region yellowish cream with dark marbling; lower surface of tail brown. For coloration in life see Fig. 4.

Variation. Measurements and scalation characters of the paratype are shown in Table 2. The following scale counts vary between the paratype and the holotype: interorbitals 22–26, scale rows from mental to the front of cloacal slit 165–174, ventrals 32–40, and precloacal pores 1–5.

Distribution. *Gekko thakhekensis* **sp. nov.** is currently known only from the type locality in Khammouane Province, Laos (Fig. 5).

Ecological notes. The type specimens were collected at night, between 1.5–2.0 m above the ground in a small belt of the secondary vegetation in front of a limestone cliff, at elevations of 168–170 m a.s.l.

Etymology. The specific epithet *thakhekensis* refers to the name of the type locality, Thakhek Town, Khammouane Province, Laos. Suggested common name: Thakhek Gecko.

TABLE 3. Morphological comparisons among the species of the *Gekko japonicus* group (modified after Nguyen *et al.* 2013, abbreviations defined in text, - = data unavailable)

Character	<i>Gekko</i> sp. nov.	<i>adleri</i>	<i>auriverrucosus</i>	<i>canhi</i>	<i>chinensis</i>	<i>japonicus</i>	<i>hokouensis</i>	<i>liboensis</i>	<i>melli</i>	<i>palmaris</i>	<i>scabridus</i>	<i>scientiadventura</i>
Maximum SVL (mm)	79.2	75.3	69	99.2	72	74	70	85	84.6	79.7	77	73
SPL (min)	10	10	9	14	10	9	10	12	10	11	9	12
SPL (max)	13	15	11	14	14	13	14	12	13	15	11	14
IFL (min)	9	9	9	10	9	8	8	11	9	9	9	9
IFL (max)	11	13	11	12	13	13	11	11	12	13	11	13
Nostril touching rostral	1	1	0	1	1	1	1	1	1	1	1	1
N (min)	3	3	3	3	2	3	3	3	3	3	3	3
N (max)	3	3	3	3	3	3	3	3	3	3	3	3
I (min)	0	1	0	1	1	0	1	0	1	0	1	0
I (max)	0	1	1	1	1	1	2	0	1	3	2	0
IO (min)	22	27	25	49	35	32	30	40	34	27	30	41
IO (max)	26	36	25	50	48	35	33	40	40	36	30	51
Postmentals (enlarged = 1, not enlarged = 0)	1	1	0	1	1	0	0	0	0	1	0	1
DTR (min)	0	7	16	11	10	9	12	10	0	4	17	0
DTR (max)	0	11	20	12	10	14	18	10	0	12	21	0
SMC (min)	165	168	-	168	156	169	153	-	181	160	-	118
SMC (max)	174	190	-	170	167	188	174	-	200	194	-	140
SR (min)	110	123	-	205	118	130	119	-	147	116	-	139
SR (max)	116	144	-	227	140	144	130	-	160	147	-	143
V (min)	32	35	-	49	37	39	36	-	43	36	-	38

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TABLE 3. (Continued)

Character	<i>Gekko</i> sp. nov.	<i>auriverrucosus</i>	<i>canhi</i>	<i>chinensis</i>	<i>japonicus</i>	<i>hokouensis</i>	<i>liboensis</i>	<i>melli</i>	<i>palnatus</i>	<i>scabridus</i>	<i>scientiadvventura</i>
V (max)	40	-	51	39	44	43	-	49	47	-	48
LT 1 (min)	11	6	13	8	10	8	8	10	10	6	12
LT1 (max)	13	8	16	10	12	11	8	12	13	9	15
LT 4 (min)	14	6	14	9	14	15	9	11	10	7	14
LT4 (max)	15	8	17	12	16	18	9	14	16	9	17
Toes webbed	1	0	0	1	0	0	0	1	1	0	1
Tubercles on fore-limbs (present = 1, absent = 0)	0	1	0	0	1	0	0	0	0	1	0
Tubercles on hind limbs (present = 1, absent = 0)	0	1	1	1	1	0	0	0	0	1	0
PP (in males, min)	1	8	5	17	6	5	-	9	23	10	5
PP (in males, max)	5	11	5	27	9	9	-	11	30	15	8
PAT (min)	2	2	2	1	2	1	1	1	1	1	2
PAT (max)	2	3	3	1	4	1	1	1	1	3	3
Tubercles on dorsal surface of tail (present = 1, absent = 0)	0	1	0	1	1	1	-	0	1	1	0
Subcaudals enlarged	1	1	1	1	1	1	-	1	1	1	1
Marking on upper side of head	0	0	0	0	0	0	0	1	0	0	1
Back flecked or blotched	1	0	1	1	0	1	0	0	1	1	1
Back banded	0	1	1	0	1	0	1	1	1	1	0
Tail banded	1	1	1	1	1	1	-	1	1	1	1

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TABLE 3. (continued)

Character	<i>Gekko</i> sp. nov.	<i>shibatatai</i>	<i>similignum</i>	<i>subpalmatum</i>	<i>swinhonis</i>	<i>taibaiensis</i>	<i>tawaensis</i>	<i>vertebralis</i>	<i>wenxianensis</i>	<i>yakuensis</i>
Maximum SVL (mm)	79.2	70.9	58.9	72	66	69	71	69.2	59	72
SPL (min)	10	10	12	8	7	9	13	10	12	12
SPL (max)	13	13	14	12	12	10	13	15	12	13
IFL (min)	9	10	11	7	7	8	15	10	11	9
IFL (max)	11	14	11	12	11	10	15	15	11	13
Nostril touching rostral	1	1	1	1	1	1	1	1	1	1
N (min)	3	3	3	3	-	-	-	3	-	3
N (max)	3	3	3	3	-	-	-	3	-	3
I (min)	0	0	1	1	-	-	2	0	1	1
I (max)	0	1	1	1	-	-	2	2	1	1
IO (min)	22	37	46	32	23	28	-	35	-	-
IO (max)	26	52	48	32	24	28	-	50	-	-
Postmentals	1	0	0	0	0	-	0	0	-	0
(enlarged = 1, not enlarged = 0)										
DTR (min)	0	5	11	0	6	-	0	2	10	-
DTR (max)	0	14	11	0	8	-	0	12	10	-
SMC (min)	165	-	-	-	-	-	-	-	-	-
SMC (max)	174	-	-	-	-	-	-	-	-	-
SR (min)	110	114	144	-	-	-	-	112	-	-
SR (max)	116	134	153	-	-	-	-	139	-	-
V (min)	32	-	-	48	40	-	-	-	42	-

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TABLE 3. (Continued)

Character	<i>Gekko</i> sp. nov.	<i>shibatai</i>	<i>similignum</i>	<i>subpalmaris</i>	<i>swinhonis</i>	<i>taibaiensis</i>	<i>tawaensis</i>	<i>vertebralis</i>	<i>wenxianensis</i>	<i>yakuensis</i>
V (max)	40	-	-	48	40	-	-	-	44	-
LT 1 (min)	11	-	11	7	6	6	10	-	6	10
LT1 (max)	13	-	13	9	9	7	10	-	6	10
LT 4 (min)	14	9	12	7	6	7	12	9	9	15
LT4 (max)	15	16	14	10	9	8	12	17	9	15
Toes webbed	1	0	1	1	0	-	0	0	0	0
Tubercles on fore-limbs (present = 1, absent = 0)	0	0	0	0	1	-	0	0	0	0
Tubercles on hind limbs (present = 1, absent = 0)	0	0	0	0	1	-	0	0	1	0
PP (in males, min)	1	0	17	5	7	4	0	0	6	6
PP (in males, max)	5	3	17	11	9	6	0	1	8	8
PAT (min)	2	1	1	1	2	-	1	1	2	1
PAT (max)	2	1	1	1	3	-	1	2	3	1
Tubercles on dorsal surface of tail (present = 1, absent = 0)	0	1	1	0	-	-	0	0	-	1
Subcaudals enlarged	1	1	1	1	1	-	1	1	-	1
Marking on upper side of head	0	0	0	0	0	0	0	0	0	0
Back flecked or blotched	1	1	1	1	1	1	1	1	1	1
Back banded	0	0	0	1	0	1	1	0	0	0
Tail banded	1	1	1	1	1	1	1	-	1	1



FIGURE 5. Map showing the type locality of *Gekko thakhekensis* in Khammouane Province, Laos.

Comparisons. We compared the undescribed gecko species from Khammouane Province, central Laos with all other members of the *Gekko japonicus* group based on examination of specimens and data obtained from the literature (Boulenger 1907; Ota *et al.* 1995; Rösler *et al.* 2005, 2010, 2011; Yang *et al.* 2012, Nguyen *et al.* 2013). Although only two male specimens were available for morphological comparisons, the undescribed species from Laos clearly differs from the remaining species of the *G. japonicus* group by a unique suite of features.

The new *Gekko* species differs from the members of the *G. japonicus* group as follows: from *G. adleri* by lacking internasals (vs. one in *G. adleri*), dorsal tubercles absent (vs. present in *G. adleri*), fewer scale rows around midbody (110–116 vs. 123–144 in *G. adleri*), fewer precloacal pores in males (1–5 vs. 17–21 in *G. adleri*), more postcloacal tubercles (two vs. one in *G. adleri*), and tubercles on dorsal surface of hind limbs absent (present in *G. adleri*); from *G. auriverrucosus* Zhou & Liu by having a nostril touching rostral (not touching in *G. auriverrucosus*), postmentals enlarged (not enlarged in *G. auriverrucosus*), dorsal body tubercles absent (vs. present in *G. auriverrucosus*), and fewer precloacal pores in males (1–5 vs. 8–11 in *G. auriverrucosus*); from *G. canhi* Rösler, Nguyen, Doan, Ho & Ziegler by having fewer interorbitals (22–26 vs. 49–50 in *G. canhi*), internasal absent (vs. present in *G. canhi*), dorsal tubercles absent (vs. present in *G. canhi*), fewer scale rows around midbody (110–116 vs. 205–227 in *G. canhi*), fewer ventral scale rows (32–40 vs. 49–51 in *G. canhi*), and tubercles on dorsal surface of hind limbs absent (present in *G. canhi*); from *G. chinensis* Gray by lacking internasals (vs. one in *G. chinensis*), fewer interorbitals (22–26 vs. 35–48 in *G. chinensis*), dorsal tubercles absent (vs. present in *G. chinensis*), tubercles on dorsal surface of hind limbs absent (present in *G. chinensis*), fewer precloacal pores in males (1–5 vs. 17–27 in *G. chinensis*), more postcloacal tubercles (two vs. one in *G. chinensis*), and tubercles on dorsal surface of tail absent (vs. present in *G. chinensis*); from *G. japonicus* (Schlegel) by having fewer interorbitals (22–26 vs. 32–35 in *G. japonicus*), postmentals enlarged (vs. not enlarged in *G. japonicus*), dorsal tubercles absent (vs. present in *G. japonicus*), fewer scale rows around midbody (110–116 vs. 130–144 in *G. japonicus*), tubercles on dorsal surface of fore and hind limbs absent (present in *G. japonicus*), fewer precloacal pores in males (1–5 vs. 6–9 in *G. japonicus*), and tubercles on dorsal surface of tail absent (vs. present in *G. japonicus*); from *G. hokouensis* Pope by lacking internasals (vs. one or two in *G. hokouensis*), fewer interorbitals (22–26 vs. 30–33 in *G. hokouensis*), postmentals enlarged (vs. not enlarged in *G. hokouensis*), dorsal tubercle rows absent (vs. present in *G. hokouensis*), fewer precloacal pores in males (1–5 vs. 5–9 in *G. hokouensis*), more postcloacal tubercles (two vs. one present in *G. hokouensis*), and tubercles on dorsal surface of tail absent (vs. present in *G. hokouensis*); from *G. liboensis* Zhao & Li by having fewer interorbitals (22–26 vs. 40 in *G. liboensis*), dorsal tubercle rows absent (vs. present in *G. liboensis*), and more postcloacal tubercles (two vs. one in *G. liboensis*); from *G. melli* Vogt by lacking internasals (vs. one present in *G. melli*), fewer interorbitals (22–26 vs. 34–40 in *G. melli*), postmentals enlarged (vs. not enlarged in *G. melli*), fewer scales in a line from mental to the front of cloacal slit (165–174 vs. 181–200 in *G. melli*), fewer scale rows around midbody (110–116 vs. 147–160 in *G. melli*), fewer ventral scale rows (32–40 vs. 43–49 in *G. melli*), fewer precloacal pores in males (1–5 vs. 9–11 in *G. melli*), and more postcloacal tubercles (two vs. one in *G. melli*); from *G. palmatus* by having dorsal tubercle rows absent (vs. present in *G. palmatus*), fewer precloacal pores in males (1–5 vs. 23–30 in *G. palmatus*), more postcloacal tubercles (two vs. one in *G. palmatus*), and tubercles on dorsal surface of tail absent (vs. present in *G. palmatus*); from *G. scabridus* Liu & Zhou by lacking internasals (vs. present in *G. scabridus*), fewer interorbitals (22–26 vs. 30 in *G. scabridus*), postmentals enlarged (vs. not enlarged in *G. scabridus*), dorsal tubercle rows absent (vs. present in *G. scabridus*), tubercles on dorsal surface of fore and hind limbs absent (present in *G. scabridus*), fewer precloacal pores in males (1–5 vs. 10–15 in *G. scabridus*), and tubercles on dorsal surface of tail absent (vs. present in *G. scabridus*); from *G. scientiadventura* by having fewer interorbitals (22–26 vs. 41–51 in *G. scientiadventura*), more scale rows from mental to cloacal slit (165–174 vs. 118–140 in *G. scientiadventura*), fewer scale rows around midbody (110–116 vs. 139–143 in *G. scientiadventura*), and fewer precloacal pores in males (1–5 vs. 5–8 in *G. scientiadventura*); from *G. shibatai* Toda, Sengoku, Hikida & Ota by having fewer interorbitals (22–26 vs. 37–52 in *G. shibatai*), postmentals enlarged (vs. not enlarged in *G. shibatai*), dorsal tubercle rows absent (vs. present in *G. shibatai*), more postcloacal tubercles (two vs. one in *G. shibatai*), and tubercles on dorsal surface of tail absent (vs. present in *G. shibatai*); from *G. similignum* Smith by having fewer interorbitals (22–26 vs. 46–48 in *G. similignum*), lacking internasals (vs. present in *G. similignum*), postmentals enlarged (vs. not enlarged in *G. similignum*), dorsal tubercle rows absent (vs. present in *G. similignum*), fewer scale rows around midbody (110–116 vs. 144–153 in *G. similignum*), fewer precloacal pores in males (1–5 vs. 17 in *G. similignum*), more postcloacal tubercles (two vs. one in *G. similignum*), and tubercles on dorsal surface of tail absent (vs. present in *G. similignum*); from *G. subpalmatus* Günther by having fewer interorbitals (22–26 vs. 32 in *G. subpalmatus*), postmentals enlarged (vs. not enlarged in *G. subpalmatus*), internasals absent (vs. present in *G. subpalmatus*), fewer ventral scale rows (32–40 vs. 48 in *G. subpalmatus*), and fewer precloacal pores in males (1–5 vs. 5–11 in *G. subpalmatus*), and more postcloacal tubercles (two vs. one in *G. subpalmatus*); from *G. swinhonis* Günther by having postmentals enlarged (vs. not enlarged in *G. swinhonis*), dorsal tubercle rows absent (vs. present in *G. swinhonis*), tubercles on dorsal surface of

fore and hind limbs absent (present in *G. swinhonis*), and fewer precloacal pores in males (1–5 vs. 7–9 in *G. swinhonis*); from *G. taibaiensis* Song by having a larger size (SVL 79.2 vs. 69.0 mm in *G. taibaiensis*), more lamellae under first and fourth toes (11–13 vs. 6–7 and 14–15 vs. 7–8, respectively, in *G. taibaiensis*), and fewer precloacal pores in males (1–5 vs. 4–6 in *G. taibaiensis*); from *G. tawaensis* Okada by lacking internasals (vs. present in *G. tawaensis*), postmentals enlarged (vs. not enlarged in *G. tawaensis*), precloacal pores present (vs. absent in *G. tawaensis*), and more postcloacal tubercles (two vs. one in *G. tawaensis*); from *G. vertebralis* Toda, Sengoku, Hikida & Ota by having fewer interorbitals (22–26 vs. 35–50 in *G. vertebralis*), postmentals enlarged (vs. not enlarged in *G. vertebralis*), dorsal tubercle rows absent (vs. present in *G. vertebralis*), and tubercles on dorsal surface of tail absent (vs. present in *G. vertebralis*); from *G. wenxianensis* Zhou & Wang by lacking internasals (vs. present in *G. wenxianensis*), dorsal tubercle rows absent (vs. present in *G. wenxianensis*), fewer ventral scale rows (32–40 vs. 42–44 in *G. wenxianensis*), tubercles on dorsal surface of hind limbs absent (present in *G. wenxianensis*), and fewer precloacal pores in males (1–5 vs. 6–8 in *G. wenxianensis*); and from *G. yakuensis* Matsui & Okada by having internasals absent (vs. present in *G. yakuensis*), postmentals enlarged (vs. not enlarged in *G. yakuensis*), fewer precloacal pores in males (1–5 vs. 6–8 in *G. yakuensis*), more postcloacal tubercles (two vs. one in *G. yakuensis*), and tubercles on dorsal surface of tail absent (vs. present in *G. yakuensis*).

Discussion

Morphologically, *G. thakhekensis* is most similar to *G. scientiadventura*, a sympatric species occurring in Khammouane Province. However, they can be clearly distinguished from each other based on several morphological characters such as body scalation (number of scales from mental to cloacal slit, scale rows around midbody), and the number of precloacal pores in males.

The molecular analyses demonstrate that the new species falls within the *G. japonicus* species group, and is strongly supported as a sister taxon to *G. scientiadventura*. Our phylogenetic results are in agreement with those generated by Nguyen *et al.* (2013) in that the clade containing *G. adleri*, *G. chinensis*, and *G. palmatus* is strongly corroborated by both the Bayesian and MP analyses. However, the relationship between *G. subpalmatus* and *G. swinhonis* are not well supported as shown in Nguyen *et al.* (2013). In fact, beside the two strongly supported clades, all other nodes within the *G. japonicus* species complex have low levels of support from all three analyses. To resolve these issues, it will be important to include more data, including more mitochondrial and nuclear genes, in future studies. Rösler *et al.* (2011) stated that the *Gekko japonicus* group is very complex in morphology. This genetically well-defined clade is morphologically variable (e. g., nares in contact with rostral or not, broad webbing between fingers and toes or not, dorsal tubercles absent or present, and tubercles on limbs absent or present).

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APPENDIX. *Gekko* specimens examined.

- G. adleri* (25): Vietnam: Cao Bang Province: IEBR A.2012.24 (holotype), ZFMK 93993–93999, IEBR A.2012.25–2012.31, VNMN A.2012.4–2012.6 (paratypes); China: Guangxi: SYS r000456–r0000461, SYS r000263 (paratypes).
- G. canhi* (4): Vietnam: Lang Son Province: IEBR A.0910 (holotype), VNMN 1001–1002 (paratypes); Lao Cai Province: ZFMK 88879 (paratype).
- G. palmatus* (30): Vietnam: Lao Cai Province: IEBR FN.29174; Tuyen Quang Province: IEBR A.0948; Bac Kan Province: IEBR 2301, IEBR A.0950–A.0951; Lang Son Province: IEBR 2474, IEBR 3619–3623, IEBR A.0949, A.0952; Quang Ninh Province: IEBR A.0807; Bac Giang Province: IEBR 3638, 3672; Vinh Phuc Province: IEBR 3223–3224a-c, ZFMK 44210, 59214–59215, 66517, 74552–74553; Hanoi: IEBR LQV3–LQV4; Thanh Hoa Province: IEBR TH.2011.1; Nghe An Province: IEBR A.0953–A.0955; Quang Binh Province: ZFMK 82888, 86434.
- G. scientiadventura* (9): Vietnam: Quang Binh Province: IEBR A.2014.7; PNKB 2011.67; ZFMK 76198 (holotype), ZFMK 76174–76179 (paratypes); ZFMK 80651–80652. Laos: Khammouane Province: VFU 2014.1–2014.2.

Publication 6

Morphological and molecular review of the *Gekko* diversity of Laos with descriptions of three new species.

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Morphological and molecular review of the *Gekko* diversity of Laos with descriptions of three new species

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Abstract

A review of the taxonomy, phylogeny, zoogeography, and ecology of the genus *Gekko* in Laos is provided based on morphological and molecular datasets. Three new species, which are both morphologically distinctive and molecularly divergent from described congeners, are described from Khammouane Province, central Laos: two members of the *G. japonicus* group, *Gekko bonkowskii* sp. nov. and *Gekko sengchanthavongi* sp. nov., and another member of the *G. petricolus* group, *Gekko boehmei* sp. nov. *Gekko bonkowskii* sp. nov. is closely related to the recently described *G. thakekensis*, which also occurs in Khammouane Province. *Gekko sengchanthavongi* sp. nov. is supported as a sister taxon to *G. scientiadventura* and *Gekko boehmei* sp. nov. is recovered as a sister species to *G. petricolus*. In addition, a key to the currently recognized members of the genus *Gekko* from Laos is provided.

Key words: *Gekko*, morphology, taxonomy, molecular phylogeny, Khammouane Province, Laos, karst forest

Introduction

Rösler *et al.* (2011) provided a review of the taxonomy, phylogeny, and zoogeography of all currently recognized *Gekko* species based on morphological and molecular datasets. These authors assigned the members of the genus *Gekko* to six species groups, namely the *G. gekko*, *G. japonicus*, *G. monarchus*, *G. petricolus*, *G. porosus*, and *G. vittatus* groups. However, the genus *Gekko* Laurent, 1768 still remains a comparatively poorly researched lizard group, as new species are continuously described. One hot spot of *Gekko* diversity within Southeast Asia is Vietnam, with 13 currently recognized species: *G. adleri* Nguyen, Wang, Yang, Lehmann, Le, Ziegler & Bonkowski, *G. badenii* Szczerbak & Nekrasova, *G. canaensis* Ngo & Gamble, *G. canhi* Rösler, Nguyen, Doan, Ho & Ziegler, *G. gekko* (Linnaeus), *G. grossmanni* Günther, *G. palmatus* Boulenger, *G. reevesii* (Gray, 1831), *G. russelltraini* Ngo, Bauer, Wood & Grismer, *G. scientiadventura* Rösler, Ziegler, Vu, Herrmann & Böhme, *G. takouensis* Ngo & Gamble, *G. truongi* Phung & Ziegler, and *G. vietnamensis* Nguyen (see Rösler *et al.* 2011; Phung & Ziegler 2011; Nguyen *et al.* 2013). In comparison, the diversity of *Gekko* in Laos is still underestimated, with only five recognized species so far, namely *Gekko gekko* (Linnaeus), *G. scientiadventura* Rösler, Ziegler, Vu, Hermann & Böhme (Teynié *et al.* 2004), *G. petricolus* Taylor (Bain & Hurley 2011), *G. thakhekensis* Luu, Calame, Nguyen, Le, Bonkowski & Ziegler, and *G. aaronbaueri* Ngo, Pham, Phimvohan, David & Teynié (see Table 1).

During our recent field work in central Laos between 2013 and 2014, three unnamed *Gekko* populations were found in the karst forest of Khammouane Province. Two of them, from the karst forests around Bualapha and Thakhek towns, could be assigned to the *Gekko japonicus* group sensu Rösler *et al.* (2011) based on the following morphological characters: size moderate (SVL 58.2–99.2 mm); nares touching rostral; 0–21 dorsal tubercle rows at midbody; 0–32 precloacal pores; 1–4 postcloacal tubercles present; weakly developed webbing between fingers and toes; the absence of lateral fold tubercles; enlarged subcaudals; dorsal surface with blotches and bands (see Rösler *et al.* 2011; Nguyen *et al.* 2013; Luu *et al.* 2014). The third population from Bualapha town revealed to be a representative of the *Gekko petricolus* group sensu Rösler *et al.* (2011) based on the following morphological characters: size moderate (SVL 82.9–108.5 mm); nares in contact with rostral; three nasals; postmentals relatively large; dorsal tubercle rows 8–18; precloacal pores 8–15; postcloacal tubercles 1–3; webbing between fingers and toes absent; hind limb tubercles present; lateral fold tubercles absent; subcaudals enlarged; dorsal pattern of head and body more or less symmetrically blotched (see Rösler *et al.* 2011). However, all three taxa are clearly distinguished from the remaining species of the *Gekko japonicus* and *Gekko petricolus* species groups by a combination of differing morphological features together with molecular phylogenetic divergence based on the mitochondrial NADH dehydrogenase subunit 2 (ND2) gene (approximately 6.8 to 9.0 %). We thus describe these taxa as new species.

Material and methods

Sampling. Field surveys were carried out by Vinh Quang Luu and Thomas Calame in mixed secondary forest near Thakhek Town, Khammouane Province, Laos, from 1 to 15 June 2014 and by Vinh Quang Luu, Kieusomphone Thanabuaosy, and Thidtavanh Suliyavong (hereafter Luu *et al.*) in the karst forest of Bualapha Town, Khammouane Province, between 16 to 30 June 2014. Tissue samples were preserved separately in 95% ethanol and voucher specimens were fixed in approximately 85% ethanol, then transferred to 70% ethanol for permanent storage. Specimens were subsequently deposited in the collection of the Vietnam Forestry University (VFU), the Institute of Ecology and Biological Resources (IEBR), Hanoi, Vietnam, the National University of Lao PDR (NUOL), the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany and the Museum für Naturkunde, Berlin (ZMB), Germany. Other abbreviations are as follows: PNKB: Zoological Collection of the Phong Nha – Ke Bang National Park, Quang Binh Province, Vietnam; VNMN: Vietnam National Museum of Nature, Hanoi, Vietnam; ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Molecular data and phylogenetic analyses. We included samples of *Gekko scientiadventura* collected from Phong Nha – Ke Bang National Park, central Vietnam, and from Khammouane, central Laos. Additional samples of *G. adleri*, *G. palmatus*, *G. truongi*, and *G. thakhekensis* were incorporated in the analyses. We also used all sequences available from Genbank for taxa of the *Gekko japonicus* group and the *G. petricolus* complex. Two species, *Lepidodactylus moestus* Peters and *L. orientalis* Brown & Parker, were used as outgroups (Table 2). We used the protocols of Le *et al.* (2006) for DNA extraction, amplification, and sequencing. A fragment of the mitochondrial gene, the ND2, was amplified using the primer pair L4437b (Macey *et al.* 1997) and ND2r102 (Greenbaum *et al.* 2007) and a pair of newly designed primers, GF1(5'-CAAGCACHATYATYACYATAT-3') and GR1 (5'-CCTATGTGTGCGATTGATGA-3'). After sequences were aligned using 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 analysis (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 to identify more highly converged trees. The optimal model for nucleotide evolution was set to TVM+I+G as selected by Modeltest v3.7 (Posada & Crandall 1998). The cutoff point for the burn-in function was set to 8 in the Bayesian analysis, as $-\ln L$ scores reached stationarity after 8,000 generations in both runs. Nodal support was evaluated using Bootstrap replication (BP) as calculated in PAUP and posterior probability (PP) in MrBayes v3.2. Uncorrected pairwise divergences were calculated in PAUP*4.0b10 (Table 3).

Morphological characters. Measurements were taken with a digital caliper to the nearest 0.1 mm. The following abbreviations were used: Measurements: SVL = snout–vent length (from tip of snout to anterior margin of cloaca), TaL = tail length (from posterior margin of cloaca to tip of tail), AG = distance between axilla and groin,

TABLE 1. Taxonomic review of *Gekko* members from Laos (modified after Panitvong *et al.* 2010; Rösler *et al.* 2011).

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Gekko gekko group															
<i>G. gekko gekko</i>	161	11–15	9–14	0	3–6	0–3	16–28	0	11–13	135–142	81–105	30–34	0	14–19	19–23
Gekko japonicus group															
<i>G. aaronsbaueri</i>	80	13–14	10–11	1	?	0–1	34–37	1	0	?	98–104	39–43	0	14–17	14–16
<i>G. bonkowskii sp.nov.*</i>	69.2	12–14	10–11	1	3	0	26–27	1	0	154–169	117	37–40	0	11–13	15
<i>G. scientiadvventura</i>	73	12–14	9–13	1	3	0	41–51	1	0	118–140	139–143	38–48	0	12–15	14–17
<i>G. sengchanthavongi sp.nov.*</i>	77.3	8–10	6–7	1	3	0	28–32	1	0	175–184	120–135	35–43	0	12–15	13–17
<i>G. thakhekensis</i>	79.2	12–14	10–11	1	3	0	22–26	1	0	165–174	110–116	32–40	0	11–13	14–15
Gekko petricolus group															
<i>G. boehmei sp.nov.*</i>	105.3	10–15	8–12	1	3	0–1	27–32	1	12–15	137–152	101–114	30–34	0	12–16	17–19
<i>G. petricolus</i>	98	12	10–11	1	3	0–1	36–38	1	16	146–156	<161	27–32	0	12–14	20

TABLE 1. (continued)

Taxon	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Gekko gekko group														
<i>G. gekko gekko</i>	0	1	1	12–16	1–3	1	0	gray to bluish or brownish gray	1	1	1	0	1	Borikhamxay, Champasak, Vientiane provinces
Gekko japonicus group														
<i>G. aaronsbaueri</i>	1	0	0	3–4	1–2	0	1	dark brown	1	1	0	0	1	Khammouane, Borikhamxay provinces
<i>G. bonkowskii sp.nov.*</i>	1	0	0	6	0–2	0	1	black to grey	1	1	0	0	1	Khammouane Province
<i>G. scientiadvventura</i>	1	0	0	5–8	2–3	0	1	brownish to yellowish	1	1	0	0	1	Khammouane, Borikhamxay provinces
<i>G. sengchanthavongi sp.nov.*</i>	1	0	0	4–5	2	0	1	dark brown to yellowish brown	1	1	1	0	1	Khammouane Province
<i>G. thakhekensis</i>	1	0	0	1–5	2	0	1	greyish brown	1	1	0	0	1	Khammouane Province
Gekko petricolus group														
<i>G. boehmei sp.nov.*</i>	0	0	1	10–11	1–2	1	1	yellow-grey	0	1	0	0	1	Khammouane Province
<i>G. petricolus</i>	0	0	1	9–10	1	1	1	gray-brown to yellow-brown	0	1	0	0	1	Southern Laos

1—maximum snout-vent length (in mm); 2—number of supralabials; 3—number of infralabials; 4—nostril touching rostral; 5—number of nasals; 6—number of intersupranasals; 7—number of interorbitals; 8—size of postmentals (enlarged or not); 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—throat and lateral folds with tubercles; 14—number of subdigital lamellae under the first toe; 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 pores (only in males); 20—number of postcloacal tubercles; 21—tubercles on dorsal surface of tail; 22—subcaudals enlarged; 23—ground coloration of dorsum; 24—marking on upper side of head; 25—back flecked or blotched; 26—banded back; 27—striped back; 28—banded tail; 29—distribution.

*1" = presence of character state; "0" = absence of character state.

**" = contribution of this study.

HL = maximum head length (from tip of snout to posterior margin of auricular opening), HW = maximum head width, HH = maximum head height, SE = distance from snout tip to anterior corner of eye, OD = greatest diameter of orbit, TD = maximum tympanum diameter, RW = maximum rostral width, RH = maximum rostral height, MW = maximum mental width, ML = maximum mental length. Scallation: CS = ciliary spines, N = nasals (nasorostrals, supranasals, postnasals), I = intersupranasals (scales between supranasals, in contact with rostral), SPL = supralabials (number of scales from below the middle of eye to the rostral scale), IFL = infralabials (number of scales from below the middle of eye to the mental scale), IO = interorbitals (number of scales in a line between anterior corners of eyes), PO = preorbitals (number of scales in a line from nostril to anterior corner of the eye), PM = postmentals, GP = gulars bordering the postmentals, DTR = dorsal tubercle rows at midbody, GSDT = granules surrounding dorsal tubercles, SMC = scales in a line from mental to the front of cloacal slit, SR = scale rows at midbody (including ventral scales), V = ventral scale rows at midbody, LF1 = subdigital lamellae under whole first finger, LF4 = subdigital lamellae under whole fourth finger, LT1 = subdigital lamellae under whole first toe, LT4 = subdigital lamellae under whole fourth toe, PP = precloacal pores, PAT = postcloacal tubercles. Bilateral scale counts were given as left/right. Pictures of the holotype were taken with a digital microscope (Keyence VHX-500F).

Multivariate Analysis was applied for examining interspecific differences between the new species and its relatives of the *Gekko japonicus* group. Twenty two of the 28 morphological characters (Rösler *et al.* 2011) were selected for correspondence analysis and cluster analysis with 1000 bootstrap replicates, using the average linkage method and correlation based similarity matrix. All statistical analyses were performed with PAST Statistics software version 3.06 (Hammer *et al.* 2001).

TABLE 2. Samples used in molecular analyses (Names in bold indicate new species).

Species	GenBank no.	Locality	Voucher number
<i>Gekko badenii</i>	JN019065	Captive	JB13
<i>G. auriverrucosus</i>	JN019062	China, Shanxi Province	NNU Z 20050716.004
<i>G. boehmei</i> sp. nov.	KT266819-20	Las, Khammouane Province	VFU R.2014.09, IEBR A.2015.31
<i>G. bonkowskii</i> sp. nov.	KT266818	Laos, Khammouane Province	VFU R.2014.10
<i>G. chinensis</i>	JN019058	China, Hainan Province	LLG 4209
<i>G. grossmanni</i>	JN019064	Captive	FBM 9
<i>G. hokouensis</i>	JN019060	China, Anhui Province	NNU Z 20050902.001
<i>G. japonicus</i>	JQ173424	n/a	HOFH 10061402
<i>G. palmatus</i>	KP205390	Vietnam, Lang Son Province	IEBR 3622
<i>G. palmatus</i>	KP205391	Vietnam, Bac Giang Province	IEBR 3672
<i>G. petricolus</i>	JN019066-7	Thailand	JB 70, JS 5
<i>G. scientiadventura</i>	KP205392-3	Vietnam, Quang Binh Province	IEBR A.2014.7, PNKB 2011.67
<i>G. scientiadventura</i>	KP205394-5	Laos, Khammouane Province	VFU 2014.2, VFU 2014.1
<i>G. sengchanthavongii</i> sp. nov.	KT266816-17	Laos, Khammouane Province	VFU R2014.14, IEBR A.2015.33
<i>G. subpalmatus</i>	JN019063	China, Szechuan Province	AMB 6567
<i>G. swinhonis</i>	JN019061	China, Henan Province	NNU Z 20051124.001
<i>G. thakhekensis</i>	KP205396-7	Laos, Khammouane Province	IEBR A.2014.6, VFU R.2014.9
<i>G. truongi</i>	KP205398	Vietnam, Khanh Hoa Province	IEBR A.2011.1
<i>Lepidodactylus moestus</i>	JN019079	Palau, Ngerur Island	USNM 521730
<i>L. orientalis</i>	JN019080	Papua New Guinea, Sudest Island	BPBM 19794

Results and discussion

Phylogenetic analyses. The combined ND2 data matrix contained 592 aligned characters. MP analysis of the dataset recovered a single most parsimonious tree with 1274 steps (Consistency Index = 0.46; Retention Index =

0.61). One tree with a Log likelihood score of -5844.37 was retained in the ML analysis after 7217 rearrangements tried. The phylogenetic relationships within the *Gekko japonicus* species group are similar to those supported by Luu *et al.*'s (2014) study, except for the placement of *G. hokouensis* and *G. swinhonis*. The two species were clustered as sister taxa in Luu *et al.* (2014), but *G. hokouensis* was recovered as a member of a clade with *G. adleri* + *G. chinensis* + *G. palmatus* + *G. truongi* and *G. swinhonis* was grouped with *G. auriverrucosus* + *G. subpalmatus* in the MP analysis. *G. sengchanthavongi* **sp. nov.** is strongly supported as sister species to *G. scientiadventura* (BP = 95 and 88; PP = 100), while *G. bonkowskii* **sp. nov.** is highly corroborated as sister species to *G. thakhekensis* (BP = 95 and 82; PP = 97) (Fig. 1). *G. sengchanthavongi* **sp. nov.** differs from *G. scientiadventura* by minimally 8.5% and *G. bonkowskii* **sp. nov.** is divergent from *G. thakhekensis* by at least 6.6% based on the partial ND2 data (Table 3).

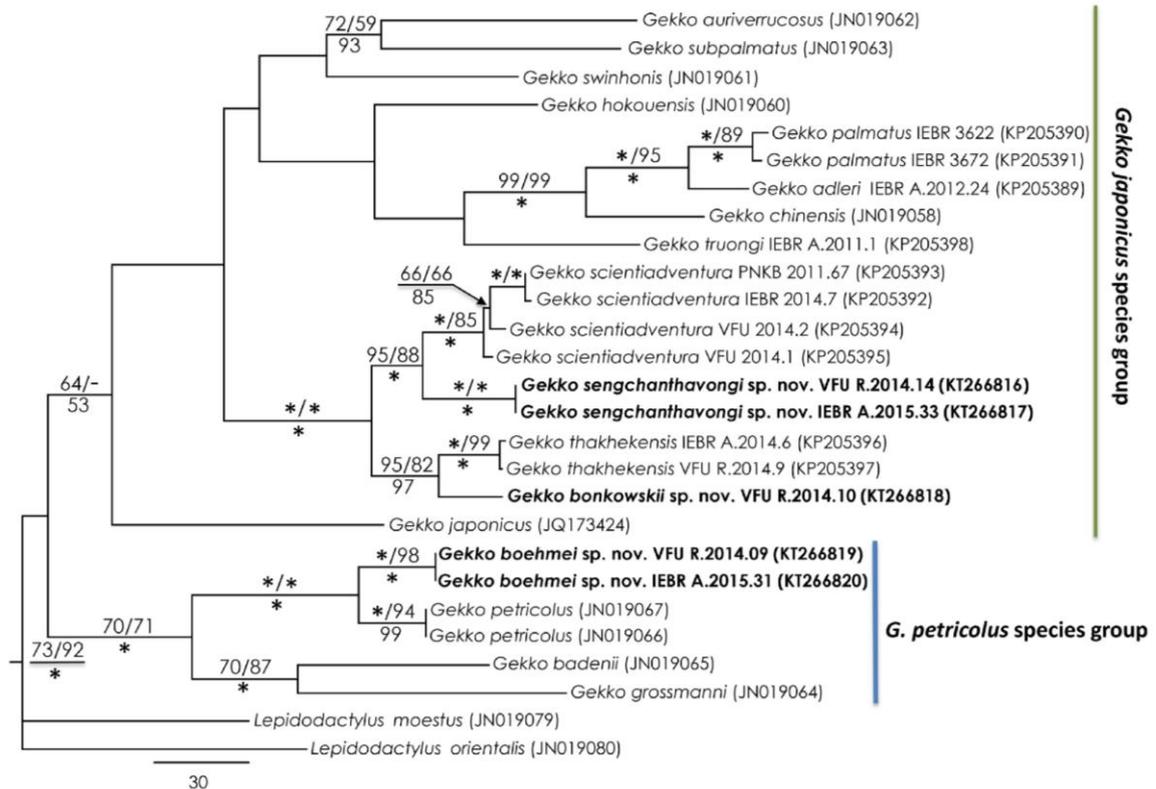


FIGURE 1. Single most parsimonious tree recovered by the MP analysis. Number above and below branches are MP/ML bootstrap values and Bayesian posterior probabilities (>50%), respectively. Asterisk denotes 100% value.

TABLE 3. Uncorrected (“p”) distance matrix showing percentage pairwise genetic divergence (COI) between new and closely related species.

Species name	1	2	3	4	5	6	7	8
1. <i>G. badenii</i> (JN019065)	-							
2. <i>G. boehmei</i> (KT266819-20)	24.9	-						
3. <i>G. bonkowskii</i> (KT266818)	23.5	25.9	-					
4. <i>G. grossmanni</i> (JN019064)	25.6	29.2	30.7	-				
5. <i>G. petricolus</i> (JN019066-7)	25.2	9.1	26.9	30.0	-			
6. <i>G. scientiadventura</i> (KP205392-5)	24.0-25.8	24.2-25.2	11.2-13.2	30.3-31.7	24.9-25.6	-		
7. <i>G. sengchanthavongi</i> (KT266816-17)	24.2	25.0	13.6	30.9	27.2	8.5-10.0	-	
8. <i>G. thakhekensis</i> (KP205396-7)	24.2-24.4	25.5-25.9	6.6-7.0	29.8-30.3	26.7-27.0	11.7-13.1	12.9	-

The topology within the *G. petricolus* species group is identical to that shown in Rösler *et al.*'s (2011) study. *Gekko boehmei* **sp. nov.** is recovered as the sister species to *G. petricolus* with strong statistical support from all three analyses (BPs = 100; PP = 100) (Fig.1). The new species is about 9.1% divergent from *G. petricolus* in terms of genetic distance in the mitochondrial fragment of ND2 (Table 3).

***Gekko bonkowskii* sp. nov.**

(Fig. 2)

Holotype. VFU R.2014.10, adult male, from the karst forest near Thakhek Town (17°27.260'N, 104°56.265'E, at an elevation of 146 m a.s.l.), Khammouane Province, central Laos, collected by Vinh Quang Luu and Thomas Calame on 6 June 2014.

Paratype. NUOL R-2015.1, adult female, the same data as the holotype.

Diagnosis. *Gekko bonkowskii* **sp. nov.** differs from its relatives by a combination of the following characters: a medium-sized gecko species (SVL 66.7 mm in the male, 69.2 mm in the female); nares touching rostral; internasals absent; postmentals enlarged; dorsal tubercles absent; ventral scale rows from mental to cloacal slit 154–169; scale rows around midbody 110–116; ventral scale rows 37–40; webbing weakly developed between fingers and toes; dorsal surface of limbs and tail without tubercles; precloacal pores six in a continuous row in the male, absent in the female; postcloacal tubercles 0–2; subcaudals enlarged; dorsum with black and grey blotches.



FIGURE 2. A) Dorsal view of the holotype (VFU R.2014.10) and B) the paratype (NUOL R-2014.5) of *Gekko bonkowskii* **sp. nov.** Photos T. Calame.

Description of holotype. An adult male with a total length of 145.9 mm (SVL 66.6 mm, TaL 79.3 mm); body slender, elongate (ratio of AG/SVL 0.48); head longer than wide (ratio of HL/HW 1.43); rostral quadrangular without suture medially, nearly twice wider than high (ratio of RW/RH 1.93) and wider than mental (ratio of RW/MW 1.29 mm), touching first supralabial and supranasal on each side; nostrils round, in contact with rostral, first supralabial, supranasal, and two enlarged nasals posteriorly, upper nasal smaller than lower nasal; posterior nasal region concave; internasal absent; preorbitals 24, preorbital region deeply concave; interorbitals 26; eye large (ratio of OD/HL 0.23), pupil vertical; ear opening oval, oblique, smaller than eye (TD/OD ratio 0.38); mental triangular, about two times wider than long (ratio of MW/ML 1.93); postmentals two, hexagonal, twice as long as wide, and longer than length of mental, touching mental, first infralabial on both sides and 6 gular scales posteriorly, outer gular scales larger than inner scales; supralabials 12/12; infralabials 10/11; dorsal scales on body smooth, round or oval, granular and juxtaposed; lateral fold present; ventrals distinctly larger than dorsal scales, smooth, imbricate, and largest in the middle of belly; ventral scale rows at midbody 37; scale rows around midbody 117; ventral scales in a row between mental and cloacal slit 154; scales on dorsal forelimbs slightly enlarged; tubercles on dorsal surface of limbs absent; scales on anterior and ventral parts of femur larger than those on posterior and dorsal parts; enlarged femoral scales absent; fingers and toes basally webbed; subdigital lamellae under first finger 12/12, under fourth finger 14/13, under first toe 12/12, under fourth toe 15/15; precloacal pores six, in a continuous row; precloacal scales enlarged; postcloacal tubercles 2/0; base of tail thickened, without tubercles on dorsal surface; subcaudals enlarged, smooth, imbricate.

Coloration in life. Dorsal surface of head brownish grey with dark and grey blotches; labials with grey bars; upper eyelids brownish black; dorsal surface of body brownish grey with black and grey blotches, in oval or round shape, forming a cross-row in anterior part, irregular in posterior part; dorsal surface of fore and hind limbs dark grey; ventral surface of head, belly, and limbs cream with black dots, chest cream with black blotches on each scale; dorsal surface of tail with six or seven grey transverse bands; ventral tail grey in forepart and with nearly closed bands in hindpart.

Sexual dimorphism. Measurements and scalation characters of the female paratype are shown in Table 4. The following scale counts slightly vary between the paratype and the holotype: scale rows from mental to the front of cloacal slit 154 (169 in the holotype), ventrals 37 (40 in the holotype), and precloacal pores absent in the female paratype. Throat and flanks of the paratype reticulated.

Comparisons. Based on examination of specimens and data obtained from the literature (Boulenger 1907; Ota *et al.* 1995; Rösler *et al.* 2005, 2010, 2011; Yang *et al.* 2012, Nguyen *et al.* 2013; Luu *et al.* 2014; Ngo *et al.* 2015; Yang 2015) we compared the new species from Laos with the remaining members of the *Gekko japonicus* group sensu Rösler *et al.* (2011) (see Table 5). Both correspondence and cluster analyses revealed that *Gekko bonkowskii* sp. nov. is closely related to *G. thakhekensis* (Figs. 3–4). Molecular phylogenetic analyses supported the sister relationship between the new species and *G. thakhekensis* (see Fig. 1). Morphologically, the new *Gekko* species can be distinguished from the species of the *G. japonicus* (following Rösler *et al.* 2011) group as follows:

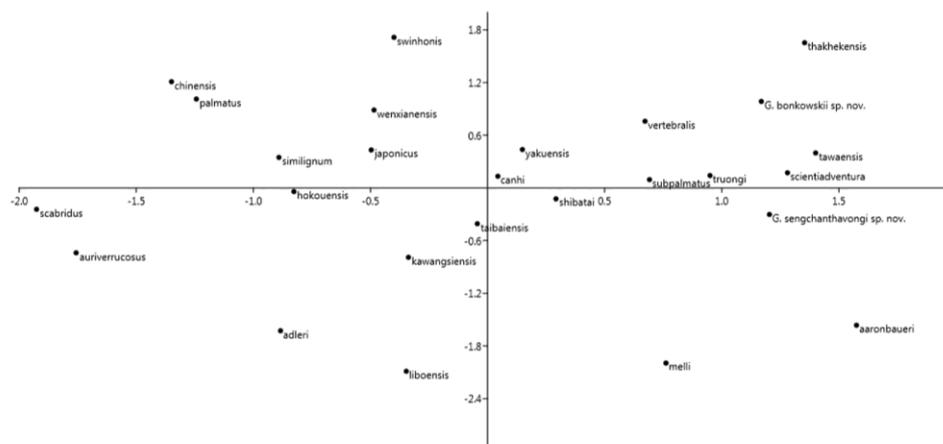


FIGURE 3. Correspondence analysis showing species association of the *Gekko japonicus* group sensu Rösler *et al.* (2011) based on morphological comparisons.

TABLE 4. Measurements (in mm) and morphological characters of the type series of *Gekko bonkowskii* **sp. nov.** and *Gekko sengchanthavongi* **sp. nov.** (for abbreviations see material and methods).

	<i>Gekko bonkowskii</i> sp. nov.		<i>Gekko sengchanthavongi</i> sp. nov.			Min–Max	M±SD	VFU R.2014.13 (paratype)
	VFU R.2014.10 (holotype)	NUOL R-2014.5 (paratype)	VFU R.2014.14 (holotype)	IEBR A.2015.33 (paratype)	NUOL R-2015.3 (paratype)			
Sex	adult male	adult female	adult male	adult male	adult male			adult female
SVL	66.7	69.2	67.7	77.3	72.8	67.7–77.3	72.6±4.8	76.8
TaL	79.2	76.0	79.1	8.0*	80.0*	79.1(n=1)	79.1±0.0	84.6
AG	31.8	31.5	29.6	32.2	29.4	29.4–32.2	30.4±1.6	35.5
HL	18.5	18.4	19.8	21.6	21	19.8–21.6	20.8±0.9	21.6
HW	12.9	12.8	13.4	14.3	17.3	13.4–17.3	15.0±2.0	13.8
HH	7.6	7.3	7.4	7.9	8.5	7.4–8.5	7.9±0.6	7.7
SE	8.5	7.7	8.6	8.4	8.9	8.4–8.9	8.6±0.3	9.2
OD	4.2	4.3	4.8	4.8	4.7	4.7–4.8	4.8±0.1	5.2
TD	1.6	1.7	2.3	2.2	2.3	2.2–2.3	2.3±0.1	2.2
RW	2.7	2.9	3.0	3.2	3.3	3.0–3.3	3.2±0.2	3.3
RH	1.4	1.4	1.4	1.2	1.5	1.2–1.5	1.4±0.2	1.4
MW	2.1	1.8	2.2	2.3	2.3	2.2–2.3	2.3±0.1	2.4
ML	1.5	1.6	1.4	1.8	1.4	1.4–1.8	1.5±0.2	1.7
CS	4/5	4/3	6/6	5/6	5/5	5–6	5.5±0.6	5/6
N	3/3	3/3	3/3	3/3	3/3	3	3.0±0.0	3/3
I	0	0	0	0	0	0	0	0
SPL	12/12	14/12	10/9	10/8	8/9	8–10	9.0±0.9	9/10
IFL	10/11	10/10	7/7	7/7	6/7	6–7	6.8±0.4	7/7
PO	24	24	17/17	18/18	18/18	17–18	17.7±0.5	18/18
IO	26	27	28	30	32	28–32	30.0±2.0	32
PM	2	2	2	2	2	2	2.0±0.0	2
GP	6	6	6	7	6	6–7	6.3±0.6	7
DTR	0	0	0	0	0	0	0	0
GSDT	0	0	0	0	0	0	0	0
SMC	154	169	179	184	182	179–184	181.7±2.5	175
SR	117	117	126	120	135	120–135	127.0±7.6	130
V	37	40	35	40	43	35–43	39.3±4.0	42
LF1	12/12	10/10	12/11	11/10	15/13	10–15	12.0±1.8	12/11
LF4	14/13	13/14	14/13	13/12	15/15	12–15	13.7±1.2	13/13
LT1	12/12	13/11	13/11	12/11	13/14	11–14	12.3±1.2	13/13
LT4	15/15	15/15	14/15	14/13	17/16	13–17	14.8±1.5	15/15
PP	6	0	3+2	3+2	3+1	4–5	4.7±0.6	0
PAT	2/0	2/0	2/2	2/2	2/2	2	2.0±0.0	2/2

G. bonkowskii **sp. nov.** can be distinguished from *G. aaronbaueri* Ngo, Pham, Phimvohan, David & Teynié by its smaller size (SVL reaching 69.2 *versus* 80.0 mm), having fewer interorbital scales (26–27 *versus* 34–37), more

scale rows around midbody (117 *versus* 98–104), fewer subdigital lamellae under first toe (11–13 *versus* 14–17), and more precloacal pores in males (6 *versus* 3–4); from *G. adleri* by the absence of internasals, tubercles on dorsal surface of limbs and tail (*versus* present), having fewer scale rows around midbody (117 *versus* 123–144) and fewer precloacal pores in males (6 *versus* 17–21); from *G. auriverrucosus* Zhou & Liu by having more supralabials (12–14 *versus* 9–11), nostril touching rostral (*versus* not touching), postmentals enlarged (*versus* not enlarged), lacking dorsal tubercles (*versus* present), fewer precloacal pores in males (6 *versus* 8–11), and fewer postcloacal tubercles (0–2 *versus* 2–3); from *G. canhi* by having a smaller size (SVL reaching 69.2 mm *versus* 99.2 mm), the absence of internasals and dorsal tubercles (*versus* present), fewer scale rows around midbody (117 *versus* 205–227), fewer ventral scales (37–40 *versus* 49–51), and the absence of tubercles on dorsal surface of hind limbs (*versus* present); from *G. chinensis* Gray by the absence of internasals (*versus* present), fewer interorbital scale rows (26–27 *versus* 35–48), the absence of tubercles on dorsal surface of body, hind limbs, and tail (*versus* present), and fewer precloacal pores in males (6 *versus* 17–27); from *G. japonicus* (Schlegel) by having postmentals enlarged (*versus* not enlarged), the absence of tubercles on dorsal surface of body, limbs, and tail (*versus* present), fewer scales around midbody (117 *versus* 130–144), fewer precloacal pores in males (6 *versus* 6–9), and fewer postcloacal tubercles (0–2 *versus* 2–4); from *G. hokouensis* Pope by the absence of internasals and dorsal tubercles (*versus* present), fewer interorbitals (26–27 *versus* 30–33), postmentals enlarged (*versus* not enlarged), and the absence of tubercles on dorsal surface of tail (*versus* present); from *G. kwangsiensis* Yang by the absence of tubercles on dorsal surface of body (*versus* present in *G. kwangsiensis*), fewer scales from mental to cloacal slit (154–169 *versus* 185–208), fewer ventral scales (37–40 *versus* 41–45), and fewer precloacal pores in males (6 *versus* 9–11); from *G. liboensis* Zhao & Li by its smaller size (SVL reaching 69.2 *versus* 85.0 mm), having fewer interorbitals (26–27 *versus* 40), and the absence of tubercles on dorsal surface of body (*versus* present); from *G. melli* Vogt by its smaller size (SVL reaching 69.2 *versus* 84.6 mm), internasals absent (*versus* present), postmentals enlarged (*versus* not enlarged), fewer scales from mental to cloacal slit (154–169 *versus* 181–200), fewer scale rows around midbody (117 *versus* 147–160), fewer ventral scale rows (37–40 *versus* 43–49), and fewer precloacal pores in males (6 *versus* 9–11); from *G. palmatus* by its smaller size (SVL reaching 69.2 *versus* 79.7 mm), the absence of tubercles on dorsal surface of body and tail (*versus* present), and fewer precloacal pores in males (6 *versus* 23–30); from *G. scabridus* Liu & Zhou by the absence of internasals (*versus* present), postmentals enlarged (*versus* not enlarged), the absence of tubercle on dorsal surface of body, limbs, and tail (*versus* present), and fewer precloacal pores in males (6 *versus* 10–15); from *G. scientiaventura* by having fewer interorbitals (26–27 *versus* 41–51), more scales from mental to cloacal slit (154–169 *versus* 118–140), and fewer scale rows around midbody (117 *versus* 139–143); from *G. shibatai* Toda, Sengoku, Hikida & Ota by having fewer interorbitals (26–27 *versus* 37–52), postmentals enlarged (*versus* not enlarged), the presence of toe webbing (*versus* absent), the absence of tubercles on dorsal surface of body and tail (*versus* present), and more precloacal pores (6 *versus* 0–3); from *G. similignum* Smith by its larger size (SVL reaching 69.2 *versus* 58.9 mm), having fewer interorbitals (26–27 *versus* 46–48), the absence of internasals (*versus* present), postmentals enlarged (*versus* not enlarged), the absence of tubercles on dorsal surface of body and tail (*versus* present), fewer scale rows around midbody (117 *versus* 144–153), and fewer precloacal pores in males (6 *versus* 17); from *G. subpalmatus* Günther by having fewer interorbitals (26–27 *versus* 32), postmentals enlarged (*versus* not enlarged), the absence of internasals (*versus* present), and fewer ventral scales (37–40 *versus* 48); from *G. swinhonis* Günther by having postmentals enlarged (*versus* not enlarged), the absence of dorsal tubercle rows on body and limbs (*versus* present), fewer precloacal pores in males (6 *versus* 7–9), and fewer postcloacal tubercles (0–2 *versus* 2–3); from *G. taibaiensis* Song by having more lamellae under first and fourth toes (11–13 *versus* 6–7 and 15 *versus* 7 or 8, respectively) and more precloacal pores in males (6 in a continuous series *versus* 4–6 in interrupted series); from *G. tawaensis* Okada by the lack of internasals (*versus* 2), postmentals enlarged (*versus* not enlarged), and precloacal pores present (*versus* absent); from *G. thakhekensis* by its smaller size (SVL reaching 69.2 *versus* 79.2 mm), having toe webbing developed only basally (ca. one seventh) (*versus* one fifth of length of digits), and more precloacal pores in males (6 *versus* 1–5); from *G. truongi* by its smaller size (SVL reaching 69.2 *versus* 95.9 mm), having fewer scale rows around midbody (117 *versus* 131–143), and fewer precloacal pores in males (6 *versus* 10–11); from *G. vertebralis* Toda, Sengoku, Hikida & Ota by having fewer interorbitals (26–27 *versus* 35–50), postmentals enlarged (*versus* not enlarged), and the absence of tubercles on dorsal surface of body and tail (*versus* present); from *G. wenxianensis* Zhou & Wang by its larger size (SVL reaching 69.2 *versus* 59.0 mm), the absence of internasals (*versus* present), the absence of tubercles on dorsal surface of body and hind limbs (*versus* present), fewer ventral

scale rows (37–40 *versus* 42–44), and fewer precloacal pores in males (6 *versus* 6–8); and from *G. yakuensis* Matsui & Okada by lacking internasals (*versus* present), having postmentals enlarged (*versus* not enlarged), fewer precloacal pores in males (6 *versus* 6–8), and the absence of tubercles on dorsal surface of tail (*versus* present).

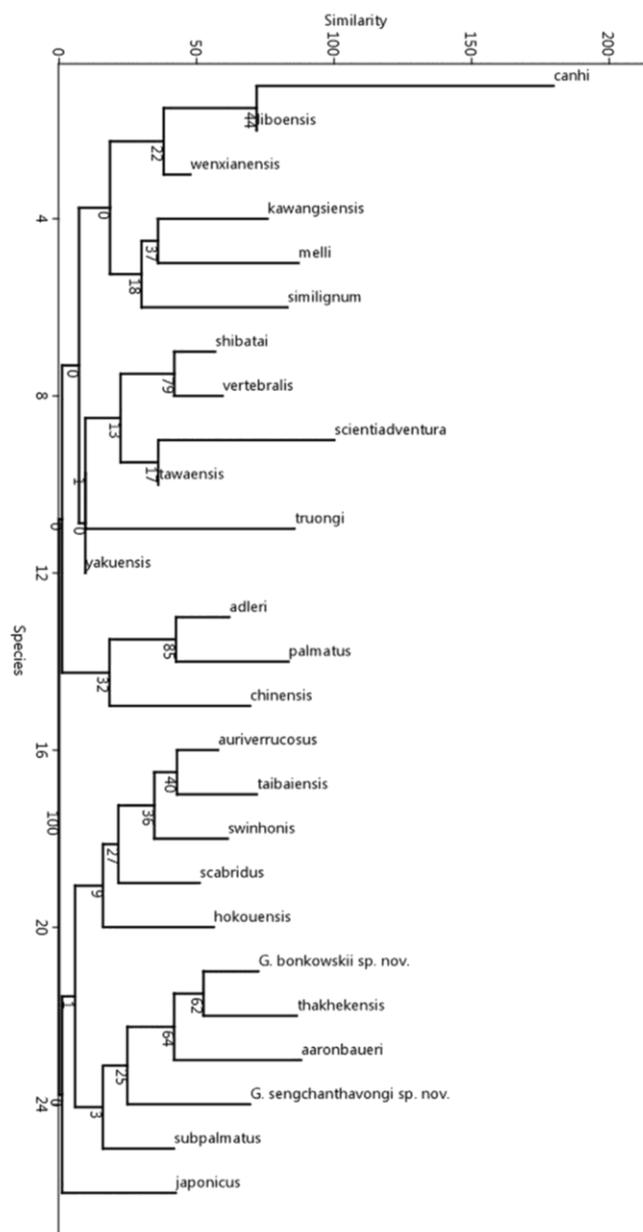


FIGURE 4. Cluster analysis showing species correlation of the *Gekko japonicus* group based on morphological comparisons (1000 bootstrap replicates).

Distribution. *Gekko bonkowskii* sp. nov. is currently known only from the type locality in Khammouane Province, central Laos (Fig. 5).

Etymology. The new *Gekko* species is named after Professor Dr. Michael Bonkowski from the Zoological Institute, University of Cologne, Germany to acknowledge his engagement for herpetological and ecological research in the Indochina region. We suggest as common names: Bonkowski’s Gecko (English), Kap Ke Bonkowski (Laotian), and Bonkowskis Gecko (German).



FIGURE 5. Map showing the type locality (black circle) of three new species of *Gekko* in Khammouane Province, central Laos.



FIGURE 6. A) Agricultural area and macrohabitat of *Gekko bonkowskii* sp. nov., B) construction works, and C) limestone exploitation for building purposes Photos V. Q. Luu.

Natural history. Specimens of *Gekko bonkowskii* were found at night between 20:00 and 21:00 on the tree trunk of shrubs, about 1.0–1.5 m above the ground, near the entrance of a karst cave at an elevation of 146 m a.s.l. Surrounding habitat was secondary forest of small hardwood and shrubs near a village (ca. 20 m) and about 40 m from the main road. The crepuscular or nocturnal new species co-occurs with at least two other gecko species in the same karstic microhabitat: *Gekko gecko* and the recently described bent-toed gecko *Cyrtodactylus jaegeri* (Luu *et al.* 2014). We also found the large huntsman spider species *Heteropoda maxima* (Jaeger) in the immediate vicinity of the observed gecko species (Fig. 6).

***Gekko sengchanthavongi* sp. nov.**
(Fig. 7)

Holotype. VFU R.2014.14, adult male, in karst forest of Bualapha Town (17°19.444'N, 105°41.576'E, at an elevation of 210 m a.s.l.), Khammouane Province, central Laos, collected by Vinh Quang Luu and Thidtavanh Suliyavong on 20 June 2014.

Paratypes. Two adult males NUOL R-2015.3, IEBR A.2015.33 and one adult female VFU R.2014.16, the same data as the holotype.

Diagnosis. *Gekko sengchanthavongi* sp. nov. can be distinguished from its congeners in the *Gekko japonicus* group by a combination of the following characters: a medium-sized gecko species (SVL 67.7–77.3 mm); nares in contact with rostral; internasals absent; postmentals enlarged; supralabials 8–10; infralabials 6 or 7; dorsal tubercles absent; ventral scale rows from mental to cloacal slit 175–184; scale rows around midbody 120–135; ventral scale rows 35–43; webbing weakly developed between fingers and toes; tubercles on dorsal surface of limbs and tail absent; precloacal pores 3+1 or 3+2 in the males, separated from each other by one poreless scales, absent in the female; postcloacal tubercles 2/2; subcaudals enlarged; dorsum with dark bars.

Description of holotype. Adult male, total length 146.8 mm (SVL 67.7 mm, TaL 79.1 mm); body slender, elongate (ratio of AG/SVL 0.44); head longer than wide (ratio of HL/HW 1.48); rostral quadrangular, two times wider than high (ratio of RW/RH 2.14) and wider than mental (ratio of RW/MW 1.36 mm), without medial suture; rostral bordered by first supralabial and supranasal on each side; nostrils round, surrounded by rostral, first supralabial, supranasal, and two enlarged nasals posteriorly; posterior nasal region deeply concave; internasals absent; preorbital scales 17, preorbital region slightly concave; interorbital scales 28; eye large (ratio of OD/HL 0.24), pupil vertical, superciliaries with six tiny spines posteriorly; ear oval-shaped, oblique, approximately half of eye diameter (ratio of TD/OD 0.48); mental triangular, wider than long (ratio of MW/ML 1.57); enlarged postmentals two, hexagonal, two times longer than wide, bordered by mental, first infralabial on each side and 6 gular scales posteriorly, outer gular scales larger than inner scales; supralabials 10/9; infralabials 7/7; dorsal scales smooth, small, round or oval, granular and juxtaposed; lateral skin folds present; ventral scales smooth, medial scales 3 or 4 times larger than dorsal scales, and largest in the middle of belly; ventral scales at midbody 35; scale rows around midbody 126; ventral scale rows between mental and cloacal slit 179; scales on dorsal limbs slightly enlarged; tubercles on limbs absent; enlarged femoral scales absent; fingers and toes webbed at base; subdigital lamellae under first finger 12/11, under fourth finger 14/13, under first toe 13/11, under fourth toe 15/15; precloacal pores 3+2, separated by one poreless scale, precloacal scales enlarged; postcloacal tubercles 2/2; tail basally thickened, without dorsal tubercles; subcaudals enlarged, smooth.

Coloration in life. Ground coloration of dorsal head dark brown; dorsal head and neck with dark and grey spots; dorsum with six bands between limb insertions, edged in yellowish brown, and irregular transverse dark brown bars; dorsal surface of limbs with dark blotches; dorsal surface of tail grey with 10 or 11 dark bands, edged in white; chin, throat, dorsolateral region and lower surface of limbs grey with light spots; chest, middle of belly grey; ventral tail grey in anterior part and with nearly closed bands in posterior part.

Sexual dimorphism. Measurements and scalation characters of the female paratype are provided in Table 4. The following scale counts slightly vary between the female and males: scale rows in line from mental to the front of cloacal slit 175 (179–184 in males), and precloacal pores absent in the female paratype.

Comparisons. Based on examination of specimens and data obtained from the literature (Boulenger 1907; Ota *et al.* 1995; Rösler *et al.* 2005, 2010, 2011; Yang *et al.* 2012, Nguyen *et al.* 2013; Luu *et al.* 2014; Ngo *et al.* 2015; Yang 2015) we compared the new species from Laos with its congeners of the *Gekko japonicus* group sensu Rösler *et al.* (2011) (see Table 5).

Both correspondence and cluster analyses supported *Gekko sengchanthavongi* **sp. nov.** as a sister taxon to *G. bonkowskii* **sp. nov.** and *G. thakhekensis* (Figs. 3–4). Molecular phylogenetic analyses also demonstrated the close relationships between these species (see Fig. 1).



FIGURE 7. A) Dorsal view and B) portrait of the holotype (VFU R.2014.14) of *Gekko sengchanthavongi* **sp. nov.** Photos V. Q. Luu.

Gekko sengchanthavongi **sp. nov.** is lacking dorsal tubercles, which are present in the following species: *G. adleri*, *G. auriverrucosus*, *G. canhi*, *G. chinensis*, *G. japonicus*, *G. hokouensis*, *G. kwangsiensis*, *G. liboensis*, *G. palmatus*, *G. scabridus*, *G. shibatai*, *G. similignum*, *G. swinhonis*, *G. vertebralis*, *G. wenzianensis*.

Gekko sengchanthavongi **sp. nov.** differs from *G. aaronbaueri* by having fewer supralabials and infralabials (8–10 *versus* 13 or 14 and 6 or 7 *versus* 10 or 11, respectively), fewer interorbital scales (28–32 *versus* 34–37), more scale rows around midbody (120–135 *versus* 98–104), fewer lamellae under first toes (11–14 *versus* 14–17), and more precloacal pores in males (4 or 5 *versus* 3 or 4); from *G. bonkowskii* **sp. nov.** by a larger size (SVL reaching 77.3 *versus* 69.2), having fewer supralabials and infralabials (8–10 *versus* 12–14 and 6 or 7 *versus* 10 or 11, respectively), more interorbitals (28–32 *versus* 26 or 27), more scales from mental to cloacal slit (175–184 *versus* 154–169), more scale rows around midbody (120–135 *versus* 117), and fewer precloacal pores in males (4 or 5 *versus* 6); from *G. melli* by having a smaller size (SVL reaching 77.3 *versus* 84.6 mm), the absence of internasal (*versus* present), postmentals enlarged (*versus* not enlarged), fewer infralabials (6 or 7 *versus* 9–12), fewer scale rows around midbody (120–135 *versus* 147–160), fewer ventral scales (35–43 *versus* 43–49), and fewer precloacal pores in males (4 or 5 *versus* 9–11); from *G. scientiaventura* by its larger size (SVL reaching 77.3 *versus* 73.0 mm), having fewer interorbitals (28–32 *versus* 41–51), more scales from mental to cloacal slit (175–184 *versus* 118–140), fewer scale rows around midbody (120–135 *versus* 139–143), and fewer precloacal pores in males (4 or 5 *versus* 5–8); from *G. subpalmatus* by the absence of internasals (*versus* present), having fewer infralabials (6 or 7 *versus* 7–12), postmentals enlarged (*versus* not enlarged), fewer ventral scales (35–43 *versus* 48), and fewer precloacal pores in males (4 or 5 *versus* 5–11); from *G. taibaiensis* by its larger size (SVL reaching 77.3 *versus* 69.0 mm), having fewer infralabials (6 or 7 *versus* 8–10), having more lamellae under first and fourth toes (11–14 *versus* 6 or 7 and 13–17 *versus* 7 or 8, respectively); from *G. tawaensis* by its larger size (SVL reaching 77.3 *versus* 71.0 mm) the absence of internasals (*versus* present), postmentals enlarged (*versus* not

enlarged), and the presence of precloacal pores in males (*versus* absent); from *G. thakhekensis* by having fewer infralabials (6 or 7 *versus* 10 or 11), more ventral scales between mental and cloacal slit (175–184 *versus* 165–174), more precloacal pores in males (6 *versus* 1–5), more scale rows around midbody (120–135 *versus* 110–116), and color pattern of dorsum (banded *versus* blotches); from *G. truongi* by its smaller size (SVL reaching 77.3 *versus* 95.9 mm), having more ventral scales between mental and cloacal slit (175–184 *versus* 160–172), and fewer precloacal pores in males (4 or 5 *versus* 10–11); and from *G. yakuensis* by the absence of internasals (*versus* present), having postmentals enlarged (*versus* not enlarged), fewer precloacal pores in males (4 or 5 *versus* 6–8), and the absence of dorsal tubercles on tail (*versus* present).



FIGURE 8. A) Microhabitat of the paratype (VFU R.2014.16) and B) macrohabitat of *Gekko sengchanthavongi* sp. nov. Photos V. Q. Luu.

Distribution. *G. sengchanthavongi* sp. nov. is currently known only from the type locality in Bualapha Town, Khammouane Province, central Laos (Fig. 5).

Etymology. We name the new species in honour of Mr. Sinnasone Sengchanthavong, Natural Resources and Environment Department of Khammouane Province, Laos, in recognition of his great support of our field research in Hin Nam No NPA. As common names, we suggest Sengchanthavong's Gecko (English), Kap Ke Sengchanthavong (Laotian), and Sengchanthavongis Gecko (German).

TABLE 5. Morphological comparisons among the species of the *Gekko japonicus* group (modified after Luu *et al.* 2014, extended by Ngo *et al.* 2015, Yang 2015, abbreviations defined in text, - = data unavailable).

Character	<i>G. bonkowski</i> sp. nov.	<i>G. sengchanthavongii</i> sp. nov.	<i>aaronbaueri</i>	<i>adleri</i>	<i>auriverrucosus</i>	<i>canhi</i>	<i>chinensis</i>	<i>japonicus</i>	<i>hokouensis</i>	<i>kwangsiensis</i>
Maximum SVL (mm)	69.2	77.3	80.0	75.3	69	99.2	72	74	70	69.7
SPL (min)	12	8	13	10	9	14	10	9	10	10
SPL (max)	14	10	14	15	11	14	14	13	14	12
IFL (min)	10	6	10	9	9	10	9	8	8	11
IFL (max)	11	7	11	13	11	12	13	13	11	13
Nostril touching rostral	1	1	1	1	0	1	1	1	1	1
N (min)	3	3	3	3	3	3	2	3	3	3
N (max)	3	3	3	3	3	3	3	3	3	3
I (min)	0	0	0	1	0	1	1	0	1	0
I (max)	0	0	1	1	1	1	1	1	2	1
IO (min)	26	28	34	27	25	49	35	32	30	29
IO (max)	27	32	37	36	25	50	48	35	33	31
Postmentals (enlarged = 1, not enlarged = 0)	1	1	1	1	0	1	1	0	0	1
DTR (min)	0	0	0	7	16	11	10	9	12	9
DTR (max)	0	0	0	11	20	12	10	14	18	11
SMC (min)	154	175	-	168	-	168	156	169	153	185
SMC (max)	169	184	-	190	-	170	167	188	174	208
SR (min)	117	120	98	123	-	205	118	130	119	143
SR (max)	117	135	104	144	-	227	140	144	130	156
V (min)	37	35	39	35	-	49	37	39	36	41
V (max)	40	43	43	44	-	51	39	44	43	45

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Character	<i>G. bonkowskii</i> sp. nov.	<i>G. sengchanthavongi</i> sp. nov.	<i>aaronbaueri</i>	<i>adleri</i>	<i>auriverrucosus</i>	<i>canthi</i>	<i>chinensis</i>	<i>japonicus</i>	<i>hokouensis</i>	<i>kwangsiensis</i>
LT 1 (min)	11	11	14	11	6	13	8	10	8	11
LT1 (max)	13	14	17	14	8	16	10	12	11	13
LT 4 (min)	15	13	14	11	6	14	9	14	15	13
LT4 (max)	15	17	16	15	8	17	12	16	18	18
Toes webbed	1	1	0	1	0	0	1	0	0	1
Tubercles on fore-limbs (present = 1, absent = 0)	0	0	0	0	1	0	0	1	0	0
Tubercles on hind limbs (present = 1, absent = 0)	0	0	0	1	1	1	1	1	0	0
PP (in males, min)	6	3+1	3	17	8	5	17	6	5	9
PP (in males, max)	6	3+2	4	21	11	5	27	9	9	11
PAT (min)	0	2	1	1	2	2	1	2	1	1
PAT (max)	2	2	2	1	3	3	1	4	1	1
Tubercles on dorsal surface of tail (present = 1, absent = 0)	0	0	0	1	1	0	1	1	1	1
Subcaudals enlarged	1	1	1	1	1	1	1	1	1	1
Marking on upper head	0	0	1	1	0	0	0	0	0	0
Back flecked or blotched	1	1	1	0	0	1	1	0	1	0
Back banded	0	1	0	1	1	1	0	1	0	1
Tail banded	1	1	1	1	1	1	1	1	1	1

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TABLE 5. (Continued)

Character	<i>G. bonkowskii</i> sp. nov.	<i>G. sengkhanthavongi</i> sp. nov.	<i>litboensis</i>	<i>melli</i>	<i>palmatum</i>	<i>scabridus</i>	<i>scientiadventura</i>	<i>shibatai</i>	<i>similignum</i>	<i>subpalmatum</i>
Maximum SVL (mm)	69.2	77.3	85	84.6	79.7	77	73	70.9	58.9	72
SPL (min)	12	8	12	10	11	9	12	10	12	8
SPL (max)	14	10	12	13	15	11	14	13	14	12
IFL (min)	10	6	11	9	9	9	9	10	11	7
IFL (max)	11	7	11	12	13	11	13	14	11	12
Nostril touching rostral	1	1	1	1	1	1	1	1	1	1
N (min)	3	3	3	3	3	3	3	3	3	3
N (max)	3	3	3	3	3	3	3	3	3	3
I (min)	0	0	0	1	0	1	0	0	1	1
I (max)	0	0	0	1	3	2	0	1	1	1
IO (min)	26	28	40	34	27	30	41	37	46	32
IO (max)	27	32	40	40	36	30	51	52	48	32
Postmentals (enlarged = 1, not enlarged = 0)	1	1	0	0	1	0	1	0	0	0
DTR (min)	0	0	10	0	4	17	0	5	11	0
DTR (max)	0	0	10	0	12	21	0	14	11	0
SMC (min)	154	175	-	181	160	-	118	-	-	-
SMC (max)	169	184	-	200	194	-	140	-	-	-
SR (min)	117	120	-	147	116	-	139	114	144	-
SR (max)	117	135	-	160	147	-	143	134	153	-
V (min)	37	35	-	43	36	-	38	-	-	48
V (max)	40	43	-	49	47	-	48	-	-	48

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Character	<i>G. bonkowski</i> sp. nov.	<i>G. sengchanthavongi</i> sp. nov.	<i>liboensis</i>	<i>melli</i>	<i>palmatum</i>	<i>scabridum</i>	<i>scientiaadventura</i>	<i>shibatani</i>	<i>similignum</i>	<i>subpalmatum</i>
LT1 (min)	11	11	8	10	10	6	12	-	11	7
LT1 (max)	13	14	8	12	13	9	15	-	13	9
LT4 (min)	15	13	9	11	10	7	14	9	12	7
LT4 (max)	15	17	9	14	16	9	17	16	14	10
Toes webbed	1	1	0	1	1	0	1	0	1	1
Tubercles on fore-limbs (present = 1, absent = 0)	0	0	0	0	0	1	0	0	0	0
Tubercles on hind limbs (present = 1, absent = 0)	0	0	0	0	0	1	0	0	0	0
PP (in males, min)	6	3+1	-	9	23	10	5	0	17	5
PP (in males, max)	6	3+2	-	11	30	15	8	3	17	11
PAT (min)	0	2	1	1	1	1	2	1	1	1
PAT (max)	2	2	1	1	1	3	3	1	1	1
Tubercles on dorsal surface of tail (present = 1, absent = 0)	0	0	-	0	1	1	0	1	1	0
Subcaudals enlarged	1	1	-	1	1	1	1	1	1	1
Marking on upper head	0	0	0	1	0	0	1	0	0	0
Back flecked or blotched	1	1	0	0	1	1	1	1	1	1
Back banded	0	1	1	1	1	1	0	0	0	1
Tail banded	1	1	-	1	1	1	1	1	1	1

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TABLE 5. (continued)

Character	<i>G. bonkowskii</i>		<i>G. sengchanthavongii</i>		<i>swinhonis</i>	<i>taibaiensis</i>	<i>tawaensis</i>	<i>thabhekensis</i>	<i>truongi</i>	<i>vertebralis</i>	<i>wenxianensis</i>	<i>yakuensis</i>
	sp. nov.	69.2	sp. nov.	77.3								
Maximum SVL (mm)	69.2	71	69	71.3	66	69	71	79.2	95.9	69.2	59	72
SPL (min)	12	13	9	8	7	9	13	12	13	10	12	12
SPL (max)	14	13	10	10	12	10	13	14	15	15	12	13
IFL (min)	10	15	8	6	7	8	15	10	11	10	11	9
IFL (max)	11	15	10	7	11	10	15	11	13	15	11	13
Nostril touching rostral	1	1	1	1	1	1	1	1	1	1	1	1
N (min)	3	-	-	3	-	-	-	3	3	3	-	3
N (max)	3	-	-	3	-	-	-	3	4	3	-	3
I (min)	0	2	-	0	-	-	2	0	0	0	1	1
I (max)	0	2	-	0	-	-	2	0	1	2	1	1
IO (min)	26	-	28	28	23	28	-	22	45	35	-	-
IO (max)	27	-	28	32	24	28	-	26	48	50	-	-
Postmentals (enlarged = 1, not enlarged = 0)	1	0	-	1	0	-	0	1	1	0	-	0
DTR (min)	0	6	-	0	6	-	0	0	0	2	10	-
DTR (max)	0	8	-	0	8	-	0	0	0	12	10	-
SMC (min)	154	175	-	175	-	-	-	165	160	-	-	-
SMC (max)	169	184	-	184	-	-	-	174	172	-	-	-
SR (min)	117	120	-	120	-	-	-	110	131	112	-	-
SR (max)	117	135	-	135	-	-	-	116	143	139	-	-
V (min)	37	40	-	40	40	-	-	32	35	-	42	-
V (max)	40	43	-	43	40	-	-	40	36	-	44	-

.....continued on the next page

Continued.

Character	<i>G. bonkowskii</i> sp. nov.		<i>G. sengchanthavongii</i> sp. nov.		<i>swinhonis</i>	<i>taibatensis</i>	<i>tawaensis</i>	<i>thakhekensis</i>	<i>truongi</i>	<i>vertebralis</i>	<i>wenxianensis</i>	<i>yakuensis</i>
	11	13	15	17								
LT 1 (min)	11	11	6	6	6	10	11	11	11	-	6	10
LT1 (max)	13	14	9	7	7	10	13	13	13	-	6	10
LT 4 (min)	15	13	6	7	7	12	14	14	15	9	9	15
LT4 (max)	15	17	9	8	8	12	15	15	17	17	9	15
Toes webbed	1	1	0	-	-	0	1	1	0	0	0	0
Tubercles on fore-limbs (present = 1, absent = 0)	0	0	1	-	-	0	0	0	0	0	0	0
Tubercles on hind limbs (present = 1, absent = 0)	0	0	1	-	-	0	0	0	0	0	1	0
PP (in males, min)	6	3+1	7	4	4	0	1	1	10	0	6	6
PP (in males, max)	6	3+2	9	6	6	0	5	5	11	1	8	8
PAT (min)	0	2	2	-	-	1	2	2	1	1	2	1
PAT (max)	2	2	3	-	-	1	2	2	1	2	3	1
Tubercles on dorsal surface of tail (present = 1, absent = 0)	0	0	-	-	-	0	0	0	0	0	-	1
Subcaudals enlarged	1	1	1	-	-	1	1	1	1	1	-	1
Marking on upper side of head	0	0	0	0	0	0	0	0	0	0	0	0
Back flecked or blotched	1	1	1	1	1	1	1	1	1	1	1	1
Back banded	1	1	0	1	1	1	0	0	1	0	0	0
Tail banded	1	1	1	1	1	1	1	1	1	-	1	1

Natural history. Specimens of *G. sengchanthavongi* were collected on karst walls at night from 20:00 to 21:30 during small rain, ca. 1.5–4 m above the ground, at an elevation of ca. 210 m a.s.l. The surrounding area was disturbed secondary forest (Fig. 8).

***Gekko boehmei* sp. nov.**

(Fig. 9)

Holotype. VFU R.2014.09, adult male, in karst forest of Bualapha Town (17°18.312'N, 105°43.726'E, at an elevation of 196 m a.s.l.), Khammouane Province, central Laos, collected by Vinh Quang Luu and Kieusomphone Thanabuaosy on 19 June 2014.

Paratypes. Two adult males ZFMK 97195 and IEBR A.2015.31, one adult female ZMB 82028, and one subadult female NUOL R-2015.2, the same data as the holotype.

Diagnosis. *Gekko boehmei* sp. nov. is distinguished from its congeners in the *Gekko petricolus* group by a combination of the following characters: a medium-sized gecko species (maximum SVL 105.3 mm); supralabials 10–15; infralabials 8–11; dorsal tubercle rows 12–15; ventral scale rows from mental to cloacal slit 141–152; scale rows at midbody 101–114; ventral scales 30–34; webbing weakly developed between fingers and toes; dorsal surface of hindlimbs and tail with enlarged tubercles; precloacal pores 10 or 11 in males, absent in females; postcloacal tubercles 1 or 2; subcaudals enlarged; vertebral part with a row of oval grey and dark dots from nape to sacrum, vertical yellow blotches on flank.

Description of holotype. Size moderate, total length 227.4 mm (SVL 102.6 mm, TaL 124.8); body robust, elongate (ratio of AG/SVL 0.46); head longer than wide (ratio of HL/HW 1.38); rostral rectangular, nearly two times wider than high (ratio of RW/RH 1.98), and wider than mental (ratio of RW/MW 1.54 mm), with a medial suture in Y-shape; nostril surrounded by rostral, first supralabial scales, supranasal, and two nasals posteriorly; posterior nasal region concave; supranasals in contact anteriorly and slightly separated by a small scale posteriorly; interorbitals 27–32; preorbital region concave; eye large (OD/HL ratio 0.22), pupil vertical; ear opening oblique; mental triangular, wider than long (MW/ML ratio 1.10); postmentals 2, rhomboid, twice as long as wide; postmental in contact with six gular scales posteriorly, outer scales larger than inner ones; supralabials 15/15; infralabials 11/11; dorsal tubercle rows 12, 3 or 4 times larger than adjacent scales, surrounded by nine dorsal scales; enlarged tubercles present on dorsal surface of hindlimbs; lateral fold weakly developed, without tubercles; ventral scales 30; scale rows around midbody 101; ventral scales in a row from mental to cloacal slit 141; webbing between fingers and toes weakly developed; claw absent on inner finger and toe; lamellae under first finger 13/13, under fourth finger 16/16, under first toe 14/15, under fourth toe 17/17; precloacal pores 11; femoral pores absent; enlarged scales from precloacal pores towards cloaca in 6 rows; postcloacal tubercle one; tail thickened at base, enlarged tubercles present on dorsal surface of tail base; subcaudals flat, enlarged.

Coloration in life. Dorsal surface of head dark grey with light and black blotches; lateral head with some grey lines radiating from orbit; dorsal part of body with light and black spots together along backbone, lateral sides with yellow symmetrical patches; limbs mottled and marked with irregular dark blotches; dorsal tail with 13 yellowish light bands; throat, venter, precloacal region, and underside of tail yellowish grey with dark marbling near lateral fold.

Sexual dimorphism. Measurements and scalation characters of the paratypes are given in Table 6. The males differ from females by having a larger size (SVL: 93.9–105.3 in males *versus* 68.0–89.6 in females), and precloacal pores present in males (*versus* absent in females). The remaining paratypes have intersupranasals in contact with rostral except for the holotype and one paratype ZFMK 96123. In addition, ZFMK 96123 has a pair of postcloacal tubercles on each side (*versus* one on each side in other type specimens).

Comparisons. Based on examination of specimens and data obtained from the literature (Panitvong *et al.* 2010; Ngo & Gamble 2011) we compared the new species from Laos with the remaining congeners of the *Gekko petricolus* group sensu Rösler *et al.* (2011) (see Table 7).

Gekko boehmei sp. nov. has enlarged tubercles on the dorsal surface of hindlimbs, and thus differs from *G. badenii*, *G. canaensis*, *G. grossmanni*, *G. lauhachindaei* Panitvong, Sumontha, Konler & Kunya, *G. russelltraini*, and *G. takouensis*, which are absent in the latter ones.

TABLE 6. Measurements (in mm) and morphological characters of the type series of *Gekko boehmei* sp. nov. (for abbreviations see material and methods, ** = regenerated).

Sex	VFU R-2014.09		ZFMK 97195		IEBR A.2015.31		Min-Max		M±SD		ZMB 82028		NUOL R-2015.2	
	(holotype)	male	(paratype)	male	(paratype)	male	(paratype)	(paratype)	(paratype)	(paratype)	female	female	subadult female	
SVL	102.6	105.3	93.9	93.9	93.9–105.3	100.6±6.0	89.6	68.0						
TaL	124.8	113.9	78.8*	78.8*	113.9–124.8 (n=2)	119.4±7.7	110.9	74.1						
AG	47.5	45	42.4	42.4	42.4–47.5	45.0±2.6	39.3	28.8						
HL	28.2	29.6	28.1	28.1	28.1–29.6	28.6±0.8	25.4	19.3						
HW	20.5	20.8	18.7	18.7	18.7–20.8	20.0±1.1	17.5	12.3						
HH	12.3	12.8	11.1	11.1	11.1–12.8	12.1±0.9	10	7.6						
SE	12.5	12.3	12	12	12.0–12.5	12.3±0.3	10.9	8.5						
OD	6.3	6.6	6.1	6.1	6.1–6.6	6.3±0.3	5.8	4.3						
RW	4.30	4.00	4.00	4.00	4.0–4.3	4.1±0.2	3.2	2.4						
RH	2.2	2.1	1.9	1.9	1.9–2.2	2.1±0.2	1.7	1.4						
MW	3.2	2.9	2.6	2.6	2.6–3.2	2.9±0.3	2.5	1.9						
ML	2.9	2.3	2.3	2.3	2.3–2.9	2.5±0.4	2	1.5						
N	3/3	3/3	3/3	3/3	3–3	3.0±0.0	3/3	3/3						
I	0.00	0.00	1.00	1.00	0–1	0.3±0.6	1	1						
SPL	15/15	12/10	11/12	11/12	10–15	12.5±2.1	14/13	12/12						
IFL	11/11	11/11	8/8	8/8	8–11	10.0±1.6	12/12	11/10						
IO	32	30	27	27	27–32	29.7±2.5	27	30						
PM	2	2	2	2	2–2	2.0±0.0	2	2						
GP	6	6	5	5	5–6	5.5±0.7	3	5						
DTR	12	13	13–15	13–15	12–15	13.2±1.1	12	10–11						
GSDT	9	9	9–10	9–10	9–10	9.3±0.5	9	8–9						
SMC	141	152	143	143	141–152	145.3±5.9	145	137						
SR	101	114	102–105	102–105	101–114	105.3±6.2	103	104						
V	30	34	32	32	30–34	32.0±2.0	30	31						
LF1	13/13	13/12	12/13	12/13	12–13	12.7±0.5	12/12	14/14						
LF4	16/16	16/16	15/16	15/16	15–16	15.8±0.4	14/16	15/14						
LTI	14/15	14/16	15/missing	15/missing	14–16	14.8±0.8	16/16	13/12						
LT4	17/17	18/18	18/missing	18/missing	17–18	17.6±0.6	19/17	17/17						
PP	11	10	10	10	10–11	10.3±0.6	0	0						
PAT	1/1	2/2	1/1	1/1	1–2	1.2±0.4	1/1	1/1						
Hinlimb tubercles	present	present	present	present	present	present	present	present						

TABLE 7. Comparisons of selected characteristics among *Gekko petricolus* – species group. n/a = data not available (modified after Panitvong *et al.* 2010; Ngo & Gamble 2011).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Gekko boehmei</i> sp. nov.*	105.3	12–15	30–34	101–114	10–11	17–18	10–15	8–11	27–32	1–2	1.86–1.98	1	0	1	1	Laos
<i>G. badenii</i>	108.0	8–13	29–35	114–136	10–18	15–20	11–15	9–14	30–46	n/a	n/a	0	1	1	0	Vietnam
<i>G. conaensis</i>	108.5	10–14	30–32	86–93	14–18	17–19	14–17	11–15	32–34	2	1.37–1.75	1	1	1	0	Vietnam
<i>G. grossmanni</i>	89.0	presence	26–31	116–135	8–14	18–20	11–13	9–11	38–48	n/a	1.06–1.38	1	0	0	0	Vietnam
<i>G. lathachindai</i>	98.0	14	32	112–121	12–14	13–15	11–12	11	36–40	1	1.20–1.30	1	1	1	0	Thailand
<i>G. petricolus</i>	98.0	16	27–32	<161	9–10	20	12	10–11	36–38	1	1.44–1.52	1	0	0	1	Thailand, Laos
<i>G. russelltrairi</i>	82.9	12–16	28–30	90–107	8–11	17–19	12–15	11–14	30–34	2	1.50–1.91	1	0	1	0	Vietnam
<i>G. takouensis</i>	107.0	14–17	30–34	83–93	11–14	18–20	13–16	10–12	36–40	1	1.20–1.30	1	1	1	0	Vietnam
<i>G. vietnamensis</i>	91.0	presence	n/a	28–30	0	18–20	11–12	10–11	30–46	n/a	n/a	0	1	1	0	Vietnam

1—maximum snout-vent length (in mm); 2—number of dorsal tubercle rows; 3—number of ventrals; 4—number of scales around midbody; 5—number of preloacal pores (only in males); 6—number of subdigital lamellae under the fourth toe; 7—number of supralabials; 8—number of sublabials; 9—number of interorbitals; 10—number of postloacal tubercles; 11—ratio of SE/OD; 12—vertebral on dorsum light marking; 13—transverse bars on dorsum; 14—vertical bars on flank; 15—tubercles on hind limbs; 16—distribution.

“1” = presence of character state; “0” = absence of character state.

“**” = contribution of this study.

Gekko boehmei sp. nov. is most similar to *G. petricolus* Taylor in the presence of dorsal tubercles on hindlimbs and the number of cloacal and femoral pores in males. However, the new species can be distinguished from the latter by its larger size (SVL up to 105.3 *versus* 98.0 mm), more precloacal pores in males (10–11 *versus* 9–10), the absence of precloacal pores in females (*versus* present in females), fewer interorbital scales (27–32 *versus* 36–40), and the presence of light bars on flank (*versus* absent).



FIGURE 9. A) Dorsal view of the holotype (VFU R.2014.09) and B) the paratype (IEBR A.2015.31) of *Gekko boehmei* sp. nov. Photos V. Q. Luu.

Distribution. The new species is only known from the type locality in Khammouane Province, central Laos (Fig. 5).

Etymology. The specific epithet honors Professor Dr. Wolfgang Böhme from the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK), Bonn, Germany to acknowledge his great contributions to herpetological research. In particular we dedicate the new species to Wolfgang on the occasion of his 70th birthday. We suggest as common names: Boehme's Gecko (English), Kap Ke Boehme (Laotian), and Böhmes Gecko (German).

Natural history. The specimens of *Gekko boehmei* were collected on karst walls between 20:00 and 21:00 after heavy rain, from 1.5 to 3 m above the forest floor, at an elevation of 196 m. The location was close to rice fields and about 100 m distant from the main road (Fig. 10).

Zoogeography and niche segregation of the genus *Gekko* from Laos

Rösler *et al.* (2011) indicated that members of the *G. japonicus* group have been recorded from Japan, Korea, China, and Taiwan to Vietnam. Our findings of *Gekko bonkowskii*, *G. sengchanthavongi*, and *G. thakhekensis* (Luu *et al.* 2014) extended the distribution range of this group to Laos. In terms of microhabitat occupation, *G. bonkowskii* and *Cyrtodactylus jaegeri* (Luu *et al.* 2014) are occurring sympatrically within the karst forest near Thakhek Town in Khammouane Province, but they are segregated by habitat preference. Specimens of *G. bonkowskii* were found on tree trunks, whereas specimens of *C. jaegeri* were collected on limestone cliffs. This phenomenon could point to strict microhabitat preference (Randall 1978) but needs further research.

Gekko boehmei is closely related to *G. petricolus* from Cambodia, Laos, and Thailand (Rösler *et al.* 2011), but

G. boehmei inhabits karst habitat in central Laos (*versus* *G. petricolus* being reported from sandstone habitat). The karst mountains in Khammoune Province in central Laos are upland formations and separated from the lowlands of southern Laos, which include the type locality of *G. petricolus* (Bain & Hurley 2011). Here, adaptation of the species to karst forest environment may have been the leading force for speciation (Nakarato *et al.* 2010; Zhang *et al.* 2014).

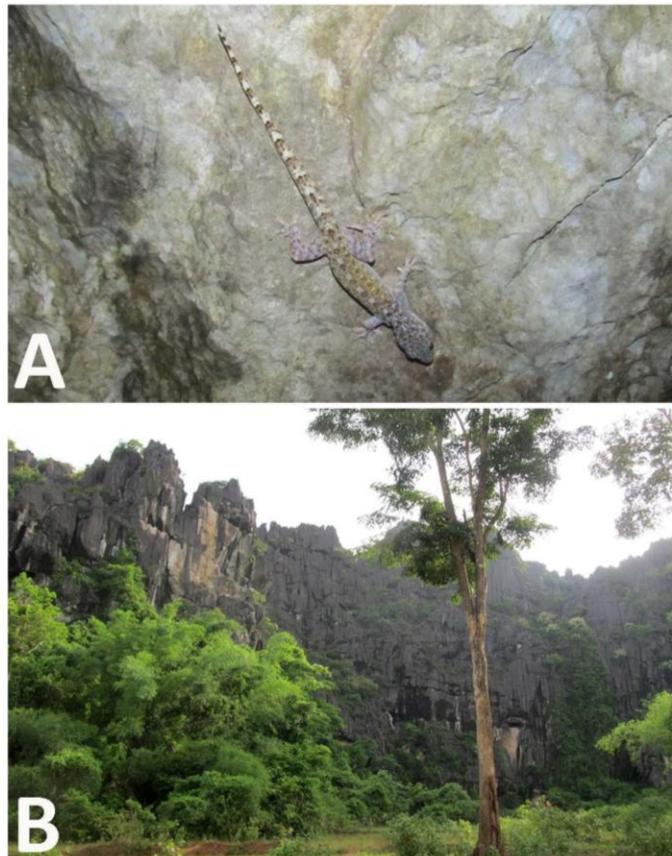


FIGURE 10. A) Microhabitat of the holotype (VFU R.2014.09) and B) macrohabitat of *Gekko boehmei* sp. nov. Photos V. Q. Luu.

Phylogeny of the genus *Gekko* from Laos

The molecular analyses show that two new species, i.e., *Gekko bonkowskii* and *G. sengchanthavongi*, belong to the *G. japonicus* species group. The other new species, *G. boehmei*, falls within the *G. petricolus* species complex. However, while the *G. petricolus* clade receives strong statistical support from all three analyses (BP > 70, PP > 95), the *G. japonicus* clade is weakly corroborated by all analyses (Fig. 1). This low level of support could result from a small number of informative characters available in our dataset, as the *G. japonicus* clade was recovered with high statistical values from all analyses using a larger data set (Rösler *et al.* 2011). However, the *G. japonicus* group is the most diverse group in the genus *Gekko* with a total of 24 recognized species including the taxa described herein (Rösler *et al.* 2011; Nguyen *et al.* 2013; Luu *et al.* 2014; Ngo *et al.* 2015). In this study we also could assign *G. truongi*, for the first time, to the *G. japonicus* species group by molecular means. It represents the 25th species of the *G. japonicus* species group. As the group is morphologically quite inconsistent, with a wide character range (see Rösler *et al.* 2011) this group concept should be tested in the future.

A total of five species of the genus *Gekko* is currently known from Laos and this number is relatively low in comparison with the species richness of the genus from Vietnam, a neighbouring country, with 13 recognized *Gekko* species so far. It is noted that more than half of the members of this group were found in limestone karst

forests of Vietnam (8 species) and Laos (2 species). Therefore, further studies are needed to discover the actual species diversity of *Gekko* from Laos, particularly in karst forests of central Laos.

Key to members of the genus *Gekko* reported from Laos

1	SVL > 160 mm; nares in contact with rostral only; iris yellow	<i>G. gekko gekko</i>
1'	SVL < 160 mm; nares in contact with rostral and first supralabial; iris not yellow	2
2	SVL < 80 mm, dorsal tubercles absent	3
2'	SVL > 80 mm, dorsal tubercles present	7
3	Interorbitals 41–51; scale rows around midbody 139–143	<i>G. scientiaventura</i>
3'	Less than 41 interorbitals; less than 139 scale rows around midbody	4
4	Scale rows around midbody 120–135	<i>G. sengchanthavongi</i> sp. nov.
4'	Less than 120 scale rows around midbody	5
5	Interorbitals 34–37; scale rows around midbody 98–104	<i>G. aaronbaueri</i>
5'	Less than 34 interorbitals; more than 104 scale rows around midbody	6
6	SVL 79 mm; interorbitals 26–27; scale rows around midbody 110–116, praecloacal pores 1–5; irregular blotches	<i>G. thakhekensis</i>
6'	SVL 69 mm; interorbitals 22–26; scale rows around midbody 117; praecloacal pores 6, regular blotches	<i>G. bonkowski</i> sp. nov.
7	SVL 101 mm; interorbitals 36–38; scale rows around midbody 152–156	<i>G. petricolus</i>
7'	SVL 95 mm; interorbitals 27–32; scale rows around midbody 104–114	<i>G. boehmei</i> sp. nov.

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APPENDIX. *Gekko* specimens examined

- G. adleri* (25): Vietnam: Cao Bang Province: IEBR A.2012.24 (holotype), ZFMK 93993–93999, IEBR A.2012.25–2012.31, VNMN A.2012.4–2012.6 (paratypes); China: Guangxi: SYS r000456–r0000461, SYS r000263 (paratypes).
- G. canhi* (4): Vietnam: Lang Son Province: IEBR A.0910 (holotype), VNMN 1001–1002 (paratypes); Lao Cai Province: ZFMK 88879 (paratype).
- G. palmatus* (30): Vietnam: Lao Cai Province: IEBR FN.29174; Tuyen Quang Province: IEBR A.0948; Bac Kan Province: IEBR 2301, IEBR A.0950–A.0951; Lang Son Province: IEBR 2474, IEBR 3619–3623, IEBR A.0949, A.0952; Quang Ninh Province: IEBR A.0807; Bac Giang Province: IEBR 3638, 3672; Vinh Phuc Province: IEBR 3223–3224a-c, ZFMK 44210, 59214–59215, 66517, 74552–74553; Hanoi: IEBR LQV3–LQV4; Thanh Hoa Province: IEBR TH.2011.1; Nghe An Province: IEBR A.0953–A.0955; Quang Binh Province: ZFMK 82888, 86434.
- G. scientiaventura* (9): Vietnam: Quang Binh Province: IEBR A.2014.7; PNKB 2011.67; ZFMK 76198 (holotype), ZFMK 76174–76179 (paratypes); ZFMK 80651–80652. Laos: Khammouane Province: VFU 2014.1–2014.2.
- G. thakhekensis* (2): Laos: Khammouane Province: IEBR A.2014.6 (holotype), VFU R.2014.9 (paratype).
- G. truongi* (1): Vietnam: Khanh Hoa Province: IEBR A.2011.1 (holotype).

Publication 7

Rediscovery of the Siamese crocodile (*Crocodylus Siamensis*) in Khammouane Province, central Lao PDR

Thomas Ziegler

Vinh Quang Luu

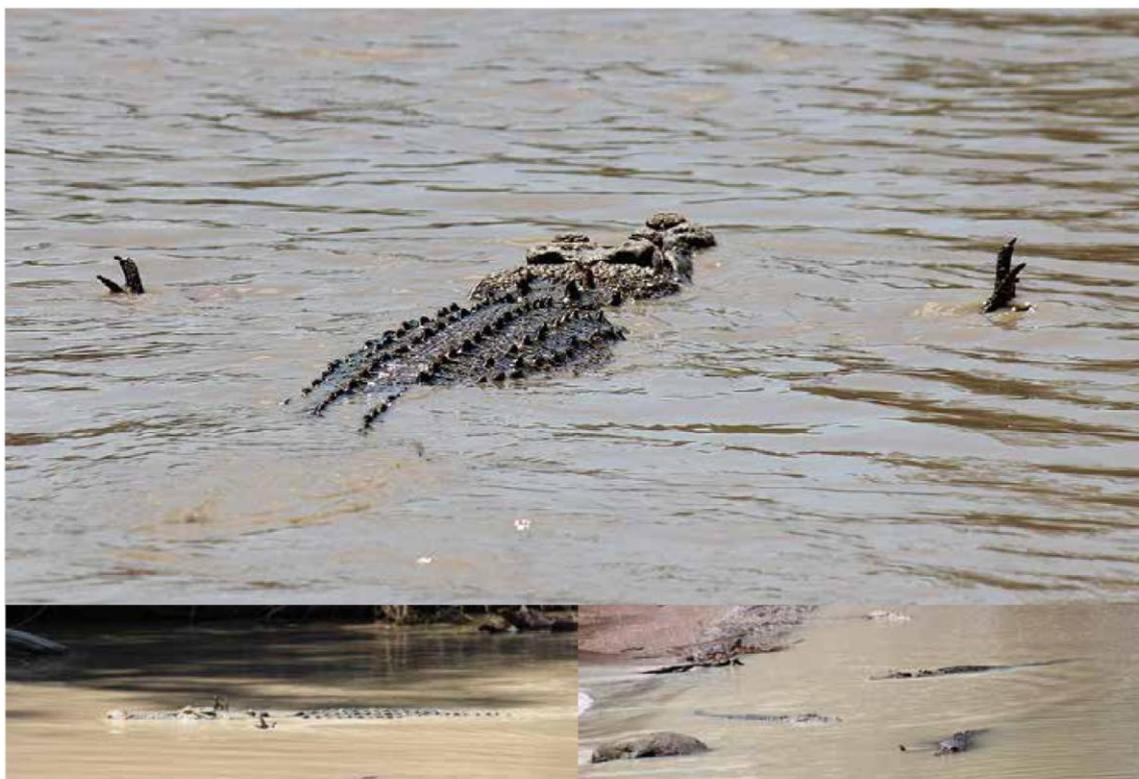
Sisomphone Soudthichak

Truong Quang Nguyen

Crocodile Specialist Group Newsletter: 34 (3), 11-13

**CROCODILE
SPECIALIST
GROUP
NEWSLETTER**

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IUCN • Species Survival Commission



Figure 1. (left) mouth transport; (centre) female crushing egg in the water of nesting enclosure with emerging young; (right) female guarding hatchlings. Photographs: Thomas Ziegler.

fed on offered crickets and earthworms during the night. The mother and offspring interactions were observed by our team by the hour and we currently are evaluating the data which will be presented in detail elsewhere.

This event represents the first successfully induced natural breeding of the Philippine crocodile in Europe. Based on this we could gather important and in part unknown data about the breeding and social behavior of this species, but also important information on how to keep the species in captivity. For example, the willingness of the mother to participate in the target training even with the freshly hatched young around her and thus the possibility to gently separate the female from the nest without interfering the breeding behavior provides important knowledge on handling the species in captivity during breeding. With our current knowledge it would have been no problem to leave the two eggs which had been incubated at lower temperatures inside the incubator and only inserting them into the nest later.

Now, with these many breeding successes in Europe in a relatively short period of time and after having had the chance to enable natural breeding in captivity, the main focus for the management of the Philippine crocodile conservation breeding will be the dispersal of the abundant offspring to other interested institutions and to build up suitable pairs in the future. As the parents of the European offspring have all been genetically screened as pure *C. mindorensis* (Hauswaldt *et al.* 2013; Ziegler *et al.* submitted), the offspring can also be considered as a valuable resource for future restocking projects in the Philippines.

This recent breeding success is dedicated to our dear friend Ralf Sommerlad, who passed away in June 2015, and who supported us so invaluablely with building up of Philippine crocodile conservation breeding and target training at Cologne Zoo.

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East and Southeast Asia

Lao PDR

REDISCOVERY OF THE SIAMESE CROCODILE (*CROCODYLUS SIAMENSIS*) IN KHAMMOUANE PROVINCE, CENTRAL LAO PDR. The Siamese crocodile (*Crocodylus siamensis*) historically occurred over much of mainland Southeast Asia as well as parts of Indonesia. Its current distribution is greatly diminished and fragmented. Extant populations are in Cambodia, Indonesia, Lao PDR and Thailand; wild populations in Vietnam are possibly extirpated (Bezuijen *et al.* 2012). The Siamese Crocodile is listed on Appendix I of CITES, and is listed on the IUCN Red List

(2015) as Critically Endangered with decreasing population trends.

In Laos, *C. siamensis* is classified “at Risk”, the highest nationally threat ranking (Bezuijen *et al.* 2006). The species was abundant in some parts of Laos until at least the early 1900s. Small breeding populations still persist, but a severe decline in range and abundance has occurred over the past century and now the species is rare or locally extinct at many sites (Bezuijen *et al.* 2013). Bezuijen *et al.* (2013) recorded the species at 13 sites in 6 river systems, with at least 36 individuals (1-11 per site) documented (Fig. 1). At all sites, crocodile densities and recruitment rates were extremely low. Thus, remnant *C. siamensis* populations in Laos are of global importance. However, Bezuijen *et al.* (2006) stated that most wetlands in Laos remain unsurveyed for crocodiles and it seems likely that other *C. siamensis* localities will be documented.

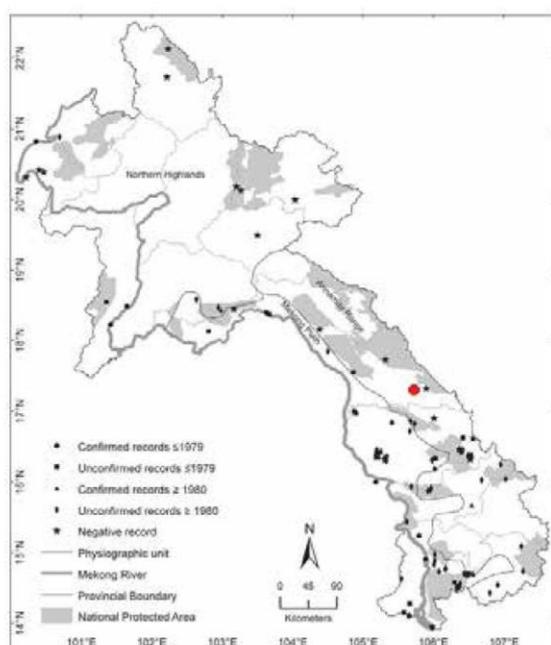


Figure 1. Distribution of *C. siamensis* in Laos (from Bezuijen *et al.* 2013); our new record is marked by the red dot.

During recent herpetological field research in central Laos we became aware of a *C. siamensis* population in Khammouane Province. Bezuijen *et al.* (2013) reported three negative records from Hin Nam No and Nakay-Nam Theun National Protected Areas and two unconfirmed records from the Nam Hin Boun River system (tributaries in Phou Hin Boun National Protected Area, previously “Khammouan Limestone National Protected Area”) in Khammouane: one record from 1960-1979, and one in 1980-1999 (Bezuijen *et al.* 2006) - no further record could be made in Khammouane for the past 16 years. Because our evidence of *C. siamensis* in Khammouane is connected with the Xebangfai River system, it thus represents an reported and overlooked population, and at the same time the rediscovery of this species from this province.

Our record was made 3–4 km from Ban Soc, Bualapha District, Khammouane Province, near Hin Nam No National Protected Area, at ca. 160-170 m asl. A crocodile of ca. 3.5 m was seen by us in a lake system (Khun Khe Lake; Fig. 2), which is subdivided into two lakes in the dry season - the larger lake is about 100 m from the smaller lake. The surface area of the smaller lake is about 1800 m² and with 1.8 m maximum water depth, and the surface area of the larger lake is about 3000 m². Another pond exists about 800 m away, and has a surface area of ca. 200 m². Lake shores consist of shallow to steep base bars intermixed with steep rock walls. Large parts of the shore are covered by vegetation (shrubs, bamboos, trees). Fish, potential prey for crocodiles, were abundant in the lake, as were frogs, snakes, softshell turtles and otters.



Figure 2. Isolated large lake of Khun Khe Lake System, where crocodile was sighted in June 2015. Photograph: Thomas Ziegler.



Figure 3. Large crocodile sighted in isolated large lake (see Fig. 2) of Khun Khe Lake System in June 2015. Photograph: Thomas Ziegler.

The crocodile was observed by us in the isolated small lake in March 2015 and in the isolated large lake in June 2015. Head crests and snout ridges were characteristic of *C. siamensis*. At the same time as the sighting of the large crocodile in March 2015, local villagers discovered another, smaller crocodile of about 2.5 m length in the separated large lake. With our current knowledge, the population covers at least two individuals, with unknown sex ratio.

Interviews with local people revealed that another individual with an injured tail was shot in the 1980s. In former times, the population must have been substantially larger. Crocodiles from that lake system were caught during the Indochinese Conflict, to supplement diet and income. An 80-year-old informant told us that crocodiles were abundant at the site during his childhood, but juveniles have not been sighted there for a long time. This supports our morphological determination, that the reported crocodiles are remnants of a natural *C. siamensis* population.

Concerning human-wildlife conflict, we saw buffalos and dogs in the surroundings of the lake, which also is used by local fishermen. Local villagers reported one non-fatal crocodile attack on a fisherman in former times. As mentioned, crocodiles were caught or shot in the area, with the last case being reported from the 1980s. We also recorded fire and forest burning as well as pollution in the immediate vicinity of the lakes. Also, Bezuijen *et al.* (2013) stated that crocodiles are under threat from a range of anthropogenic processes, mainly habitat loss and opportunistic collection. Because all documented breeding sites and most confirmed national records in Laos are in rural lands outside the national protected area system, conservation efforts require community-based approaches (Bezuijen *et al.* 2013). The latter authors also suggested that conservation approaches should first focus on protecting documented populations and their habitats.

Also the newly discovered population is currently not protected. It is located nearby a watershed protected area and is ca. 10 km distant from the border of Hin Nam No National Protected Area. Discussions with the forest resource management section led to plans to establish a provincial protected area under the management of the provincial natural resources and environment department in a first step, but which has to be decided by the Provincial Government first.

We also collected faecal samples for subsequent genetic screening to support the discovery of a natural population and to definitely exclude that the sighted crocodiles are escaped animals or hybrids. However, on the basis of the interviews with local villagers this is unlikely, but also because the closest Siamese crocodiles are about 400 km away in Vientiane Province. In Vientiane, the Ban Kuen Zoo houses the only known captive collection of *C. siamensis* in Laos (Phothitay *et al.* 2005; Thorbjarnarson 2003) - around 1000 individuals, most of which are suspected to be hybrids (Bezuijen *et al.* 2006, 2012). Thus, the absence of other crocodile institutions in Laos reduces the risk of hybridization of wild crocodiles with escaped hybrids (Bezuijen *et al.* 2006).

Besides the aforementioned, still outstanding genetical analysis, further research of the newly discovered population is desirable, in particular to document the actual population size, but also to record the surrounding fauna and flora. Results of first surveys conducted by our team revealed the existence of further so far not reported wildlife in the region, which will be dealt with in a separate article. Also educational

advertising is required to reduce human-wildlife conflicts. In case that the newly discovered crocodile population in fact only consists of two animals, which may be of the same sex, a further step could be a population restocking with genetically wild *C. siamensis* of local provenance. This could be done by the release of breeding males into the site if only females are present, or vice versa (see also Bezuijen *et al.* 2013). In that case, genetically tested zoo stock could potentially be used for future restocking efforts.

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Science



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Publication 8

**A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from
limestone forest, Khammouane Province, central Laos**

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Minh Duc Le

Michael Bonkowski

Thomas Ziegler

***Zootaxa*, 4058 (3): 388-402. DOI: [org/10.11646/zootaxa.4058.3.6](https://doi.org/10.11646/zootaxa.4058.3.6)**

<http://dx.doi.org/10.11646/zootaxa.4058.3.6>

<http://zoobank.org/urn:lsid:zoobank.org:pub:C53B8D25-3EC8-4295-8666-4D8670E07AB0>

A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from the limestone forest of Khammouane Province, central Laos

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Abstract

We describe a new species of the genus *Cyrtodactylus* on the basis of three specimens from Khammouane Province, Laos. *Cyrtodactylus soudthichaki* **sp. nov.** is distinguished from the remaining congeners by the combination of the following characters: adult SVL 69.2–70.0 mm; dorsal head and neck with dark blotches; nuchal loop present; dorsum with five brown bands between limb insertions; 19 or 20 irregular rows of dorsal tubercles; 32 or 33 ventral scale rows; ventrolateral folds present, with distinct tubercles; dorsal surface of hind limbs with tubercles; 29 precloacal and femoral pores in a continuous row in males, precloacal pores absent in the female; enlarged femoral and precloacal scales present; 4 or 5 postcloacal tubercles; and subcaudals transversely enlarged. The new species most closely resembles *Cyrtodactylus jaegeri* and *Cyrtodactylus roesleri* in overall coloration and pattern. However, they can be clearly distinguished from each other in the number of dorsal tubercle rows, ventral scales, and femoral and precloacal pores. *Cyrtodactylus soudthichaki* is the 16th species of *Cyrtodactylus* known from Laos.

Key words: *Cyrtodactylus soudthichaki* **sp. nov.**, central Laos, morphology, taxonomy

Introduction

Limestone karst forests of Lao PDR (hereafter Laos) harbour a high level of species richness, in particular Bent-toed Geckos. A total of 11 species of the genus *Cyrtodactylus* have been recorded from this habitat type in Laos, for instance from Luang Prabang Province (one species): *C. vilaphongi* Schneider, Nguyen, Le, Nophaseud, Bonkowski & Ziegler; from Luang Nam Tha Province (one species): *C. wayakonei* Nguyen, Kingsada, Rösler, Auer & Ziegler; from Vientiane Province (two species): *C. pageli* Schneider, Nguyen, Schmitz, Kingsada, Auer & Ziegler and *C. spelaeus* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov; from Borikhamxay Province (one species): *C. teyniei* David, Nguyen, Schneider & Ziegler and from Khammouane Province (six species): *C. roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz (Teynié & David 2010), *C. lomyenensis* Ngo & Pauwels, *C. jaegeri* Luu, Calame, Bonkowski, Nguyen & Ziegler, *C. multiporus* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, *C. darevskii* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, and *C. khammouanensis* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov.

Our recent field work in the karst forest of Phou Hin Poun National Protected Area, Khammouane Province, central Laos led to the discovery of another, morphologically distinct new species of *Cyrtodactylus* which is described below.

Material and methods

Sampling. Field surveys were conducted in Phou Hin Poun National Protected Area (NPA), Khammouane Province, Laos in April 2015. Specimens were anaesthetized and fixed in approximately 85% ethanol, then later transferred to 70% ethanol for permanent storage. Specimens were subsequently deposited in the collections of the Vietnam Forestry University (VFU), Hanoi, Vietnam; the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology, Hanoi, Vietnam; and the National University of Laos (NUOL), Vientiane, Laos.

Morphological characters. Measurements were taken with a digital calliper to the nearest 0.1 mm. Abbreviations are as follows: snout–vent length (SVL), from tip of snout to anterior margin of cloacal opening; tail length (TaL), from posterior margin of cloacal opening 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 process; maximum head width (HW); greatest diameter of orbit (OD); snout to eye distance (SE), from tip of snout to anterior margin of eyeball; eye to ear distance (EyeEar), from anterior edge of ear opening to posterior margin of eyeball; ear length (EarL), maximum diameter of ear; 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 counting rostral and labial), i.e. nasorostral, supranasal, postnasals (N); postrostrals or internasals (IN); postmentals (PM); dorsal tubercle rows (DTR), granular scales surrounding dorsal tubercles (GST); ventral scales in longitudinal rows at midbody (V); number of scales along the midbody from mental to anterior edge of cloaca opening (SLB); number of scale rows at 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.

Results

Cyrtodactylus soudthichaki sp. nov.

(Figs. 1–3)

Holotype. VFU R.2015.18, adult male, Khun Don region (17°33.731'N, 104°52.360'E, elevation 167 m a.s.l.) within Phou Hin Poun NPA, Khammouane Province, central Laos, collected during night time between 19:00 and 21:00 on 4 April 2015 by V. Q. Luu and T. Calame.

Paratypes. IEBR A.2015.34, adult female and NUOL R-2015.5, subadult male, bearing the same data as the holotype.

Diagnosis. The new species can be distinguished from all other members of the genus *Cyrtodactylus* from the mainland Indochina region by a combination of the following characters: adult SVL 69.2–70.0 mm; dorsal head and neck with dark blotches; nuchal loop present; dorsum with five brown bands between limb insertions; 19 or 20 irregular rows of dorsal tubercles; 32 or 33 ventral scale rows; ventrolateral folds present with distinct tubercles; dorsal surface of hind limbs with tubercles; 29 precloacal and femoral pores in a continuous row in males, precloacal pores absent in the female; enlarged femoral and precloacal scales present; 4 or 5 postcloacal tubercles; subcaudals transversely enlarged.

Description of the holotype. Adult male, snout-vent length (SVL) 69.2 mm; body elongate (TrunkL/SVL 0.41); head elongate (HL/SVL 0.28), relatively narrow (HW/HL 0.63), depressed (HH/HL 0.33), distinct from neck; loreal region inflated, posterior nasal region concave; snout long (SE/HL 0.44), obtuse, longer than diameter of orbit (OD/SE 0.63); snout scales small, rounded, homogeneous, granular, larger than those on frontal and parietal regions; eye large (OD/HL 0.27), pupils vertical; eyelid fringe with tiny spines posteriorly; ear oval-shaped, small (EarL/HL 0.11); rostral wider than high with a medial suture; supranasals in contact medially; rostral bordered by first supralabial and nostril on each side; nares oval, surrounded by supranasal, rostral, first supralabial, and two enlarged postnasals; mental triangular, as wide as rostral (RW 3.0, MW 2.9); postmentals two, enlarged, in broad contact posteriorly, bordered by mental anteriorly, first two infralabials laterally; supralabials 10/

11; infralabials 8/8. Dorsal scales small, granular to flattened; dorsal tubercles conical, round, present on occipital region, dorsum and tail base, those on the sides larger, each surrounded by 9 granular scales, in 20 irregular longitudinal rows at midbody; ventral scales smooth, medial scales 2 or 3 times larger than dorsal scales, round, subimbricate, in 32 longitudinal rows at midbody; lateral skin folds distinct, with tubercles; gular region with homogeneous, smooth scales; ventral scales between mental and cloacal slit 170; precloacal groove absent; a series of distinctly enlarged femoral scales present; femoral and precloacal pores 29, in a continuous row.

TABLE 1. Measurements (in mm) and morphological characters of the type series of *Cyrtodactylus soudthichaki* sp. nov. (* = regenerated, for other abbreviations see material and methods).

Character	VFU R.2015.18 Holotype	IEBR A.2015.34 Paratype	NUOL R-2015.5 Paratype
Sex	male	female	subadult male
SVL	69.2	70.0	56.8
TaL	95.2	95.1*	71.2
HH	6.4	7.0	6.0
HL	19.3	19.8	16.5
HW	12.2	13.0	10.4
OD	5.3	5.1	4.3
SE	8.4	8.2	7.0
EyeEar	4.9	5.3	4.5
EarL	2.1	1.9	1.5
TrunkL	28.5	30.5	25.5
ForeL	11.2	12.0	9.0
FemurL	15.0	16.4	12.2
CrusL	13.5	15.2	11.9
LD4A	7.0	6.3	5.9
LD4P	8.9	8.3	8.0
RW	3.0	3.4	2.6
RH	2.6	2.1	1.5
MW	2.9	3.0	2.5
ML	2.7	2.4	2.0
SL	10/11	11/11	10/11
IL	8/8	9/9	9/9
N	3/3	3/3	3/3
IN	0	1	0
PM	2	2	2
DTR	20	19	20
GST	9	10	9
V	32	33	33
SLB	170	169	165
SR	78	85	78
FP+PP	29	0	29
PAT	5/5	4/4	5/5
LD4	18/18	18/16	18/17
LT4	18/18	18/18	18/18

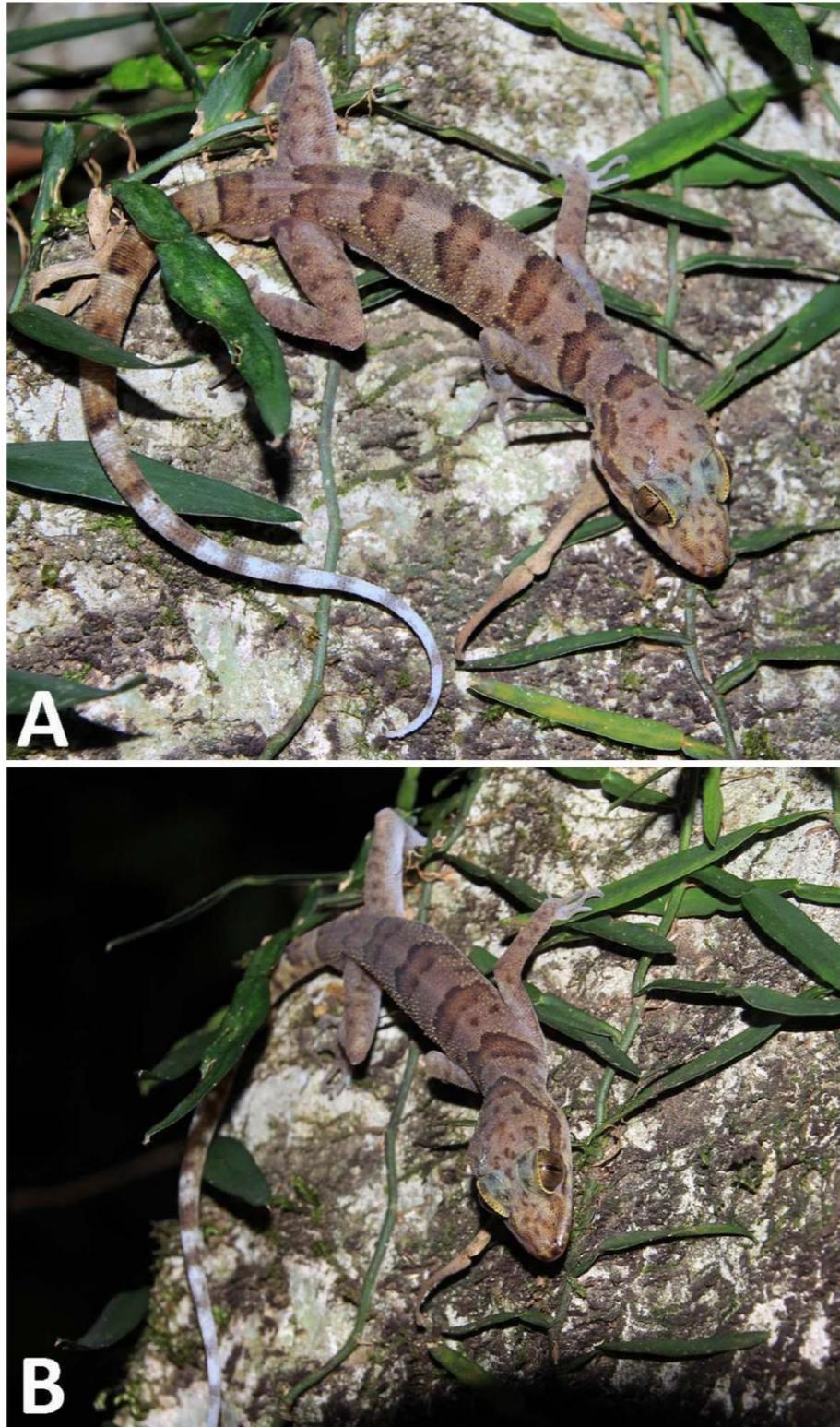


FIGURE 1. Adult male holotype of *Cyrtodactylus soudthichaki* sp. nov. (VFU R.2015.18) in life: A) dorsal view, and B) lateral view. Photos V. Q. Luu.

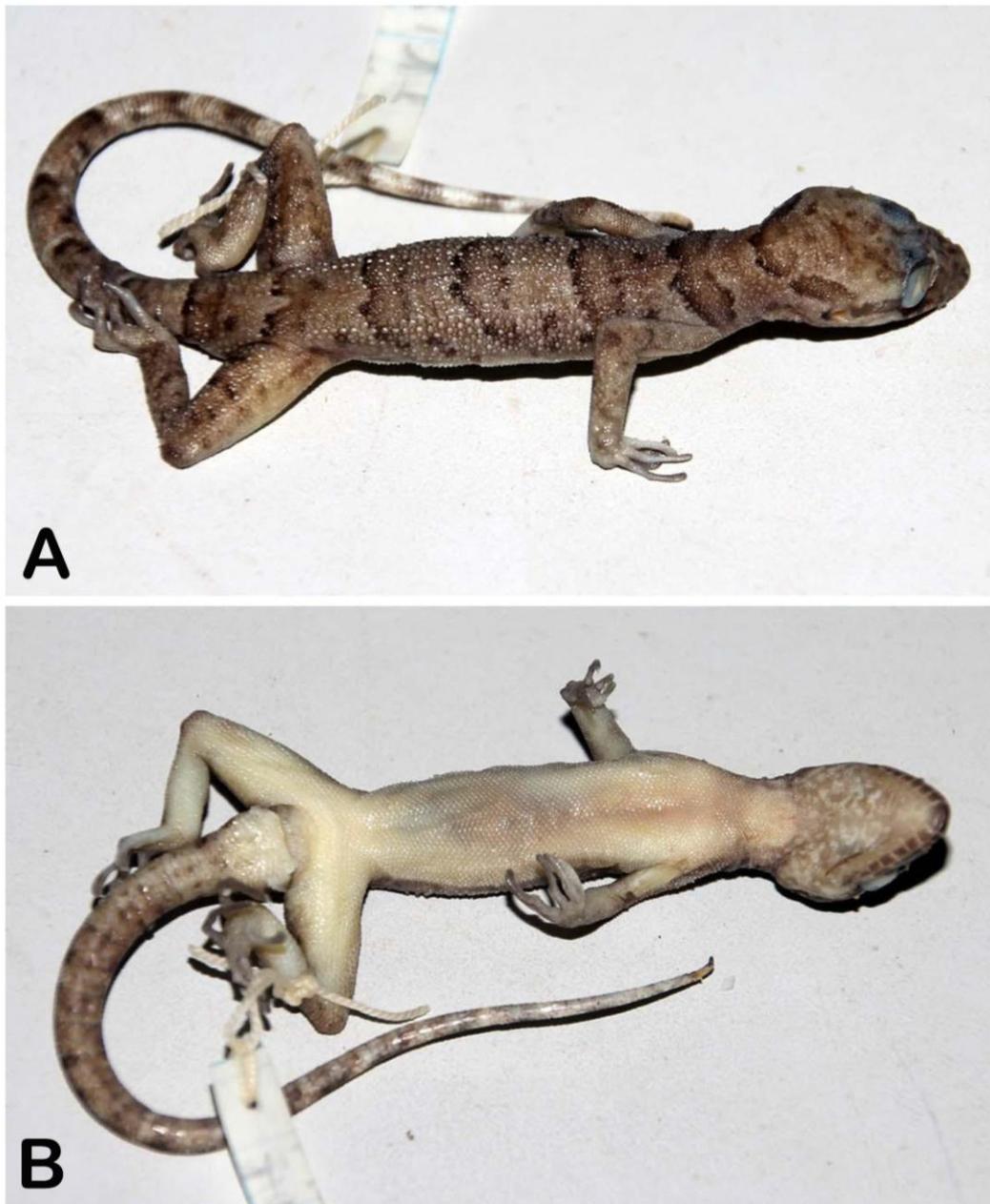


FIGURE 2. Adult male holotype of *Cyrtodactylus soudthichaki* **sp. nov.** (VFU R.2015.18) in preservative: A) dorsal view, and B) ventral view. Photos V. Q. Luu.

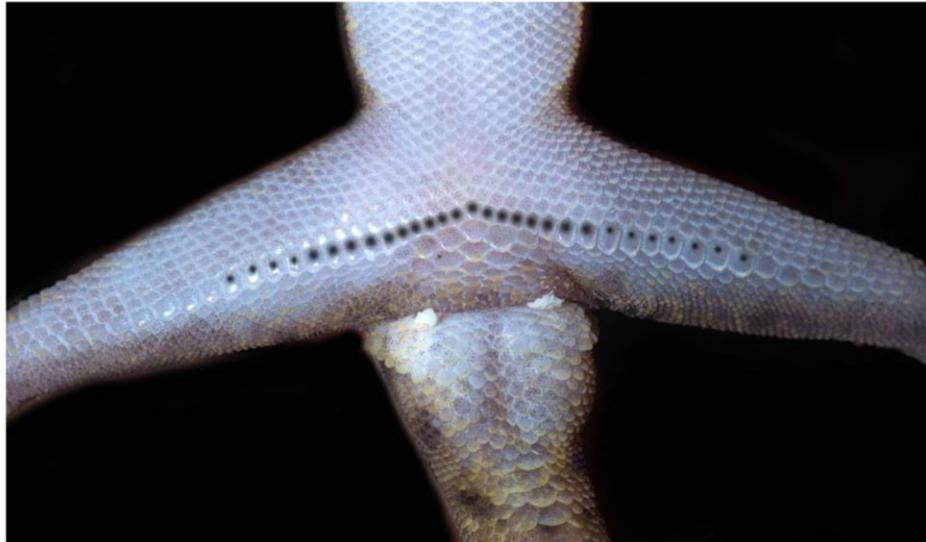


FIGURE 3. Cloacal region of the holotype of *Cyrtodactylus soudthichaki* sp. nov. (VFU R.2015.18) in life; pores are marked by black dots. Photo T. Calame.

Fore- and hind limbs moderately slender (ForeL/SVL 0.16, CrusL/SVL 0.20), femur longer than crus (FemurL/CrusL 1.34); dorsal surface of forelimbs with slightly developed tubercles; dorsal surface of hind limbs covered by distinctly developed tubercles; fingers and toes without distinct webbing; toe IV longer than finger IV (LD4P/LD4A 1.27); lamellae under fourth finger and fourth toe 18/18.

Tail longer than snout–vent length (TaL 95.2 mm, TaL/SVL 1.38); postcloacal tubercles 5/5; dorsal surface of tail with distinct tubercles at base; subcaudals distinctly transversely enlarged, flat, smooth.

Coloration in life. Ground color of dorsal surface of head and body greyish brown; dorsal head with irregular dark brown marking; nuchal loop dark brown, in U-shape, extending from posterior corner of eye, partly above tympanum to the neck; labials brown; five distinct dark transverse bands between limb insertions, normally with indentations in the posterior part of the dorsal bands at midbody; small tubercles at midbody brown; tubercles on sides yellow; dorsal surface of fore- and hind limbs with dark blotches; dorsal surface of tail grey with 15 dark bands, edged in white; posterior half of the tail white with only faint dark bands transversally; chin, throat, chest, belly and ventral surface of limbs greyish cream; ventral tail grey with dark and yellow blotches.

Sexual dimorphism. The female differs from the males by the absence of femoral and precloacal pores (*versus* 29 pores in males) and the absence of hemipenial swellings at the tail base (see Tables 1&2).

Comparisons. In the following we compare the new species with its congeners from Laos and neighbouring countries from the mainland Indochina region, including Vietnam, Cambodia, and Thailand based on examination of specimens (see Appendix) and data obtained from the literature (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) (see Table 3).

Morphologically, *Cyrtodactylus soudthichaki* sp. nov. closely resembles *C. jaegeri* Luu, Calame, Bonkowski, Nguyen & Ziegler and *C. roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz in overall coloration and pattern. However, the new species can be distinguished from *C. jaegeri* by having fewer femoral and precloacal pores in males (29 *versus* 44 in *C. jaegeri*), more dorsal tubercle rows on body (19–20 *versus* 15–17 in *C. jaegeri*) and the absence of femoral and precloacal pores in the female (present in *C. jaegeri*), and from *C. roesleri* by having transverse dorsal bands between limb insertions with indentations in the posterior part of dorsal bands at the vertebral region (*versus* without indentations in *C. roesleri*) (see Ziegler *et al.* 2010), fewer ventral scale rows (32–33 *versus* 34–40 in *C. roesleri*), more femoral and precloacal pores in males (29 *versus* 20–28 in *C. roesleri*), and the absence of femoral pores in the female (present in *C. roesleri*). For further distinguishing characters see Table 4 and Fig. 4.

TABLE 3. Morphological comparisons between *Cyrtodactylus souldhichaki* sp. nov. and its 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). Abbreviations are as follows: m = male; f = female; – = characters unobtainable from literature; * = tail regenerated, for other abbreviations see material and methods.

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
<i>Cyrtodactylus souldhichaki</i> sp. nov.	69.2–70.0	95.1*–95.2	32–33	present	Present (in males)	29 (FP+PP)	absent	16–18	18	banded	present
<i>C. angularis</i>	80.0–92.0	92–95.2	40–45	present	absent	3	3	18–19	18–19	banded	present
<i>C. astrum</i>	46.4–108.3	99.0*–109.0*	31–46	–	present	31–38 (FP+PP)	–	–	20–24	banded	present
<i>C. auribalteatus</i>	82.8–98.1	106.5–138.7	38–40	5–7	4–5 (in males)	6	absent	–	18–21	banded	present
<i>C. badenensis</i>	59.3–74.1	58.6–82.4	25–29	absent	absent	0	0	–	18–22	banded	present
<i>C. bichnganae</i>	95.3–99.9	96.3–115.6	30–31	11–13	18	10	8	18–20	16–20	banded	present
<i>C. bidoupimontis</i>	74.0–86.3	75.0–86.0	38–43	6–8	absent	4–6	0	15–20	18–23	banded	absent
<i>C. brevipalmatus</i>	64.0–72.0	77.0	35–44	present	present	6+9+7	6+9+7	–	–	blotched	present
<i>C. bugiamapensis</i>	58.6–76.8	65.3–83.0	36–46	6–10	absent	7–8	0–7	15–17	17–20	blotched	absent
<i>C. buchardi</i>	60.0–65.0	46.0–54.0	30	absent	absent	9	0	14	12	blotched	absent
<i>C. caovansungi</i>	90.4–94.0	120.0	38–44	8	6	9	0	22	23–25	banded	present
<i>C. cattienensis</i>	43.5–69.0	51.0–64.7	28–42	3–8	absent	6–8	0	12–16	14–19	banded	absent
<i>C. chanhomeae</i>	69.9–78.8	74.4–74.7	36–38	present	present	32 (FP+PP)	34 (FP+PP)	18–20	21–23	banded	present
<i>C. chaiquangensis</i>	90.9–99.3	97.0–108.3	36–38	absent	absent	6	7	16–18	19–23	banded	present
<i>C. cryptus</i>	62.5–90.8	63.5–88.4	47–50	absent	absent	9–11	0	18–19	20–23	banded	absent
<i>C. cucdongensis</i>	55.8–65.9	22.1–27.8	35–44	present	absent	5–6	4–6	8–11	15–20	banded	absent
<i>C. cucphuongsensis</i>	96.0	79.3*	42	14	absent	0	–	21	24	banded	present
<i>C. darevskii</i>	84.6–100.0	95.0–113.0	38–46	present	present	38–44 (FP+PP)	24–34	17–20	18–22	banded	present
<i>C. dumuii</i>	76.2–84.2	100.2*	40	present	present in males/absent in females	6+5–6+6–7	0–7	16	19	banded	present
<i>C. eisenmanae</i>	76.8–89.2	91.0–103.8	44–45	4–6	absent	0	0	18–20	17–18	banded	present
<i>C. erythrops</i>	78.4	83.0*	28	present	present	10+9+9 (PP+FP)	–	16	20	blotched	present

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TABLE 3. (Continued)

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	L74	Color pattern of dorsum	Enlarged subcaudals
<i>C. grismeri</i>	68.3–95.0	111.3–115.1	33–38	absent	–	0	0	16–18	16–19	banded	present
<i>C. huongsonensis</i>	73.4–89.8	90.5	41–48	7–9	15–17	6	8	17–19	20–23	banded	present
<i>C. huynhi</i>	54.8–79.8	61.5–78.6	43–46	3–5	3–8	7–9	0–8	14–17	17–21	banded	absent
<i>C. interdigitalis</i>	59.0–80.0	71.0–90.0	37–42	present	16–18	14	0	17–22	16–20	banded	present
<i>C. intermedius</i>	61.0–85.0	80.0–110.0	40–50	6–10	–	8–10	–	20	22	banded	present
<i>C. irregularis</i>	72.0–86.0	66.0–74.0	38–45	7–8	–	5–7	0–6	15–16	18–19	blotched	absent
<i>C. jaegeri</i>	60.0–68.5	82.4–83.4	31–32	17–19	present	44 (FP+PP)	21	17–19	20–23	banded	present
<i>C. jarujini</i>	85.0–90.0	105.0–116.0	32–38	present	present	52–54 (PP+FP)	0	15–17	18–19	blotched	present
<i>C. khammouanensis</i>	70.8–73	83.0–95.0	32–38	present	present	40–44 (PP+FP)	0	18–20	20–23	banded	present
<i>C. khelangensis</i>	72.8–95.3	max. 96.0*	32–35	present	present	6+2–5+6–7 (PP+FP)	2+6+1 (PP+FP)	18	22	banded	present
<i>C. kingsadai</i>	83.0–94.0	max. 117.0	39–46	9–12	0–7	7–9 (PP+FP)	4–8	19–21	21–25	banded	present
<i>C. lekaguli</i>	80.5–103.5	115.0–125.0	31–43	present	present	30–36 (PP+FP)	0	–	20–25	banded	present
<i>C. lomyensis</i>	57.7–71.2	72.2–86.1	35–36	17–18	present	39–40 (PP+FP)	32	16–19	19–23	banded	present
<i>C. martini</i>	64.4–96.2	76.0–101.2	39–43	14–18	absent	4 (PP+FP)	0	19–23	22–24	banded	present
<i>C. multiporus</i>	81.0–98.0	97.0–105.0	30–38	present	present	58–60 (PP+FP)	0	18–20	18–22	banded	present
<i>C. nigriocularis</i>	82.7–107.5	70.6–121	42–49	absent	absent	0–2	0	–	17–21	uniformly brown	present
<i>C. oldhami</i>	63.0–68.0	69*–70*	34–38	present	absent	1–4	–	–	–	striped and spots	present
<i>C. pagli</i>	76.2–81.8	85.4*–113.2*	41–44	absent	absent	4	4	19–23	19–23	banded	present
<i>C. paradoxus</i>	52.0–84.0	80.8–111.0	32–40	present	absent	0–4	0	15–18	17–23	banded	present
<i>C. phonghakebangensis</i>	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
<i>C. phuocbinhensis</i>	46.0–60.4	76.1	43–47	5	absent	7	0	16–21	17–19	blotched	absent

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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
<i>C. pseudoquadrivirgatus</i>	48.6–83.3	55.7–82.3	41–57	absent	absent	5–9	5–10	15–21	16–25	blotched	absent
<i>C. puhensis</i>	79.2	82.59	36	present	absent	5	–	18	23	banded	present
<i>C. quadrivirgatus</i>	39.0–67.0	77.0	40	present	absent	4	4	–	–	striped	absent
<i>C. ramongensis</i>	56.9–59.6	66.0–67.1	35–40	present	0	0	0	17	18	blotched	absent
<i>C. roesleri</i>	51.1–75.3	63.4–101.0	34–40	7–10	present	20–28	17–22	17–19	17–21	banded	present
<i>C. saiyok</i>	56.7–61.0	66.7–67.5	23–24	present	absent	5	–	–	16–17	banded	present
<i>C. samroiyot</i>	63.2–66.9	78.8–87.5	33–34	present	absent	7	6	18	19	banded	present
<i>C. sanook</i>	72.9–79.5	104.2	27–28	present	absent	3–4	absent	–	19–20	banded	present
<i>C. spelaeus</i>	88.9–91.0	max. 83*	36–39	absent	absent	8–9	0	19–20	22–24	banded	present
<i>C. sumonthai</i>	61.5–70.7	89.9–94.0	33–36	absent	absent	2	0	16	18	banded	present
<i>C. takouensis</i>	74.7–81.1	77.7–91.0	39–40	3–5	0–2	3–4	0	16–17	18–20	banded	present
<i>C. taynguyenensis</i>	60–85	66–94	42–49	absent	absent	6	0	13–18	17–21	blotched	absent
<i>C. teyniei</i>	89.9	ca. 110.0	38	23	absent	unknown	13	17–18	19–20	blotched	present
<i>C. thuongae</i>	57.3–77.6	max. 78.1	29–44	2–5	0–3	0–1	0	14–17	14–20	blotched	absent
<i>C. wayakonei</i>	72.0–86.8	76.8–89.0	31–35	absent	absent	6–8	7	17–18	19–20	banded	present
<i>C. thirakhupti</i>	72.0–79.6	99.1	37–40	present	absent	absent	absent	16	20	banded	present
<i>C. tigroides</i>	74.3–83.2	108.5–117.0	34	present	present	6+8+7	5+9+7	18–19	20–22	banded	present
<i>C. vilaphongi</i>	60.9–86.1	61.2–68.1	34–36	0	–	–	0	18–19	18–20	banded	absent
<i>C. yanghayensis</i>	78.5–92.3	91.3–109.1	39–46	5–16	0–2	6–8	0	16–19	15–17	banded	present
<i>C. ziegleri</i>	84.6–93.0	95.0–107.0	33–39	8–10	0–6	5–8	0–8	16–19	18–21	banded	absent

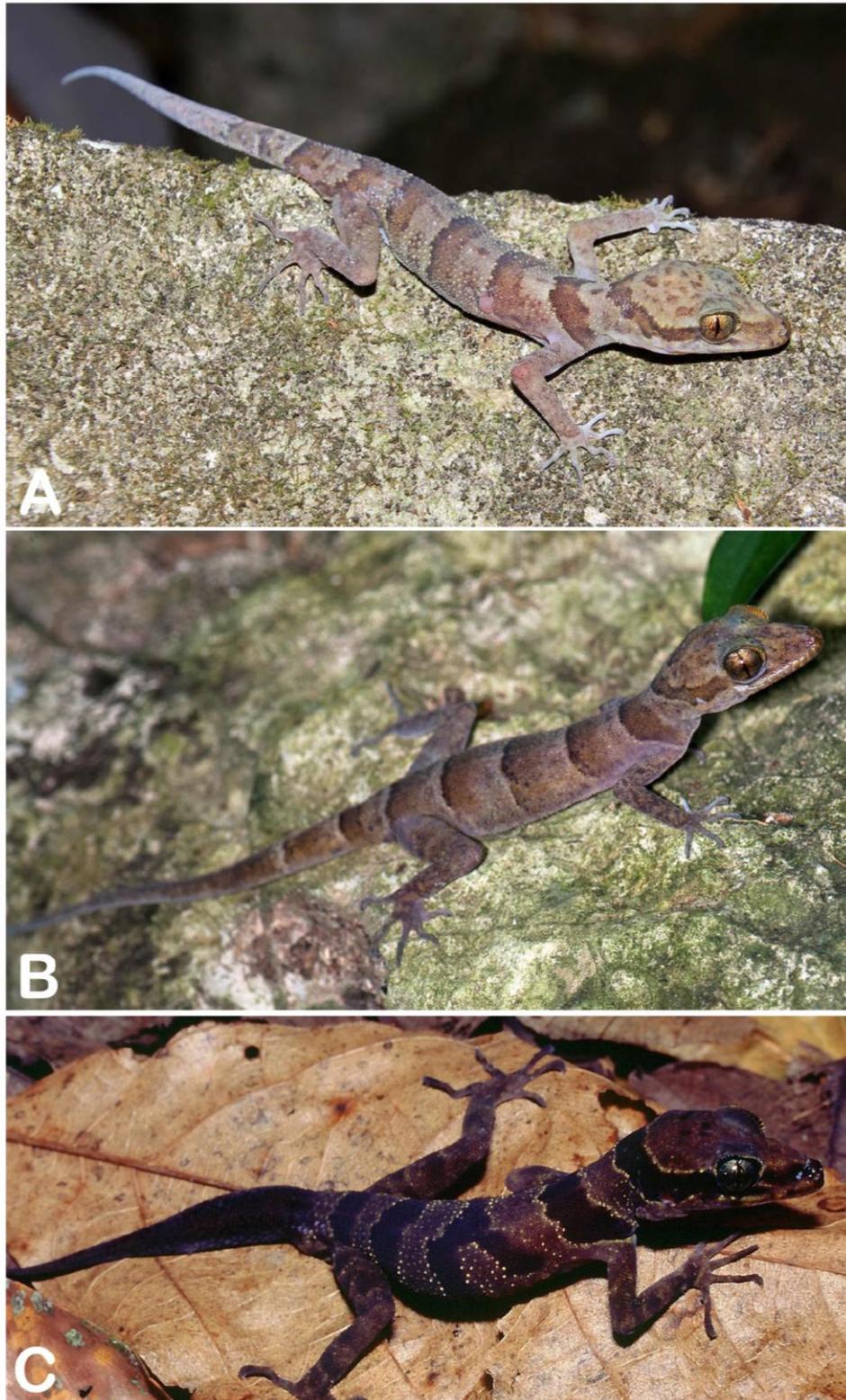


FIGURE 4. Dorsal pattern of three morphologically similar *Cyrtodactylus* species: A) *Cyrtodactylus soudthichaki* **sp. nov.** (adult female paratype: IEBR A.2015.34); B) *C. jaegeri*; and C) *C. roesleri* from Vietnam. Photos V. Q. Luu, T. Calame & T. Ziegler.

TABLE 4. Different diagnostic characters between *Cyrtodactylus soudthichaki* sp. nov., *C. jaegeri* and *C. roesleri* (after Ziegler *et al.* 2010, and own data).

Character	<i>Cyrtodactylus soudthichaki</i> sp. nov.	<i>C. jaegeri</i>	<i>C. roesleri</i>
Dorsal tubercle rows	19–20	15–17	13–19
Transverse dorsal bands between limbs	5, normally with indentations in mid-dorsal region	4, normally without indentations in mid-dorsal region	4–5, normally without indentations in mid-dorsal region
V	32–33	31–32	34–40
PP + FP (in males)	29	44	20–28
PP + FP (in females)	0	21	17–22
PAT	4–5	3–6	5–8

Cyrtodactylus soudthichaki sp. nov. has enlarged subcaudals, which are absent in the following species: *C. bidoupimontis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, *C. buchari* David, Teynié & Ohler, *C. bugiamapensis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, *C. cattienensis* Geissler, Nazarov, Orlov, Böhme, Phung, Nguyen & Ziegler, *C. cucdongensis* Schneider, Phung, Le, Nguyen & Ziegler, *C. cryptus* Heidrich, Rösler, Vu, Böhme & Ziegler, *C. huynhi* Ngo & Bauer, *C. irregularis* (Smith), *C. phuocbinhensis* Nguyen, Le, Tran, Orlov, Lathrop, Macculloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, *C. pseudoquadrivirgatus* Rösler, Vu, Nguyen, Ngo & Ziegler, *C. quadrivirgatus* Taylor, *C. ranongensis* Sumontha, Pauwels, Panitvong, Kunya & Grismer, *C. taynguyenensis* Nguyen, Le, Tran, Orlov, Lathrop, Macculloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, *C. thuongae* Phung, van Schingen, Ziegler & Nguyen, *C. vilaphongi*, and *C. zieglerei* Nazarov, Orlov, Nguyen & Ho.

The new species has femoral and preloacal pores in males and thus differs from the following species which do not possess such pores in males: *C. angularis* (Smith), *C. badenensis* Nguyen, Orlov & Darevsky, *C. chauquangensis* Hoang, Orlov, Ananjeva, Johns, Hoang & Dau, *C. cucphuongensis* Ngo & Chan, *C. eisenmanae* Ngo, *C. grismeri* Ngo, *C. martini* Ngo, *C. nigriocularis* Nguyen, Orlov & Darevsky, *C. oldhami* (Theobald), *C. pageli* Schneider, Nguyen, Schmitz, Kingsada, Auer & Ziegler, *C. paradoxus* (Darevsky & Szczerbak), *C. puhensis* Nguyen, Yang, Le, Nguyen, Orlov, Hoang, Nguyen, Jin, Rao, Hoang, Che, Murphy & Zhang, *C. sai yok* Panitvong, Sumontha, Tunprasert & Pauwels, *C. samroi yot* Pauwels & Sumontha, *C. sanook* Pauwels, Sumontha, Latinne & Grismer, *C. spelaeus*, *C. sumonthai* Bauer, Pauwels & Chanhome, *C. teyniei*, *C. wayakonei*, *C. thirakhupti* Pauwels, Bauer, Sumontha & Chanhome.

The new species differs from *C. astrum* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Ahmad, Bauer, Wangkulangkul, Grismer & Pauwels by its smaller size (SVL reaching 70.0 mm *versus* 108.3 mm), and fewer femoral and preloacal pores in males (29 *versus* 31–38); from *C. auribalteatus* Sumontha, Panitvong & Deen by having fewer ventral scale rows (32–33 *versus* 38–40), and more femoral and preloacal pores in males (29 *versus* 10–11); from *C. bichnganae* Ngo & Grismer by its smaller size (SVL 69.2–70.0 mm *versus* 95.3–99.9 mm), and the absence of femoral and preloacal pores in the female (*versus* present); from *C. brevipalmatus* (Smith) by having fewer ventral scale rows (32–33 *versus* 35–44), more femoral and preloacal pores in males (29 *versus* 22), and the absence of femoral and preloacal pores in females (*versus* present); from *C. caovansungi* Orlov, Nguyen, Nazarov, Ananjeva & Nguyen by its smaller size (SVL 69.2–70.0 mm *versus* 90.4–94.0 mm), having fewer ventral scale rows (32–33 *versus* 38–44), and more femoral and preloacal pores in males (29 *versus* 15); from *C. chanhomeae* Bauer, Sumontha & Pauwels by having fewer ventral scale rows (32–33 *versus* 36–38), fewer femoral and preloacal pores in males (29 *versus* 32), and the absence of femoral and preloacal pores in the female (*versus* present); from *C. darevskii* by its smaller size (SVL 69.2–70.0 mm *versus* 84.6–100.0 mm), having fewer ventral scale rows (32–33 *versus* 38–46), and fewer femoral and preloacal pores in males (29 *versus* 38–44); from *C. dumnuui* Bauer, Kunya, Sumontha, Niyomwan, Pauwels, Chanhome & Kunya by its smaller size (SVL 69.2–70.0 mm *versus* 76.2–84.2 mm), having fewer ventral scale rows (32–33 *versus* 40), and femoral and preloacal pores in a continuous row in males (*versus* discontinuous row); from *C. erythropros* Bauer, Kunya, Sumontha, Niyomwan, Panitvong, Pauwels, Chanhome & Kunya by its smaller size (SVL 69.2–70.0 mm *versus* 78.4 mm), having more ventral scale rows (32–33 *versus* 28), and femoral and preloacal pores in a continuous row in males (*versus* discontinuous row); from *C. huongsonensis* Luu, Nguyen, Do & Ziegler by having fewer ventral scale rows (21–23 *versus* 41–48), more femoral and preloacal pores in males (29 *versus* 21–23), and the absence of femoral and

preloacal pores in the female (*versus* present); from *C. interdigitalis* Ulber by its smaller size (SVL reaching 70.0 mm *versus* 80.0 mm), having fewer ventral scale rows (32–33 *versus* 37–42), and a slightly lower number of femoral and preloacal pores in males (29 *versus* 30–32); from *C. intermedius* (Smith) by its smaller size (SVL reaching 70.0 mm *versus* 85.0 mm) and by having fewer ventral scale rows (32–33 *versus* 40–50); from *C. jarujini* Ulber by its smaller size (SVL reaching 70.0 mm *versus* 90.0 mm) and having fewer femoral and preloacal pores in males (29 *versus* 52–54); from *C. khammouanensis* by having fewer ventral scales (32–33 *versus* 32–38) and fewer femoral and preloacal pores in males (29 *versus* 40–44); from *C. khelangensis* Pauwels, Sumontha, Panitvong & Varaguttanonda by its smaller size (SVL 69.2–70.0 mm *versus* 72.8–95.3 mm in *C. khelangensis*), femoral and preloacal pores in a continuous row in males (*versus* discontinuous row), and the absence of femoral and preloacal pores in the female (*versus* present); from *C. kingsadai* Ziegler, Phung, Le & Nguyen by its smaller size (SVL reaching 70.0 mm *versus* 94.0 mm), having fewer ventral scales (32–33 *versus* 39–46), and more femoral and preloacal pores in males (29 *versus* 0–16); from *C. lekaguli* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Ahmad, Bauer, Wangkulangkul, Grismer & Pauwels and *C. lomyenensis* in having fewer femoral and preloacal pores in males (29 *versus* 30–36 in *C. lekaguli* and 39–40 in *C. lomyenensis*), and the absence of femoral and preloacal pores in the female (*versus* present in *C. lekaguli* and *C. lomyenensis*); from *C. multiporus* by its smaller size (SVL reaching 70.0 mm *versus* 98.0 mm), having fewer ventral scale rows (32–33 *versus* 39–43), and fewer femoral and preloacal pores in males (29 *versus* 58–60); from *C. phonghakebangensis* Ziegler, Rösler, Herrmann & Vu by its smaller size (SVL reaching 70.0 mm *versus* 96.3 mm), having fewer femoral and preloacal pores in males (29 *versus* 32–42), and the absence of femoral and preloacal pores in the female (*versus* present); from *C. takouensis* Ngo & Bauer by its smaller size (SVL 69.2–70.0 mm *versus* 74.7–81.1 mm), having fewer ventral scales (32–33 *versus* 39–40) and more femoral and preloacal pores in males (29 *versus* 3–6); from *C. tigroides* Bauer, Sumontha & Pauwels by having a smaller size (SVL 69.2–70.0 mm *versus* 74.3–83.2 mm) and more femoral and preloacal pores in males (29 *versus* 21); and from *C. yangbayensis* Ngo & Chan by having fewer ventral scale rows (32–33 *versus* 39–46) and more femoral and preloacal pores in males (29 *versus* 4–14).

Distribution. *Cyrtodactylus soudthichaki* sp. nov. is currently known only from the type locality in Khun Don Mountain, Phou Hin Poun NPA, Khammouane Province, central Laos (Fig. 5).

Etymology. This species is named in honour of Mr. Sisomphone Soudthichak, from the Natural Resources and Environment Department of Khammouane Province, Laos, who provided great support for our field research in Laos since 2013. As common names, we suggest Soudthichak's Bent-toed Gecko (English) and Soudthichak's Ki Chiem (Laotian).

Natural history. The specimens were found between 19:00 and 21:00, on the branches of shrubs and karst boulders in a karst forest, approximately 0.3 m above the forest floor, between 150 and 170 m a.s.l. The karst forest included species of the dominated families Ebenaceae, Dracaenaceae, Arecaeae, Poaceae, Meliaceae, and Moraceae. The humidity at the time of collection was approximately 85% and the air temperature ranged from 23 to 26°C.

Discussion

At first glance, *Cyrtodactylus soudthichaki* is phenotypically most similar to the karst-dwelling species *C. jaegeri* and *C. roesleri*. However, the new species is clearly distinguishable from them in the number of ventral scale and dorsal tubercle rows, and preloacal-femoral pores. The type locality of *C. soudthichaki* is only approximately 20 km distant from the type locality of *C. jaegeri* in Thakhek Town, about 90 km distant from the type locality of *C. roesleri* in Phong Nha - Ke Bang National Park, Vietnam, and about 40 km distant from the nearest concrete record of *C. roesleri* in Laos (Konglor Cave, Kounkham District, see Teynié & David 2010). However, the type locality of *C. soudthichaki* is separated from the occurrences of *C. jaegeri* and *C. roesleri* by the Hin Boun River. Limestone mountains in Khammouane Province are not only isolated from each other by river systems, but also by intensively cultivated farmland and thus can be regarded as island-like structures (Timmins 1997; Luu *et al.* 2014). In addition, in contrast to *C. roesleri* and *C. jaegeri* which on karst cliffs and karst outcrops (Ziegler *et al.* 2010; Luu *et al.* 2014), *C. soudthichaki* occupies a different ecological niche, as known specimens were found on the branches of shrubs.

Cyrtodactylus soudthichaki is the 16th species of the genus *Cyrtodactylus* known from Laos. This is also the seventh Bent-toed Gecko species recorded from Khammouane Province apart from *C. lomyenensis*, *C. roesleri*, *C. jaegeri*, *C. khammouanensis*, *C. darevskii*, and *C. multiporus* (Ngo & Pauwels 2010; Teynié & David 2010; Luu *et al.* 2014; Nazarov *et al.* 2014). All *Cyrtodactylus* species from Khammouane Province have been discovered in the karst forests during the two recent decades. In conclusion, the karst forests of the Truong Son Range (Annamite Mountains) in Khammouane Province seem to play a vital role in *Cyrtodactylus* speciation and evolution. However, compared with the numerous *Cyrtodactylus* species discovered so far from the Vietnamese side of the Truong Son Range, further studies are required in the karst forests of Khammouane to elucidate the actual number, distribution ranges and niche segregation of *Cyrtodactylus* species occurring there.



FIGURE 5. Map showing the type locality of *Cyrtodactylus soudthichaki* sp. nov. in Phou Hin Poun NPA (black circle), Khammouane Province, Laos.

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APPENDIX. Comparative specimens examined.

- Cyrtodactylus jaegeri*. Laos: Khammouane: Thakhek: IEBR A.2013.55 (holotype), NUOL R-2013.1 (paratype)
C. jarujini. Thailand: Nong Khai: Bung Ban: ZMB 50648 (holotype).
C. huongsonensis. Vietnam: Hanoi: Huong Son: IEBR A.2011.3 (holotype), ZFMK 92293 (paratype).
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. 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. 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).

Publication 9

***Cyrtodactylus rufford*, a new cave-dwelling bent-toed gecko (Squamata:
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Cyrtodactylus rufford, a new cave-dwelling bent-toed gecko (Squamata: Gekkonidae) from Khammouane Province, central Laos

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Abstract

We describe a new species of the gekkonid genus *Cyrtodactylus* from Khammouane Province, central Laos based on morphological and molecular data. Morphologically, *Cyrtodactylus rufford* sp. nov. differs from its congeners by a unique combination of the following characters: medium size, SVL reaching 72.5 mm; dorsal pattern with three or four light transverse bands between limb insertions; one intersupranasal; 14–16 irregular dorsal tubercle rows at midbody, weakly developed in the paravertebral region; 27–29 ventral scale rows between ventrolateral folds; 42–43 precloacal and femoral pores in a continuous row in males, enlarged femoral and precloacal scales present; 4 or 5 postcloacal tubercles on each side; dorsal tubercles present at base of tail; medial subcaudal scales enlarged. Molecular analyses show that the new species is closely related to *C. khammouanensis*, which was originally described from Khammouane Province.

Key words: *Cyrtodactylus rufford* sp. nov., Khammouane Province, morphology, phylogeny, taxonomy

Introduction

Within the last five years, eight bent-toed geckos of the genus *Cyrtodactylus* have been recorded from Khammouane Province in Lao PDR (hereafter Laos), accounting for 50% of the total *Cyrtodactylus* species number recorded from the country. They include *C. lomyenensis* Ngo & Pauwels, *C. interdigitalis* Ulber, *C. roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz, *C. jaegeri* Luu, Calame, Bonkowski, Nguyen & Ziegler, *C. khammouanensis* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, *C. darevskii* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, *C. multiporus* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, and *C. soudthichaki* Luu, Calame, Nguyen, Bonkowski & Ziegler (Ngo & Pauwels 2010; Teynié & David 2010; Luu *et al.* 2014; Nazarov *et al.* 2014; Luu *et al.* 2015). Most of the aforementioned species are associated with karstic and limestone cave formations.

Pursuing our on-going research on taxonomy and zoogeography of the herpetofauna from Laos (Nguyen *et al.* 2010; Luu *et al.* 2014, Schneider *et al.* 2014), we investigated diverse localities in Khammouane Province, central Laos, with a special emphasis on karst formations and associated limestone forests. The field surveys yielded a

number of distinct species. As a result, we herein describe a cave-dwelling *Cyrtodactylus* species from an isolated karst mountain in the Gnommalath District, which was neither morphologically nor genetically assignable to any other recognized congener.

Material and methods

Sampling. Field research was conducted in Nang Log Cave, near Daen Village, Gnommalath District, Khammouane Province, Laos in March 2015. Specimens were euthanized and fixed in approximately 85% ethanol, then later transferred to 70% ethanol for permanent storage. Tissue samples of collected bent-toed geckos were preserved separately in 95% ethanol. Specimens were subsequently deposited in the collections of the Vietnam Forestry University (VFU), Hanoi, Vietnam; the Institute of Ecology and Biological Resources (IEBR), Vietnam Academy of Science and Technology, Hanoi, Vietnam; and the National University of Laos (NUOL), Vientiane, Lao PDR. Other abbreviations are as follows: PNKB: Zoological Collection of the Phong Nha-Ke Bang National Park, Quang Binh Province, Vietnam; ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZIN: Zoological Institute, St. Petersburg, Russian Academy of Sciences, Russia; ZMMU: Zoological Museum, Lomonosov Moscow State University, Moscow, Russia.

Molecular data and phylogenetic analyses. Since the new taxon is morphologically similar to species of the *C. phongnhakebangensis* group (Nazarov *et al.* 2014), we included taxa assigned to the group, consisting of eight *Cyrtodactylus* species from Laos and two species from Vietnam (Table 1). The species *C. elok* Dring, 1979 was used as an outgroup.

TABLE 1. Samples used in molecular analyses (for abbreviations see Material and Methods).

Species	GenBank no.	Locality	Voucher number
<i>C. elok</i>	HM888479	Malaysia	ZMMU RAN 1992
<i>C. elok</i>	HM888478	Malaysia	ZMMU RAN 1992
<i>C. darevskii</i>	HQ967221	Laos: Khammouane Province	ZIN FN 256
<i>C. darevskii</i>	HQ967223	Laos: Khammouane Province	ZIN FN 223
<i>C. lomyenensis</i>	KJ817436	Laos: Khammouane Province	IEBR KM2012.54
<i>C. lomyenensis</i>	KP199942	Laos: Khammouane Province	IEBR KM2012.52
<i>C. jaegeri</i>	KT004364	Laos: Khammouane Province	IEBR A.2013.55
<i>C. jaegeri</i>	KT004365	Laos: Khammouane Province	NUOL R.2013.1
<i>C. jaegeri</i>	KT004366	Laos: Khammouane Province	VFU TK914
<i>C. khammouanensis</i>	HM888467	Laos: Khammouane Province	ZIN FN 191
<i>C. khammouanensis</i>	HM888469	Laos: Khammouane Province	ZIN FN 257
<i>C. multiporus</i>	HM888472	Laos: Khammouane Province	ZIN FN 3
<i>C. multiporus</i>	HM888471	Laos: Khammouane Province	ZIN FN 2
<i>C. pageli</i>	KJ817431	Laos: Vientiane Province	ZFMK 91827
<i>C. phongnhakebangensis</i>	KF929526	Vietnam: Quang Binh Province	PNKB2011.30
<i>C. phongnhakebangensis</i>	KF929527	Vietnam: Quang Binh Province	PNKB2011.32
<i>C. roesleri</i>	KF929532	Vietnam: Quang Binh Province	PNKB2011.34
<i>C. roesleri</i>	KF929531	Vietnam: Quang Binh Province	PNKB2011.3
<i>Cyrtodactylus. rufford sp. nov.</i>	KU175572	Laos: Khammouane Province	VFU R.2015.14
<i>C. teyniei</i>	KJ817430	Laos: Khammouane Province	IEBR KM2012.77
<i>C. teyniei</i>	KP199945	Laos: Khammouane Province	IEBR KM2012.77

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 analysis (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 9 in the Bayesian analysis, as $-\ln L$ scores reached stationarity after 9,000 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. <i>C. darevskii</i> (HQ967221&3)	-				
2. <i>C. khammouanensis</i> (HM888467 & 9)	15.0–15.1	-			
3. <i>C. jaegeri</i> (KT004364 & 5 & 6)	16.9	14.8–15.0	-		
4. <i>C. lomyenensis</i> (KJ817436/KP199942)	13.6–13.7	16.2–16.4	16.3–16.6	-	
5. <i>C. multiporus</i> (HM888471 & 2)	15.6	16.2–16.4	16.2–16.3	14.7–15.1	-
6. <i>C. pageli</i> (KJ817431)	18.3–18.8	17.7–18.5	16.8–18.8	17.0–18.3	16.4–17.3
7. <i>C. phongnhakebangensis</i> (KF929526 & 7)	9.7	15.5–15.7	16.7	14.5–14.6	15.3
8. <i>C. roesleri</i> (KF929531 & 2)	17.3	9.7–10.0	15.3–15.4	17.4–17.6	16.9–17.1
9. <i>Cyrtodactylus. rufford sp. nov.</i> (KU175572)	18.2	11.9–12.1	14.6–14.7	17.8–17.9	16.7
10. <i>C. teyniei</i> (KJ817430/KP199945)	15.4–15.5	16.5–16.9	17.1–17.7	14.3–14.7	6.6–7.0

continued.

Species name	6	7	8	9	10
1. <i>C. darevskii</i> (HQ967221&3)					
2. <i>C. khammouanensis</i> (HM888467 & 9)					
3. <i>C. jaegeri</i> (KT004364 & 5 & 6)					
4. <i>C. lomyenensis</i> (KJ817436/KP199942)					
5. <i>C. multiporus</i> (HM888471 & 2)					
6. <i>C. pageli</i> (KJ817431)	-				
7. <i>C. phongnhakebangensis</i> (KF929526 & 7)	17.7–17.8	-			
8. <i>C. roesleri</i> (KF929531 & 2)	16.1–17.6	15.3	-		
9. <i>Cyrtodactylus. rufford sp. nov.</i> (KU175572)	16.9–18.7	17.6	16.3	-	
10. <i>C. teyniei</i> (KJ817430/KP199945)	17.1–18.0	15.3–15.3	17.5–17.7	17.5–17.9	-

Morphological characters. Measurements were taken with digital calipers 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 process; maximum head width (HW); greatest diameter of orbit (OD); snout to orbit distance (SE), from tip of snout to anterior corner of orbit; orbit to ear distance (EyeEar), from anterior edge of ear opening to posterior corner of orbit; ear length (EarL), maximum diameter of ear; 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) counted from the first labial scale to the corner of mouth; nasal scales surrounding nares, from rostral to labial (not counting rostral and labial), i.e. nasorostral, supranasal, postnasals (N); postrostrals or internasals (IN); postmentals (PM); dorsal tubercle rows (DTR) counted transversely across the mid-length 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 mid-length of the abdomen from one ventrolateral fold to the other; number of scales along the midbody from mental (not included) 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) counted from the base of the first phalanx to the claw. Bilateral scale counts were given as left/right.

Results

Phylogenetic analyses. The final matrix consisted of 670 aligned characters, of which 229 are parsimony informative. The alignment did not contain any gaps. MP analysis of the dataset recovered three most parsimonious trees with 640 steps (CI = 0.57; RI = 0.76). The topology derived from the Bayesian analysis (Fig. 1) is almost identical to that of clade A in Nguyen *et al.* (2015), except that the position of *C. pageli* was resolved as the sister taxon to the clade containing *C. khammouanensis*, *C. jaegeri*, *C. roesleri*, and *Cyrtodactylus rufford sp. nov.* In Nguyen *et al.* (2015), *C. pageli* was recovered as the basal taxon to all taxa presented in this study, except for *Cyrtodactylus rufford sp. nov.* and the outgroups with strong support from the Bayesian analysis (PP = 99). The new species is strongly corroborated as the sister taxon of *C. khammouanensis* in MP and Bayesian analyses, and the former is about 11.9–12.1% divergent from the latter based on COI data (Table 2).

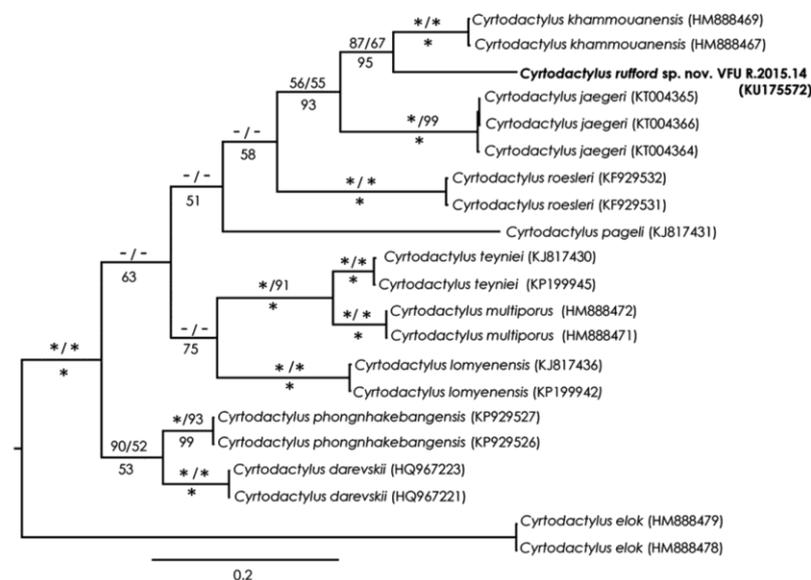


FIGURE 1. Phylogram based on the Bayesian analysis. Number above and below branches are MP/ML bootstrap values and Bayesian posterior probabilities (>50%), respectively. Asterisk denotes 100% value.

Cyrtodactylus rufford sp. nov. (Figs. 2–3)

Holotype. VFU R.2015.14, adult male, on a karst cliff, near the entrance of Nang Log cave (17°30.282'N, 105°23.107'E, elevation 160 m a.s.l.), Gnommalath District, Khammouane Province, central Laos, was collected on 29 March 2015 by V. Q. Luu, T. Calame and K. Thanabuao.

Paratypes. IEBR R.2015.35, adult male, and NUOL R.2015.15, subadult male; same collection data as was provided for the holotype.

Diagnosis. The new species differs from other congeners of the genus *Cyrtodactylus* by the following combination of characters: medium size, SVL reaching 72.5 mm; dorsal pattern consisting of three or four light transverse bands between limb insertions; one intersupranasal; 14–16 irregular dorsal tubercle rows at midbody,

weakly developed in the paravertebral region; 27–29 ventral scale rows between ventrolateral folds; 42–43 precloacal and femoral pores in a continuous row in males, enlarged femoral and precloacal scales present; 4 or 5 postcloacal tubercles on each side; dorsal tubercles present at base of tail; subcaudal scales medially enlarged.

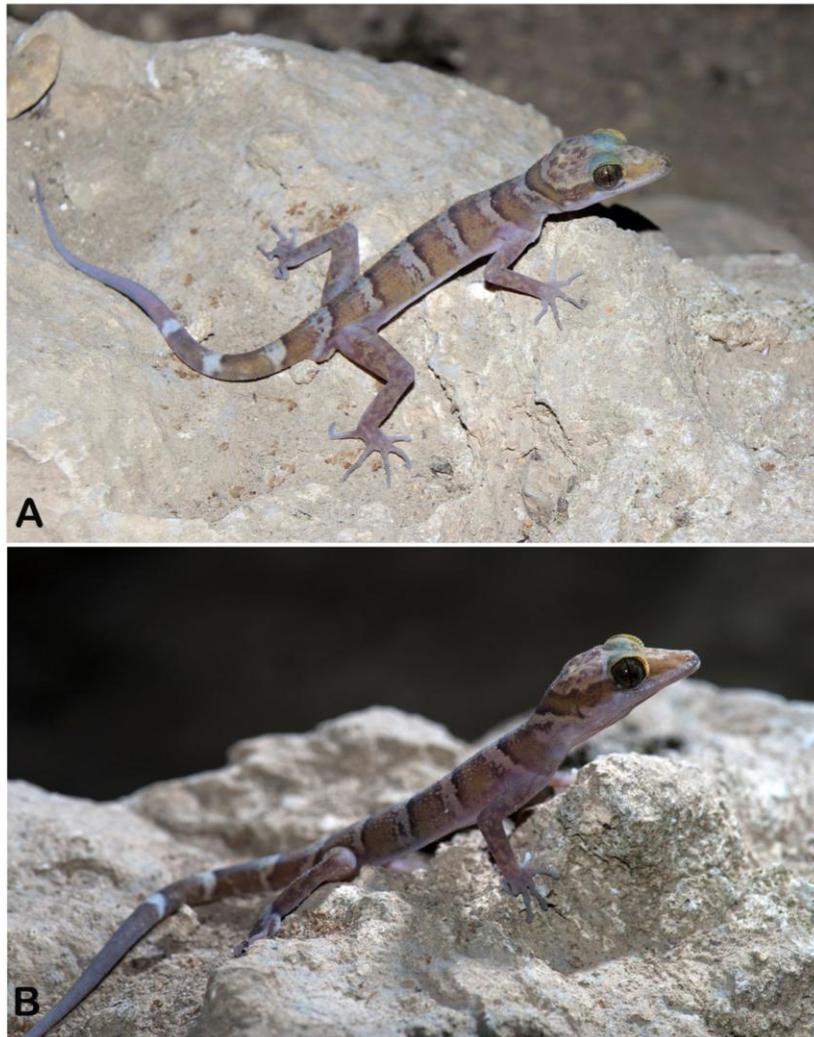


FIGURE 2. Adult male holotype of *Cyrtodactylus rufford* sp. nov. (VFU R.2015.14) in life from Khammouane Province, central Laos: A) dorsal view, and B) lateral view. Photos: V. Q. Luu and T. Calame.

Description of the holotype. Adult male, SVL 68.3 mm; body slender, elongate (TrunkL/SVL ratio 0.47); head elongate (HL/SVL ratio 0.29), relatively narrow (HW/HL ratio 0.57), depressed (HH/HL ratio 0.36), distinct from neck; loreal region inflated, posterior nasal region concave; snout long (SE/HL ratio 0.47), obtuse, longer than orbit diameter (OD/SE ratio 0.57); scales on snout small, rounded, homogeneous, granular, larger than those on frontal and parietal regions; eye large (OD/HL ratio 0.27), pupils vertical; supraciliaries with tiny spines posteriorly; ear opening oval, small (EarL/HL ratio 0.10); rostral wider than high with a shallow inverted Q-shaped medial suture; supranasals separated from each other by one small scale; rostral in contact with first supralabial and nostril on each side; nostrils oval, each surrounded by supranasal, rostral, first supralabial, and two enlarged postnasals; mental triangular, as wide as rostral (RW 2.8, MW 2.7); one pair of enlarged postmentals, in broad contact posteriorly, bordered laterally by first infralabials and triangular mental anteriorly; supralabials 11/12; infralabials 10/11. Dorsal scales granular to weakly conical; intermixed with conical, round dorsal tubercles (2–3 times larger than adjoining scales) present from occipital region to dorsum and base of tail, tubercles in 16 rows at midbody, larger on flanks, each surrounded by 9 granular scales; ventrals larger than lateral scales, smooth, round,

largest posteriorly, in 28 longitudinal scale rows between ventrolateral folds; gular region with homogeneous, smooth scales; ventral scales from mental to cloacal slit 153; precloacal groove lacking; enlarged femoral and cloacal scales present; femoral and precloacal pores 43, in a continuous row.

Fore and hind limbs moderately slender (ForeL/SVL ratio 0.17, CrusL/SVL 0.20); dorsum of forelimbs with weakly developed tubercles; hind limbs dorsally with distinct tubercles; interdigital webbing slightly developed; lamellae under fourth finger 19/19; lamellae under fourth toe 19/18.

Tail partly regenerated, longer than SVL (TaL 94.5 mm, TaL/SVL ratio 1.38); 5/4 postcloacal tubercles; tubercles present at base of tail dorsum; subcaudals transversely enlarged in the middle, flat, smooth.



FIGURE 3. Dorsal view of the paratype of *Cyrtodactylus rufford* sp. nov. (IEBR R.2015.34) in life from Khammouane Province, central Laos. Photo: V. Q. Luu.

Coloration in life. Head dorsally greyish brown with dark blotches; nuchal loop brown, uninterrupted, in U-shape; labials grey; three light transverse bands between limb insertions, edged in black anteriorly, somewhat irregular in the posterior parts of the dorsal bands; tubercles at midbody brown; tubercles on body bands grey; dorsal surface of fore- and hind- limbs with dark reticulated markings; dorsal surface of tail brown with light rings (2–3 times narrower than dark bands), ventral surface of head, body and limbs greyish cream; venter of tail grey.

Variation: The adult male paratype (IEBR R.2015.35) has wider light bands on the midbody with dark spots within each band compared to those of the holotype and subadult male paratype (NUOL R.2015.15). Further morphological characters of the paratypes are provided in Table 3.

Comparisons. We compared *Cyrtodactylus rufford* sp. nov. to other species of *Cyrtodactylus* 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.* 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) (see Table 4).

Cyrtodactylus rufford sp. nov. has distinctly enlarged median subcaudals and thus differs from the following species which are lacking enlarged median subcaudals: *C. bidoupimontis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, *C. bobrovi* Nguyen, Le, Pham, Ngo, Hoang, Pham & Ziegler, *C. buchardi* David, Teynié & Ohler, *C. bugiamapensis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, *C. cattienensis* Geissler, Nazarov, Orlov, Böhme, Phung, Nguyen & Ziegler, *C. cudongensis* Schneider, Phung, Le, Nguyen & Ziegler, *C. cryptus* Heidrich, Rösler, Vu, Böhme & Ziegler, *C. huynhi* Ngo & Bauer, *C. irregularis* (Smith), *C. otai* Nguyen, Le, Pham, Ngo, Hoang, Pham & Ziegler, *C. phuocbinhensis* Nguyen, Le, Tran, Orlov, Lathrop, Macculloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, *C. pseudoquadriregatus* Rösler, Vu, Nguyen, Ngo & Ziegler, *C. quadriregatus* Taylor, *C. ranongensis* Sumontha, Pauwels, Panitvong, Kunya & Grismer, *C. taynguyenensis* Nguyen, Le, Tran, Orlov, Lathrop, Macculloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, *C. thuongae* Phung, van Schingen, Ziegler & Nguyen, *C. vilaphongi* Schneider, Nguyen, Le, Nophaseud, Bonkowski & Ziegler, and *C. zieglerei* Nazarov, Orlov, Nguyen & Ho.

TABLE 3. Measurements (in mm) and morphological characters of the type series of *Cyrtodactylus rufford* sp. nov. (* = partly regenerated, for other abbreviations see material and methods).

Character	VFU R.2015.14 Holotype	IEBR R.2015.34 Paratype	NUOL R.2015.15 Paratype
Sex	male	male	subadult male
SVL	68.3	72.5	56.5
TaL	94.5*	96.8	84.6
HH	7.1	6.7	5.3
HL	19.5	20.6	16.3
HW	11.2	12.9	9.8
OD	5.2	5.6	4.8
SE	9.1	8.6	7.0
EyeEar	4.9	5.3	4.3
EarL	2.0	2.3	1.8
TrunkL	32.2	31.3	27.4
ForeL	11.5	10.9	9.5
FemurL	15.2	15.0	11.4
CrusL	13.9	14.2	10.6
LD4A	6.5	6.2	5.9
LD4P	8.3	8.1	7.2
RW	2.8	2.8	2.3
RH	1.4	1.8	1.3
MW	2.7	2.7	2.4
ML	2.2	2.2	1.4
SL	11/12	12/12	11/12
IL	10/11	9/9	11/11
N	3/3	3/3	3/3
IN	1	1	1
PM	2	2	2
DTR	16	14	15
GST	9	9	9
V	28	27	29
SBL	153	167	156
SR	78	74	79
FP+PP	43	42	43
PAT	5/4	5/5	5/5
LD4	19/19	19/19	20/19
LT4	19/18	19/18	18/18

Cyrtodactylus rufford sp. nov. has femoral and precloacal pores in males, both of which are lacking in the following species: *C. angularis* (Smith), *C. badenensis* Nguyen, Orlov & Darevsky, *C. chauquangensis* Hoang, Orlov, Ananjeva, Johns, Hoang & Dau, *C. cucphuongensis* Ngo & Chan, *C. eisenmanae* Ngo, *C. grismeri* Ngo, *C. martini* Ngo, *C. nigriocularis* Nguyen, Orlov & Darevsky, *C. oldhami* (Theobald), *C. pageli* Schneider, Nguyen, Schmitz, Kingsada, Auer & Ziegler, *C. paradoxus* (Darevsky & Szczerbak), *C. puhuenensis* Nguyen, Yang, Le, Nguyen, Orlov, Hoang, Nguyen, Jin, Rao, Hoang, Che, Murphy & Zhang, *C. saiyok* Panitvong, Sumontha, Tunprasert & Pauwels, *C. samroiyo*t Pauwels & Sumontha, *C. sanook* Pauwels, Sumontha, Latinne & Grismer,

TABLE 4. Morphological comparisons between *Cyrtodactylus rufford* sp. nov. and its congeners from Laos and neighbouring countries in the Indochina region (compiled after Lau *et al.* 2014; Nazarov *et al.* 2014; Nguyen *et al.* 2014; Panitwong *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). Abbreviations are as follows: FPI = femoral pores in the left side; FPr = femoral pores in the right side; – = characters unobtainable from literature; * = tail regenerated, for other abbreviations see material and methods.

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
<i>Cyrtodactylus rufford</i> sp. nov.	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
<i>C. sordidhichaki</i>	69.2–70.0	95.1*–95.2	32–33	present	present (in males)	29 (FP+PP)	absent	1618	18	banded	present
<i>C. angularis</i>	80.0–92.0	92–95.2	40–45	present	absent (in males)	3 (FP+PP)	3	18–19	18–19	banded	present
<i>C. astrum</i>	46.4–108.3	99.0*–109.0*	31–46	–	present	31–38 (FP+PP)	–	–	20–24	banded	present
<i>C. auribaiteatus</i>	82.8–98.1	106.5–138.7	38–40	5–7	4–5 (in males)	6	absent	–	18–21	banded	present
<i>C. badensis</i>	59.3–74.1	58.6–82.4	25–29	absent	absent	0	0	–	18–22	banded	present
<i>C. bichnganae</i>	95.3–99.9	96.3–115.6	30–31	11–13	18	10	8	18–20	16–20	banded	present
<i>C. bidoupimontis</i>	74.0–86.3	75.0–86.0	38–43	6–8	absent	4–6	0	15–20	18–23	banded	absent
<i>C. bobrovi</i>	75.2–96.4	80.8–90.3	40–45	0	0	5	0	19–21	21–22	banded	absent
<i>C. brevipalmatus</i>	64.0–72.0	77.0	35–44	present	present	6+9+7 (FPI+PP+FPPr)	6+9+7 (FPI+PP+FPPr)	–	–	blotched	present
<i>C. bugiamapensis</i>	58.6–76.8	65.3–83.0	36–46	6–10	absent	7–8	0–7	15–17	17–20	blotched	absent
<i>C. buchardi</i>	60.0–65.0	46.0–54.0	30	absent	absent	9	0	14	12	blotched	absent
<i>C. caovansingj</i>	90.4–94.0	120.0	38–44	8	6	9	0	22	23–25	banded	present
<i>C. cattienensis</i>	43.5–69.0	51.0–64.7	28–42	3–8	absent	6–8	0	12–16	14–19	banded	absent
<i>C. chanhomeae</i>	69.9–78.8	74.4–74.7	36–38	present	present	32 (FP+PP)	34 (FP+PP)	18–20	21–23	banded	present
<i>C. chauquangensis</i>	90.9–99.3	97.0–108.3	36–38	absent	absent	6	7	16–18	19–23	banded	present
<i>C. cryptus</i>	62.5–90.8	63.5–88.4	47–50	absent	absent	9–11	0	18–19	20–23	banded	absent
<i>C. cucdongensis</i>	55.8–65.9	22.1–27.8	35–44	present	absent	5–6	4–6	8–11	15–20	banded	absent
<i>C. cucphuongensis</i>	96.0	79.3*	42	14	absent	0	–	21	24	banded	present
<i>C. darevskii</i>	84.6–100.0	95.0–113.0	38–46	present	present	38–44 (FP+PP)	24–34	17–20	18–22	banded	present
<i>C. dumuii</i>	76.2–84.2	100.2*	40	present	present in males/absent in females	6+5–6+6–7 (FPI+PP+FPPr)	0–7	16	19	banded	present

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TABLE 4. (Continued)

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
<i>C. eisenmanae</i>	76.8–89.2	91.0–103.8	44–45	4–6	absent	0	0	18–20	17–18	banded	present
<i>C. erythropis</i>	78.4	83.0*	28	present	present	10+9+9 (FP+PP+FPPr)	–	16	20	blotched	present
<i>C. grisei</i>	68.3–95.0	111.3–115.1	33–38	absent	–	0	0	16–18	16–19	banded	present
<i>C. huongsonensis</i>	73.4–89.8	90.5	41–48	7–9	1.5–17	6	8	17–19	20–23	banded	present
<i>C. huynhi</i>	54.8–79.8	61.5–78.6	43–46	3–5	3–8	7–9	0–8	14–17	17–21	banded	absent
<i>C. interdigitalis</i>	59.0–80.0	71.0–90.0	37–42	present	16–18	14	0	17–22	16–20	banded	absent
<i>C. intermedius</i>	61.0–85.0	80.0–110.0	40–50	6–10	–	8–10	–	20	22	banded	present
<i>C. irregularis</i>	72.0–86.0	66.0–74.0	38–45	7–8	–	5–7	0–6	15–16	18–19	blotched	absent
<i>C. jaegeri</i>	60.0–68.5	82.4–83.4	31–32	17–19	present	44 (FP+PP)	21	17–19	20–23	banded	present
<i>C. jarujini</i>	85.0–90.0	105.0–116.0	32–38	present	present	5254 (PP+FP)	0	15–17	18–19	blotched	present
<i>C. khammouanensis</i>	70.8–73	83.0–95.0	32–38	present	present	40–44 (PP+FP)	017	18–20	20–23	banded	present
<i>C. khlangensis</i>	72.8–95.3	max. 96.0*	32–35	present	present	6+2–5+6–7 (FP+PP+FPPr)	2+6+1 (FP+PP+FPPr)	18	22	banded	present
<i>C. kingsadai</i>	83.0–94.0	max. 117.0	39–46	9–12	0–7	7–9	4–8	19–21	21–25	banded	present
<i>C. lekaguli</i>	80.5–103.5	115.0–125.0	31–43	present	present	30–36 (PP+FP)	0	–	20–25	banded	present
<i>C. lomyenensis</i>	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
<i>C. martini</i>	64.4–96.2	76.0–101.2	39–43	14–18	absent	4	0	19–23	22–24	banded	present
<i>C. multiporus</i>	81.0–98.0	97.0–105.0	30–38	present	present	58–60 (PP+FP)	0	18–20	18–22	banded	present
<i>C. nigriocularis</i>	82.7–107.5	70.6–121	42–49	absent	absent	0–2	0	–	17–21	uniformly brown	present
<i>C. oldhami</i>	63.0–68.0	69*–70*	34–38	present	absent	1–4	–	–	–	striped and spotted	present
<i>C. otai</i>	85.2–90.6	89.7–97.6	38–43	absent	absent	7–8	0	16–19	19–22	banded	absent
<i>C. pageli</i>	76.2–81.8	85.4*–113.2*	41–44	absent	absent	4	4	19–23	19–23	banded	present
<i>C. paradoxus</i>	52.0–84.0	80.8–111.0	32–40	present	absent	0–4	0	15–18	17–23	banded	present
<i>C. phongthakebangensis</i>	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

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TABLE 4. (Continued)

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males)	PP (in females)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
<i>C. phuoabinhensis</i>	46.0–60.4	76.1	43–47	5	absent	7	0	16–21	17–19	blotched	absent
<i>C. pseudoquadrivirgatus</i>	48.6–83.3	55.7–82.3	41–57	absent	absent	5–9	5–10	15–21	16–25	blotched	absent
<i>C. puhensis</i>	79.2	82.59	36	present	absent	5	–	18	23	banded	present
<i>C. quadrivirgatus</i>	39.0–67.0	77.0	40	present	absent	4	4	–	–	striped	absent
<i>C. ranongensis</i>	56.9–59.6	66.0–67.1	35–40	present	0	0	0	17	18	blotched	absent
<i>C. roestleri</i>	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
<i>C. saiyok</i>	56.7–61.0	66.7–67.5	23–24	present	absent	5	–	–	16–17	banded	present
<i>C. samroirot</i>	63.2–66.9	78.8–87.5	33–34	present	absent	7	6	18	19	banded	present
<i>C. sanook</i>	72.9–79.5	104.2	27–28	present	absent	3–4	absent	–	19–20	banded	present
<i>C. spelaetus</i>	88.9–91.0	max. 83*	36–39	absent	absent	8–9	0	19–20	22–24	banded	present
<i>C. sumonthai</i>	61.5–70.7	89.9–94.0	33–36	absent	absent	2	0	16	18	banded	present
<i>C. takonensis</i>	74.7–81.1	77.7–91.0	39–40	3–5	0–2	3–4	0	16–17	18–20	banded	present
<i>C. taynguyenensis</i>	60–85	66–94	42–49	absent	absent	6	0	13–18	17–21	blotched	absent
<i>C. teyniei</i>	89.9	ca. 110.0	38	23	absent	unknown	13	17–18	19–20	blotched	present
<i>C. thongae</i>	57.3–77.6	max. 78.1	29–44	2–5	0–3	0–1	0	14–17	14–20	blotched	absent
<i>C. wayakonei</i>	72.0–86.8	76.8–89.0	31–35	absent	absent	6–8	7	17–18	19–20	banded	present
<i>C. thirakhupti</i>	72.0–79.6	99.1	37–40	present	absent	absent	absent	16	20	banded	present
<i>C. tigroides</i>	74.3–83.2	108.5–117.0	34	present	present	6+8+7 (FP+PP+FPt)	5+9+7 (FP+PP+FPt)	18–19	20–22	banded	present
<i>C. vilaphongi</i>	60.9–86.1	61.2–68.1	34–36	0	–	–	0	18–19	18–20	banded	absent
<i>C. yangbayensis</i>	78.5–92.3	91.3–109.1	39–46	5–16	0–2	6–8	0	16–19	15–17	banded	present
<i>C. ziegleri</i>	84.6–93.0	95.0–107.0	33–39	8–10	0–6	5–8	0–8	16–19	18–21	banded	absent

C. spelaeus Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, *C. sumonthai* Bauer, Pauwels & Chanhome, *C. wayakonei* Nguyen, Kingsada, Rösler, Auer & Ziegler, *C. takouensis* Ngo & Bauer, *C. thirakhupti* Pauwels, Bauer, Sumontha & Chanhome, and *C. yangbayensis* Ngo & Chan.

Cyrtodactylus rufford **sp. nov.** has a contiguous series of femoral and precloacal pores in males and thus differs from the following species which have poreless scales separating femoral from precloacal pores: *C. bichnganae* Ngo & Grismer, *C. brevipalmatus* (Smith), *C. dumnuui* Bauer, Kunya, Sumontha, Niyomwan, Pauwels, Chanhome & Kunya, *C. erythropros* Bauer, Kunya, Sumontha, Niyomwan, Panitvong, Pauwels, Chanhome & Kunya, *C. huongsonensis* Luu, Nguyen, Do & Ziegler, *C. interdigitalis*, *C. khelangensis* Pauwels, Sumontha, Panitvong & Varaguttanonda, and *C. tigroides* Bauer, Sumontha & Pauwels.

Cyrtodactylus rufford **sp. nov.** has 42–43 femoral and precloacal pores in males and thus differs from the following species which have distinctly fewer femoral and precloacal pores: *C. auribalteatus* Sumontha, Panitvong & Deein (10–11), *C. caovansungi* Orlov, Nguyen, Nazarov, Ananjeva & Nguyen (15), *C. chanhomeae* Bauer, Sumontha & Pauwels, *C. intermedius* (Smith) (8–10), *C. kingsadai* Ziegler, Phung, Le & Nguyen (7–16), *C. roesleri* (20–28), and *C. soudthichaki* (29).

Cyrtodactylus rufford **sp. nov.** can be distinguished from *C. astrum* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Ahmad, Bauer, Wangkulangkul, Grismer & Pauwels by its smaller size (maximum SVL 72.5 mm *versus* 108.3 mm), having fewer ventral scale rows (27–29 *versus* 31–46), fewer lamellae under the fourth toe (18–19 *versus* 20–24), and more femoral and precloacal pores in males (42–43 *versus* 31–38); from *C. jarujini* Ulber by its smaller size (maximum SVL 72.5 mm *versus* 90.0 mm), having fewer ventral scale rows (27–29 *versus* 32–38), and fewer femoral and precloacal pores in males (42–43 *versus* 52–54); from *C. lekaguli* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Ahmad, Bauer, Wangkulangkul, Grismer & Pauwels by its smaller size (SVL reaching 72.5 mm *versus* 103.5 mm), having fewer ventral scales (27–29 *versus* 31–43), and more femoral and precloacal pores in males (42–43 *versus* 30–36); from *C. multiporus* by its smaller size (maximum SVL 72.5 mm *versus* 98.0 mm), having fewer ventral scale rows (27–29 *versus* 30–38), and fewer femoral and precloacal pores in males (42–43 *versus* 58–60); from *C. teyniei* David, Nguyen, Schneider & Ziegler by its smaller size (maximum SVL 72.5 mm *versus* 89.9 mm), having fewer ventral scale rows (27–29 *versus* 38), the presence of a nuchal band (*versus* being absent), and having a banded dorsal pattern (*versus* blotched).

Cyrtodactylus rufford **sp. nov.** is similar to the members of the *C. phongnhakebangensis* group (Nazarov *et al.* 2014) including *C. khammouanensis*, *C. lomyenensis*, *C. jaegeri*, *C. darevskii*, and *C. phongnhakebangensis* Ziegler, Rösler, Herrmann & Vu in having a high number of femoral and precloacal pores and in the dorsal pattern. However, the new species can be distinguished from *C. khammouanensis* by having fewer ventral scale rows (27–29 *versus* 32–38), fewer dorsal tubercles at midbody (14–16 *versus* 16–21), fewer lamellae under the fourth toe (18–19 *versus* 20–23), dorsum of head with dark blotched markings (*versus* absent), having light transverse bands between limb insertions with wavy margins (*versus* transverse bands with smooth margins), and tail with light rings (*versus* light bands); from *C. lomyenensis* by having fewer ventral scale rows (27–29 *versus* 35–36), fewer supralabials (10–12 *versus* 13–14), and more femoral and precloacal pores in males (42–43 *versus* 39–40); from *C. darevskii* by its smaller size (maximum SVL 72.5 mm *versus* 100.0 mm), having fewer ventral scale rows (27–29 *versus* 38–46), and fewer ventral scales between mental and cloacal slit (153–167 *versus* 180–208); from *C. jaegeri* by having fewer ventral scale rows (27–29 *versus* 31–32), fewer femoral and precloacal pores in males (42–43 *versus* 44), fewer lamellae under the fourth toe (18–19 *versus* 20–23), and having irregular shaped light transverse bands between limb insertions (*versus* regular shaped light transverse bands); and from *C. phongnhakebangensis* by its smaller size (maximum SVL 72.5 mm *versus* 96.3 mm), having fewer ventral scale rows (27–29 *versus* 32–42), generally more femoral and precloacal pores in males (42–43 *versus* 32–42), and fewer ventral scales between mental and cloacal slit (153–167 *versus* 180–208). For more details see Table 5.

Distribution. *Cyrtodactylus rufford* **sp. nov.** is currently known only from the type locality in the karst forest near Daen Village, Gnommalath District, Khammouane Province, central Laos (Fig. 4).

Etymology. The new species is named in honour of the Rufford Foundation (UK) for its support to herpetofaunal research and conservation in Laos. The species epithet is to be treated as a noun in apposition, invariable. As common names, we suggest Ki Chiem Rufford (Laotian) and Rufford Bent-toed Gecko (English).

Natural history. The type series of the new species was found between 20:00 and 21:00, on a karst cliff near the entrance of Nang Log Cave, from 0.3 m to 2 m height above the forest floor, at elevations between 160 and 180 m a.s.l. Nang Log Cave is situated within an isolated karst mountain surrounded by secondary forest, plantations,

and some huts for tourists. The cave is a tourism site, only 50 m distant from Road 12 and 64 km from the border of Vietnam. The humidity was approximately 80% and the air temperature ranged from 24 to 26°C (Fig. 5). Other species found on the same karst wall within a 300 meters range of the type locality were the lizard *Gekko gekko* (Linnaeus), and the tree frog species *Rhacophorus spelaesus* Orlov, Gnophanxay, Phimminith & Phomphoumy, as well as the Huntsman Spider *Heteropoda maxima* Jaeger, and the long-legged cave centipede *Thereuopoda longicornis* (Fabricius).

TABLE 5. Comparison of *Cyrtodactylus rufford* sp. nov. with other members of the *C. phongnhakebangensis* group (data obtained from Ziegler *et al.* 2002; Ngo & Pauwels 2010; Luu *et al.* 2014, Nazarov *et al.* 2014; and own data based on specimens examined, see Appendix).

Character	<i>Cyrtodactylus rufford</i> sp. nov.	<i>C. khammouanensis</i>	<i>C. lomyenensis</i>
V	27–29	32–38	35–36
DTR	14–16	16–21	20–24
PP + FP (in males)	42–43	40–44	39–40
SLB	153–167	155–172	–
PAT	4–5	5–6	5
Rostral suture	Q	Y	Y
LT4	18–19	20–23	19–23
Transverse dorsal bands between limbs	3 or 4 light sometimes irregular shaped bands	4 light bands	4 light bands
Tail pattern	light rings	light bands	light rings

continued.

Character	<i>C. jaegeri</i>	<i>C. darevskii</i>	<i>C. phongnhakebangensis</i>
V	31–32	38–46	32–42
DTR	15–17	16–20	11–20
PP + FP (in males)	44	38–44	32–42
SLB	156–164	180–208	–
PAT	3–6	4–5	4–5
Rostral suture	I	Y	I
LT4	20–23	18–22	18–26
Transverse dorsal bands between limbs	4 light bands	3–4 sometimes irregular shaped light bands	2–3 light bands
Tail pattern	light rings	light bands	light bands

Discussion

Cyrtodactylus rufford is closely related to *C. khammouanensis* but differs in dorsal head and body pattern, ventral scales, and number of dorsal tubercles. The species occurs in the area about 50 km (Daen Village, Gnommalath District) from the type locality of *C. khammouanensis* (Na Phao Village, Boulapha District), Khammouane Province, Laos (see Fig. 4) and the two species are isolated from one another by the Xebangfai river system. In addition, molecular data show large genetic divergence, approximately 12%, between the new species and *C. khammouanensis*. This level of divergence is much higher than that of some other species pairs within the genus *Cyrtodactylus*, e.g., *C. otai* and *C. bobrovi* ~ 4% (Nguyen *et al.* 2015), *C. dati* and *C. huynhi* ~ 4% (Nguyen *et al.* 2014), and *C. multiporus* and *C. teyniei* ~ 6% (Nazarov *et al.* 2014).



FIGURE 4. Map showing the type locality of *Cyrtodactylus rufford* sp. nov. (red circle) and the type locality of *Cyrtodactylus khammouanensis* (white circle) in Khammouane Province, central Laos.

With the description of *Cyrtodactylus rufford*, 17 species of the genus *Cyrtodactylus* have been recorded from Laos. At present, nine bent-toed gecko species are known to occur in Khammouane Province. Eight of them have been recorded from limestone caves and karstic forested formations, and only *C. interdigitalis* has been reported as a non-karst dwelling species (Teynié & David 2010). Specimens of *C. jaegeri*, *C. soudthichaki*, and the new species have been seen and captured from outside caves or cave entrances. However, these animals have not been observed to forage inside the caves. The data show that they might use the caves for sheltering and breeding, but forage outside of the cave at night. Due to their behavior, they are considered to be troglonexenes (cave guests) (e.g., Ellis & Pauwels 2012).

In many areas of Khammouane Province in central Laos, the karst mountains are isolated hills and outcrops that might have influenced *Cyrtodactylus* speciation (Bauer *et al.* 2009; Ellis & Pauwels 2012), especially within the *C. phongnhakebangensis* species group. For example, *C. jaegeri* and *C. soudthichaki* have been discovered at two karst localities only a few kilometres apart. In addition, *C. jaegeri* has only been recorded from three caves within an isolated limestone mountain. Threats to these isolated and thus apparently small populations include burning of forests for agricultural development and quarrying for construction. Therefore, further studies both focusing on distribution and population status of the micro-endemic and highly vulnerable bent-toed geckos are urgently required to design appropriate conservation measures.



FIGURE 5. Habitat of *Cyrtodactylus rufford* sp. nov. at its type locality. Photo: V. Q. Luu.

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APPENDIX. Comparative specimens examined.

- Cyrtodactylus jaegeri*. Laos: Khammouane Province: Thakhek: IEBR A.2013.55 (holotype), NUOL R-2013.1 (paratype).
- C. jarujini*. Thailand: Nong Khai Province: Bung Ban: ZMB 50648 (holotype).
- C. lomyenensis*. Laos: Khammouane Province: Huong Son: IEBR A.2011.3 (holotype), ZFMK 92293 (paratype).
- 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. 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. soudthichaki*. Laos: Khammouane: Thakhek: VFU R.2015.18 (holotype), IEBR A.2015.34, NUOL R-2015.15 (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 Province: Vieng Phoukha: IEBR A.2010.01 (holotype), ZFMK 91016, MTD 47731, NUOL 2010.1 (paratypes).

Publication 10

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A new species of karst-dwelling bent-toed gecko (Squamata: Gekkonidae) from Khammouane Province, central Laos

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Abstract

We describe a new species of the genus *Cyrtodactylus* from Khammouane Province, central Laos based on morphological features and molecular data. Morphologically, *Cyrtodactylus bansocensis* **sp. nov.** is differentiated from other congeners by a unique combination of the following characters: medium size, SVL reaching 74.0 mm; dorsal pattern consisting of four light transverse bands between limb insertions; supranasals in contact with each other; dorsal tubercles at midbody in 14–15 irregular rows; lateral folds present without interspersed tubercles; ventral scales between ventrolateral folds 34–35; precloacal and femoral pores in males 34, separated by four poreless scales in the male holotype and in a continuous row in the male paratype; enlarged femoral and precloacal scales present; postcloacal tubercles 5–7 on each side; dorsal tubercles present at tail base; and subcaudal scales transversely enlarged. Molecular analyses revealed the new species to be closely related to *Cyrtodactylus rufford*, which is also found in Khammouane Province.

Key words: *Cyrtodactylus bansocensis* **sp. nov.**, limestone karst, morphology, phylogeny, taxonomy

Introduction

Recent herpetological fieldwork in Khammouane Province in central Laos has revealed that this karst region represents a hotspot of bent-toed gecko (*Cyrtodactylus*) diversity. Six species have been described from this province during the past two years—*C. darevskii* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, *C. khammouanensis* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, *C. multiporus* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, *C. jaegeri* Luu, Calame, Bonkowski, Nguyen & Ziegler, *C. soudthichaki* Luu, Calame, Nguyen, Bonkowski & Ziegler, and *C. rufford* Luu, Calame, Nguyen, Le, Bonkowski & Ziegler (Nazarov *et al.* 2014; Luu *et al.* 2014; Luu *et al.* 2015; Luu *et al.* 2016). Recent field surveys in the karst forest near Ban Soc Village, Bualapha District, approximately 10 km from the border of Hin Nam No National Protected Area (NPA) led to the discovery of another unnamed *Cyrtodactylus* population, which differs from its congeners by morphological and molecular characters. Thus, we herein describe the karst-dwelling *Cyrtodactylus* population from Ban Soc as a new species.

Material and methods

Sampling. Field research was carried out in the forest, near Ban Soc Village, Bualapha District, Khammouane Province, Laos in March 2015. Specimens were euthanized, and fixed in approximately 85% ethanol, then later transferred to 70% ethanol for permanent storage. Tissue samples were preserved separately in 95% ethanol. Specimens were subsequently deposited in the collections of the Vietnam National University of Forestry (VFU), Hanoi, Vietnam; National University of Laos (NUOL), Vientiane, Lao PDR. Other abbreviations for collections are as follows: IEBR: the Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Hanoi, Vietnam; Department of Herpetology and Ichthyology, Muséum d'histoire naturelle, Geneva (MHNG); Switzerland, Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde (MTD), Dresden, Germany; NEM: Namlik Ecovillage Museum, Ban That Wang Monh, Vientiane Province, Laos; PNKB: Zoological Collection of the Phong Nha – Ke Bang National Park, Quang Binh Province, Vietnam; ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; and the Museum für Naturkunde, Berlin (ZMB), Germany.

Molecular data and phylogenetic analyses. Molecular analyses using the cytochrome c oxidase subunit 1 (COI) gene has been demonstrated to be useful in characterizing new taxa in the genus *Cyrtodactylus* when molecular results are combined with morphological comparisons (e.g., Nazarov *et al.* 2014; Nguyen *et al.* 2014, Nguyen *et al.* 2015; Luu *et al.* 2016). We also analyzed data under a phylogenetic framework to provide objective hypotheses of relationships among closely related taxa. Since the new taxon is morphologically similar to members of the *Cyrtodactylus phongnhakebangensis* species group (sensu Nazarov *et al.* 2014; see also Luu *et al.* 2016), we included species previously assigned to the group, consisting of nine species from Laos and two species from Vietnam (Table 1). *Cyrtodactylus elok* Dring, 1979, was used as outgroup.

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

Species	GenBank no.	Locality	Voucher number
<i>Cyrtodactylus bansocensis</i> sp. nov.	KU175573	Laos: Khammouane Province	VFU R.2015.20
<i>Cyrtodactylus bansocensis</i> sp. nov.	KU175574	Laos: Khammouane Province	NUOL R-2015.21
<i>C. darevskii</i>	HQ967221	Laos: Khammouane Province	ZIN FN 256
<i>C. darevskii</i>	HQ967223	Laos: Khammouane Province	ZIN FN 223
<i>C. elok</i>	HM888479	Malaysia	ZMMU RAN 1992
<i>C. elok</i>	HM888478	Malaysia	ZMMU RAN 1992
<i>C. lomyenensis</i>	KJ817436	Laos: Khammouane Province	IEBR KM2012.54
<i>C. lomyenensis</i>	KP199942	Laos: Khammouane Province	IEBR KM2012.52
<i>C. jaegeri</i>	KT004364	Laos: Khammouane Province	IEBR A.2013.55
<i>C. jaegeri</i>	KT004365	Laos: Khammouane Province	NUOL R.2013.1
<i>C. jaegeri</i>	KT004366	Laos: Khammouane Province	VFU TK914
<i>C. multiporus</i>	HM888472	Laos: Khammouane Province	ZIN FN 3
<i>C. multiporus</i>	HM888471	Laos: Khammouane Province	ZIN FN 2
<i>C. pageli</i>	KJ817431	Laos: Vientiane Province	ZFMK 91827
<i>C. phongnhakebangensis</i>	KF929526	Vietnam: Quang Binh Province	PNKB2011.30
<i>C. phongnhakebangensis</i>	KF929527	Vietnam: Quang Binh Province	PNKB2011.32
<i>C. roesleri</i>	KF929532	Vietnam: Quang Binh Province	PNKB2011.34
<i>C. roesleri</i>	KF929531	Vietnam: Quang Binh Province	PNKB2011.3
<i>C. rufford</i>	KU175572	Laos: Khammouane Province	VFU R.2015.14
<i>C. teyniei</i>	KJ817430	Laos: Khammouane Province	IEBR KM2012.77
<i>C. teyniei</i>	KP199945	Laos: Khammouane Province	IEBR KM2012.77

We used the protocols of Le *et al.* (2006) for DNA extraction, amplification, and sequencing. A fragment of the COI gene 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 analysis (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 13 in the Bayesian analysis, as $-\ln L$ scores reached stationarity after 13,000 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 *Cyrtodactylus bansocensis* sp. nov. and closely related species.

Species name	1	2	3	4	5
1. <i>Cyrtodactylus bansocensis</i> sp. nov. (KU175573 & 4)	-				
2. <i>C. darevskii</i> (HQ967221&3)	16.5–16.9	-			
3. <i>C. khammouanensis</i> (HM888467 & 9)	12.1–12.4	15.0–15.1	-		
4. <i>C. jaegeri</i> (KT004364 & 5 & 6)	14.6–15.5	16.9	14.8–15.0	-	
5. <i>C. lomyenensis</i> (KJ817436/KP199942)	15.3–16.1	13.6–13.7	16.2–16.4	16.3–16.6	-
6. <i>C. multiporus</i> (HM888471 & 2)	16.2–16.3	15.6	16.2–16.4	16.2–16.3	14.7–15.1
7. <i>C. pageli</i> (KJ817431)	16.8–19.1	18.3–18.8	17.7–18.5	16.8–18.8	17.0–18.3
8. <i>C. phongnhakebangensis</i> (KF929526 & 7)	15.4	9.7	15.5–15.7	16.7	14.5–14.6
9. <i>C. roesleri</i> (KF929531 & 2)	15.8–15.9	17.3	9.7–10.0	15.3–15.4	17.4–17.6
10. <i>C. rufford</i> (KU175572)	11.2–11.6	18.2	11.9–12.1	14.6–14.7	17.8–17.9
11. <i>C. teynieii</i> (KJ817430/KP199945)	17.6–17.8	15.4–15.5	16.5–16.9	17.1–17.7	14.3–14.7

continued.

Species name	6	7	8	9	10	11
1. <i>Cyrtodactylus bansocensis</i> sp. nov. (KU175573 & 4)						
2. <i>C. darevskii</i> (HQ967221&3)						
3. <i>C. khammouanensis</i> (HM888467 & 9)						
4. <i>C. jaegeri</i> (KT004364 & 5 & 6)						
5. <i>C. lomyenensis</i> (KJ817436/KP199942)						
6. <i>C. multiporus</i> (HM888471 & 2)	-					
7. <i>C. pageli</i> (KJ817431)	16.4–17.3	-				
8. <i>C. phongnhakebangensis</i> (KF929526 & 7)	15.3	17.7–17.8	-			
9. <i>C. roesleri</i> (KF929531 & 2)	16.9–17.1	16.1–17.6	15.3	-		
10. <i>C. rufford</i> (KU175572)	16.7	16.9–18.7	17.6	16.3	-	
11. <i>C. teynieii</i> (KJ817430/KP199945)	6.6–7.0	17.1–18.0	15.3–15.3	17.5–17.7	17.5–17.9	-

Morphological characters. Measurements were taken with a digital calliper 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 process; 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; forearm length (ForeaL), from base of palm to elbow; femur length (FemurL); crus length (CrusL), from base of heel to knee.

Scale counts were taken as follows: supralabials (SL) and infralabials (IL) counted from the first labial scale to the corner of mouth; nasal scales surrounding nare, from rostral to supralabial (except counting rostral and supralabial), including 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 ventral scales along the midbody from mental to anterior edge of cloaca (SLB); number of scale rows around midbody (SR); femoral pores (FP); preloacal pores (PP); postloacal tubercles (PAT); number of subdigital lamellae on fourth finger (LD4) and number of subdigital lamellae on fourth toe (LT4) counted from the base of the first phalanx to the claw. Bilateral scale counts were given as left/right.

Results

Phylogenetic analyses. The final matrix consisted of 669 aligned characters, of which 237 are parsimony informative. The alignment did not contain any gaps. Maximum Parsimony analysis of the dataset recovered a single most parsimonious tree with 687 steps (CI = 0.54; RI = 0.76). In the ML analysis, the score of the single best tree found was 3738.98 after 4237 arrangements were tried. The topology derived from the Bayesian analysis (Fig. 1) is almost identical to that in Luu *et al.* (2016). The new species was weakly recovered in a clade together with *C. khammouanensis* (Nazarov *et al.* 2014) and *C. rufford* (Luu *et al.* 2016). The new species is most closely related to *C. rufford* in terms of genetic distance based on COI gene sequences, and is diverged about 11.2–11.6% from the latter, respectively (Table 2).

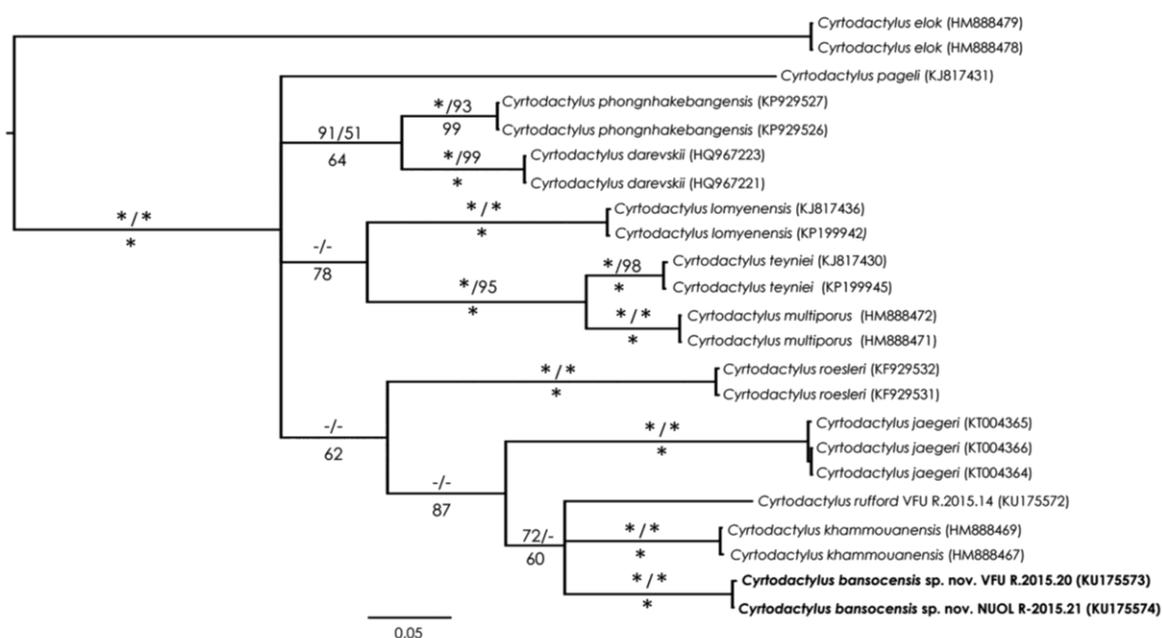


FIGURE 1. Phylogram of *Cyrtodactylus* based on the Bayesian analysis of 669 aligned characters of the mitochondrial COI gene. Number above and below branches are MP/ML bootstrap values and Bayesian posterior probabilities (>50%), respectively. Asterisk denotes 100% value. Hyphen indicates the statistical support value lower than 50%. Scale bar shows the number of expected substitutions per position.

***Cyrtodactylus bansocensis* sp. nov.**

(Figs. 2–4)

Holotype. VFU R.2015.20, adult male, on karst cliff, above the entrance of Peopalame cave (17°27.101'N, 105°35.393'E, 195 m elevation), near Ban Soc Village, Bualapha District, Khammouane Province, central Laos, collected on 17 March 2015 by V. Q. Luu and K. Thanabuaosy.

Paratype. NUOL R-2015.21, adult male, same collection data as the holotype.

Diagnosis. The new species can be distinguished from congeners by the following combination of characters: medium size, SVL reaching 74.0 mm; dorsal pattern with four light transverse bands between limb insertions; supranasals in contact; 14–15 irregular dorsal tubercle rows at midbody; lateral skin fold present without tubercles; 34–35 ventral scale rows between ventrolateral folds; 34 preloacal and femoral pores in a continuous row in the paratype and interrupted by four poreless scales in the holotype, enlarged femoral and preloacal scales present; 5–7 postloacal tubercles on each side; dorsal tubercles present at base of tail; subcaudal scales transversely enlarged, widely entire under tail surface.



FIGURE 2. Dorsal view of the adult male holotype of *Cyrtodactylus bansocensis* sp. nov. (VFU R.2015.20) in life. Photo: V. Q. Luu.

Description of the holotype. Adult male, medium size (SVL 71.0 mm); body elongate (TrunkL/SVL 0.42); head distinct from neck, elongate (HL/SVL 0.28), relatively wide (HW/HL 0.64), depressed (HH/HL 0.41); loreal region concave; snout long (SE/HL 0.41), obtuse anteriorly, longer than diameter of orbit (OD/SE 0.64); scales on snout small, round, granular, bigger than those on frontal and parietal regions; eye large (OD/HL 0.26), pupils vertical; supraciliaries with spinuous scales posteriorly; ear oval-shaped, small (EarL/HL 0.11); rostral wider than high with a half median suture, in contact with first supralabial and nostril on each side; supranasals in broad contact; nostril opening oval, bordered by supranasal, rostral, first supralabial, and two enlarged postnasals; mental triangular, wider than long (ML/MW 0.86); two enlarged postmentals; supralabials 8/9; infralabials 8/8.

Dorsal scales granular; dorsal tubercles round, conical, present from occipital region to tail base, tubercles in 14 irregular rows at midbody, each surrounded by nine granular scales; lateral folds without tubercles; ventral scales smooth, round, largest posteriorly, in 35 longitudinal scales at midbody; gular region with homogeneous and smooth scales; 170 ventral scales from mental to cloacal slit; preloacal groove absent; enlarged femoral and cloacal scales present; total femoral and preloacal pores 34, on distal thigh, pore-bearing series interrupted by single scales lacking pores (1 + 1 + 29 + 3) (Fig. 4).

Fore- and hindlimbs moderately slender (ForeL/SVL 0.17, CrusL/SVL 0.20); forelimbs lacking tubercles; dorsal surface of thigh and shank with distinctly developed tubercles, the same size to those on flanks; digits webbed basally; lamellae under fourth finger 16/17; lamellae under fourth toe 18/19.

Tail longer than SVL (TaL 98.5 mm, TaL/SVL 1.39); postloacal tubercles 6/7; caudal tubercles present at the dorsum of the first segment of tail, extending from body; subcaudal scales transversely enlarged, three to four times as wide as long at base of tail, flat, smooth.

Coloration in life. Head dorsally greyish brown with dark blotches; distinct brown nuchal loop, widened in the nape, with dark edge, U-shaped, stretching from posterior edge of orbit to nape; labials grey. Dorsum with four light transverse bands between limb insertions, edged darker anteriorly, dark spots within two enlarged bands at

midbody; tubercles at midbody yellowish brown; dorsal surface of fore and hind limbs with grey reticulated markings; tail greyish brown dorsally with 13 light rings (2–3 times narrower than dark tail bands); ventral surface of head, body and limbs cream; ventral surface of tail grey.

Variation: Light bands at midbody of the paratype (NUOL R-2015.21) are less distinctly defined at the posterior edges. The paratype also has precloacal and femoral pores in a continuous row (*versus* series interrupted by 4 poreless scales in the holotype). For further morphological characters of the paratype see Table 3.

TABLE 3. Measurements (in mm) and morphological characters of the type series of *Cyrtodactylus bansocensis* sp. nov. (for other abbreviations see material and methods).

Character	VFU R.2015.20 holotype	NUOL R-2015.21 paratype
Sex	male	male
SVL	71.0	74.0
TaL	98.5	103.5
HH	8.3	7.5
HL	20.2	21.0
HW	13.0	13.3
OD	5.3	5.5
SE	8.3	8.7
EyeEar	5.7	5.3
EarL	2.3	2.4
TrunkL	29.8	33.4
ForeL	12.2	11.7
FemurL	15.7	16.7
CrusL	14.1	15.7
RW	3.1	2.8
RH	1.6	2.0
MW	2.9	3.3
ML	2.5	2.2
SL	8/9	9/10
IL	8/8	8/8
N	3/3	3/3
IN	0	0
PM	2	2
DTR	14	15
GST	9	9
V	35	34
SLB	170	158
SR	87	86
FP+PP	34	34
PAT	6/7	6/5
LD4	16/17	18/19
LT4	18/19	21/20

Comparisons. We compared *Cyrtodactylus bansocensis* sp. nov. with other species of *Cyrtodactylus* from Laos and neighbouring countries in the mainland Indochina region (Vietnam, Cambodia, and Thailand). Comparisons were based on examination of museum specimens (see Appendix) and data from taxonomic

publications (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.* 2016) (see Table 4).

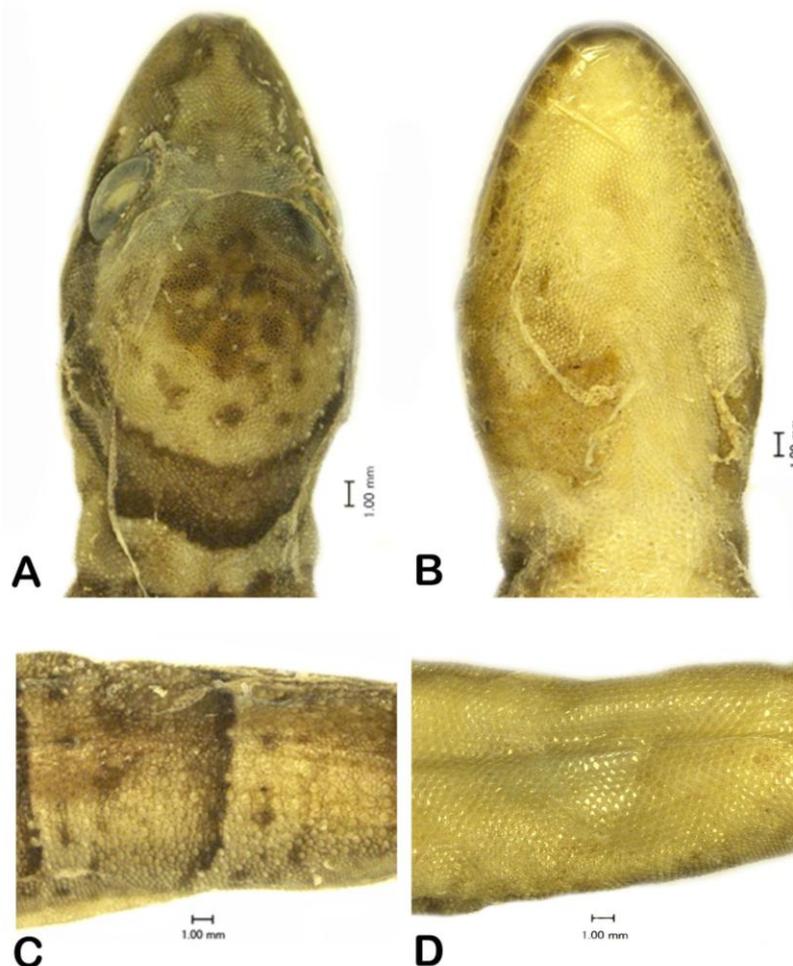


FIGURE 3. Details of the holotype of *Cyrtodactylus bansocensis* sp. nov. (VFU R.2015.20) A) Dorsal head; B) ventral head; C) dorsal body; D) ventral body. Photos: V. Q. Luu.

Cyrtodactylus bansocensis sp. nov. has enlarged subcaudal scales and thus differs from the following species which lack this character state: *C. bidoupimontis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, *C. bobrovi* Nguyen, Le, Pham, Ngo, Hoang, Pham & Ziegler, *C. buchari* David, Teynié & Ohler, *C. bugiamapensis* Nazarov, Poyarkov, Orlov, Phung, Nguyen, Hoang & Ziegler, *C. cattienensis* Geissler, Nazarov, Orlov, Böhme, Phung, Nguyen & Ziegler, *C. cryptus* Heidrich, Rösler, Vu, Böhme & Ziegler, *C. cucdongensis* Schneider, Phung, Le, Nguyen & Ziegler, *C. huynhi* Ngo & Bauer, *C. interdigitalis* Ulber, *C. irregularis* (Smith), *C. otai* Nguyen, Le, Pham, Ngo, Hoang, Pham & Ziegler, *C. phuocbinhensis* Nguyen, Le, Tran, Orlov, Lathrop, Macculloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, *C. pseudoquadrivirgatus* Rösler, Vu, Nguyen, Ngo & Ziegler, *C. quadrivirgatus* Taylor, *C. ranongensis* Sumontha, Pauwels, Panitvong, Kunya & Grismer, *C. taynguyenensis* Nguyen, Le, Tran, Orlov, Lathrop, Macculloch, Le, Jin, Nguyen, Nguyen, Hoang, Che, Murphy & Zhang, *C. thuongae* Phung, van Schingen, Ziegler & Nguyen, *C. vilaphongi* Schneider, Nguyen, Le, Nophaseud, Bonkowski & Ziegler, and *C. zieglerei* Nazarov, Orlov, Nguyen & Ho.

The new species has femoral and precloacal pores in males, which are absent in the following species: *C. angularis* (Smith), *C. badenensis* Nguyen, Orlov & Darevsky, *C. chauquangensis* Hoang, Orlov, Ananjeva, Johns, Hoang & Dau, *C. cucphuongensis* Ngo & Chan, *C. eisenmanae* Ngo, *C. grismeri* Ngo, *C. martini* Ngo, *C.*

nigriocularis Nguyen, Orlov & Darevsky, *C. oldhami* (Theobald), *C. pageli* Schneider, Nguyen, Schmitz, Kingsada, Auer & Ziegler, *C. paradoxus* (Darevsky & Szczerbak), *C. puhuensis* Nguyen, Yang, Le, Nguyen, Orlov, Hoang, Nguyen, Jin, Rao, Hoang, Che, Murphy & Zhang, *C. sai yok* Panitvong, Sumontha, Tunprasert & Pauwels, *C. samroi yot* Pauwels & Sumontha, *C. sanook* Pauwels, Sumontha, Latinne & Grismer, *C. spelaeus* Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov & Chulisov, *C. sumonthai* Bauer, Pauwels & Chanhome, *C. wayakonei* Nguyen, Kingsada, Rösler, Auer & Ziegler, and *C. thirakhupti* Pauwels, Bauer, Sumontha & Chanhome.

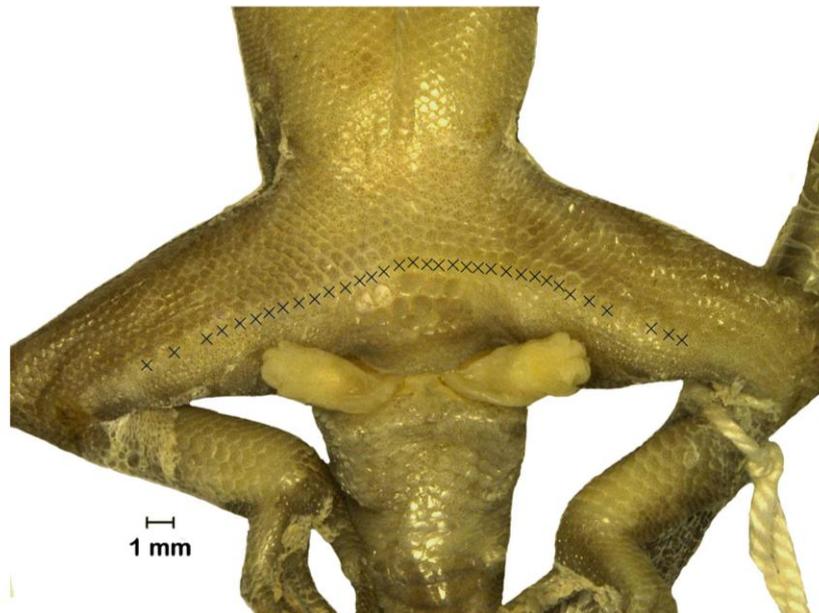


FIGURE 4. Cloacal region of the holotype of *Cyrtodactylus bansocensis* sp. nov. (VFU R.2015.20) (preloacal and femoral pores marked with x). Photo: V. Q. Luu.

The new species has 34 femoral and preloacal pores in males and thus differs from the following species which have distinctly fewer femoral and preloacal pores: *C. auribalteatus* Sumontha, Panitvong & Deein (10–11), *C. bichnganae* Ngo & Grismer (28), *C. brevipalmatus* (Smith) (22), *C. caovansungi* Orlov, Nguyen, Nazarov, Ananjeva & Nguyen (15), *C. dummui* Bauer, Kunya, Sumontha, Niyomwan, Pauwels, Chanhome & Kunya (19), *C. erythropros* Bauer, Kunya, Sumontha, Niyomwan, Panitvong, Pauwels, Chanhome & Kunya (28), *C. huongsonensis* Luu, Nguyen, Do & Ziegler (21–23), *C. intermedius* (Smith) (8–10), *C. khelangensis* Pauwels, Sumontha, Panitvong & Varaguttanonda (14–18), *C. kingsadai* Ziegler, Phung, Le & Nguyen (7–16), *C. roesleri* Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh & Schmitz (20–28), *C. takouensis* Ngo & Bauer (3–6), *C. tigroides* Bauer, Sumontha & Pauwels (21), and *C. yangbayensis* Ngo & Chan (6–10).

The new species has 34 femoral and preloacal pores in males and thus differs from the following species which have higher counts of femoral and preloacal pores: *C. darevskii* (38–44), *C. jaegeri* (44), *C. jarujini* Ulber (52–54), and *C. multiporus* (58–60).

The new species differs from *C. chanhomeae* Bauer, Sumontha & Pauwels by having fewer ventral scales (30–35 versus 36–38), fewer dorsal tubercles (14–15 versus 16–18), brown nuchal loop with dark edge (versus yellow edge), and white-grey body bands between limb insertions (versus yellow); from *C. lomyenensis* Ngo & Pauwels by having fewer dorsal tubercle rows (14–15 versus 20–24), fewer supralabials and infralabials (8–10 versus 13–14; 8 versus 11, respectively), and fewer femoral and preloacal pores in males (34 versus 39–40); from *C. phongnhakebangensis* Ziegler, Rösler, Herrmann & Vu by its smaller size (maximum SVL 74.0 mm versus 96.3 mm), the absence of tubercles on lateral folds (versus present), enlarged nuchal loop in neck region absent (versus present), four light transverse bands between limb insertions (versus 2–3), and tail with light rings (versus bands); and from *C. teymiei* David, Nguyen, Schneider & Ziegler by its smaller size (maximum SVL 74.0 mm versus 89.9 mm), having fewer ventral scale rows (34–35 versus 38), the presence of a nuchal band (versus being absent), and having a banded dorsal pattern (versus blotched).

TABLE 4. Morphological comparisons between *Cyrtodactylus bansocensis* sp. nov. and its 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; Nguyen *et al.* 2015; Sumontha *et al.* 2015; Nguyen *et al.* 2015; Luu *et al.* 2015; Luu *et al.* 2016. 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; FPI = 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
<i>Cyrtodactylus bansocensis</i> sp. nov.	71.0–74.0	98.5–103.5	34–35	present	present	34 (FP+PP)	unknown	16–19	18–21	banded	present
<i>C. rufford</i>	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
<i>C. soudhichaki</i>	69.2–70.0	95.1*–95.2	32–33	present	present (in males)	29 (FP+PP)	absent	16–18	18	banded	present
<i>C. angularis</i>	80.0–92.0	92–95.2	40–45	present	absent	3	3	18–19	18–19	banded	present
<i>C. astrum</i>	46.4–108.3	99.0*–109.0*	31–46	–	present	31–38 (FP+PP)	–	–	20–24	banded	present
<i>C. auribalteatus</i>	82.8–98.1	106.5–138.7	38–40	5–7	4–5 (in males)	6	absent	–	18–21	banded	present
<i>C. badensis</i>	59.3–74.1	58.6–82.4	25–29	absent	absent	0	0	–	18–22	banded	present
<i>C. bichanganae</i>	95.3–99.9	96.3–115.6	30–31	11–13	18	10	8	18–20	16–20	banded	present
<i>C. bidoupimontis</i>	74.0–86.3	75.0–86.0	38–43	6–8	absent	4–6	0	15–20	18–23	banded	absent
<i>C. bobrovi</i>	75.2–96.4	80.8–90.3	40–45	0	0	5	0	19–21	21–22	banded	absent
<i>C. brevipalmatus</i>	64.0–72.0	77.0	35–44	present	present	6+9+7 (FPI+PP+FPr)	6+9+7 (FPI+PP+FPr)	–	–	blotched	present
<i>C. bugiamapensis</i>	58.6–76.8	65.3–83.0	36–46	6–10	absent	7–8	0–7	15–17	17–20	blotched	absent
<i>C. buchardi</i>	60.0–65.0	46.0–54.0	30	absent	absent	9	0	14	12	blotched	absent
<i>C. caovansungi</i>	90.4–94.0	120.0	38–44	8	6	9	0	22	23–25	banded	present
<i>C. cattienensis</i>	43.5–69.0	51.0–64.7	28–42	3–8	absent	6–8	0	12–16	14–19	banded	absent
<i>C. chanhomeae</i>	69.9–78.8	74.4–74.7	36–38	present	present	32 (FP+PP)	34 (FP+PP)	18–20	21–23	banded	present
<i>C. chauquangensis</i>	90.9–99.3	97.0–108.3	36–38	absent	absent	6	7	16–18	19–23	banded	present
<i>C. cryptus</i>	62.5–90.8	63.5–88.4	47–50	absent	absent	9–11	0	18–19	20–23	banded	absent
<i>C. cucdongensis</i>	55.8–65.9	22.1–27.8	35–44	present	absent	5–6	4–6	8–11	15–20	banded	absent
<i>C. cucphuongensis</i>	96.0	79.3*	42	14	absent	0	–	21	24	banded	present
<i>C. darevskii</i>	84.6–100.0	95.0–113.0	38–46	present	present	38–44 (FP+PP)	24–34	17–20	18–22	banded	present

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TABLE 4. (Continued)

Taxa	SVL (mm)	TaL (mm)	V	EFS	FP	PP (in males) (FP+PP+FPPr)	PP (in females) (0-7)	LD4	LT4	Color pattern of dorsum	Enlarged subcaudals
<i>C. dumitui</i>	76.2-84.2	100.2*	40	present	present in males/absent in females	6+5-6+6-7 (FP+PP+FPPr)	0-7	16	19	banded	present
<i>C. eisenmanae</i>	76.8-89.2	91.0-103.8	44-45	4-6	absent	0	0	18-20	17-18	banded	present
<i>C. erythrops</i>	78.4	83.0*	28	present	present	10+9+9 (FP+PP+FPPr)	-	16	20	blotched	present
<i>C. grisei</i>	68.3-95.0	111.3-115.1	33-38	absent	-	0	0	16-18	16-19	banded	present
<i>C. huongsonensis</i>	73.4-89.8	90.5	41-48	7-9	15-17	6	8	17-19	20-23	banded	present
<i>C. huynhi</i>	54.8-79.8	61.5-78.6	43-46	3-5	3-8	7-9	0-8	14-17	17-21	banded	absent
<i>C. interdigitalis</i>	59.0-80.0	71.0-90.0	37-42	present	16-18	14	0	17-22	16-20	banded	absent
<i>C. intermedius</i>	61.0-85.0	80.0-110.0	40-50	6-10	-	8-10	-	20	22	banded	present
<i>C. irregularis</i>	72.0-86.0	66.0-74.0	38-45	7-8	-	5-7	0-6	15-16	18-19	blotched	absent
<i>C. jaegeri</i>	60.0-68.5	82.4-83.4	31-32	17-19	present	44 (FP+PP)	21	17-19	20-23	banded	present
<i>C. jarujini</i>	85.0-90.0	105.0-116.0	32-38	present	present	52-54 (PP+FP)	0	15-17	18-19	blotched	present
<i>C. khammouanensis</i>	70.8-73	83.0-95.0	32-38	present	present	40-44 (PP+FP)	0-17	18-20	20-23	banded	present
<i>C. khelangensis</i>	72.8-95.3	max. 96.0*	32-35	present	present	6+2-5+6-7 (FP+PP+FPPr)	2+6+1	18	22	banded	present
<i>C. kingsadai</i>	83.0-94.0	max. 117.0	39-46	9-12	0-7	7-9	4-8	19-21	21-25	banded	present
<i>C. lekaguli</i>	80.5-103.5	115.0-125.0	31-43	present	present	30-36 (PP+FP)	0	-	20-25	banded	present
<i>C. lomyenensis</i>	57.7-71.2	72.2-86.1	35-36	17-18	present	39-40 (PP+FP)	32	16-19	19-23	banded	present
<i>C. martini</i>	64.4-96.2	76.0-101.2	39-43	14-18	absent	4	0	19-23	22-24	banded	present
<i>C. multiporus</i>	81.0-98.0	97.0-105.0	30-38	present	present	58-60 (PP+FP)	0	18-20	18-22	banded	present
<i>C. nigriocularis</i>	82.7-107.5	70.6-121	42-49	absent	absent	0-2	0	-	17-21	uniformly brown	present
<i>C. oldhami</i>	63.0-68.0	69*-70*	34-38	present	absent	1-4	-	-	-	striped and spotted	present
<i>C. otai</i>	85.2-90.6	89.7-97.6	38-43	absent	absent	7-8	0	16-19	19-22	banded	absent
<i>C. pageli</i>	76.2-81.8	85.4*-113.2*	41-44	absent	absent	4	4	19-23	19-23	banded	present

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TABLE 4. (Continued)

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

Cyrtodactylus bansocensis **sp. nov.** is morphologically similar to *C. rufford* (Luu *et al.* 2016), *C. khammouanensis*, and *C. soudthichaki* in the dorsal colour pattern and/or numbers of femoral and precloacal pores. However, the new species can be distinguished from *C. rufford* by having more ventral scale rows (34–35 *versus* 27–29), fewer supralabials (8–10 *versus* 10–12), fewer infralabials (8 *versus* 9–11), fewer femoral and precloacal pores in males (34 *versus* 42–43), and more postcloacal tubercles on each side (5–7 *versus* 4–5); *C. khammouanensis* by having fewer dorsal tubercle rows (14–15 *versus* 16–21), having fewer supralabials and infralabials (8–10 *versus* 11–12; 8 *versus* 9–10, respectively), fewer femoral and precloacal pores in males (34 *versus* 40–44), and tail with light rings (*versus* light bands); and from *C. soudthichaki* by its larger size (SVL reaching 74.0 mm *versus* 70.0 mm), having fewer dorsal tubercle rows (14–15 *versus* 19–20), more femoral and precloacal pores in males (34 *versus* 29), slightly higher number of ventral scales (34–35 *versus* 32–33), more subdigital lamellae on fourth toe (18–21 *versus* 18), more postcloacal tubercles on each side (5–7 *versus* 4–5), and tail with light rings (*versus* light bands). For more details see Table 5.

TABLE 5. Comparison of *Cyrtodactylus bansocensis* **sp. nov.** with other morphologically similar species of *Cyrtodactylus* (data obtained from Nazarov *et al.* 2014; Luu *et al.* 2015; Luu *et al.* 2016 and own data).

Character	<i>Cyrtodactylus bansocensis</i> sp. nov.	<i>C. rufford</i>	<i>C. khammouanensis</i>	<i>C. soudthichaki</i>
Number of specimens	2	3	4	3
Maximal snout–vent length (mm)	74.0	72.5	73.0	70.0
Ventral scales	34–35	27–29	32–38	32–33
Dorsal tubercle rows	14–15	14–16	16–21	19–20
Supralabials	8–10	10–12	11–12	10–11
Infralabials	8	9–11	9–10	8–9
Femoral and precloacal pores (in males)	34	42–43	40–44	29
Postcloacal tubercles	5–7	4–5	5–6	4–5
Transverse dorsal color pattern between limbs	light bands narrower than dark bands with dark spots in the mid-dorsal region	light thin sometimes irregular shaped bands as narrow as haft dark bands	light regular bands nearly as wide as dark bands	light bands wider than dark bands with dark blotches in the dorsolateral region
Tail color pattern	light rings	light rings	light bands	light bands

Distribution. *Cyrtodactylus bansocensis* **sp. nov.** is currently known only from the type locality in the karst forest near Ban Soc Village, Bualapha District, Khammouane Province, central Laos (Fig. 5).

Etymology. We name this species after its type locality, Ban Soc limestone forest to underline the importance of this area (see also Ziegler *et al.* 2015) for biodiversity and nature conservation. We suggest as common names: Ki Chiem Ban Soc (Laotian), and Ban Soc Bent-toed Gecko (English).

Natural history. The type specimens of the new species were collected between 20:00 and 21:00, on karst outcrops above the entrance of Peopalam cave, at an elevation of 195 m a.s.l. The surrounding habitat was secondary forest dominated by the species of Ebenaceae, Arecaeae, Poaceae, Meliaceae, and Moraceae. The bent-toed geckos were actively foraging on surfaces of karst outcrops. They were fast and difficult to approach and catch (Fig. 6).

Discussion

Cyrtodactylus bansocensis most closely resembles other karst-dwelling species—*C. rufford*, *C. khammouanensis*, and *C. soudthichaki*. Preliminary comparison between COI sequences of *C. soudthichaki* and those of other species in the group show that this species is most closely related to *C. bansocensis* with the genetic distance of approximately 12% separating the two taxa. More detailed analyses of the species group are underway, and the

results will be discussed in our upcoming papers. The type locality of the species is about 40 km distant from the type locality of *C. rufford* in Nang Log Cave (17°30.282'N, 105°23.107'E), Gnommalath District, in approximately 30 km distance from the type locality of *C. khammouanensis* in Na Phao Village, Bualapha district (17°34'57.1"N, 105°44'37.3"E), and in around 200 km from the type locality of *C. soudthichaki* in Khun Don region (17°33.731'N, 104°52.360'E), Hinboun District. The type localities of three latter species are separated from the new species by the Xebangfai river (Fig. 5), which derives from the Truong Son Range on the border between Vietnam and Laos and drains through Khammouane and Savannakhet provinces to the Mekong River. The river and its many tributaries flow through a wide range of ecosystems and geographical features with a total area of about 9,500 km², and form many karst caves in these provinces (Claridge & Tsechalicha 1997; Pollack *et al.* 2009). The limestone karst forest in Khammouane Province harbors a high number of microendemic species and further research in this region may reveal further new bent-toed gecko species. Our recent discovery brings the number of *Cyrtodactylus* reported from Khammouane Province to nine, and the total number from Laos to 18.

The limestone karst forests surrounding Ban Soc Village, the type locality of *C. bansocensis*, seem to be an extraordinary area in terms of biodiversity. According to interviews with local people and the staff of the Provincial Natural Resources and Environment Department, the area houses several flagship mammal species for Laos, such as the Laotian Rock Rat *Laonastes aenigmamus* Jenkins, Kilpatrick, Robinson & Timmins, the Red-shanked Douc Langur *Pygathrix nemaeus* (Linnaeus), and the Southern White-cheeked Gibbon *Nomascus siki* Delacour. We also uncovered a so far overlooked population of the Siamese crocodile *Crocodylus siamensis* (Schneider) near the type locality of the new bent-toed gecko species, which highlights the importance of this region in terms of conservation (Ziegler *et al.* 2015). In order to protect the biodiversity of this region, the establishment of a provincial protected area should be considered by the provincial authority of Khammouane Province in the near future.

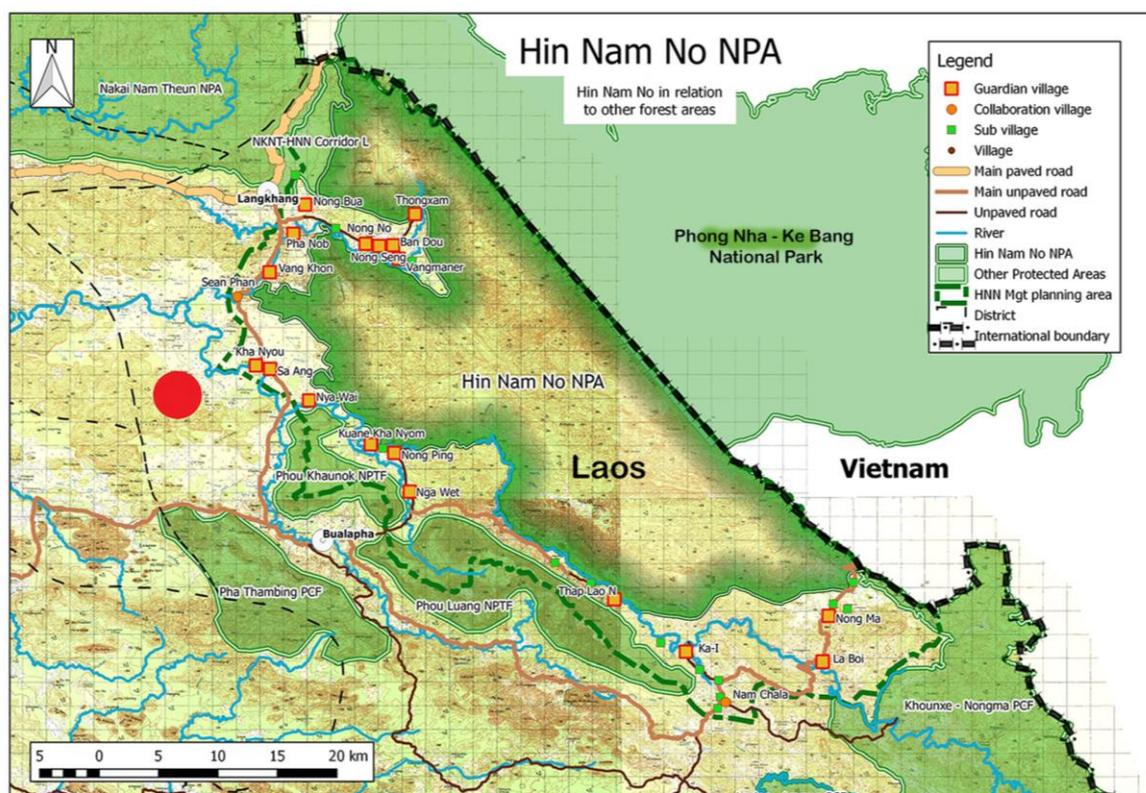


FIGURE 5. Type locality (red circle) of *Cyrtodactylus bansocensis* in Khammouane Province, central Laos.



FIGURE 6. Habitat of *Cyrtodaactylus bansocensis*. Photo: V. Q. Luu.

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APPENDIX. Comparative specimens examined.

- Cyrtodactylus jaegeri*. Laos: Khammouane Province: Thakhek: IEBR A.2013.55 (holotype), NUOL R-2013.1 (paratype).
C. jarujini. Thailand: Nong Khai Province: Bung Ban: ZMB 50648 (holotype).
C. lomyenensis. Laos: Khammouane Province: Huong Son: IEBR A.2011.3 (holotype), ZFMK 92293 (paratype).
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. 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: Gnommalath: VFU R.2015.14 (holotype), IEBR R.2015.35, NUOL R-2015.15 (paratypes).
C. soudthichaki. Laos: Khammouane: Thakhek: 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 Province: Vieng Phoukha: IEBR A.2010.01 (holotype), ZFMK 91016, MTD 47731, NUOL 2010.1 (paratypes).

Publication 11

**Evolution in karst massifs: Cryptic diversity among bent-toed geckos along
the Truong Son Range with descriptions of three new species
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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 *Cyrtodactylus 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 *Cyrtodactylus* 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 truongsongensis* (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. phonghakebangensis* 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. phonghakebangensis*, *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
<i>C. badenensis</i>	KF929505	Vietnam: Tay Ninh Province	KIZ13689
<i>C. bansocensis</i>	KU175573	Laos: Khammouane Province	VFU R.2015.20
<i>C. bansocensis</i>	KU175574	Laos: Khammouane Province	NUOL R-2015.21
<i>C. bobrovi</i>	KT004368	Vietnam: Hoa Binh Province	IEBR A.2015.30
<i>C. bobrovi</i>	KT004369	Vietnam: Hoa Binh Province	VNMN A.2015.61
<i>Cyrtodactylus calamei</i> sp. nov.	KX064043	Laos: Khammouane Province	NUOL R-2015.22
<i>Cyrtodactylus calamei</i> sp. nov.	KX064044	Laos: Khammouane Province	VNUF R.2015.28
<i>C. cryptus</i>	KF169971	Vietnam: Quang Binh Province	PNKB3
<i>C. cryptus</i>	KF169972	Vietnam: Quang Binh Province	PNKB4
<i>C. cryptus</i>	KX064038	Laos: Khammouane Province	VNUF R.2014.69
<i>C. elok</i>	HM888478	Malaysia	ZMMU RAN 1991
<i>C. elok</i>	HM888479	Malaysia	ZMMU RAN 1992
<i>C. darevskii</i>	HQ967221	Laos: Khammouane Province	ZIN FN 256
<i>C. darevskii</i>	HQ967223	Laos: Khammouane Province	ZIN FN 223
<i>Cyrtodactylus hinnamnoensis</i> sp. nov.	KX064045	Laos: Khammouane Province	IEBR A.2013.89
<i>Cyrtodactylus hinnamnoensis</i> sp. nov.	KX064046	Laos: Khammouane Province	IEBR A.2013.90
<i>Cyrtodactylus hinnamnoensis</i> sp. nov.	KX064047	Laos: Khammouane Province	VNUF R.2015.11
<i>Cyrtodactylus hinnamnoensis</i> sp. nov.	KX064048	Laos: Khammouane Province	VNUF R.2015.3
<i>Cyrtodactylus hinnamnoensis</i> sp. nov.	KX064049	Laos: Khammouane Province	NUOL R-2015.9
<i>C. lomyenensis</i>	KJ817436	Laos: Khammouane Province	IEBR KM2012.54
<i>C. lomyenensis</i>	KP199942	Laos: Khammouane Province	IEBR KM2012.52
<i>C. interdigitalis</i>	KX077901	Laos: Khammouane Province	VNUF R.2014.50

.....continued on the next page

TABLE 1. (Continued)

Species	GenBank no.	Locality	Voucher number
<i>C. jaegeri</i>	KT004364	Laos: Khammouane Province	IEBR A.2013.55
<i>C. jaegeri</i>	KT004365	Laos: Khammouane Province	NUOL R.2013.1
<i>C. jaegeri</i>	KT004366	Laos: Khammouane Province	VFU TK914
<i>C. cf. jarujini</i>	KX077907	Laos: Bolikhamxay Province	VNUF R.2015.7
<i>C. khammouanensis</i>	HM888467	Laos: Khammouane Province	ZIN FN 191
<i>C. khammouanensis</i>	HM888469	Laos: Khammouane Province	ZIN FN 257
<i>C. kingsadai</i>	KF188432	Vietnam: Phu Yen Province	IEBR A.2013.3
<i>C. cf. martini</i>	KF929537	China: Yunnan	KIZ201103
<i>C. multiporus</i>	HM888472	Laos: Khammouane Province	ZIN FN 3
<i>C. multiporus</i>	HM888471	Laos: Khammouane Province	ZIN FN 2
<i>C. otai</i>	KT004370	Vietnam: Hoa Binh Province	IEBR A.2015.26
<i>C. otai</i>	KT004371	Vietnam: Hoa Binh Province	IEBR A.2015.27
<i>C. puhuensis</i>	KF929529	Vietnam: Thanh Hoa Province	KIZ 11665
<i>C. pulchellus</i>	HQ967202	Malaysia	ZMMU R-12643-3
<i>C. pulchellus</i>	HQ967203	Malaysia	ZMMU R-12643-4
<i>C. pageli</i>	KJ817431	Laos: Vientiane Province	ZFMK 91827
<i>C. pageli</i>	KX077902	Laos: Vientiane Province	NQT 2010.36
<i>C. pageli</i>	KX077903	Laos: Vientiane Province	NQT 2010.37
<i>C. phongnhakebangensis</i>	KF929526	Vietnam: Quang Binh Province	PNKB2011.30
<i>C. phongnhakebangensis</i>	KF929527	Vietnam: Quang Binh Province	PNKB2011.32
<i>C. pseudoquadrivirgatus</i>	KF169963	Vietnam: Hue Province	ITBCZ3001
<i>C. cf. pseudoquadrivirgatus</i>	KP199949	Vietnam	ZMMU R-13095-2
<i>C. quadrivirgatus</i>	HM888465	Malaysia	ZMMU RAN 1989
<i>C. quadrivirgatus</i>	HM888466	Malaysia	ZMMU RAN 1990
<i>C. roesleri</i>	KF929532	Vietnam: Quang Binh Province	PNKB2011.34
<i>C. roesleri</i>	KF929531	Vietnam: Quang Binh Province	PNKB2011.3
<i>C. rufford</i>	KU175572	Laos: Khammouane Province	VFU R.2015.14
<i>Cyrtodactylus sommerladi</i> sp. nov.	KX064039	Laos: Khammouane Province	IEBR A.2015.37
<i>Cyrtodactylus sommerladi</i> sp. nov.	KX064040	Laos: Khammouane Province	VNUF R.2013.22
<i>Cyrtodactylus sommerladi</i> sp. nov.	KX064041	Laos: Khammouane Province	VNUF R.2013.87
<i>Cyrtodactylus sommerladi</i> sp. nov.	KX064042	Laos: Khammouane Province	IEBR A.2015.39
<i>C. spelaeus</i>	KP199947	Laos: Vientiane Province	ZMMU R-13980-3
<i>C. spelaeus</i>	KP199948	Laos: Vientiane Province	ZMMU R-13980-1
<i>C. soudthichaki</i>	KX077904	Laos: Khammouane Province	NUOL R-2015.5
<i>C. soudthichaki</i>	KX077905	Laos: Khammouane Province	VFU R.2015.18
<i>C. soudthichaki</i>	KX077906	Laos: Khammouane Province	IEBR A.2015.34
<i>C. teynie</i>	KJ817430	Laos: Khammouane Province	IEBR KM2012.77
<i>C. teynie</i>	KP199945	Laos: Khammouane Province	IEBR KM2012.77
<i>C. vilaphongi</i>	KJ817434	Laos: Luang Prabang	NUOL R-2013.5
<i>C. vilaphongi</i>	KJ817435	Laos: Luang Prabang	IEBR A.2013.103
<i>C. wayakonei</i>	KJ817438	Laos: Luang Nam Tha Province	ZFMK 91016
<i>C. wayakonei</i>	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 $-lnL$ 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. <i>Cyrtodactylus calamei</i> sp. nov. (KX064043 & 4)	-				
2. <i>C. darevskii</i> (HQ967221 & 3)	5.2–5.3	-			
3. <i>Cyrtodactylus hinnamnoensis</i> sp. nov. (KX064045-9)	5.1–5.4	4.0–4.1	-		
4. <i>C. cf. jarujini</i> (KX077907)	16.2–16.3	16.3	16.0–16.5	-	
5. <i>C. lomyenensis</i> (KJ817436/KP199942)	14.2–14.5	13.6–13.7	14.2–14.7	15.1–15.4	-
6. <i>C. multiporus</i> (HM888471 & 2)	15.1–15.3	15.6	14.7–15.4	9.6	14.7–15.1
7. <i>C. pageli</i> (KJ817431/KX077902 & 3)	16.5–17.5	18.3–18.8	18.6–19.4	17.1–17.8	17.1–18.3
8. <i>C. phongnhakebangensis</i> (KF929526 & 7)	7.9	9.7	8.6–9.3	17.0	14.5–14.6
9. <i>C. roesleri</i> (KF929531 & 2)	15.5	17.3	16.9–17.1	17.2–17.3	17.4–17.6
10. <i>Cyrtodactylus sommerladi</i> 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. <i>C. teynieii</i> (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. <i>Cyrtodactylus calamei</i> sp. nov. (KX064043 & 4)						
2. <i>C. darevskii</i> (HQ967221 & 3)						
3. <i>Cyrtodactylus hinnamnoensis</i> sp. nov. (KX064045-9)						
4. <i>C. cf. jarujini</i> (KX077907)						
5. <i>C. lomyenensis</i> (KJ817436/KP199942)						
6. <i>C. multiporus</i> (HM888471 & 2)	-					
7. <i>C. pageli</i> (KJ817431/KX077902 & 3)	16.4–17.3	-				
8. <i>C. phongnhakebangensis</i> (KF929526 & 7)	15.3	17.7–17.8	-			
9. <i>C. roesleri</i> (KF929531 & 2)	16.9–17.1	16.1–17.5	15.3	-		
10. <i>Cyrtodactylus sommerladi</i> sp. nov. (KX064039-42)	16.9–17.0	15.0–16.6	16.2–16.3	5.9–6.2	-	
11. <i>C. teynieii</i> (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).

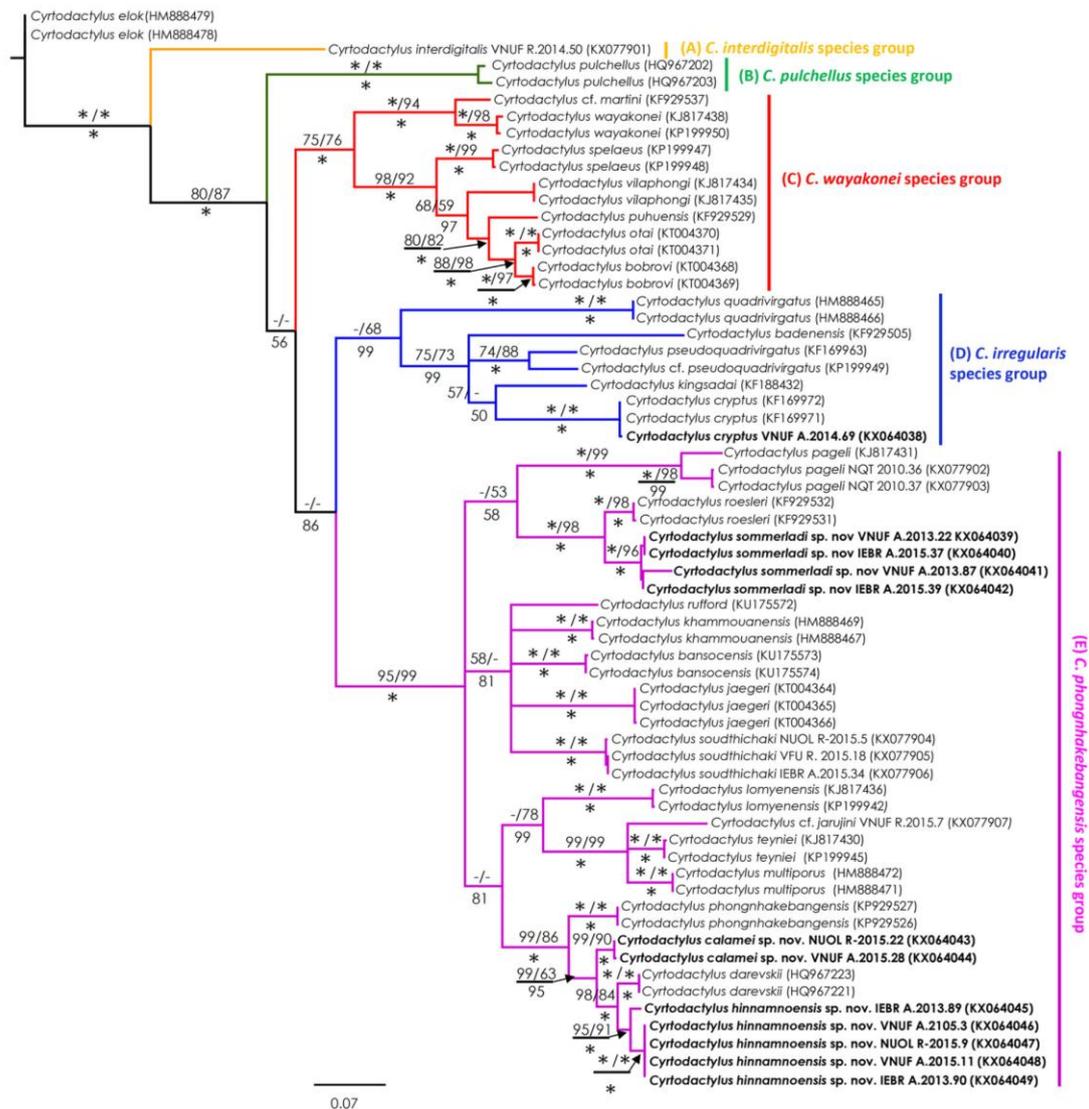


FIGURE 1. Phylogram based on the Bayesian analysis. Number above and below branches are MP/ML bootstrap values and Bayesian posterior probabilities (>50%), respectively. Asterisk denotes 100% value. Hyphen indicates the statistical support value lower than 50%. Scale shows the number of expected substitutions 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* versus *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 begun at different levels, and thus are described in the following.

TABLE 3. Morphological comparisons between *Cyrtodactylus calamei* sp. nov., *Cyrtodactylus himmoensis* 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 = preloacal pores; LD4 = subdigital lamellae on fourth finger; TL4 = subdigital lamellae on fourth toe; FPI = 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
<i>Cyrtodactylus calamei</i> 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
<i>Cyrtodactylus himmoensis</i> 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
<i>Cyrtodactylus sommerladi</i> 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
<i>C. bansocensis</i>	71.0–74.0	98.5–103.5	34–35	present	present	34 (FP+PP)	unknown	16–19	18–21	banded	present
<i>C. rufford</i>	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
<i>C. sordhichaki</i>	69.2–70.0	95.1*–95.2	32–33	present	present (in males)	29 (FP+PP)	absent	16–18	18	banded	present
<i>C. angularis</i>	80.0–92.0	92–95.2	40–45	present	absent (in males)	3	3	18–19	18–19	banded	present
<i>C. astrum</i>	46.4–108.3	99.0*–109.0*	31–46	–	present	31–38 (FP+PP)	–	–	20–24	banded	present
<i>C. auribalteatus</i>	82.8–98.1	106.5–138.7	38–40	5–7	4–5 (in males)	6	absent	–	18–21	banded	present
<i>C. badensis</i>	59.3–74.1	58.6–82.4	25–29	absent	absent	0	0	–	18–22	banded	present
<i>C. bichinganae</i>	95.3–99.9	96.3–115.6	30–31	11–13	18	10	8	18–20	16–20	banded	present
<i>C. bidoupimontis</i>	74.0–86.3	75.0–86.0	38–43	6–8	absent	4–6	0	15–20	18–23	banded	absent
<i>C. bobrovi</i>	75.2–96.4	80.8–90.3	40–45	0	0	5	0	19–21	21–22	banded	absent
<i>C. brevipalmatus</i>	64.0–72.0	77.0	35–44	present	present	6+9+7 (FPI+PP+FPPr)	6+9+7 (FP+PP+FPPr)	–	–	blotched	present
<i>C. bugiamapensis</i>	58.6–76.8	65.3–83.0	36–46	6–10	absent	7–8	0–7	15–17	17–20	blotched	absent
<i>C. buchari</i>	60.0–65.0	46.0–54.0	30	absent	absent	9	0	14	12	blotched	absent
<i>C. caovansungi</i>	90.4–94.0	120.0	38–44	8	6	9	0	22	23–25	banded	present
<i>C. cattienensis</i>	43.5–69.0	51.0–64.7	28–42	3–8	absent	6–8	0	12–16	14–19	banded	absent
<i>C. chanhomeae</i>	69.9–78.8	74.4–74.7	36–38	present	present	32 (FP+PP)	34 (FP+PP)	18–20	21–23	banded	present
<i>C. chauquangensis</i>	90.9–99.3	97.0–108.3	36–38	absent	absent	6	7	16–18	19–23	banded	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
<i>C. cryptus</i>	62.5–90.8	63.5–88.4	47–50	absent	absent	9–11	0	18–19	20–23	banded	absent
<i>C. cucdongensis</i>	55.8–65.9	22.1–27.8	35–44	present	absent	5–6	4–6	8–11	15–20	banded	absent
<i>C. cucphuongsensis</i>	96.0	79.3*	42	14	absent	0	–	21	24	banded	present
<i>C. darevskii</i>	84.6–100.0	95.0–113.0	38–46	present	present	38–44 (FP+PP)	24–34	17–20	18–22	banded	present
<i>C. dummuui</i>	76.2–84.2	100.2*	40	present	present in males/absent in females	6+5–6+6–7 (FPI+PP+FPPr)	0–7	16	19	banded	present
<i>C. eisemannae</i>	76.8–89.2	91.0–103.8	44–45	4–6	absent	0	0	18–20	17–18	banded	present
<i>C. erythropros</i>	78.4	83.0*	28	present	present	10+9+9 (FPI+PP+FPPr)	–	16	20	blotched	present
<i>C. grismeri</i>	68.3–95.0	111.3–115.1	33–38	absent	–	0	0	16–18	16–19	banded	present
<i>C. huongsonensis</i>	73.4–89.8	90.5	41–48	7–9	15–17	6	8	17–19	20–23	banded	present
<i>C. huynhi</i>	54.8–79.8	61.5–78.6	43–46	3–5	3–8	7–9	0–8	14–17	17–21	banded	absent
<i>C. interdigitalis</i>	59.0–80.0	71.0–90.0	37–42	present	16–18	14	0	17–22	16–20	banded	absent
<i>C. intermedius</i>	61.0–85.0	80.0–110.0	40–50	6–10	–	8–10	–	20	22	banded	present
<i>C. irregularis</i>	72.0–86.0	66.0–74.0	38–45	7–8	–	5–7	0–6	15–16	18–19	blotched	absent
<i>C. jaegeri</i>	60.0–68.5	82.4–83.4	31–32	17–19	present	44 (FP+PP)	21	17–19	20–23	banded	present
<i>C. jarujini</i>	85.0–90.0	105.0–116.0	32–38	present	present	52–54 (PP+FP)	0	15–17	18–19	blotched	present
<i>C. khammouanensis</i>	70.8–73	83.0–95.0	32–38	present	present	40–44 (PP+FP)	0–17	18–20	20–23	banded	present
<i>C. khelangensis</i>	72.8–95.3	max. 96.0*	32–35	present	present	6+2–5+6–7 (FPI+PP+FPPr)	2+6+1	18	22	banded	present
<i>C. kingsadai</i>	83.0–94.0	max. 117.0	39–46	9–12	0–7	7–9	4–8	19–21	21–25	banded	present
<i>C. lekaguli</i>	80.5–103.5	115.0–125.0	31–43	present	present	30–36 (PP+FP)	0	–	20–25	banded	present
<i>C. lomynensis</i>	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
<i>C. martini</i>	64.4–96.2	76.0–101.2	39–43	14–18	absent	4	0	19–23	22–24	banded	present
<i>C. multiporus</i>	81.0–98.0	97.0–105.0	30–38	present	present	58–60 (PP+FP)	0	18–20	18–22	banded	present
<i>C. nigriocularis</i>	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 and striped and spotted	Enlarged subcaudals
<i>C. oldhami</i>	63.0–68.0	69*–70*	34–38	present	absent	1–4	–	–	–	striped and spotted	present
<i>C. otai</i>	85.2–90.6	89.7–97.6	38–43	absent	absent	7–8	0	16–19	19–22	banded	absent
<i>C. pageli</i>	76.2–81.8	85.4*–113.2*	41–44	absent	absent	4	4	19–23	19–23	banded	present
<i>C. paradoxus</i>	52.0–84.0	80.8–111.0	32–40	present	absent	0–4	0	15–18	17–23	banded	present
<i>C. phonghakebangensis</i>	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
<i>C. phuocbinhensis</i>	46.0–60.4	76.1	43–47	5	absent	7	0	16–21	17–19	blotched	absent
<i>C. pseudoquadrivirgatus</i>	48.6–83.3	55.7–82.3	41–57	absent	absent	5–9	5–10	15–21	16–25	blotched	absent
<i>C. phuensis</i>	79.2	82.59	36	present	absent	5	–	18	23	banded	present
<i>C. quadrivirgatus</i>	39.0–67.0	77.0	40	present	absent	4	4	–	–	striped	absent
<i>C. ranongensis</i>	56.9–59.6	66.0–67.1	35–40	present	0	0	0	17	18	blotched	absent
<i>C. roesleri</i>	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
<i>C. sai yok</i>	56.7–61.0	66.7–67.5	23–24	present	absent	5	–	–	16–17	banded	present
<i>C. samroi yot</i>	63.2–66.9	78.8–87.5	33–34	present	absent	7	6	18	19	banded	present
<i>C. sanook</i>	72.9–79.5	104.2	27–28	present	absent	3–4	absent	–	19–20	banded	present
<i>C. speilaus</i>	88.9–91.0	max. 83*	36–39	absent	absent	8–9	0	19–20	22–24	banded	present
<i>C. stannothai</i>	61.5–70.7	89.9–94.0	33–36	absent	absent	2	0	16	18	banded	present
<i>C. takouensis</i>	74.7–81.1	77.7–91.0	39–40	3–5	0–2	3–4	0	16–17	18–20	banded	present
<i>C. taynguyenensis</i>	60–85	66–94	42–49	absent	absent	6	0	13–18	17–21	blotched	absent
<i>C. teyniei</i>	89.9	ca. 110.0	38	23	absent	unknown	13	17–18	19–20	blotched	present
<i>C. thuangae</i>	57.3–77.6	max. 78.1	29–44	2–5	0–3	0–1	0	14–17	14–20	blotched	absent
<i>C. wayakonei</i>	72.0–86.8	76.8–89.0	31–35	absent	absent	6–8	7	17–18	19–20	banded	present
<i>C. thirakhupti</i>	72.0–79.6	99.1	37–40	present	absent	absent	absent	16	20	banded	present
<i>C. tigroides</i>	74.3–83.2	108.5–117.0	34	present	present	6+8+7 (FP+PP+FPPr)	5+9+7 (FP+PP+FPPr)	18–19	20–22	banded	present
<i>C. vilaphongi</i>	60.9–86.1	61.2–68.1	34–36	0	–	–	0	18–19	18–20	banded	absent
<i>C. yangbaysensis</i>	78.5–92.3	91.3–109.1	39–46	5–16	0–2	6–8	0	16–19	15–17	banded	present
<i>C. ziegleri</i>	84.6–93.0	95.0–107.0	33–39	8–10	0–6	5–8	0–8	16–19	18–21	banded	absent

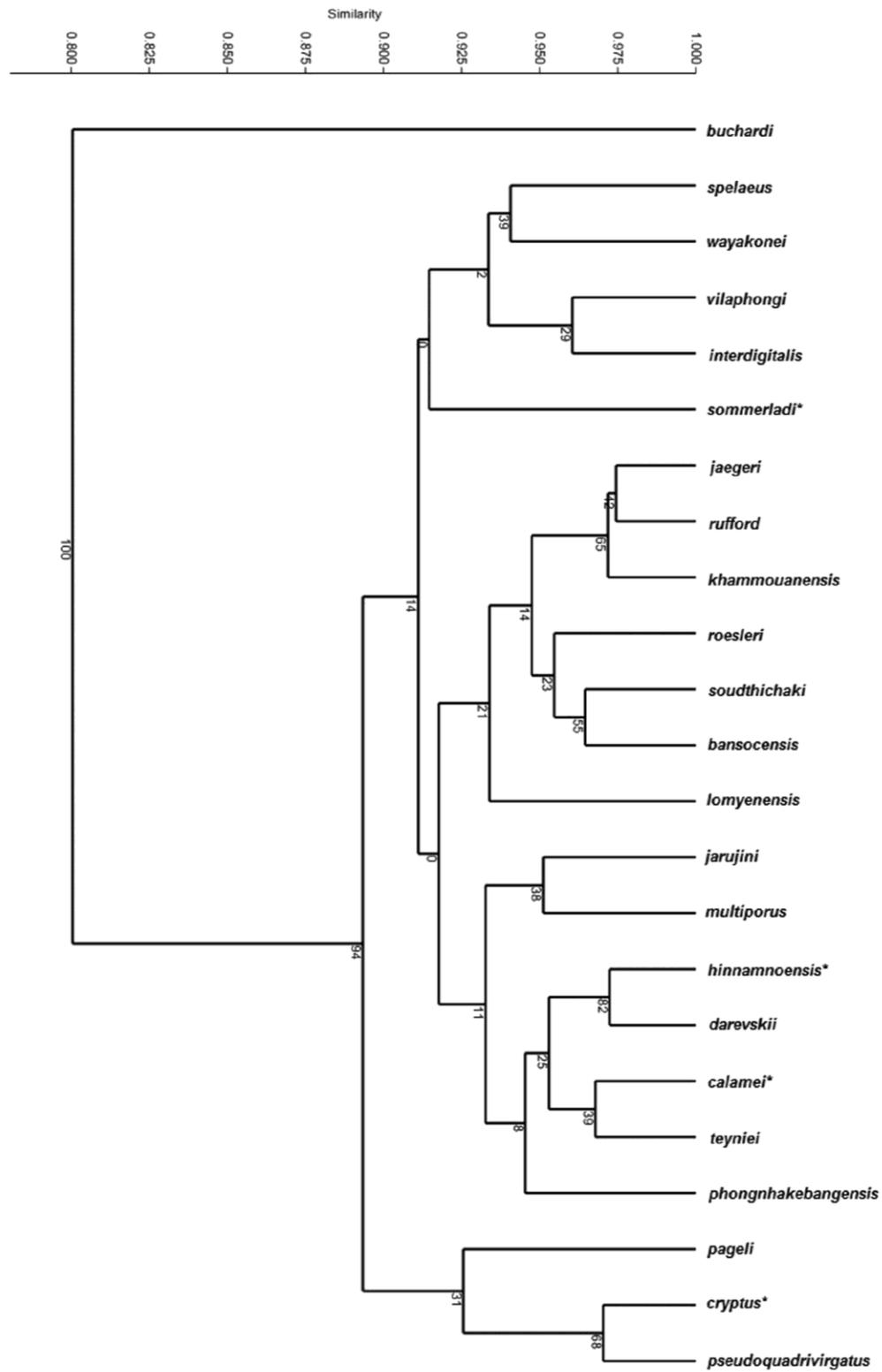


FIGURE 2. Cluster analysis showing species correlation of the *Cyrtodactylus* species based on morphological comparisons (1000 bootstrap replicates).

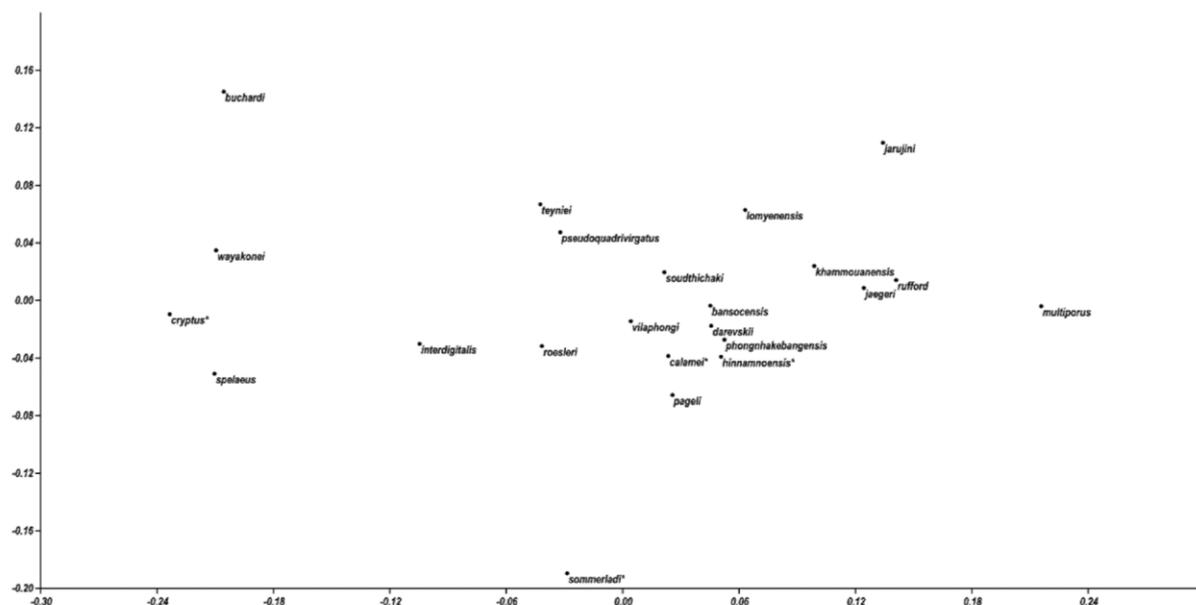


FIGURE 3. Correspondence analysis showing species association of *Cyrtodactylus* from Laos (except for *Cyrtodactylus phonghakebangensis* and *C. roesleri* which are from Vietnam) based on morphological comparisons.

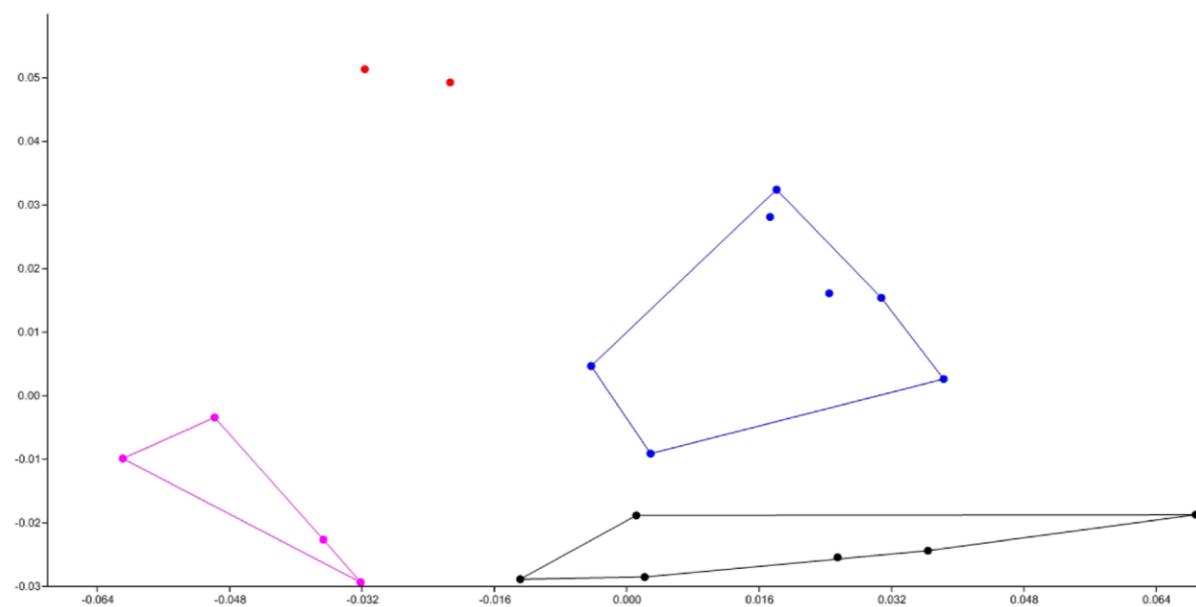


FIGURE 4. Correspondence analysis comparing all adult male measurements of four *Cyrtodactylus* sibling species: *Cyrtodactylus hinnamnoensis* **sp. nov.** (blue dots); *Cyrtodactylus darevskii* (pink dots); *Cyrtodactylus calamei* **sp. nov.** (red dots); and *Cyrtodactylus phonghakebangensis* (black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

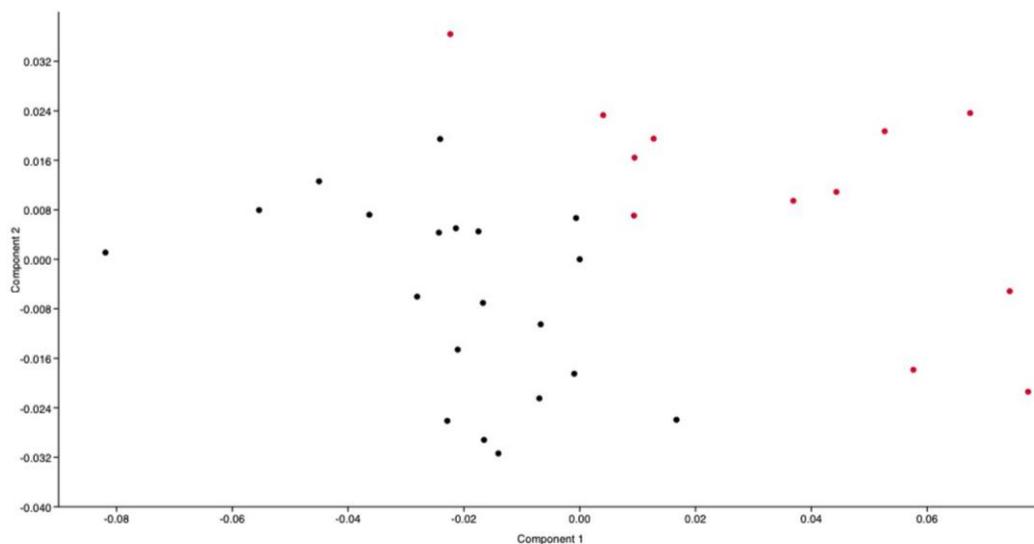


FIGURE 5. Principal components analysis comparing head shape of *Cyrtodactylus sommerladi* sp. nov. (red dots) and *Cyrtodactylus roesleri* (black dots) based on relative head width and head height.

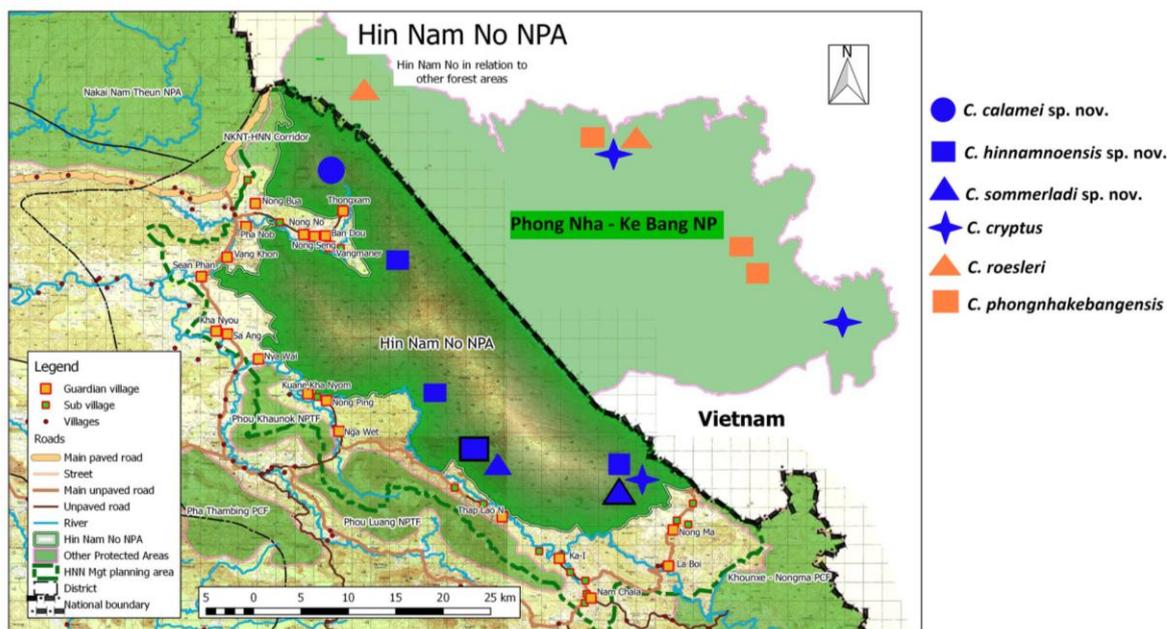


FIGURE 6. Map showing the localities (blue) of the three new *Cyrtodactylus* species (type localities are encircled with black line) and the new *Cyrtodactylus* country record from Khammouane Province, central Laos.

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. Thanabuaoasy.

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 \pm 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).

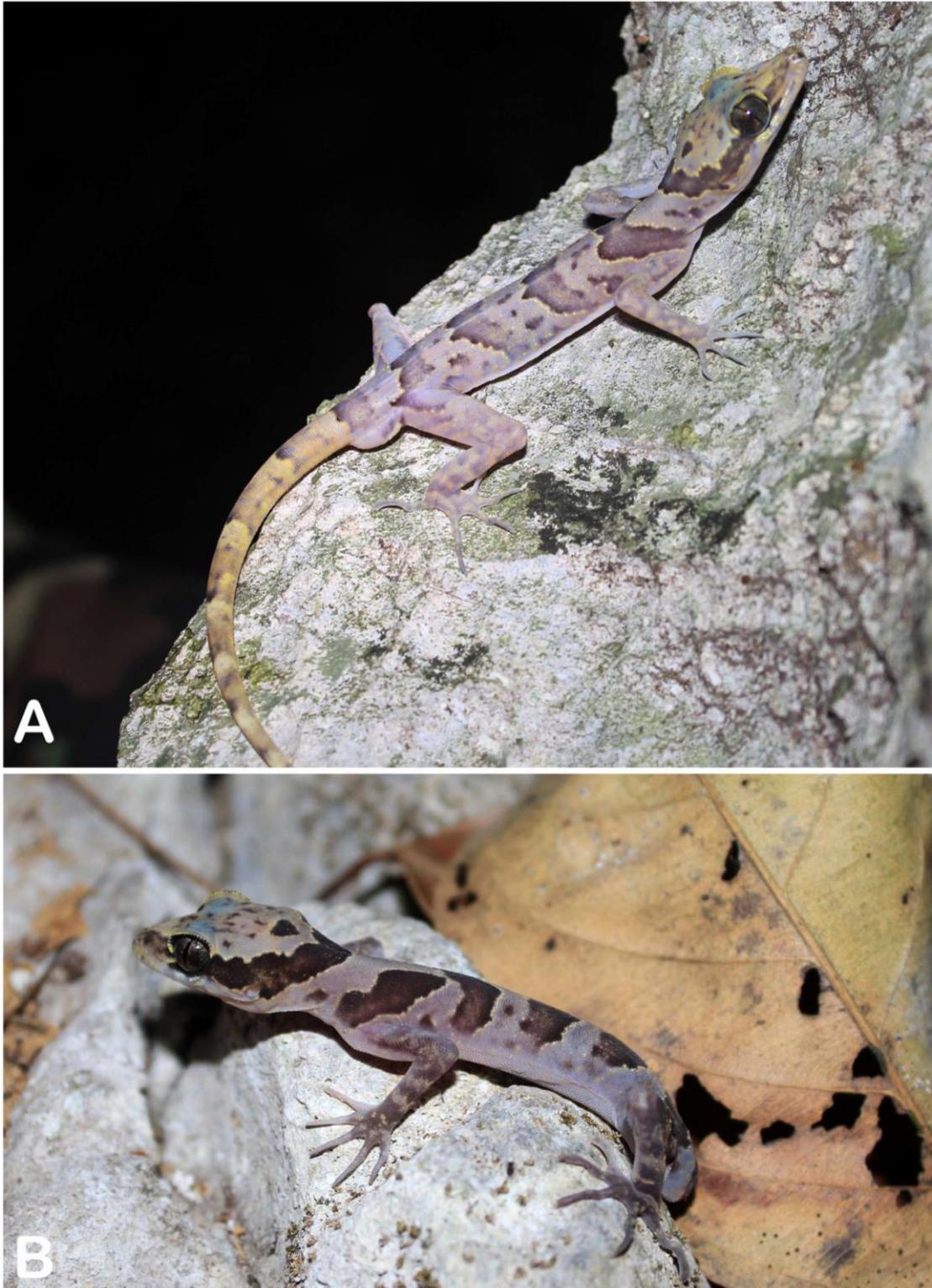


FIGURE 7. A) Dorsolateral view of the holotype (VNUF R.2015.28); B) lateral view of the paratype (NUOL R.2015.22) of *Cyrtodactylus calamei* sp. nov. in life. Photos: V. Q. Luu.

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 26°C (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
<i>Cyrtodactylus calamei</i> 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
<i>Cyrtodactylus calamei</i> sp. nov.					
1	VNUF R.2015.28	25°C	85%	210 m	karst cliff ca. 1 m height
2	IEBR A. 2015.36	26°C	87%	205 m	karst cliff ca. 0.5 m height
3	NUOL R-2015.22	26°C	81%	193 m	small tree ca. 0.2 m height
4	VNUF R.2015.27	25.5°C	86%	260 m	karst cliff ca. 0.3 m height

***Cyrtodactylus hinnammoensis* 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 hinnammoensis* **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.

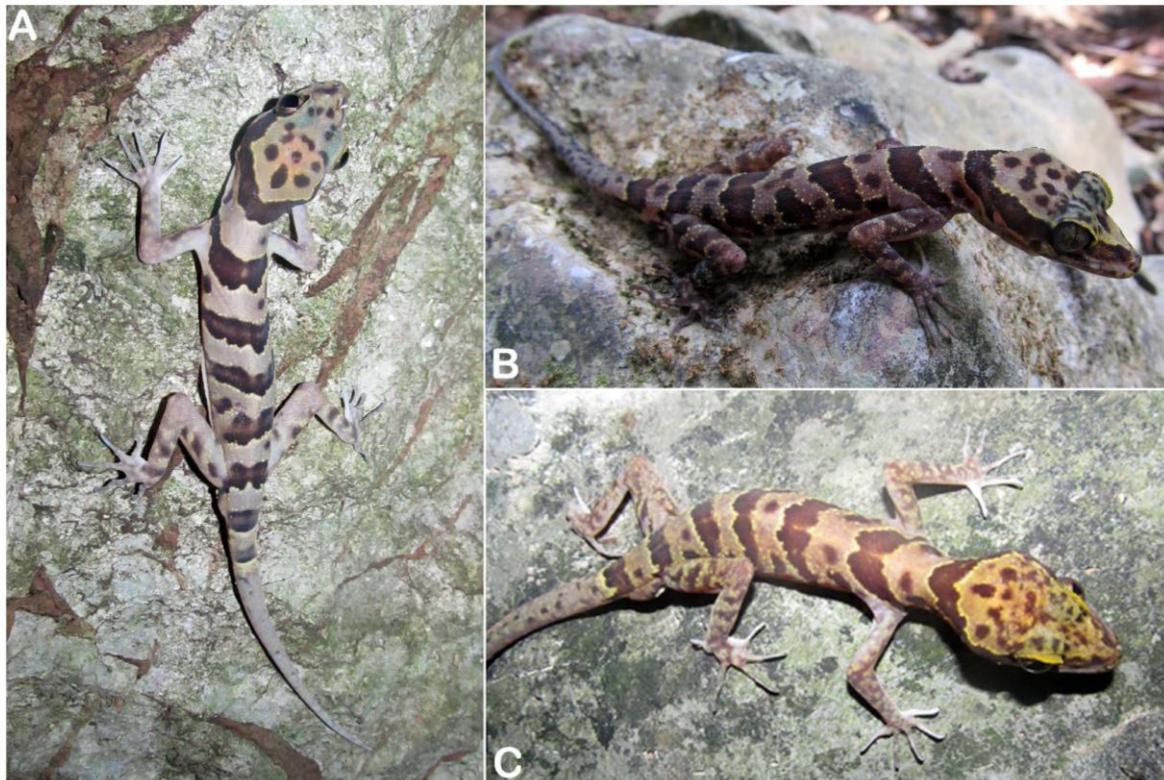


FIGURE 8. A) Dorsal view of the holotype (IEBR A.2013.90); and dorsal views of the paratypes of *Cyrtodactylus hinnamnoensis* sp. nov. in life B) VNUF R.2014.99; and C) VNUF R.2013.3. Photos: V. Q. Luu.

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).

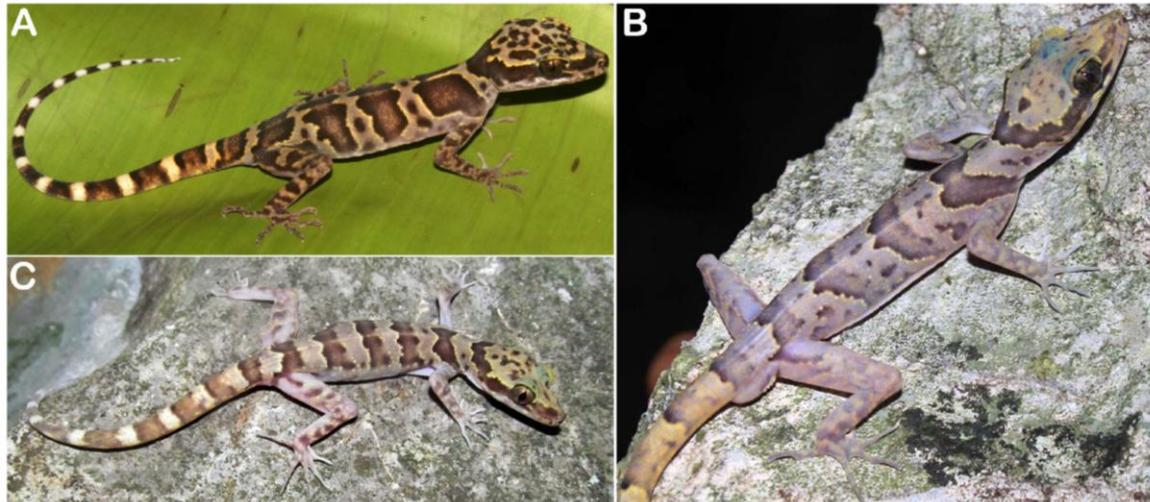


FIGURE 9. Dorsal pattern of three *Cyrtodactylus* sibling species: A) *Cyrtodactylus phongnhakebangensis* from Vietnam (Phong Nha-Ke Bang National Park); B) *Cyrtodactylus calamei* **sp. nov.**; and C) *Cyrtodactylus hinnamnoensis* **sp. nov.** (VNUF R.2013.4), from Laos. Photos: T. Ziegler & V. Q. Luu.

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

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TABLE 6. (Continued)

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

TABLE 7. Comparison of *Cyrtodactylus calamei* **sp. nov.** and *Cyrtodactylus himmaoensis* **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	<i>Cyrtodactylus calamei</i> sp. nov.	<i>Cyrtodactylus himmaoensis</i> sp. nov.	<i>C. darevskii</i>	<i>C. phongnhakebangensis</i>
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 himmaoensis* **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 measurements 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 \pm 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.

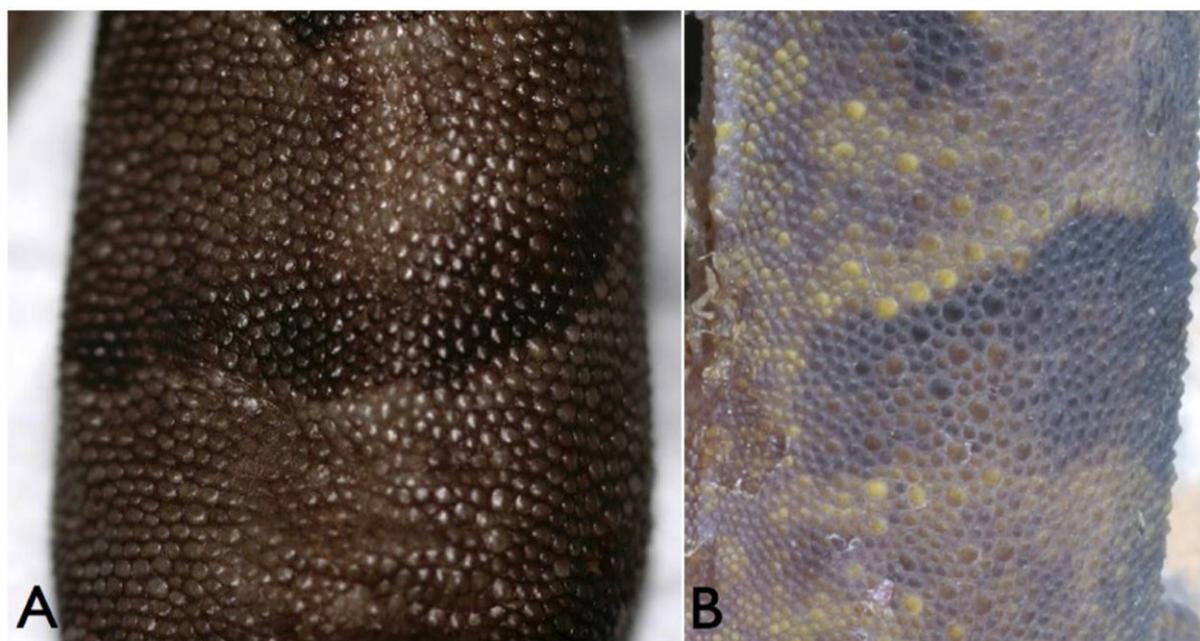


FIGURE 11. Comparison of dorsal scale structure of *Cyrtodactylus sommerladi* sp. nov. (A: with homogenous tubercle-like scales) and *C. roesleri* (B: with distinct dorsal tubercle rows). Photos: N. Schneider & T. Ziegler.

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

.....continued on the next page

TABLE 9. (Continued)

Character	NUOL	IEBR	VNUF	ZFMK97197	IEBR	VNUF	VNUF	VNUF	NUOL	VNUF	m±SD	min-max
	R-2013.23 paratype sub., male	A.2015.38 paratype female	R.2013.104 paratype female	paratype female	A.2015.40 paratype female	R.2013.104 paratype female	R.2014.89 paratype female	R.2013.21 paratype female	R.2013.67 paratype female			
Sex												
SVL	61.8	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*	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	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	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	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	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	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	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	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	29.1	34.1	26.4	27	30.6	35.2	29.9	30.9±3.3	26.4–35.2		
ForeaL	9.4	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	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	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	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	7.9	7.7	7.5	7.2	7.5	8.9	9.0	8.0±0.7	7.2–9.0		
RW	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	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	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	2.4	1.9	2.7	2.4	1.9	2.6	2.5	2.3±0.3	1.9–2.7		
SL	9/10	10/9	10/11	10/10	11/9	10/11	9/9	9/10	9.7±0.8	9–11		
IL	7/8	8/8	8/8	8/8	8/8	9/9	9/8	8/7	8.1±0.6	7–9		
N	3	3	3	3	3	3	3	3	3.0±0.0	3–3		
IN	0	0	0	0	0	0	0	0	0	0		
PM	2	2	2	2	2	2	2	2	2.0±0.0	2–2		
DTR	no	no	no	no	no	no	no	4-5				
GST	no	no	no	no	no	no	7.00	8.00				
V	35	37	34	33	32	31	34	32	33.3±2.0	31–37		
SLB	191	179	189	170	184	186	188	183	182.7±6.5	170–189		
SR	87	87	93	78	87	78	86	88	85.3±5.5	78–93		
FP+PP	23	19	21	18	17	21	21	20	19.6±1.6	17–21		
PAT	5/5	4/4	4/4	4/4	5/5	4/5	5/6	5/5	5.0±0.6	4–6		
LD4	16/17	17/17	17/17	17/16	17/16	17/17	19/20	17/18	17.2±1.0	16–20		
LT4	23/21	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 29.9°C (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 (17°17.328'N, 106°09.909'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 (17°17.394'N, 106°09.980'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).

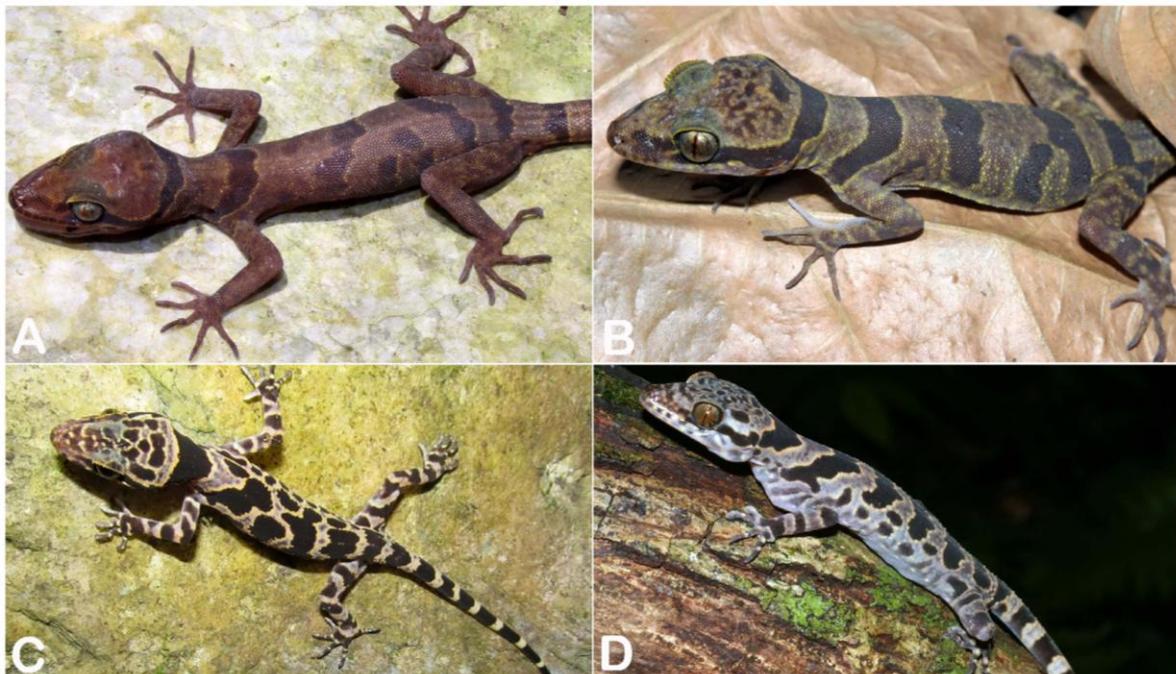


FIGURE 12. Dorsal pattern of two *Cyrtodactylus* pairs from Hin Nam No NPA (left side) and Phong Nha-Ke Bang NP (right side): A) Paratype of *Cyrtodactylus sommerladi* sp. nov. (NUOL R-2013.21) from Laos and B) paratype of *Cyrtodactylus roesleri* (ZFMK 86433) from Vietnam; C) *Cyrtodactylus cryptus*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

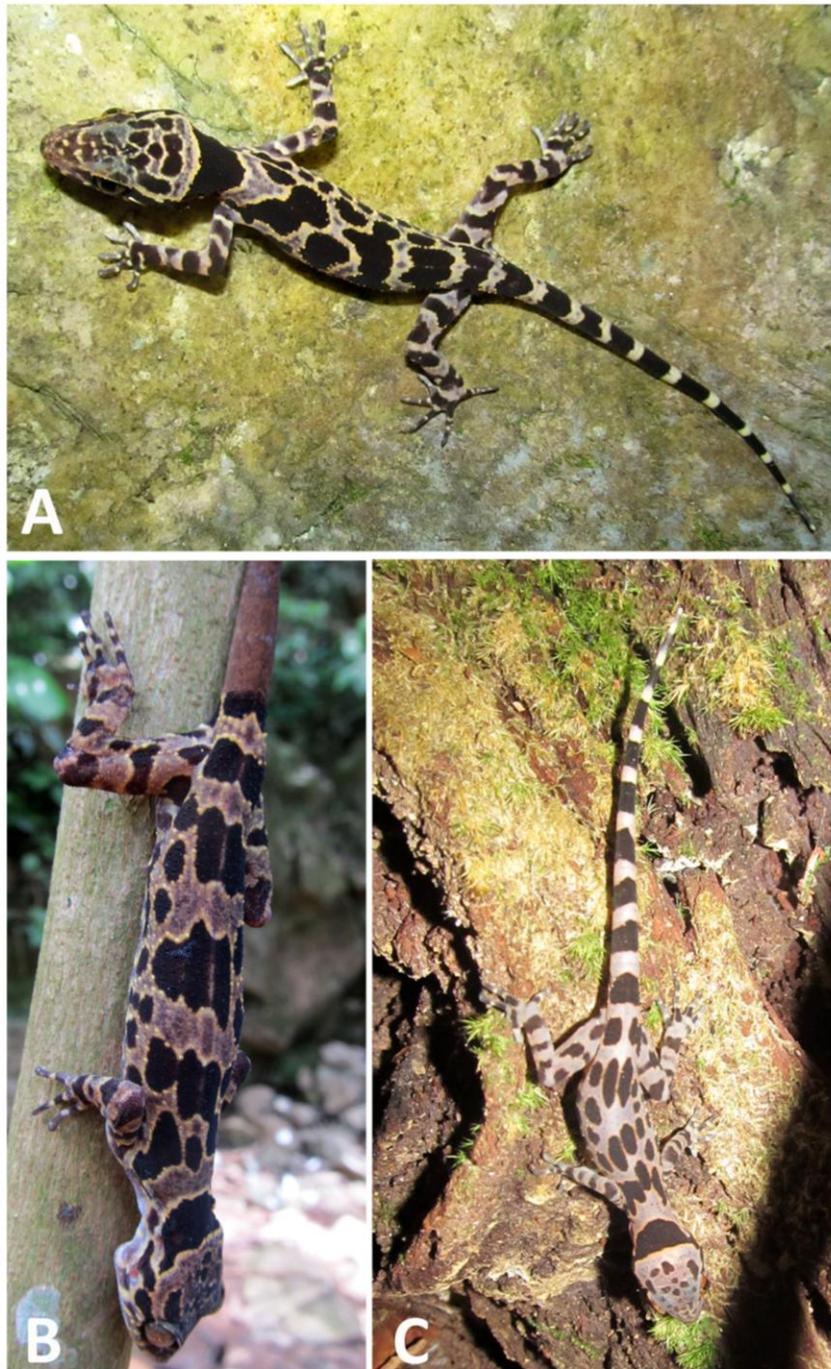


FIGURE 13. A) Adult male (VNUF R.2014.86); B) adult female (VNUF R.2014.69); and C) juvenile (VNUF R.2014.68) of *Cyrtodactylus cryptus* from Laos in life. Photos: V. Q. Luu.

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
<i>Cyrtodactylus cryptus</i>						
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	
<i>Cyrtodactylus cryptus</i>						
1	VNUF R.2014.86	27°C	81%	587 m	on the karst cliff ca. 0.3 m height	
2	VNUF R.2014.69	27.3°C	81%	592 m	on the trunk of a small tree, ca.0.2 m height	
3	NUOL R-2014.68	27.3°C	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 phonghakebangensis 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 phonghakebangensis* 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 precloacal 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
<i>Cyrtodactylus phonghakebangensis</i> species group															
<i>C. bansoensis</i>	74	103.5	8-10	8	3	0	3	0	14-15	158-170	86-87	34-35	0	16-19	18-21
<i>Cyrtodactylus calamei</i> 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
<i>C. darenskii</i>	100	113	10-12	9-11	3	0	4-5	1	16-20	190-216	-	38-46	0	17-20	18-22
<i>Cyrtodactylus hinnaoensis</i> 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
<i>C. jaegeri</i>	68.5	83.4	10-11	9-11	3	0-1	5	1	15-16	156-164	-	31-32	1	17-19	20-23
<i>C. jarujini</i>	90	116	12-16	10-12	4	1	0	0	18-20	169	-	32-38	0	15-17	18-19
<i>C. khammouanensis</i>	73	95	11-12	9-10	3	0	4-5	0	16-21	155-172	-	32-38	0	18-20	20-23
<i>C. lomyenensis</i>	71.2	86.1	13-14	11	3	0-1	4	0	20-24	-	-	35-36	0	16-19	19-23
<i>C. multiporus</i>	98	105	9-11	9-11	4	0	6-8	0	16-20	164-181	-	30-38	0	18-20	18-22
<i>C. pageli</i>	81.8	113.2	9-11	9	4	0	5	0	10-14	216-239	115-122	41-44	0	19-23	19-23
<i>C. phonghakebangensis</i>	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
<i>C. roesleri</i>	73.5	101	10-12	7-10	3	0-1	4-5	1	13-19	158-187	-	34-40	0	17-19	17-20
<i>C. rufford</i>	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
<i>Cyrtodactylus sommertadi</i> sp. nov.*	80.3	89.9	9-11	8-9	2-3	0-1	5-6	0	0-5	168-192	76-93	31-32	0	16-20	17-24
<i>C. southchicki</i>	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
<i>C. teyniei</i>	89.9	110	10	9	4	0	0	0	19	184	108	38	0	17-18	19-20
<i>Cyrtodactylus irregularis</i> species group															
<i>C. bucharidi</i>	65	54	13-14	10-11	4	1	0	0	25	-	-	30	0	14	12
<i>C. cryptus</i> *	83.6	73	7-8	6-7	4	1	0	0	15-17	211-218	122-131	40-43	0	17-19	17-19
<i>C. pseudoquadrivirgatus</i>	83.8	72.6	8-10	7-10	4	1	0	0	17-18	-	-	39-40	1	16-19	17-20
<i>Cyrtodactylus wayakonei</i> species group															
<i>C. spelaeus</i>	91	83	9-12	8-10	3	1	0	0	10	156-183	-	36-39	0	19-20	22-24
<i>C. vilaphongi</i>	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
<i>C. wayakonei</i>	86.8	89	7-8	9-10	4	0	0	0	17-19	151-163	85-98	31-35	1	17-18	19-20
<i>Cyrtodactylus interdigitalis</i> species group															
<i>C. interdigitalis</i>	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
<i>Cyrtodactylus phongthakebangensis</i> species group															
<i>C. bansocensis</i>	0	0	1	34	5-7	1	2	Greyish brown	1	0	1	0	0	Khammouane Province	Luu <i>et al.</i> 2016b
<i>Cyrtodactylus calamei</i> sp. nov.*	0	1	1	35-39	4	0	2	Grey	1	1	1	0	0	Khammouane Province	This paper
<i>C. darenskii</i>	0	0	1	38-44	4-5	0	1	Brownish grey	1	1	1	0	0	Khammouane Province	Nazarov <i>et al.</i> 2014
<i>Cyrtodactylus hinnamoensis</i>	0	1	1	36-44	4-6	0	2	Yellowish brown	1	0	1	0	1	Khammouane Province	This paper
sp.nov.*															
<i>C. jaegeri</i>	0	1	1	44	3-6	1	2	Greyish brown	0	0	1	0	0	Khammouane Province	Luu <i>et al.</i> 2014a
<i>C. jarujini</i>	0	1	1	52-54	4	1	2	Grey brown	1	1	0	0	1	Bolikhamxay Province	Bain & Hurley 2011
<i>C. khammoianensis</i>	0	0	1	40-44	5-6	0	1	Brown	0	0	1	0	1	Khammouane Province	Nazarov <i>et al.</i> 2014
<i>C. lomyenensis</i>	0	0	1	39-40	5	0	1	Brownish grey	1	0	1	0	0	Khammouane Province	Ngo & Pauwels 2010
<i>C. multiporus</i>	0	1	1	58-60	5-6	0	2	Brown	1	1	1	0	0	Khammouane Province	Nazarov <i>et al.</i> 2014
<i>C. pageli</i>	0	0	0	4	4	1	1	Light brown	1	0	0	0	1	Vientiane Province	Schneider <i>et al.</i> 2011
<i>C. phongthakebangensis</i>	0	0	1	32-42	4-5	0	2	Dark grey	1	1	1	0	1	Invalid	Luu <i>et al.</i> 2013
<i>C. roesteri</i>	0	0	1	20-28	5-8	1	2	Brownish grey	0	0	1	0	1	Invalid	Teynié & David 2010
<i>C. rufford</i>	0	0	1	42-43	4-5	0	1	Brown-Grey	1	0	1	0	0	Khammouane Province	Luu <i>et al.</i> 2016a
<i>Cyrtodactylus sommerladi</i> sp. nov.*	0	0	1	20-26	4-6	0	2	Yellowish grey	0	0	1	0	0	Khammouane Province	This paper
<i>C. soudthichaki</i>	0	1	1	29	4-5	1	2	Greyish brown	1	0	1	0	1	Khammouane Province	Luu <i>et al.</i> 2015a
<i>C. teyniei</i>	0	0	1	-	3	1	1	Greyish brown	1	1	0	0	1	Borikhamxay Province	David <i>et al.</i> 2011
<i>Cyrtodactylus irregularis</i> species group															
<i>C. buchardi</i>	0	1	1	9	-	1	0	Dark tan	0	1	0	1	1	Champasak Province	David <i>et al.</i> 2004
<i>C. cryptus</i> *	0	0	1	8-11	3-4	1	0	Brownish grey	1	1	0	0	1	Khammouane Province	This paper
<i>C. pseudoquadrivirgatus</i>	0	1	1	-	2-3	1	0	Blackish brown	1	1	0	0	1	Salavan Province	Luu <i>et al.</i> 2013
<i>Cyrtodactylus wayakonei</i> species group															
<i>C. spelaeus</i>	0	1	1	8	2-3	0	1	Grey brown	1	1	0	0	0	Vientiane Province	Nazarov <i>et al.</i> 2014
<i>C. vilaphongi</i>	0	1	1	-	2	1	1	Blackish brown	1	1	1	0	0	Luang Prabang Province	Schneider <i>et al.</i> 2014
<i>C. wayakonei</i>	0	1	1	6-8	4	1	1	Grey-brown	1	1	1	0	0	Luang Nam Tha Province	Nguyen <i>et al.</i> 2010
<i>Cyrtodactylus interdigitalis</i> species group															
<i>C. interdigitalis</i>	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 tail; 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 preloacal and femoral pores (only in males); 20—number of postloacal 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 preacoal 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 preacoal 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 \pm SD 84.1 \pm 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 \pm SD 72.3 \pm 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 \pm SD 76.6 \pm 9.8 mm SVL), and the non-sympatric *C. calamei* (mean \pm SD 80.0 \pm 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).

Publication 12

**A new species of the genus *Lycodon* Boie, 1826 (Serpentes: Colubridae)
from Khammouane Province, central Laos**

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***Zootaxa*, in review**

A new species of the genus *Lycodon* Boie, 1826 (Serpentes: Colubridae) from Khammouane Province, central Laos

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Abstract

We describe a new species of the genus *Lycodon* Boie based on an adult male specimen from Khammouane Province, central Laos. *Lycodon banksi* **sp. nov.** is distinguished from its congeners by a combination of the following characters: (1) SVL 415 mm; (2) dorsal scales in 17–17–15 rows, dorsal scales on the anterior 2/3 of the body length smooth, the six central dorsal scale rows of the posterior 1/3 of the body length feebly keeled; (3) supralabials 8; (4) infralabials 10; (5) loreal in contact with the eye; (6) cloacal single; (7) ventral scales 241; (8) subcaudals 26+, paired (tail tip lost); (9) dorsal surface of body with 87 greyish yellow blotches; (10) dorsal surface of tail with 11+ light bands (tail tip lost); (11) ventral surface of body and tail uniformly grey cream. Based on the molecular comparisons, *Lycodon banksi* **sp. nov.** is placed in a clade with other species previously considered to be members of the separate genus *Dinodon*, except for *L. futsingensis*. The new species is at least about 9% genetically divergent from other species within this clade as shown by a fragment of the mitochondrial cytochrome *b*. Morphologically, the new species is distinguishable by its size, scalation, and colour pattern. This discovery increases the number of *Lycodon* species known from Laos to eleven species.

Key words: New species, *Lycodon*, Laos, karst forest, morphology, phylogeny, taxonomy.

Introduction

The genus *Lycodon* Boie is known as one of the most diverse genera of colubrid snakes, with currently 50 species being recognized (Uetz and Hošek 2015). This genus has a widespread distribution through eastern Iran to southern China and Japan, southward to the Philippines as well as the Indo-Australian Archipelago (Lanza 1999; Silver *et al.* 2013; Neang *et al.* 2014). Six species of *Lycodon* have been recently described within the last five years, namely *Lycodon synaptor* Vogel & David, 2010, *L. gongshan* Vogel & Luo, 2011 and *L. liuchengchaoi* Zhang, Jiang, Vogel & Rao, 2011 from China; *L. davidi* Vogel, Nguyen, Kingsada & Ziegler, 2012 from Laos; *L. zoosvictoriae* Neang, Hartmann, Hun, Souter & Furey, 2014 from Cambodia; and *L. cavernicolus* Grismer, Quah, Anuar, Muin, Wood & Nor, 2014 from Malaysia.

From Laos, ten species and subspecies of *Lycodon* have been reported to date comprising *L. capucinus* (Boie), *L. davidi*, *L. fasciatus* (Anderson), *L. futsingensis* (Pope), *L. laoensis* Günther, *L. meridionalis* (Bourret), *L. rufozonatus* Cantor, *L. ruhstrati abditus* Vogel, David, Pauwels, Sumontha, Norval, Hendrix, Vu & Ziegler, *L. subcinctus* Boie, and *L.*

septentrionalis Günther (Deuve 1970; Vogel *et al.* 2012; Siler *et al.* 2013; Luu *et al.* 2013; Teynié *et al.* 2014).

Our recent field surveys in the karst forest of Phou Hin Poun National Protected Area (NPA), Khammouane Province, central Laos led to the discovery of one snake specimen near the mouth of Khun Don cave, which revealed to be a representative of the genus *Lycodon* according to the following characters: orbit round with a vertically elliptical pupil; nostril enlarged; robustly arched upper maxillary bone with an inward curve in the anterior part; anterior and posterior maxillary teeth interrupted by a diastema; dorsal scales smooth or weakly keeled, bearing 17 rows anteriorly and at mid body, and posteriorly 15 rows; ventral scales weakly notched (Lanza 1999; Grismer *et al.* 2014). Although only a single specimen was available, its morphological characters distinctly differed from *L. meridionalis* and all remaining species of the genus *Lycodon*. The morphological findings were supported by molecular analyses so that we describe the single adult male from Phou Hin Poun, Khammouane Province, central Laos as a new *Lycodon* species.

Material and methods

Sampling. Field survey was conducted by Vinh Quang Luu and Thomas Calame in the Khun Don cave area within Phou Hin Poun NPA, Khammouane Province, central Laos in April 2016. Liver tissue sample was preserved separately in 95% ethanol and voucher specimen was fixed in approximately 85% ethanol, and subsequently transferred to 70% ethanol for permanent storage. The specimen from Phou Hin Poun NPA, central Laos was deposited in the collections of the Vietnam National University of Forestry (VNUF), Hanoi, Vietnam.

Morphological analysis. Measurements were taken following Vogel *et al.* (2009) with a digital calliper to the nearest 0.1 mm, except body and tail lengths. These measurements included: head length (HL, from snout tip to jaw angles); head width (HW, maximum head width at posterior margin of parietals); head height (HH, vertical height between upper and under sides of head were measured at HW); interorbital distance (IO, the distance between outer edges of supraoculars); eye–nostril distance (EN, from anterior edge of the orbit to posterior edge of nostril); internarial distance (IN, horizontal diameter between nostrils); eye diameter (ED, horizontal diameter of the orbit); snout length (SnL, from the tip of rostral to the anterior edge of the orbit); snout-vent length (SVL, from tip of snout to the vent); tail length (TaL); ratio of tail length / total length (TaL/TL); total length (TL).

Scale counts were taken following Vogel *et al.* (2009), except for ventral scales (VEN) which were counted according to Dowling (1951); formula of dorsal scale rows (DSR):

number of dorsal scale rows at neck (ASR, at one head length behind head), number of dorsal scales at midbody (MSR, at number of VEN/2), and number of dorsal scale rows before the vent (PSR, at one head length before the vent); supralabials (SL, counted on upper lips); infralabials (IL, counted on lower lips); loreals (Lor); loreal scale touching the orbit (yes or no); preoculars (PreOc); postoculars (PosOc); temporals (Temp, counted immediately behind postoculars and between posterior SL and parietals). Bilateral scale counts were given as left/right. Keel (keeled dorsal scale rows); PreVEN (preventral scales); VEN notched (present or absent); VEN keeled (present or absent); SC (subcaudal scales); numbers of pattern–units (like crossbars or vertebral blotches) are provided as number on body + numbers on tail.

Morphological and colour pattern data for comparisons were gained from Boulenger 1893; Smith (1943); Orlov & Ryabov (2004); Neang *et al.* (2014); Grismer *et al.* (2014); see also specimens listed in the Appendix.

Museum abbreviations are as follows: CAS–California Academy of Sciences; GP–Guo Peng; LSUMZ–The Louisiana State University Museum of Natural Science; MNHN–Muséum National d'Histoire Naturelle, Paris, France.

Molecular data and phylogenetic analyses.

Mitochondrial cytochrome *b* gene was employed in this study, because it has been widely used in previous molecular analyses of *Lycodon* (e.g., Guo *et al.* 2013, Siler *et al.* 2013). We included three new sequences from samples collected in Laos and Vietnam (Table 1). Other sequences of related species were obtained from GenBank. Three species, *Ahaetulla prasina*, *Boiga cynodon*, and *Dispholidus typus*, were assigned as outgroups based on their phylogenetic relationships to the genus *Lycodon* (Guo *et al.* 2013, Siler *et al.* 2013) (Table 1).

We used the protocols of Le *et al.* (2006) for DNA extraction, amplification, and sequencing. A fragment of the mitochondrial cytochrome *b* was amplified using the primer pair L14910/H160 64 (Burbrink *et al.* 2000). 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 analysis (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 and the number of bootstrap replicates in ML to 1000. The optimal model for nucleotide evolution was set to TVM+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. $BP \geq 70\%$ and $PP \geq 95\%$ are regarded as strong support for a clade. Uncorrected pairwise divergences were calculated in PAUP*4.0b10 (Table 2).

Results

Molecular data, Phylogenetic analysis

The final matrix consisted of 1100 aligned characters, of which 345 were parsimony informative. The alignment did not contain gaps. Maximum parsimony analysis of the dataset recovered two most parsimonious trees with 1094 steps (CI = 0.58; RI = 0.6). In the ML analysis, the score of the single best tree found was 6016.87 after 1581 arrangements were tried. The topology derived from the MP analysis (Fig. 1) was similar to that in Guo *et al.* (2013), but nodes of the phylogeny received lower statistical support. The new species was recovered in a clade together with other species, which were previously placed in the genus *Dinodon* (see Siler *et al.* 2013; Guo *et al.* 2013), except for *L. futsingensis*. This clade was strongly supported only by the MP analysis (BP = 85%) (Fig. 1). The new species is most closely related to *L. meridionalis* in terms of genetic distance based on cytochrome *b* data, and is diverged about 9.0–9.2% from the latter (Table 2).

Taxonomic account

Lycodon banksi sp. nov.

(Figs. 2–4)

Holotype. VNUF R.2015.20 (field number: TK 20.15), adult male, collected on 4 April 2015 by Vinh Quang Luu and Thomas Calame in the karst forest, at the mouth of Khun Don cave (17°33.731' N, 104°52.360' E), Phou Hin Poun NPA, near Ban Ha Village, Hinboun District, Khammouane Province, central Laos, at an elevation of 167 m a.s.l.

Diagnosis. *Lycodon banksi* sp. nov is characterized by the following morphological characters: (1) SVL 415 mm (2) dorsal scales in 17–17–15 rows, dorsal scales on the anterior 2/3 of the body length smooth, the six central dorsal scale rows of the posterior 1/3 of the body length feebly keeled; (3) supralabials 8; (4) infralabials 10; (5) loreal entering orbit; (6) cloacal single; (7) ventral scales 241; (8) subcaudals 26+, paired (tail tip lost); (9) dorsal surface of body with 87 greyish yellow blotches; (10) dorsal surface of tail with 11+ light bands (tail tip lost); (11) ventral surface of body and tail uniformly grey cream.

Description of the holotype. Head elongate (HL 15.3 mm), moderately distinct from the neck, rather flattened, longer than wide (HW/HL ratio 0.71), depressed (HH/HL ratio 0.40), narrow anteriorly (IN/IO ratio 0.65); snout elongate (SnL/HL ratio 0.39); nostril lateral, oval shaped, located in the middle of the nasal; eye large (ED/HL ratio 0.17), pupils vertically elliptic; rostral triangular, much broader than high, hardly visible from above; nasal divided into two scales by a vertical ridge along posterior edge of nostril; two square internasals, as wide as long, bordered by two large, subpentagonal prefrontals posteriorly; frontal single, enlarged, pentagonal, narrowed posteriorly; parietals longer than wide, in contact with each other medially, with upper anterior and posterior temporals, paraparietal laterally and four nuchal scales posteriorly; loreal 1/1, elongate, entering orbit; supralabials 8/8, first and second in contact with nasal, third to fifth entering orbit, sixth largest; infralabials 10/10, first pairs in broad contact with each other, first to fifth in contact with chin shields; first and second pairs of chin shields elongate, of the same size and shape, separated by a medial groove, first pair larger than the second; preocular 1/1; postoculars 2/2, of the same size, bordering anterior temporals; anterior temporals 2/2, posterior temporals 3/3, upper ones smaller than lower ones.

Body elongate, SVL 415 mm; TaL >50 mm (tail tip lost); ventrals 241 (including two preventrals); subcaudals at least 26, divided, weakly notched in lateral sides; cloacal single; DSR 17–17–15; dorsal scales on the anterior 2/3 of the body length smooth, the six central dorsal scale rows of the posterior 1/3 of the body length feebly keeled; the vertebral scales not enlarged.

Colouration in life. Head dark grey, without vertical light nuchal band; dorsal surface of body dark grey-yellow with 87 greyish yellow irregular dorsal blotches; first body blotch starting at ventral scale 13, a half vertebral scale covered by this blotch; two yellow stripes on each side, from behind the neck to vent, indistinct posteriorly; ventral scales grey cream; dorsal surface of tail with at least eleven greyish yellow tail blotches, ventral surface of tail grey cream.

Hemipenis. The left hemipenis is partially everted and shows spinose ornamentation.

Comparisons. In our phylogenetic analysis, *Lycodon banksi* sp. nov. is closely related to *L. meridionalis*, *L. rufozonatus*, *L. semicarinatus* (Cope), and *L. futsingensis*. However, the new species differs from *L. meridionalis* by having a distinctly smaller size (SVL 415.0 mm *versus* 1295.0 mm maximum length in *L. meridionalis*), loreal entering the orbit (*versus* separated from the orbit), dorsal scales on the anterior 2/3 of the body length smooth, the six

central dorsal scale rows on the posterior body third feebly keeled (*versus* distinctly keeled), dorsal head pattern uniform dark grey (*versus* with yellow-black marbling in *L. meridionalis*), and ventral surface grey cream (*versus* yellow with dark spots posteriorly) (see Bourret 1935; Orlov & Ryabov 2004); from *L. rufozonatus* by its distinctly smaller size (SVL 415 *versus* 830 mm), having loreal entering the orbit (*versus* usually separated), a distinctly higher ventral scale count (241 *versus* 185–204), dorsal scales feebly keeled in the posterior body part (*versus* all smooth), dorsal head pattern uniform dark grey (*versus* dark brown with yellowish borders), and body bands greyish yellow (*versus* dark brown); from *L. semicarinatus* by its distinctly smaller size (SVL 415 *versus* 870 mm), having loreal touching the orbit (*versus* separated), a higher ventral scale count (241 *versus* 211–234), dorsal scale rows keeled along posterior 1/3 (*versus* keeled along anterior half), belly pattern uniform grey cream (*versus* yellowish), and body bands greyish yellow (*versus* yellowish brown); from *L. futsingensis* by having loreal entering the orbit (*versus* separated), a higher ventral scale count (241 *versus* 209), dorsal scales feebly keeled in the posterior body part (*versus* all smooth), lower number of body bands (22 *versus* 87), and body bands greyish yellow (*versus* light grey) (Table 4).

The new species differs from *L. flavozonatus* by its much smaller size (SVL 415 *versus* 990–1170 mm), having loreal in contact with the orbit (*versus* separated), cloacal single (*versus* divided), six dorsal scale rows on the posterior third of the body feebly keeled (*versus* 10–12 keeled dorsal scale rows at midbody), dorsal head dark grey (*versus* black with light markings), and belly pattern uniform grey cream (*versus* yellow with large black spots). The new species can be distinguished from *L. capucinus* by having more ventrals (241 *versus* 182–211) fewer supralabials (8/8 *versus* 9–10), cloacal single (*versus* divided), dorsal blotches 87 (*versus* reticulated), and greyish yellow blotched body pattern (*versus* reticulated) (see Neang *et al.* 2014).

The new species can be distinguished from all species of the *L. ruhstrati* group (Vogel *et al.* 2009) by having a loreal entering the orbit (*versus* separated from the orbit). The new species differs from *L. butleri* Boulenger, *L. fasciatus*, *L. gongshan*, and *L. luichengchaoi* of the *L. fasciatus* group (Vogel *et al.* 2009) by having more ventrals (241 *versus* 128–227, collectively), the absence of a nuchal band (*versus* present), more dorsal blotches (87 *versus* 19–45 bands, collectively), and belly and ventral surface of tail without bands (*versus* banded); from *L. cavernicolus* by having slightly fewer ventrals (241 *versus* 245), dorsal head uniformly dark grey (*versus* light brown), fewer supralabials (8 *versus* 9 or 10), more dorsal blotches (87 *versus* 36–45 bands), dorsal scales on the anterior 2/3 of the body length smooth,

the six central dorsal scale rows of the posterior 1/3 of the body length feebly keeled (*versus* keeled), and greyish yellow blotched pattern on the body (*versus* white bands).

Distribution. *Lycodon banksi* sp. nov. is currently known only from the type locality in Phou Hin Poun NPA, Khammouane Province, central Laos (Fig. 5).

Etymology. The species naming is dedicated to our friend and colleague Chris Banks, International Coordinator, Philippine Crocodile National Recovery Team, Zoos Victoria, Australia, for his outstanding contributions towards amphibian and reptile conservation, in particular of the Philippine Crocodile. We propose the following common names: Banks' Wolf Snake (English), Banks Wolfszahnatter (German).

Natural history. The specimen was found at 20:39, crawling on a limestone outcrop in the karst forest, approximately 0.3 m above the forest floor, at an elevation of 167 m a.s.l. The humidity at the time of collection was approximately 85% and the air temperature ranged from 23 to 26°C (Fig. 6).

Discussion

In our phylogenetic analyses, *Lycodon banksi* is placed in a clade with other species previously considered to be members of the separate genus *Dinodon*, except for *L. futsingensis*. In addition, the specimen of *L. meridionalis* from Bac Kan Province, Vietnam was nested in the same clade with *L. flavozonatus* from Guangdong and Guangxi provinces in southern China. The genetic distance between the Vietnamese and Chinese samples is approximately 1.4 – 2.4% (2.6% between two Chinese samples). Morphological features of the specimen from Bac Kan Province (VNFU R.2012.4) are consistent with those in the descriptions of *L. meridionalis* by Bourret (1935) and Orlov & Ryabov (2004) in the following characters: snout-ventlength in males reaching 1295 mm; dorsal head with yellow-black marble markings; transverse bands on body 86–115; ventral scales 234–245; cloacal plate single; belly pattern uniform yellow with dark spots posteriorly (Table 4). Therefore, we herein initially assign two specimens (GP 1939, 2279) from China to *L. meridionalis* based on molecular data, although this placement needs to be confirmed by further morphological studies.

Superficially, the new species is most similar to *L. meridionalis* in the dorsal pattern. However, they are clearly distinguishable in other morphological features, e.g., the snout-vent length, dorsal scalation, dorsal head, and belly patterns. Although the new species has no sister species as supported by phylogenetic analyses, it is most closely related to *L. meridionalis* in terms of genetic distance, but distinctly differing from the latter (ca. 9%).

The new species seems to be a nocturnal and terrestrial snake, endemic to the northern Truong Son Range. It is a karst-dweller, as are *L. davidi* and *L. ruhstrati abditus* (Vogel *et al.* 2012; Luu *et al.* 2013). *L. banksi* has a unique pattern of dark grey and yellow colouration on its dorsal surface, which offers a perfect camouflage among litter on the forest ground. Moreover, the species has indistinct banding on the dorsal surface in comparison with its congeners of the *L. ruhstrati* and *L. fasciatus* groups.

The discovery of this new species increases the number of *Lycodon* species from Laos to eleven. In the same area, we recently discovered two new bent-toed geckos (*Cyrtodactylus jaegeri* Luu, Calame, Bonkowski, Nguyen & Ziegler, *Cyrtodactylus soudthichaki* Luu, Calame, Nguyen, Bonkowski & Ziegler) and two new true gecko species (*Gekko thakhekensis* Luu, Calame, Nguyen, Le, Bonkowski & Ziegler, *Gekko bonkowskii* Luu, Calame, Nguyen, Le, Bonkowski & Ziegler) (Luu *et al.* 2014a,b; Luu *et al.* 2015a,b). These recent discoveries together with the new *Lycodon* species provide strong evidence that the northern Truong Son

Range, and especially the extensive limestone karst formations in Khammouane Province, central Laos is a hotspot of endemic biodiversity.

The finding of this new *Lycodon* species with its unusual colour pattern and morphology suggests that the morphological and genetic diversity within the genus *Lycodon* might be far greater than commonly assumed. Our study further underlines the need to combine detailed morphological and molecular data to delineate species complexes. Unfortunately, it was not possible to obtain molecular data from all investigated reference species (e.g., *Lycodon fasciatus* specimen MNHN 1928.69 from Xieng Khoang Province, northern Laos) due to its age and formalin-fixed condition. Therefore, further field studies are needed to accurately assess the diversity of *Lycodon* in this poorly studied karst forest systems of central Laos.

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Appendix. Comparative specimens examined

Lycodon capucinus. Laos: Bolikhamxay Province: Tad Leuk: VNUF R.2015.15 (field number: PKK06.15).

Lycodon fasciatus. Laos: Xieng Khoang Province: MNHN1928.69

Lycodon fasciatus. China: Yunnan Province: MNHN1919.148

Lycodon fasciatus. China: Tibet: MNHN1912.465

Lycodon fasciatus. China: Tibet: MNHN1912.466

Lycodon fasciatus. India: MNHN1928.69

Lycodon futsingensis. Laos: Khammouane Province: VFU A.2013.4

Lycodon meridionalis. Vietnam: Bac Kan Province: Ba Be National Park: VNUF R.2012.4 (field number: BBR4).

Figure Captions

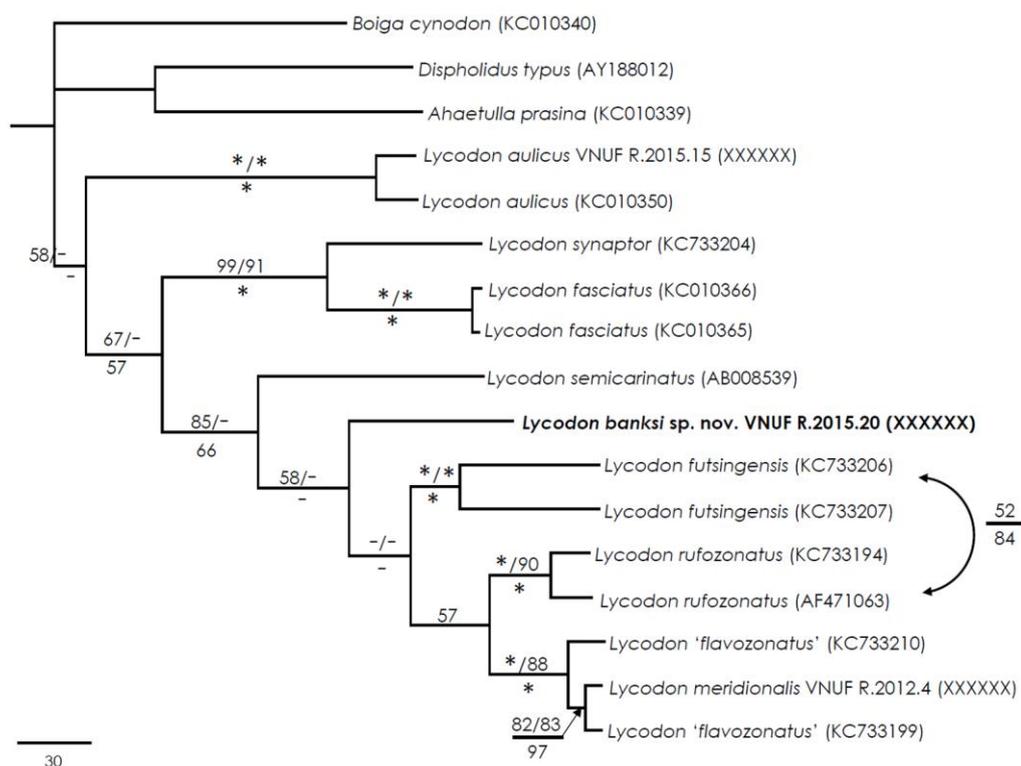


FIGURE 1. One of the two most parsimonious maximum parsimony trees based on the partial cytochrome *b* gene. Numbers above and below branches are bootstrap values of MP/ML analyses (>50%) and Bayesian posterior probabilities, respectively. The arrow and numbers indicate the sister relationship between two taxa and the BP (above) and PP (below) values supported by the ML and Bayesian analyses, respectively. Asterisk denotes 100% value.



FIGURE 2. Adult male holotype of *Lycodon banksi* **sp. nov.** (VNUF R.2015.20) in life: A) dorsolateral view; B) head in dorsolateral; and C) head in dorsal view. Photos: V. Q. Luu

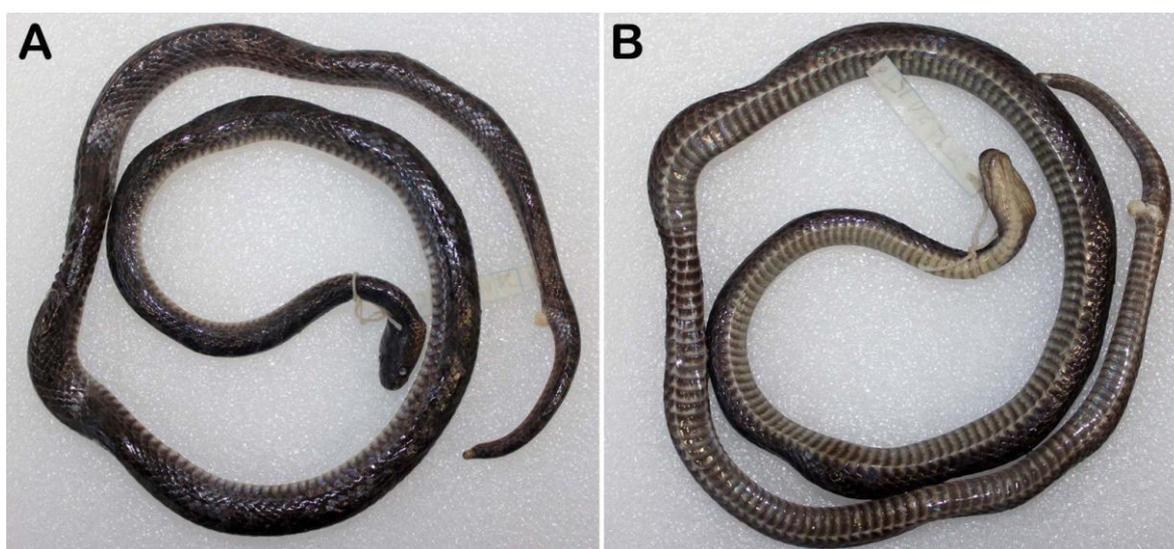


FIGURE 3. Adult male holotype of *Lycodon banksi* **sp. nov.** (VNUF R.2015.20) in preserved state: A) dorsal view; and B) ventral view. Photos: V. Q. Luu

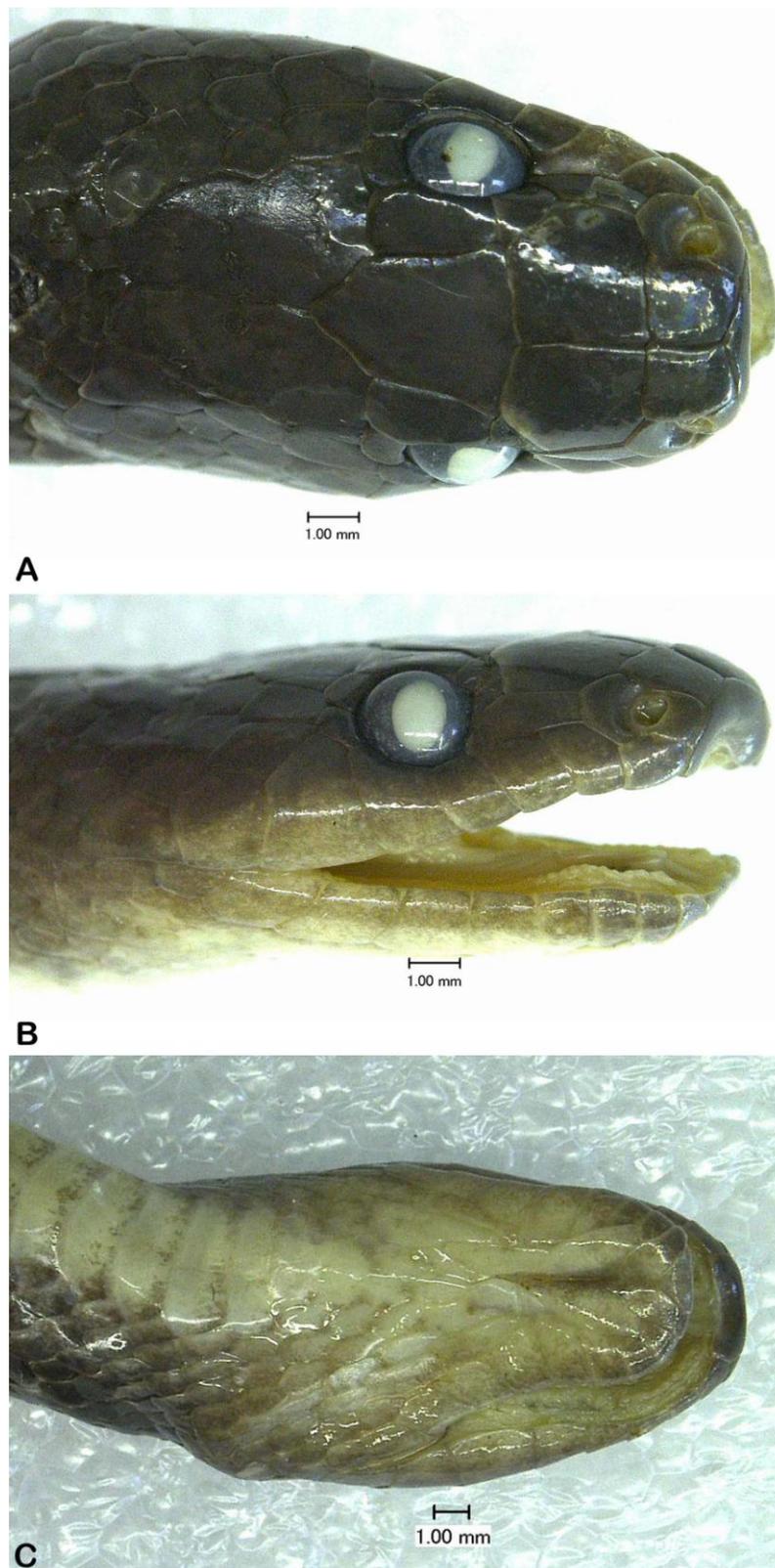


FIGURE 4. Head portraits of the preserved holotype of *Lycodon banksi* sp. nov. (VNUF R.2015.20): A) dorsal view; B) lateral view; and C) ventral view. Photos: V. Q. Luu



FIGURE 5. Map showing the type locality of *Lycodon banksi* sp. nov. in Khammouane Province, Laos.



FIGURE 6. Habitat of *Lycodon banksi* **sp. nov.** at its type locality. Photo: V. Q. Luu.

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

Species	GenBank no.	Locality	Voucher number
<i>Ahaetulla prasina</i>	KC010339	Philippines: Palawan Province	KU 326673
<i>Boiga cynodon</i>	KC010340	Philippines: Negros Occidental Province	KU:324614
<i>Dispholidus typus</i>	AY188012	Not reported	Not reported
<i>Lycodon aulicus</i>	KC010350	Philippines: Romblon Province	KU:315378
<i>L. aulicus</i>	XXXXXX	Laos: Bolikhamxay Province	VNUF R.2015.15
<i>Lycodon banksi</i> sp. nov.	XXXXXX	Laos: Khammouane Province	VNUF R.2015.20
<i>L. fasciatus</i>	KC010366	Myanmar: Chin State	CAS 234957
<i>L. fasciatus</i>	KC010365	Myanmar: Chin State	CAS 234875
<i>L. futsingensis</i>	KC733206	China: Zhejiang	GP 2216
<i>L. futsingensis</i>	KC733207	China: Guangdong	GP 2226
<i>L. 'flavozonnatus'</i>	KC733210	China: Guangdong	GP2279
<i>L. meridionalis</i>	XXXXXX	Vietnam: Bac Kan Province	VNUF R.2012.4
<i>L. 'flavozonnatus'</i>	KC733199	China: Guangxi	GP 1939
<i>L. rufozonatus</i>	KC733194	China: Sichuan	GP 133
<i>L. rufozonatus</i>	AF471063	Not reported	LSUMZ:44977
<i>L. semicarinatus</i>	AB008539	Not reported	Not reported
<i>L. synaptor</i>	KC733204	China: Yunnan	GP 2188

TABLE 2. Uncorrected (“p”) distance matrix showing percentage pairwise genetic divergence (cytochrome *b*) between new and closely related species.

Species name	1	2	3	4	5
1. <i>Lycodon banksi</i> sp. nov.	–				
2. <i>L. meridionalis</i> & <i>L. 'flavozonnatus'</i>	9.0–9.2	–			
3. <i>L. futsingensis</i>	9.6	8.5–8.7	–		
4. <i>L. rufozonatus</i>	10.6–11.1	7.4–8.2	8.7–9.2	–	
5. <i>L. semicarinatus</i>	10.9	9.8–10.3	10.3	9.3–10.2	–

TABLE 3. Measurements (in mm) and morphological characters of the holotype of *Lycodon banksi* **sp. nov.** (measurements in mm; for other abbreviations see material and methods; * tail tip lost).

<i>Lycodon banksi</i> sp. nov.	
Character	VNUF R.2015.20
Sex	male
SVL	415.0
TaL	50.0*
TL	465.0
TaL/TL	0.108*
HL	15.3
HW	10.8
HH	6.1
IO	6.3
EN	3.3
IN	4.1
ED	2.6
SnL	6.0
DSR	
ASR (neck)	17
MSR (midbody)	17
PSR (precloacal)	15
Keel	6 dorsal scale rows on the posterior body third feebly keeled
VEN	241
PrVEN	2
Ventral notched	present
Ventral keeled	absent
SC	26*
divided	yes
Cloacal (single/divided)	1
Loreal (left/right)	1/1
Loreal entering orbit	yes
SL (left/right)	8/8
entering orbit left	3,4,5
entering orbit right	3,4,5
largest scales (L/R)	6/6
IL (left/right)	10/10

IL s incotact with 1st chin shield	1–5
PreOc (L/R)	1/1
PostOc (L/R)	2/2
Temporal scales	
anterior	2/2
posterior	3/3
Paras (scales around paraparietal)	5/7
Parab (scales between parietals)	4
Nuchal band	absent
Body bands	87 (yellow blotches)
Tail blotches/bands	15*
Belly pattern	grey cream
Belly bands	absent
Ventral tail pattern	grey cream
First body blotch/band position (at VEN)	13
First band width (vertebral scales)	0.5

TABLE 4. Diagnostic characters separating *Lycodon banksi* **sp. nov.** from closely related species (data obtained from Boulenger 1893; Smith 1943; Orlov & Ryabov 2004; Luu *et al.* 2013 and own data).

Characters	<i>Lycodon banksi</i> sp. nov.	<i>L. meridionalis</i>	<i>L. rufozonatus</i>	<i>L. semicarinatus</i>	<i>L. futsingensis</i>	<i>L. flavozonatus</i>
Maximum snout-vent length (mm)	415	1295	830	870	603	901
Loreal scale touching the orbit	yes	no	no (rarely yes)	no	no	no
Head pattern	dark grey	yellow-black marble markings	dark brown with yellowish borders	black	black	black with light markings and yellow collar on the nape
Ventral scales	241	234–246	185–204	211–234	209	202–225
Cloacal plate	single	single	single	single	single	double
Supralabials	8	8	8	8	8	not reported
Infralabials	10	9–10	5	5	9	not reported
Number of keeled dorsal scale	6 dorsal rows on the posterior body third feebly keeled	9 (distinctly keeled)	0	keeled in anterior half	0	10–12
Number of blotches or bands on body	87	86–115	not reported	not reported	22	51–78
Belly pattern	uniform grey cream	uniform yellow with dark spots posteriorly	not reported	yellowish	cream, speckled posteriorly	yellow with large black spots
Blotch/band colour	greyish yellow	yellow	dark brown	yellowish brown	light grey	yellow

Publication 13

**First record of *Gracixalus quyeti* (Amphibia: Anura: Rhacophoridae) from
Laos: molecular consistency versus morphological divergence between
populations on both sides of the Annamite Range**

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Revue Suisse de Zoologie, in review

First record of *Gracixalus quyeti* (Amphibia: Anura: Rhacophoridae) from Laos: molecular consistency versus morphological divergence between populations on both sides of the Annamite Range

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ABSTRACT

We report the first country record of the poorly known *Gracixalus quyeti* from Laos based on a recently collected specimen from Khammouane Province, central Laos. While the genetic analysis revealed nearly identical sequences, we recorded some differences in body ratios and colour patterns among the specimen from Laos and type specimens from the eastern side of the Annamite Range in Vietnam.

Key words. *Gracixalus quyeti*, biogeography, distribution, new record, Annamite Range, Laos.

INTRODUCTION

Although the knowledge of amphibian diversity in Laos has strikingly increased within the last two decades, information is lacking on distribution patterns and natural history (Luu et al. 2014). It is known that studies on geographic distribution of species are essential for understanding their evolution and ecology and are furthermore crucially required for effective conservation (Nguyen et al. 2014, Rowley et al. 2015). The rhacophorid genus *Gracixalus* currently contains 11 species whose range is restricted to lowland and montane forests in China, Thailand, Vietnam and Laos (Nguyen et al. 2008, Rowley et al. 2011, Frost 2014, Matsui et al. 2015). However, relatively little is known about this genus, and distribution ranges of the species within the genus are still poorly understood. For example, *G. supercornutus* (Orlov, Ho & Nguyen, 2004) has been recently recorded from Laos, but was previously known only from Vietnam (Luu et al. 2014). While *G. supercornutus* has been the only recorded species of this genus from Laos until now, four other species are currently known only from Vietnam, including *G. lumarius* (Rowley, Le, Dau, Hoang & Cao, 2014), *G. waza* (Nguyen, Le, Pham, Nguyen, Bonkowski & Ziegler, 2013), *G. quangi* (Rowley, Dau, Nguyen, Cao & Nguyen, 2011) and *G. quyeti* (Nguyen, Hendrix, Böhme, Vu & Ziegler, 2008).

In this study, we report *Gracixalus quyeti*, a recently described and poorly known species from Phong Nha – Ke Bang National Park (NP) in central Vietnam, for the first time from Hin Nam No National Protected Area (NPA) in central Laos on the western side of the Annamite Range, only 80 km straight line distance apart from the type locality in Phong Nha – Ke Bang NP.

MATERIAL AND METHODS

A single female specimen of *Gracixalus quyeti* (VNUF A.2014.73) was collected by Vinh Quang Luu, Thomas Calame, Dung Van Phan and Kieusomphone Thanabuaosy during a field survey in May 2014 in Noong Ma Village (17°17.394' N, 106°09.980' E, recorded by a Garmin GPSMAP 60CSx GPS receiver and recorded in datum WGS 84), within Hin Nam No NPA, Boualapha District, Khammouane Province, central Laos. The specimen was anaesthetized in a closed vessel with a piece of cotton wool containing ethyl acetate. After taking photographs, the specimen was fixed in 80% ethanol and subsequently transferred into 70% ethanol for permanent-storage. A tissue sample was preserved separately in 95% ethanol. The specimen has been deposited in the collection of the Vietnam National University of Forestry (VNUF), Hanoi, Vietnam.

Molecular analysis. Total genomic DNA was extracted from a tissue sample using a commercially available DNeasy Tissue Kit following manufacturer's instructions (QIAGEN Inc., Valencia, CA, USA). A fragment of 16S gene was amplified using the primer pair 16Sar + 16Sbr (Palumbi et. al 1991). The standard PCR conditions used for 16S were: 95° C for 5', 40 cycles of [95° C for 30'', 50° C for 45'', 72° C for 60''] and 72° C for 6'. All PCR products were visualized on a gel before sequencing. Successful amplifications were purified to eliminate PCR components using GeneJET™ PCR Purification kit (Fermentas, Canada). Purified PCR products were sent to Macrogen Inc. (Seoul, South Korea) for sequencing. The obtained sequence was compared to those available from other species using the BLAST search in GenBank.

Morphological analysis. Determination of morphological characters followed Ohler et al. (2002) and Nguyen et al. (2008). Measurements were taken by the first author with a digital caliper to the nearest 0.1 mm. Abbreviations were used as follows: SVL: snout-vent length; HL: head length (from the back of mandible to the tip of snout); HW: head width (across angle of jaws); MN: distance from the back of mandible to the nostril; MFE: distance from the back of mandible to the front of eye; MBE: distance from the back of mandible to the back of eye; IFE: distance between the front of eyes; IBE: distance between the back of eyes; IN: internasal distance; EN: distance from the front of eye to the nostril; EL: horizontal eye diameter; NS: distance from nostril to the tip of snout; SL: distance from the front of eye to the tip of snout; TYD: greatest tympanum diameter; TYE: distance from tympanum to the back of eye; IUE: minimum distance between upper eyelids; UEW: maximum width of upper

eyelid. Forelimb: HAL: hand length (from the base of outer palmar tubercle to the tip of fourth toe); FLL: forelimb length (from the elbow to the base of outer tubercle); TFL: third finger length (from the base of the first subarticular tubercle to the tip of third toe); fd1-4: width of discs of fingers I-IV; fw1-4: width of fingers I-IV (measured at the narrowest point of the distant phalanx). Hindlimb: FL: femur length (from vent to knee); TL: tibia length; TW: tibia width; FOL: foot length (from the base of inner metatarsal tubercle to the tip of fourth toe); FTL: fourth toe length (from the base of the first subarticular tubercle to the tip of fourth toe); TFOL: distance from the base of tarsus to the tip of fourth toe; IMT: length of the inner metatarsal tubercle; ITL: inner toe length; td1-4: width of discs of toes I-IV; fw1-4: width of toes I-IV (measured at the narrowest point of the distant phalanx). Webbing: MTTF: distance from the distal edge of metatarsal tubercle to the maximum incurvation of web between third and fourth toes; TFTF: distance from the maximum incurvation of web between third and fourth toes to the tip of fourth toe; MTFF: distance from the distal edge of metatarsal tubercle to the maximum incurvation of web between fourth and fifth toes; FFTF: distance from the maximum incurvation of the web between fourth and fifth to the tip of fourth toe. Webbing formula description followed Glaw & Vences (2007). Comparative character data were taken from Nguyen et al. (2008). Institutional abbreviations are as follows: ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; VNUH: Vietnam National University, Hanoi, Vietnam.

RESULTS

The Laotian specimen has been found at night (20:30) while sitting on a branch of a shrub, ca. 0.5 m above an outcrop at an elevation of 592 m above sea level. The air temperature was 27.3°C and the humidity was 80%. The locality was surrounded by limestone cliffs and karst vegetation, mainly consisting of species of Ebenaceae, Dracaenaceae, Arecaeae, Meliaceae, and Moraceae.

Comparative analysis of the obtained sequence with those from GenBank (ZFMK 82999: EU871429.1, VNUH 160706: EU871428.1) showed 99% similarity between the newly collected specimen from Laos (VFU A. 2014.73) and the holotype (ZFMK 82999) as well as the paratype (VNUH 160706) of *Gracixalus quyeti* from Vietnam.

The morphological diagnosis coincided with the original description of *G. quyeti* from central Vietnam (Nguyen et al. 2008) in the following characters: Small rhacophorid (ZFMK 82999 SVL 34 mm, VFU A. 2014.73 SVL 31.4 mm), vomerine teeth absent. Snout rounded, longer

than the diameter of eye. Nostrils closer to tip of snout than to eye. Pupil oval and horizontal. Tympanum distinct, rounded and wider than disc of finger III. Dorsal surface of head, back and upper portion of flanks covered with small sharp tubercles. Dark pattern forming an inverse Y, triangular spot between eyes bifurcating into two bands continuing posteriorly onto the back. Brown marbling on margin of throat and throat. Webbing moderately developed: $1i(1)-(2)j2e(0.5)-(1\frac{2}{3})j3e(0.5)-(2)j4e(2)-(0.5)j5$.

Despite the high genetical correspondence, we also noted some differences in morphology and colour pattern between the examined specimen from Laos and the type specimens of *G. quyeti* (Nguyen et al. 2008): Body ratios: Head wider than long, in contrast to longer than wide in the type specimens. Forelimb slightly shorter, same as hand length with 27% of SVL (holotype 30%, paratype 28%). Length of finger III 16% of SVL and remarkably shorter than in the specimens from Vietnam (holotype 24%, paratype 19%). Hind limb approximately 1.45 times longer than SVL, shorter than in specimens from Vietnam (holotype: 1.6, paratype: 1.7). Tibia 1.5 times thinner than in the holotype. Length of toe IV 23% of SVL, remarkably shorter than in the holotype (37%) and slightly shorter compared to the paratype (25%). Fingers and toes approximately 2 to 4 times thinner than in the holotype (Tab. 1).

Coloration in life: Dorsal surface of head and body is greenish beige to grayish light-brown with a grayish dark-brown blotching pattern as described above, whereas it is brownish to moss-green with a dark brown pattern in the adult holotype and moss-green with an indistinct pattern in the subadult paratype. Forelimb and dorsal part of hindlimbs are beige to grayish light-brown with grayish dark-brown bands, moss-green with dark brown bands in the holotype and the subadult paratype. Ventral surface can only be described based on preserved specimens: Belly, chest and throat slightly white to yellowish white with brown marbling on margin of throat and throat, background color more yellowish in the preserved holotype and more bluish in the paratype (Fig. 1A-B).

DISCUSSION

The record of *Gracixalus quyeti* in Hin Nam No NPA, Laos is approximately 80 km straight line distance apart from the type locality in Quang Binh Province, central Vietnam (Fig. 2). It is likely that *G. quyeti* is more widespread across the Annamite's extensive limestone areas of central Vietnam and central Laos. The species might potentially be endemic to these fragmented lowland and montane forest habitats, while its occurrence seems to be relatively rare within this presumed distribution range.

According to Rowley et al. (2011), molecular distances vary along and within species of the genus *Gracixalus*. Within the group of *Gracixalus jinxiuensis*, individuals with 0.2 – 0.6% genetic divergence in the mitochondrial 16S gene have been identified as three distinct species within two genera (*G. jinxiuensis*, *Kurixalus carinensis* and *K. odontotarsus*), while specimens of *G. gracilipes* that have been collected in 75–120 km distance showed 1 – 3% molecular divergence.

All records of *G. quyeti* were derived from different elevations in the limestone area within the transition zone between the northern and central Annamite Mountains, a semiconnected array of hills and forested limestone karst outcrops. The Annamite Range generally experiences a tropical wet monsoon climate, while the eastern oceanic Phong Nha Ke – Bang NP receives more precipitation and has lower average temperatures than Hin Nam No on the western side in the rain shadow of the Annamite Range (Timmins & Cuong 2001, Sterling et al. 2006, Bain & Hurley 2011). Taking into account the climatic differences between both sides of the Annamite Range and the lack of knowledge about the genus *Gracixalus* cited above, further research must clarify if the shown morphological differences in coloration and body ratios may possibly reflect ecological adaptations to different environments, evolutionary driven morphs or likely just reflect variation within this poorly known species.

Still, our finding elevates the number of amphibian species recorded from Laos to 100, and the number of rhacophorid species known to occur in Laos to 34. Although the species number of amphibians known from Laos has nearly doubled during the last 15 years from 58 to 100 recorded species, the amphibian species richness of Laos is still underestimated (Stuart 1999, Frost 2014, Teynié et al. 2014, Luu et al. 2014). In particular big gaps remain in our knowledge of the Annamite's amphibian ecology and distribution.

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Figure Captions

Figure 1. (A) dorsolateral view, and (B) lateral view of the female of *Gracixalus quyeti* from Hin Nam No NPA, central Laos. Photos: T. Calame.

Figure 2. Map showing the distribution of *Gracixalus quyeti*, including the localities of the type series after Nguyen et al. (2008) in Quang Binh Province, Vietnam (marked with blue dots) and our first record from Khammouane Province, Laos (marked with a red dot).

Table 1. Morphological characters of the newly collected specimen of *Gracixalus quyeti* from Laos in comparison with type specimens from Vietnam (after Nguyen et al. 2008, measurements in mm, abbreviations defined in the text).

	VNUH A. 2014.73 female Hin Nam No NPA, central Laos	ZFMK 82999 female, holotype Phong Nha Ke-Bang NP central Vietnam	VNUH 160706 subadult, paratype Phong Nha Ke-Bang NP, central Vietnam
SVL	31.4	34.0	22.0
HL	10.3	12.5	8.2
HW	11.73	11.4	7.4
MN	10.3	11.2	7.4
MFE	6.96	8.4	5.4
MBE	3.86	4.5	3.3
IFE	5.45	6.9	4.3
IBE	8.5	11.0	6.8
IN	3.08	3.0	2.1
EN	2.9	3.5	2.5
EL	4.0	4.8	3.2
NS	1.34	2.1	1.3
SL	4.22	5.4	3.8
TYD	2.0	2.5	1.6
TYE	0.92	1.0	0.7
IUE	3.89	4.1	2.4
UEW	2.36	3.0	1.8
HAL	8.4	10.3	6.1
FLL	6.4	7.2	4.9
TFL	4.97	8.1	4.2
fw 1-4	0.31/0.36/0.38/0.36	0.6/0.9/1/0.9	
fd 1-4, 3	0.48/0.83/0.99/1	1/1.6/1.9/1.7	1.2

FL	15.68	18.5	11.5
TL	17.61	20.0	11.8
TW	2.57	4.2	2.0
FOL	12.21	15.2	13.9
FTL	7.1	12.5	5.6
TFOL	20.47	24.8	8.1
IMT	0.82	1.3	0.8
ITL	3.83	4.2	1.9
MTTF	7.1	9.4	3.9
MTFF	7.3	9.8	4.7
TFTF	4.71	5.6	3.0
FFTF	4.38	5.0	2.8
tw 1-5	0.28/0.29/0.36/0.49/0.4	0.8/0.9/1.1/1.3/1.1	
td 1-5	0.35/0.66/0.6/0.96/0.8	0.5/0.6/0.7/0.9/0.8	

4. Discussion

4.1 Comparison of the herpetofaunal communities between the eastern and western sides of the Truong Son Range

First of all, I compared the similarity of herpetofauna communities, measured by Sørensen similarity index to their spatial distance. The assumption was that differences between communities would increase with distance of the habitats (isolation by distance) (Wright 1943).

For this purpose I compared the relationships of community compositions of Hin Nam No (Laos) to six protected areas with similar karst forests in the central and northeastern Vietnam: Phong Nha - Ke Bang NP (Quang Binh Province) (publication 1), Kim Hy Nature Reserve (NR) and Ba Be NP (Bac Kan Province), Du Gia NR and Tay Con Linh NR (Ha Giang Province), Cat Ba NP (Hai Phong Province) (Bain & Nguyen 2004; Le *et al.* 2004; Nguyen *et al.* 2009; Ziegler *et al.* 2014; Nguyen *et al.* 2011b; Pham *et al.* 2015a-b). All protected areas were on the mainland, except for Cat Ba NP which is an isolated island area.

a) Amphibians:

With the increasing distance, the similarity level of amphibian communities decreased (Fig. 4.1). The Sørensen index for Cat Ba NP was the lowest (0.25) because Cat Ba NP is an isolated island area. For that reason, species' distribution and migration rates are limited.

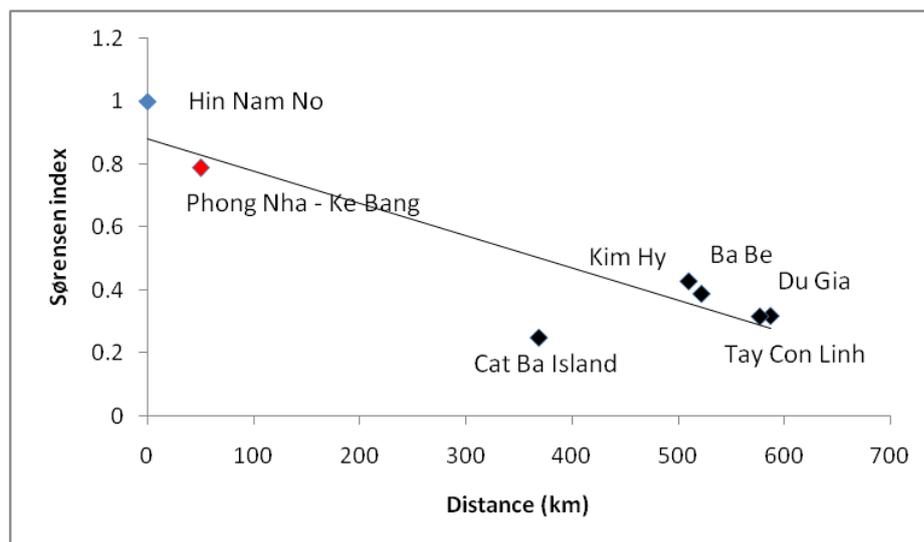


FIGURE 4.1. Relation of community similarity (Sørensen index) and distance of the amphibian faunas between Hin Nam No and similar karst forest regions in Vietnam

The higher level of amphibian species similarity between Hin Nam No and Phong Nha - Ke Bang was further supported by a cluster analysis (Fig 4.2).

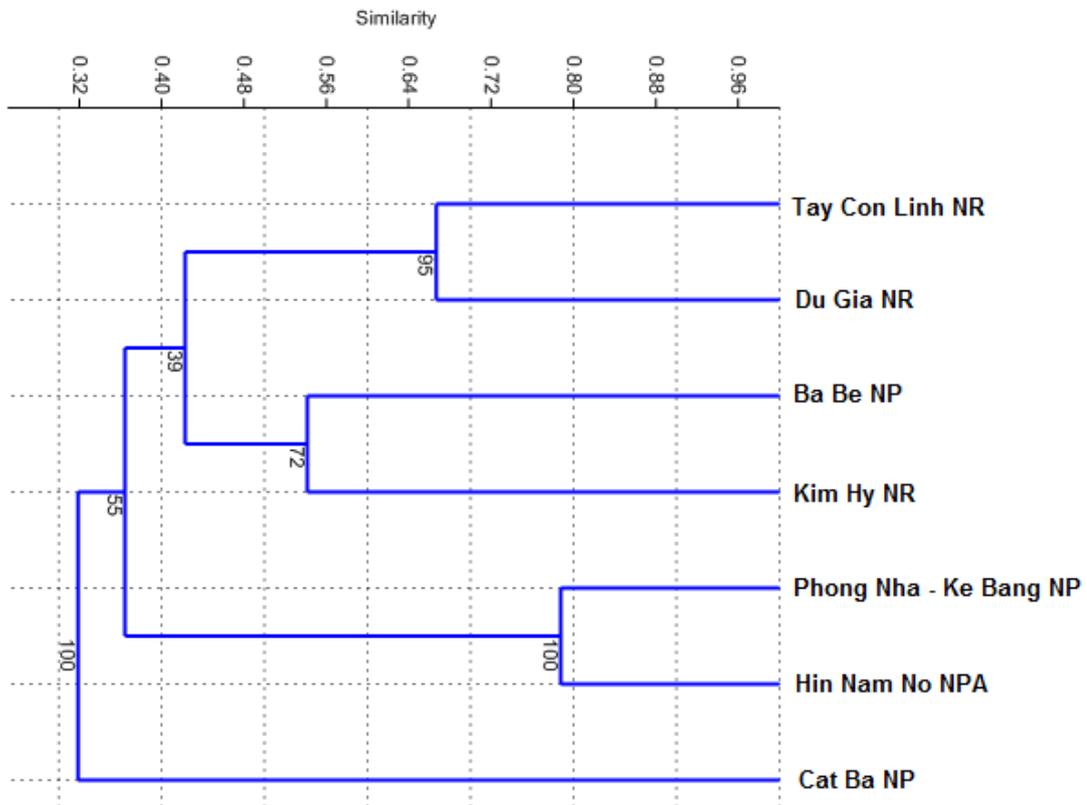


FIGURE 4.2. Cluster analysis (Sørensen index) of the amphibian faunas between Hin Nam No and and similar karst forest regions in Vietnam

Twelve amphibian species (20% of the total amphibian species numbers of both areas) were found in Phong Nha - Ke Bang (publication 1) but could not yet be recorded in Hin Nam No (Fig. 4.3). These are *Ichthyophis chaloensis*, *Brachytarsophrys intermedia*, *Hyla simplex*, *Amolops cremnobatus*, *Babina chapaensis*, *Hylarana maosonensis*, *Feihyla vittata*, *Rhacophorus annamensis*, *R. dennysi*, *R. exechopygus*, *Theلودerma corticale*, and *T. vietnamensis*. By contrast, seven amphibian species (14% of the total amphibian species numbers of both areas) are only known from Hin Nam No but have not been found in Phong Nha - Ke Bang, namely *Ichthyophis* sp., *Leptobrachium* sp., *Leptolalax minimus*, *Kaloula indochinensis*, *Hylarana erythraea*, *Rhacophorus maximus*, and *R. spelaeus*.

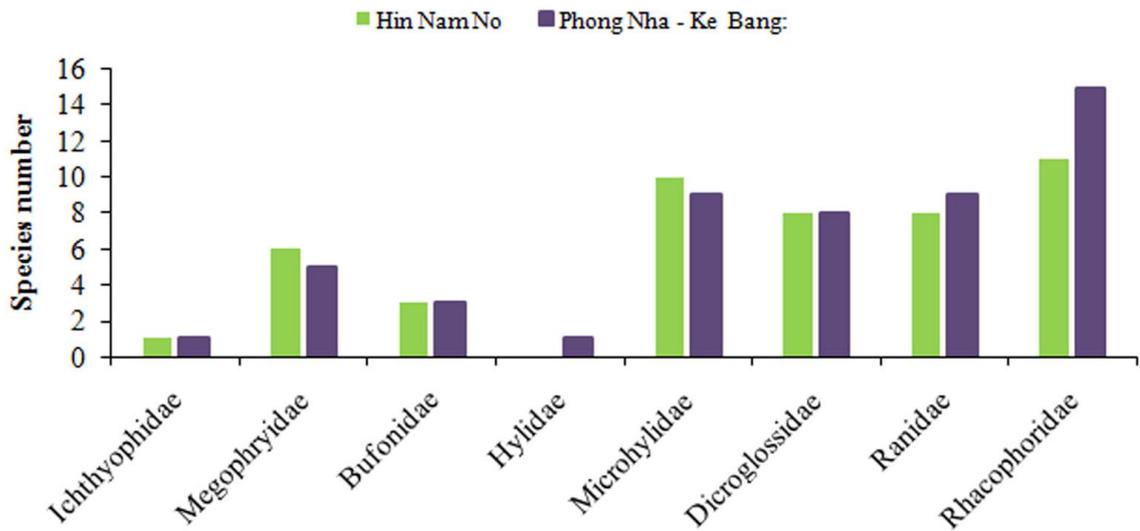


FIGURE 4.3. Comparison of amphibian species numbers between Hin Nam No and Phong Nha - Ke Bang

There are 39 species (66%) occurring in both Hin Nam No and Phong Nha - Ke Bang (similarity index 0.79, Fig. 4.4).

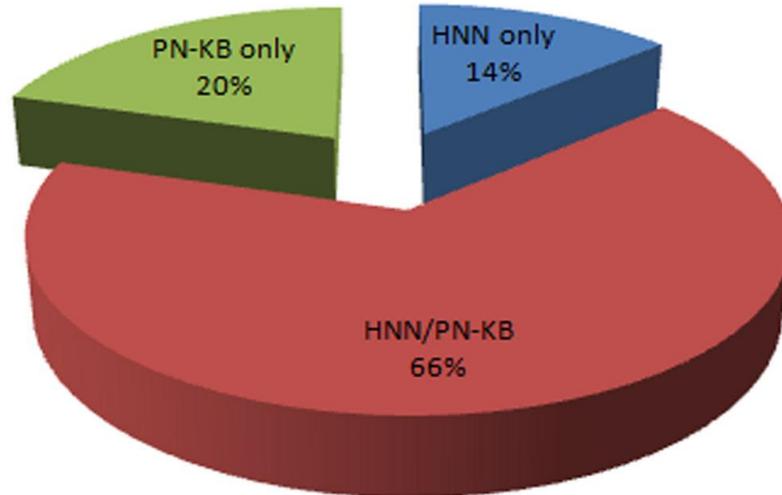


FIGURE 4.4. Comparison of the relative amounts of amphibian species (%) in Hin Nam No (HNN) to that of Phong Nha - Ke Bang (PN-KB)

b) Reptiles:

Similar to amphibians, also reptiles show a clear distance-decay in community similarity (Fig. 4.5). Interestingly, already a relative strong difference in community composition is found between Hin Nam No and Phong Nha - Ke Bang, while the reptile communities of Cat Ba Island are more similar to their closest mainland communities than it is the case for island amphibian communities. This might be explained by the fact that it is more difficult for amphibians to cross saltwater.

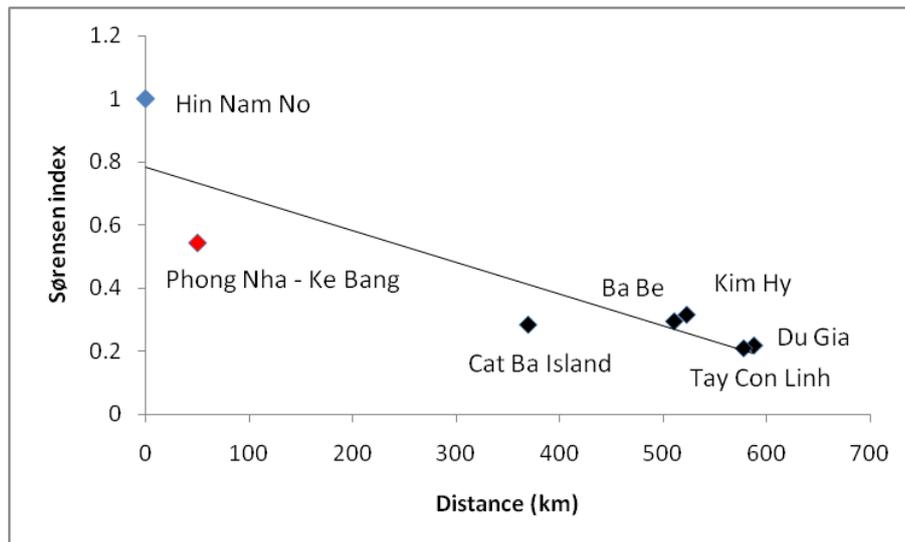


FIGURE 4.5. Relation of community similarity (Sørensen index) and distance of the reptile faunas between Hin Nam No and similar karst forest regions in Vietnam

The higher level of species similarity of the reptile fauna between Hin Nam No and Phong Nha - Ke Bang is also confirmed by a cluster analysis (Fig. 4.6).

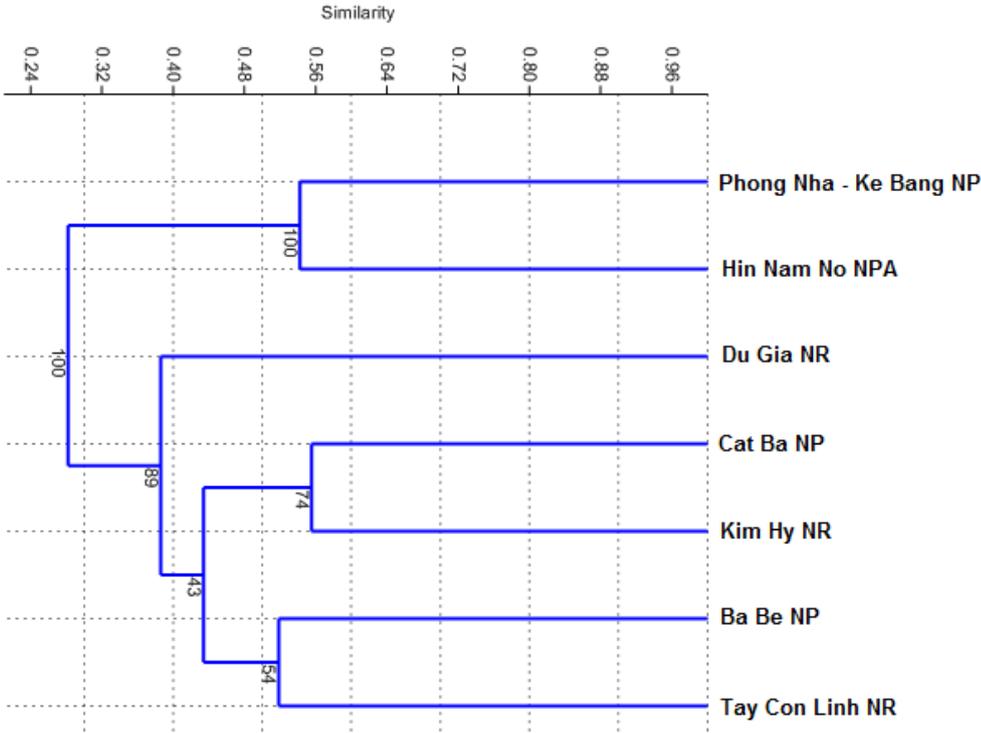


FIGURE 4.6. Cluster analysis (Sørensen index) of the reptile faunas between Hin Nam No and different regions in Vietnam with similar karst forests

Hin Nam No is currently known to house 48 reptile species (38%) together with the Phong Nha - Ke Bang NP (similarity index 0.54, Fig. 4.7).

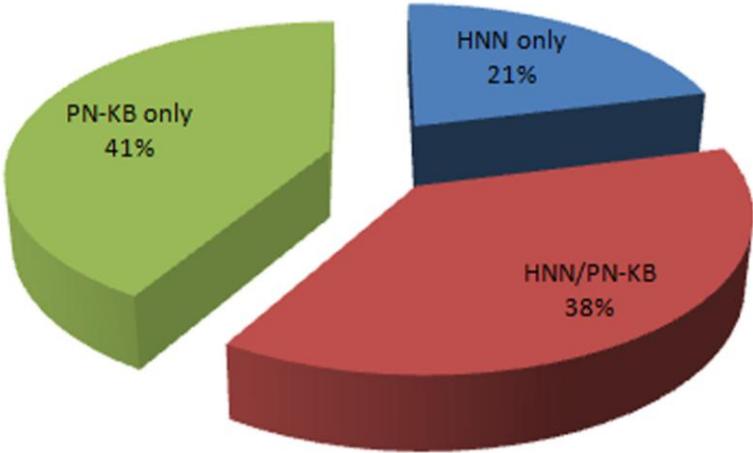


FIGURE 4.7. Comparison of the relative amounts of reptile species (%) in Hin Nam No (HNN) to that of Phong Nha - Ke Bang (PN-KB)

Fifty-three reptile species (41% of the total reptile species numbers of both areas) are currently known only from Phong Nha - Ke Bang, for example four turtles (*Platysternon*

megacephalum, *Cuora cyclornata*, *C. galbinifrons*, and *Amyda cartilaginea*), five lizards (*Cyrtodactylus phongnhakebangensis*, *C. roesleri*, *Dopasia gracilis*, *Sphenomorphus tetradactylus*, and *Tropidophorus noggei*) and two snake species (*Calamaria thanhi* and *Protobothrops cornutus*). In addition, eight families of turtles (Platysternidae), lizards (Anguidae), and snakes (Typhlopidae, Xenopeltidae, Boidae, Xenodermatidae, Lamprophiidae, and Pseudoxenodontidae) have not been proven yet for Hin Nam No. In contrast, 20 species (21% total reptile species numbers of both areas) were recorded only from Hin Nam No (e.g., *Crocodylus siamensis*, *Cyrtodactylus calamei*, *C. hinnamnoensis*, *C. sommerladi*, *Gekko boehmei*, *G. sengchanthavongi*, *Trimeresurus macrops*) (Fig. 4.8).

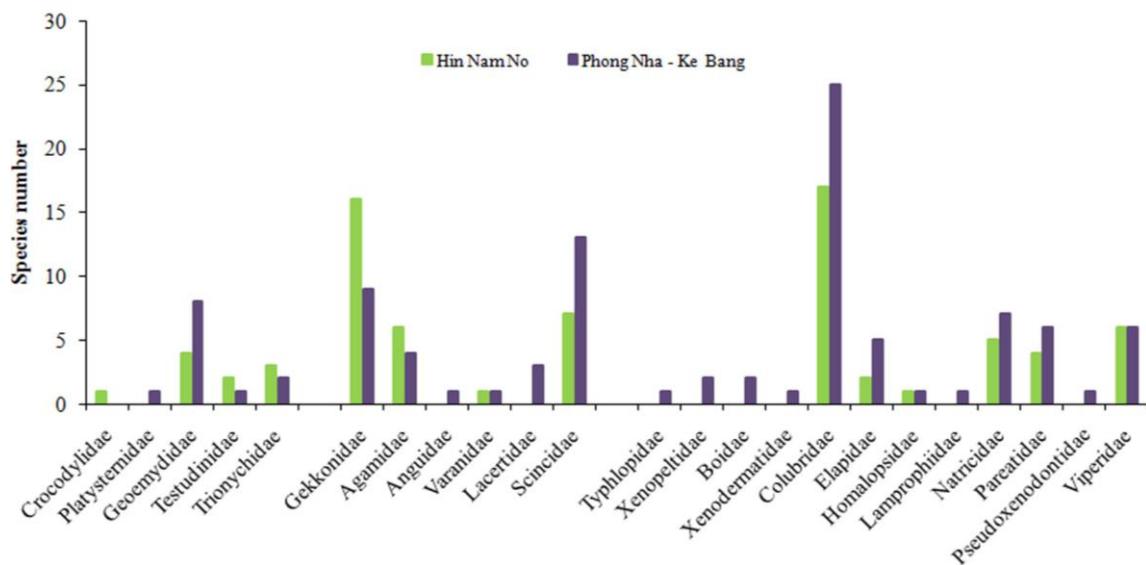


FIGURE 4.8. Species richness of reptiles from Hin Nam No and Phong Nha - Ke Bang

Higher numbers of amphibians and reptiles in Phong Nha - Ke Bang are not surprising, because intensive surveys have been implemented since 1999 (e.g., Ziegler *et al.* 2004; Hendrix *et al.* 2008; Zielger *et al.* 2007; Zielger & Vu 2009; Ziegler *et al.* 2010). By comparing the relative amounts of shared species in Hin Nam No and Phong Nha - Ke Bang, it is interesting to note that less reptile species (38%) than amphibian species (66%) are shared between both regions. This might indicate that the Truong Son Range might have acted as a stronger biogeographical barrier for reptiles (publication 11) than for amphibians (publication 13). (Hypothesis 5).

4.2 Zoogeography and distribution pattern

My own research results contributed to a better understanding of the distribution of amphibians and reptiles of the area and in part extended species records both to Laos as well as to the northern Truong Son Range. For example, three anurans species (*Rhacophorus maximus*, *Gracixalus quyeti*, and *G. supercornutus*) were recorded for the first time from Laos (publications 3 & 13). In addition, our findings of three new geckos (*Gekko bonkowskii*, *G. sengchanthavongi*, and *G. thakhekensis*) of the *G. japonicus* group extended the distribution range of this group to Laos (publications 5 & 6). In terms of colubrid snake species, *Lycodon rustrati abditus* was originally described from Phong Nha - Ke Bang on the eastern side of the Truong Son Range and only recently recorded from the western side of the Range. *Lycodon futsingensis* previously was only known from southern China to northern and central Vietnam, and only recently reported from Laos (publication 2).

Remarkably, 12 reptiles species were newly discovered from the northern Truong Son Range and their distributions are restricted to the western side of the Truong Son Range.

4.3 The Truong Son Range as a natural barrier for the distribution of amphibians and reptiles between Vietnam and Laos

Natural barriers are known to play an important role for the evolution of amphibians and reptiles in Southeast Asia. First of all the river systems hampered the exchange of reptile taxa. For example, the Red River has been shown to act as barrier for amphibians (anurans) and reptiles (agamids: *Acanthosaura*) (Bain & Hurley 2011). Further evidence shows that the Red River is separating two species of leopard geckos (*Goniurosaurus*) on the eastern side and bent-toed geckos (*Cyrtodactylus*) on the western side of the Red River (Nguyen *et al.* 2009). Also in the southern part of China, two pairs of closely related *Goniurosaurus* species are separated by a river system, namely *G. araneus* versus *G. luii* (Quangxi Region) and *G. yingdeensis* versus *Goniurosaurus* sp. (Guangdong Province) (Chen *et al.* 2014).

Also the lower Mekong River in the southern part of Indochina represents an evolutionary barrier for a number of amphibians (caecilians and anurans) and also the two squamate sister species *Calotes mystaceus* and *C. bachae*, which are known to be distributed on both sides of the river with different habitat preferences (Geissler *et al.* 2015).

The central hypothesis (Hypothesis 1) was that the Truong Son Range has acted as a biogeographic barrier for the distribution of amphibians and reptiles. It was already stated that there is a lesser amount of reptile species occurring on both sides of the range, compared to amphibians. Thus, this hypothesis currently cannot be verified for all studied groups. For

example, the forest dwellers *Cyrtodactylus cryptus* (publication 11) and *Gracixalus quyeti* (publication 13) did not speciate on both sides. But concerning single taxa and genera, the hypothesis could be verified for karst adapted gekkonids of the genera *Cyrtodactylus* and *Gekko* at least, as is shown by the species pairs of *C. hinnamnoensis* versus *C. phongnhakebangensis*; *C. sommerladi* versus *C. roesleri* (publication 11); and *G. sengchangthavongi* versus *Gekko scientadventura* (publication 6). The latter gecko species pairs represented morphologically similar, but genetically clearly different taxa. Combining the molecular data with the geographic distribution and niche separation of the species shows repeated pattern of adaptive radiation in two clades (Fig. 4.9 in publication 11).

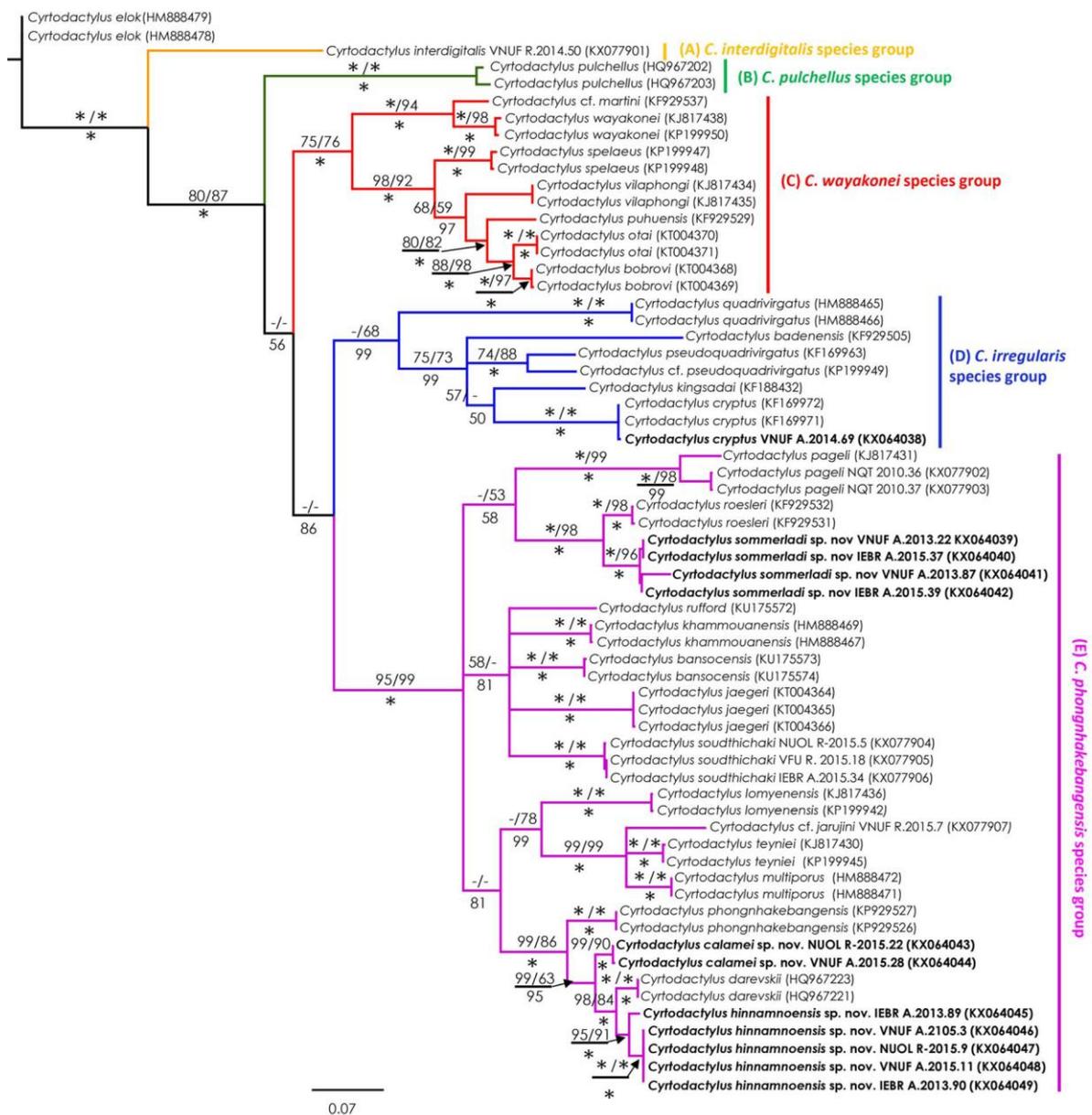


FIGURE 4.9. Phylogram based on the Bayesian analysis. Number above and below branches are MP/ML bootstrap values and Bayesian posterior probabilities (>50%), respectively. Asterisk denotes 100% value. Hyphen indicates the statistical support value lower than 50%. Scale shows the number of expected substitutions per position as calculated in MrBayes v3.2. New species and records marked in bold.

These data demonstrate that the Truong Son Range plays an important role in shaping the distribution and divergent evolution of the bent-toed geckos on the Laotian and Vietnamese sides of the range.

4.5. Species diversity

A total of 51 herpetofauna species comprising 21 amphibians and 30 reptiles have been recorded from the Hin Nam No NPA and surrounding areas (Walston & Vinton 1999; Nazarov *et al.* 2014). During the last four years, my own research contributed 26 species (55.3%) of amphibians and 45 species (60.0%) of reptiles to this list (Fig. 4.10)

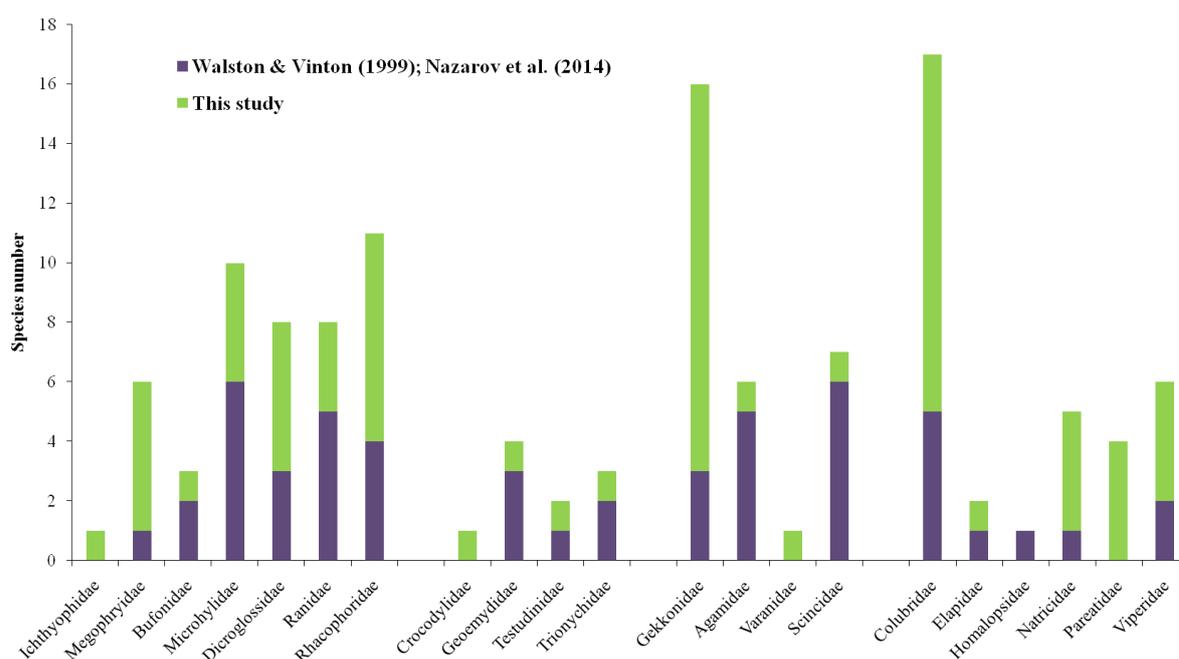


FIGURE 4.10. Species richness of amphibian and reptile families from the Hin Nam No NPA (new records marked with green coloration)

Rhacophoridae (23.4% of the Hin Nam No amphibian fauna), Microhylidae (21.2%), and both Ranidae and Dicroglossidae (each with 17.0%) are the most species-rich amphibian

families in Hin Nam No (Fig. 4.10). The Geoemydidae is the most species rich family of turtles accounting for 44,4% of the Hin Nam No turtle fauna. In particular Gekkonidae (53.3% of the Hin Nam No lizard fauna) and Colubridae (48.6% of the Hin Nam No snake fauna) stand out as the most species-rich reptile families of Hin Nam No.

Remarkably, an unknown population of the endangered *Crocodylus siamensis* was rediscovered by our team in Ban Soc, Bualapha District, near the Hin Nam No NPA (publication 7).

4.5.1 New discoveries from Laos

a) New country records: Three anuran species (*Gracixalus quyeti*, *G. supercornutus* and *Rhacophorus maximus*) (publications 3 & 13), two bent-toed geckos (*Cyrtodactylus cryptus* and *C. pseudoquadrivirgatus*) (publications 2 & 11), and two snake species (*Lycodon futsingensis* and *L. ruhstrati abditus*) (publication 2) have been recorded for the first time from Laos. All mentioned species were recorded within the Hin Nam No NPA, except for *Gracixalus supercornutus* and *Cyrtodactylus pseudoquadrivirgatus* which were from Xe Sap NPA, southern Laos.

b) New species: In this study, we have discovered 12 new species from the Hin Nam No NPA and isolated karst mountains in Khammouane Province, comprising seven bent-toed geckos (publications 4 & 8–11), four gekkonids (publications 5 & 6) and one colubrid snake (publication 12) (Hypothesis 3). Our findings bring the species number of the *Cyrtodactylus* genus from 6 to 13 in Khammouane Province. Furthermore, four of six *Gekko* species from Laos have been known to occur in Khammouane Province. These new findings have proven the extensive limestone karst formation in Khammouane Province, central Laos as a hotspot of herpetofauna biodiversity. Similarly in Phong Nha - Ke Bang NP in Vietnam, 16 new species and one subspecies have been described as new to science since 1999 (Ziegler & Vu 2009; Geissler *et al.* 2015), confirming that the whole region harbours an exceptional species-rich herpetofauna.

The limestone area of the northern Annamite's mainly consists of karst formations which are known to bear high levels of biodiversity and endemism (Clements *et al.* 2006). Karst mountains in Khammouane Province are not only isolated from each other by river systems, but also by intensively cultivated farmland and nowadays can be regarded as island-like structures (publications 4 & 7). Population fragmentation has led to species separation. Our discoveries of cryptic species provide evidence that speciation in some reptile groups in the

region occurred relatively recently (Hypothesis 2). For example, *C. sommerladi* in Laos is phenetically similar to its sibling species *C. roesleri* in Vietnam, and our phylogenetic analyses revealed them to represent distinct taxa, with slight morphological differences in dorsal pattern and tubercle arrangement (publication 11). Such ambiguous morphological characters are characteristic for initial stages of allopatric speciation, which can promote cryptic diversity (Ahmadzadeh *et al.* 2013).

c) Taxonomic revision: Using an integrative taxonomic approach by combining morphological, molecular, and ecological data, we could show that the record of *Cyrtodactylus roesleri* from Laos by Teynié & David (2010) was invalid. Similarly, *Cyrtodactylus* specimens from Hin Nam No, that were previously identified as *C. phongnhakebangensis* based on morphological characters (publication 2), had to be reassigned to a new species namely *C. hinnamnoensis* (publication 11). These results show the taxonomic difficulties for biodiversity research in these karst regions. High rates of adaptive radiation have resulted in species-complexes that cannot be separated by morphological investigations alone (Hypothesis 4).

4.5.2 Niche segregation of the herpetofauna in Hin Nam No NPA

An ecological classification of amphibians and reptiles according to, e.g., Ziegler *et al.* (2007); Fritz *et al.* (2014); IUCN (2015) and our own data during field forays revealed clear patterns of spatial and temporal adaptations of the herpetofauna.

a) Amphibians:

Most of amphibian species were found in forested areas (n=35), and two species were found in agricultural habitat, while 10 species were recorded in both habitat types (Fig. 4.11). This provides strong evidence that the protection of forests is an ultimate prerequisite of the preservation of amphibian species in karst areas.

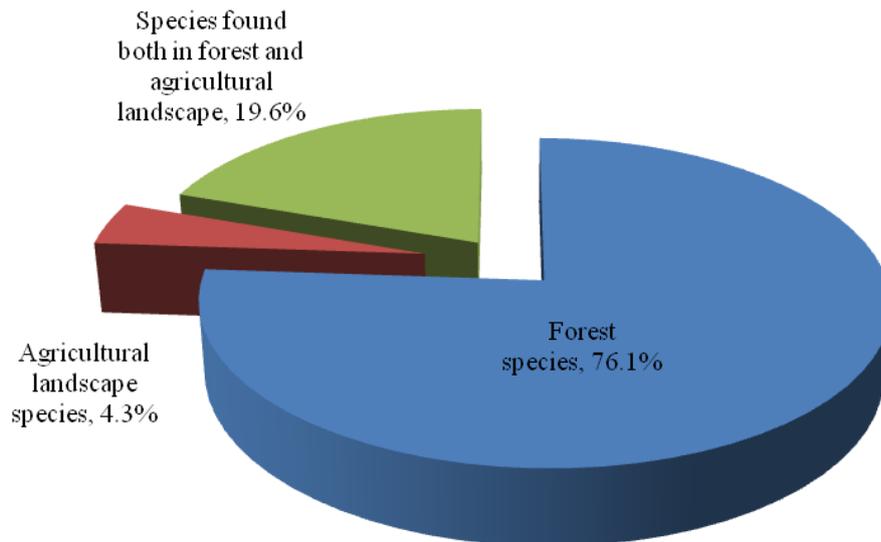


FIGURE 4.11. Relation of the occurrence of amphibian species in the Hin Nam No NPA in forest and agricultural areas.

In accordance with the high number of forest inhabitants, 11 species were adapted to arboreal life. Cavernicolous life style also plays an important role in karst environment, an example is *Rhacophorus spelaeus*, a species which lives inside caves. Thirty-five species were found on the ground where also karst caves provided an important habitat, and one species was fossorial. Most species ($n=33$) of amphibians were found at night, while 14 species were recorded to be active at day and night times. Because they are harder to see at night time and also can avoid contact with the numerous diurnal predators.

b) Reptiles:

With 56 species also by far the majority of reptiles were found in forested areas, and only three species were found exclusively in agricultural habitats, and 16 species occurred in both habitat types (Fig. 4.12).

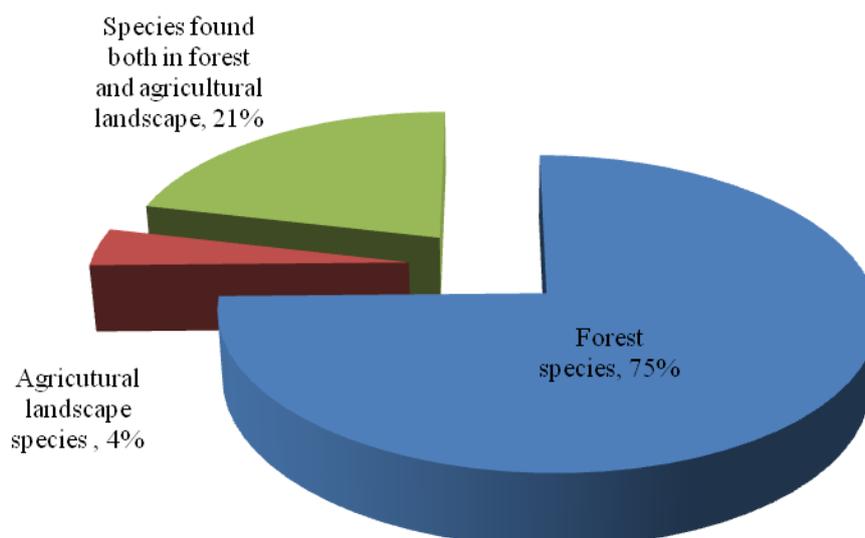


FIGURE 4.12. Relation of the occurrence of reptile species in the Hin Nam No NPA in forest and agricultural areas.

Most of reptiles species were terrestrial ($n=63$), and half of them (32 species) had an arboreal life style. The other half lived on the ground or near the caves. In the remaining 12 of 75 reptile species were semiaquatic. There are distinct differences in adaptations towards the environment, for example rock associated gekkonids (*Cyrtodactylus*) versus ground associated gekkonids (*Dixonius*). For example, a larger size and depressed body of *Cyrtodactylus* species reflects an adaptation for hunting and finding shelter in the narrow rock crevices of karst habitats (publication 4) (**Hypothesis 6**), while *Dixonius* species have a smaller size, a body square in cross-section with short limbs, likely as an adaptation to hunting on the ground.

Among the 75 reptile species recorded from the Hin Nam No NPA, 42 were nocturnal species, 24 were diurnal species, and nine species were observed both at night and during the day.

Many reptile species were found in the karst formations or near karst outcrops and caves, including all new species of the genera *Cyrtodactylus*, *Gekko*, and *Lycodon* (publications 4–6 & 8–12). The snake species *Lycodon futsingensis*, *L. ruhstrati*, *Lycodon* sp., *L. cf. subcinctus*, *Protobothrops sieversorum*, and *Trimeresurus* cf. *truongsonensis* revealed to be karst adapted. This indicates the importance of the karst formations as unique habitat for rare species.

Interspecific spatial microhabitat partitioning was found among sympatric gecko species (Hypothesis 6). For example, three bent-toed geckos (*Cyrtodactylus hinnamonensis*, *C. sommerladi*, and *C. cryptus*) co-occurred in the southern part of Hin Nam No. *C. hinnamonensis* generally occupied higher perches on cliff walls than *C. sommerladi*, while *C. cryptus* was found on ground or on tree trunks (publication 11). *Cyrtodactylus jaegeri* and *Gekko bonkowskii* are occurring sympatrically in an isolated karst near Thakhek town, but they are segregated by microhabitat preference. The former species occupied limestone cliffs, whereas the latter species preferred tree trunks (publication 6). The larger gecko species often occurred at higher perches (publications 11). Similar patterns were reported in karst forests of Phong Nha - Ke Bang (Loos *et al.* 2012). These repeated patterns of habitat partitioning among geckos indicate that competition for resources partition apparently plays a significant role for structuring extant gecko communities.

4.5 The northern Truong Son Range – a hotspot of *Cyrtodactylus* speciation and cryptic diversity

The complex topography of karst systems in the northern Truong Son Range fostered long-term isolation of populations (Bain & Hurley 2011). As a result, 16 species (about 9% of the total species numbers) of amphibians and reptiles have been found to occur in a restricted area on opposite sides of the northern Truong Son Range. On the Laotian side, nine gecko species (*Cyrtodactylus bansocensis*, *C. calamei*, *C. darevskii*, *C. hinnamnoensis*, *C. khammouanensis*, *C. multiporus*, *C. sommerladi*, *G. boehmei*, *G. sengchanthavongi*) currently have to be regarded as endemic to the Hin Nam No region. On the Vietnamese side, there are seven species including two bent-toed geckos (*Cyrtodactylus phongnhakebangensis* and *C. roesleri*), three skinks (*Lygosoma boehmei*, *Sphenomorphus tetradactylus* and *Tropidophorus noggei*), and two snakes (*Hebius andreae* and *Boiga bourreti*) currently only known from Phong Nha - Ke Bang and adjacent regions. These data indicate that the northern Truong Son Range plays an important role as a center of endemism (publication 11) (**Hypothesis 4**).

Cryptic species are characterized by being morphologically similar but genetically different. A pair of sibling species (*C. roesleri* versus *C. sommerladi*) was found on opposite sides of the Truong Son Range. Furthermore, *C. phongnhakebangensis* from Vietnam and *C. hinnamnoensis* from Laos are generally very similar in morphology, but the phylogenetic analyses revealed distinct differences (publication 11). The phenomenon, that the species have conserved phenotypes, may be due to separation of the population only recently or due to evolution under similar conditions in karst environment (**Hypothesis 7**).

4.6 Conservation issues

a) Threats to the herpetofauna

Two main threats to amphibians and reptiles in Hin Nam No and surrounding areas are habitat destruction and illegal wildlife hunting.

Habitat destruction: During the surveys, we have found that agricultural lands were created along the main road and the Ho Chi Minh trail (established from the war time) in and around Hin Nam No. When roads have opened, access to the forests is promoted. In southern Hin Nam No, each local family can have several forest lands and they can convert them into agricultural lands by burning forests and cultivate for several years and then use another forest land. In addition, karst forests decrease by limestone exploitation for building purposes (publication 6). Unfortunately, eight of twelve new species are living out of the protected areas in Khammouane Province.

Illegal wildlife hunting: The high economic species value are major subjects of hunting (e.g., turtles, snakes and geckos). Amphibians are mainly collected for food and food trade. During the survey time we observed ample proof of human activity in the forest (i.e. small traps, hunting huts and footpaths). Local people with lamps were collecting amphibians during heavy rain in the forest in Noong Ma Village. A group of hunters with guns and dogs was met in the forest in Cha Lou Village. Although the detailed information about wildlife hunting and trade are not reported, wildlife harvesting is the primary cause of reptile and amphibian population decline. It is noted that many threatened species became very rare in and around Hin Nam No because we could not find cobras, pythons, and some turtle species in the wild during the survey time.

b) Threatened species of reptiles and amphibians recorded from Hin Nam No NPA

Among 122 species recorded from the protected area, 16 species (accounting 13.1% of the species number) are globally threatened (Table 4.2):

- 16 species were listed in the IUCN Red List of Threatened Animals (2016): one critically endangered, eight endangered, six vulnerable, and one near threatened species.
- 10 species listed in the CITES appendices (2016): one species listed in the Appendix I and one species listed in the Appendix II.

TABLE 4.2. List of threatened species of reptiles and amphibians recorded from Hin Nam No region

No	Species name	Common name	IUCN (2016)	CITES (2016)
	Amphibia	Amphibian		
1	<i>Hylarana attigua</i>	Similar Frog	VU	
2	<i>Gracixalus quyeti</i>	Quyets Treefrog	EN	
3	<i>Rhacophorus kio</i>	Kio Whipping Frog	VU	
4	<i>Rhacophorus spelaeus</i>	Unkown	VU	
	Crocodylia	Crocodian		
5	<i>Crocodylus siamensis</i>	Siamese Crocodile	CR	I
	Testudines	Turtles		
6	<i>Cuora mouhotii</i>	Keeled Box Turtle	EN	II
7	<i>Cyclemys dentata</i>	Asian Leaf Turtle	NT	II
8	<i>Heosemys annamdalii</i>	Yellow-headed Temple Turtle	EN	II
9	<i>Heosemys grandis</i>	Giant Asian Pond Turtle	VU	II
10	<i>Indotestudo elongata</i>	Elongated Tortoise	EN	II
11	<i>Manouria impressa</i>	Impressed Tortoise	VU	II
12	<i>Amyda cartilaginea</i>	Asiatic Softshell Turtle	VU	II
13	<i>Palea steindachneri</i>	Wattle-necked Softshell Turtle	EN	II
14	<i>Pelochelys cantorii</i>	Cantor's Giant Softshell	EN	II
	Serpentes	Snakes		
15	<i>Protobothrops sieversorum</i>	Three Horned-scaled Pitviper	EN	
16	<i>Trimeresurus cf. truongsoneis</i>	Truong Son Pit Viper	EN	

Notes: IUCN (2016) = The IUCN Red List of Threatened Species. CR = Critically endangered, EN = Endangered, VU = Vulnerable, NT = Near threatened; CITES (2016) = Appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), update from 2 October 2013. I, II = species listed in the Appendix I and Appendix II, respectively.

With a relatively high number of threatened species, the herpetofauna of the Hin Nam No NPA contains a high level of conservation concern in Laos. However, the frequency of threatened species during the survey time was very rare (except for *Rhacophorus kio*), in particular turtle species.

c) Hot spots of the herpetofauna diversity

Identification of biodiversity hot spots plays a significant role for conservation priorities. Based on the results of my research and published literature we can define hot spots for herpetofaunal conservation in Hin Nam No and surrounding areas. Criteria for a hot spot determination include: 1) species richness, 2) number of rare and/or threatened species, 3) forest area and habitat quality, and 4) human disturbance. In each criterion, a higher number shows a better score (score ranking from 1 to 5). Following the criteria, the relative conservation value of each site is ranked as follows (Table 4.1): Southern Hin Nam No with 16 points, both central and northern Hin Nam No with 13 points, and Bualapha town with the lowest value of eight points.

TABLE 4.1. Evaluation of the hot spots for herpetofauna conservation value in Hin Nam No region

Criterion	Species richness	Number of rare/threatened species	Forest area/habitat quality	Human disturbance	Total
Northern HNN	3	4	4	2	13
Central HNN	4	3	5	1	13
Southern HNN	5	5	3	3	16
Bualapha town	1	1	2	4	8
Ban Soc	2	2	1	5	10

Most of the new species and new country records were found in southern Hin Nam No (Noong Ma Village). This area is known as a center of new species discoveries. We found 39 of a total of 47 amphibian species and 38 of a total of 75 reptile species known from Hin Nam No during the survey period (e.g., *Gracixalus quyeti*, *Rhacophorus maximus*, *Cyrtodactylus hinnamnoensis*, *C. sommerladi*, *C. cryptus*, *Lycodon* sp., *L. futsingensis*, *L. ruhstrati abditus*). In addition, two pitviper species (*Protobothrops sieversorum* and *Trimeresurus* cf. *truongsonensis*) were recorded in this area. However, these forests are facing rapid habitat fragmentation and destruction due to easy access to the area by the Ho Chi Minh trail and by burning forests for agricultural cultivation. Therefore, the southern Hin Nam No should be selected as a first priority in improved conservation of both species and their habitats.

Central Hin Nam No (Cha Lou and Noong Ping villages) harbours valleys with a dense network of streams (Kaan and Noong Choong) and mostly still undisturbed forests which are rich in old trees. The dominant habitat type is limestone forest but a small area of lowland semi-evergreen forest can be found in valleys among the limestone karst. The diversity is quite high with 20 amphibians and 19 reptiles. Most of them are vulnerable and endemic

species such as turtles (*Heosemys grandis*, *Manouria impressa*), and lizards (*Varanus nebulosus*, *Cyrtodactylus hinnamnoensis*, *C. sommerladi*).

Northern Hin Nam No (Noong Bua, Dou, Vangmano, Thong Xam villages and Phou Chuang mountain) is characterized by Phou Chuang mountain, an isolated sedimentary peak with rocky streams. The dominant habitat type is undisturbed evergreen forest of good quality with big trees. Twenty-five amphibians and 31 reptiles are found in this area with a high degree of herpetofaunal diversity, among them anurans (*Limnonectes gyldenstolpei* and *Rhacophorus orlovi*) and bent-toed geckos (*Cyrtodactylus multiporus* and *C. interdigitalis*). The remaining habitat of northern Hin Nam No is dominated by karst forest where we only have found one turtle (*Cuora mouhotii*) and one bent-toed gecko species (*Cyrtodactylus calamei*) (publication 11). In addition, two bent-toed gecko species (*Cyrtodactylus darevskii* and *C. khammouanensis*) were recently described by Nazarov *et al.* (2014).

Ban Soc village: The limestone cliffs created small ponds and caves which house a critically endangered species (*Crocodylus siamensis*) and one newly discovered species (*Cyrtodactylus bansocensis*). These species are not protected at present.

Bualapha town: The isolated karst forest is surrounded by villages and fields. Three new species are found in this area (*Gekko boehmei*, *G. scientiadventura*, *Dixonius* sp.).

d) Recommendations for further research and conservation

The Northern Truong Son Range is known as a hotspot of speciation and cryptic species. It is demonstrated by a list of 12 new species to science and seven new country records for Laos which were provided by our working group between 2013 and 2016 (Table 4.3).

TABLE 4.3. New species and new country records to Laos

No.	Classification	Year
New species		
	Gekkonidae	
1	<i>Cyrtodactylus bansocensis</i>	2016
2	<i>Cyrtodactylus calamei</i>	2016
3	<i>Cyrtodactylus hinnamnoensis</i>	2016
4	<i>Cyrtodactylus jaegeri</i>	2014
5	<i>Cyrtodactylus rufford</i>	2016
6	<i>Cyrtodactylus sommerladi</i>	2016
7	<i>Cyrtodactylus soudthichaki</i>	2015
8	<i>Gekko boehmei</i>	2015
9	<i>Gekko bonkowskii</i>	2015
10	<i>Gekko sengchanthavongi</i>	2015
11	<i>Gekko thakhekensis</i>	2014
	Colubridae	
12	<i>Lycodon banksi</i>	2016 (in review)
New country records		
	Rhacophoridae	
1	<i>Gracixalus quyeti</i>	2016 (in review)
2	<i>Gracixalus supercornutus</i>	2014
3	<i>Rhacophorus maximus</i>	2014
	Gekkonidae	
4	<i>Cyrtodactylus cryptus</i>	2016
5	<i>Cyrtodactylus pseudoquadrivirgatus</i>	2013
	Colubridae	
6	<i>Lycodon futsingensis</i>	2013
7	<i>L. ruhstrati abditus</i>	2013

Although the number of amphibians and reptiles in the Laotian side rapidly increase, further research is still needed because research efforts mainly focused on Hin Nam No NPA during a four-year period in comparison with efforts of a more than 10 years lasting study in Phong Nha - Ke Bang.

Of particular conservation importance are endemic species (publication 11) and species listed in IUCN & CITES Appendices (Table 4.2).

We have named two representative gecko species after their type locality and the protected area, viz., *Gekko thakhekensis* and *Cyrtodactylus hinnamnoensis* (publications 4 & 11). These species have conservation flagship species potential (usually attractive and threatened species). With such actions, we have the chance to highlight both sites and species and raise awareness for conservation matters.

Priorities for conservation should be in the endemic species richest parts of Hin Nam No, such as southern Hin Nam No. In addition, Ban Soc should be among the conservation priorities as well as this region in Khammouane Province, houses a so far overlooked population of the Critically Endangered Siamese crocodile. We currently are cooperating with our partners from the National University of Laos in Vientiane and the local authorities in Khammouane in establishing a reserve and engaging in further *in situ* conservation activities.

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6. Summary / Zusammenfassung

Summary

In this thesis the mostly unknown herpetofauna in Hin Nam No National Protected Area Laos in the northern Truong Son Range was for the first time intensively investigated, and its diversity was compared to the bordering, and well-investigated Phong Nha - Ke Bang National Park in Vietnam.

Twelve new vertebrate species were described comprising 11 geckonids (*Cyrtodactylus bansocensis*, *C. calamei*, *C. hinnamnoensis*, *C. jaegeri*, *C. rufford*, *C. sommerladi*, *C. soudthichaki*, *Gekko boehmei*, *G. bonkowskii*, *G. sengchanthavongi*, *G. thakhekensis*, *Lycodon banksi* and one colubrid snake (*Lycodon banksi*). Seven species were discovered for the first time in Laos including three frogs (*Gracixalus quyeti*, *G. supercornutus*, *Rhacophorus maximus*), two geckos (*Cyrtodactylus cryptus*, *C. pseudoquadrivirgatus*) and two snakes (*Lycodon futsingensis*, *L. ruhstrati abditus*).

The main hypothesis that the Truong Son Range acted as a biogeographic barrier for the distribution of amphibians and reptiles could be confirmed at least for karst adapted gekkonids. Compared to other herpetofaunal groups the number of gekkonids in karst formations was particularly high (seven bent-toed geckos, four true geckos). By comparing the relative amounts of shared species in Hin Nam No and Phong Nha - Ke Bang, it is interesting to note that fewer reptile species (38%) than amphibian species (66%) were shared between both regions. This might indicate that the Truong Son Range acts as a stronger biogeographical barrier for reptiles than for amphibians.

Two pairs of karst-adapted cryptic gecko species (i.e. species with distinct genetic differences, but a similar phenotype) occurred on both sides of the Truong Son Range. Only in one case these were sibling species (*Cyrtodactylus sommerladi* in Laos versus *C. roesleri* in Vietnam), but not in the other (*C. hinnamnoensis* in Laos versus *C. phongnhakebangensis* in Vietnam).

On the Laotian side, nine gecko species (*Cyrtodactylus bansocensis*, *C. calamei*, *C. darevskii*, *C. hinnamnoensis*, *C. khammouanensis*, *C. multiporus*, *C. sommerladi*, *G. boehmei*, *G. sengchanthavongi*) currently have to be regarded as endemic to the Hin Nam No region. On the Vietnamese side, seven species including two bent-toed geckos (*Cyrtodactylus phongnhakebangensis* and *C. roesleri*), three skinks (*Lygosoma boehmei*, *Sphenomorphus tetradactylus* and *Tropidophorus noggei*), and two snakes (*Hebius andreae* and *Boiga bourreti*) are currently only known from Phong Nha - Ke Bang and adjacent regions. These

high numbers of potential endemic species together with the cryptic species complex in *Cyrtodactylus* provide strong evidence that the karst formations in the northern Truong Son Range represent a hot spot of reptile diversity and of speciation in *Cyrtodactylus* in particular.

Correct species identification is a fundamental requirement for conservation measures. The discovery of cryptic species complexes poses a challenge for alpha taxonomy and species conservation, because the true distribution ranges of the species are in fact much smaller than previously assumed. Species conservation in this area of Laos is facing a number of further problems. New and potentially endemic species were discovered in highly populated and disturbed areas. Conversion of the Ho Chi Minh Trail into a highway provided easy access for farmers and still continues to accelerate the destruction of remote forest areas. Southern Hin Nam No with its high diversity of endemic species was identified as the first priority area for conservation. Also Ban Soc, an area isolated from Hin Nam No, should be among the conservation priorities because this region houses a so far overlooked population of the critically endangered Siamese crocodile. Efforts to establish a legal conservation status for this habitat are in progress.

Zusammenfassung

In der vorliegenden Arbeit wurde die noch weitgehend unbekannte Herpetofauna im Hin Nam No Schutzgebiet, im Gebirgszug der nördlichen Annamiten (vietnamesisch: Truong Son Range) in Laos, erstmals umfassend erforscht, und mit der Herpetofauna des angrenzenden, gut erforschten Phong Nha - Ke Bang Nationalparks in Vietnam verglichen.

Hieraus resultierten Artbeschreibungen von insgesamt 12 neue Wirbeltierarten, darunter 11 Geckos (*Cyrtodactylus bansocensis*, *C. calamei*, *C. hinnamnoensis*, *C. jaegeri*, *C. rufford*, *C. sommerladi*, *C. soudthichaki*, *Gekko boehmei*, *G. bonkowskii*, *G. sengchanthavongi*, *G. thakhekensis*, *Lycodon banksi*) und einer Schlange aus der Familie der Nattern (*Lycodon banksi*). Darüber hinaus wurden 7 beschriebene Arten zum ersten Mal für Laos nachgewiesen, darunter 3 Froscharten (*Gracixalus quyeti*, *G. supercornutus*, *Rhacophorus maximus*), 2 Bogenfingergeckos (*Cyrtodactylus cryptus*, *C. pseudoquadrivirgatus*) und 2 Schlangen (*Lycodon futsingensis*, *L. ruhstrati abditus*).

Die Hypothese, dass die nördlichen Annamiten eine Barriere für die Evolution der Herpetofauna bildete konnte zumindest für an Karstgebiete adaptierte Geckos bestätigt werden. Insbesondere die Artenzahl von Geckos (7 Bogenfingergeckos, 4 echte Geckos) war in den Karstgebieten hoch. Wenn man die relativen Anteile der gleichen Arten in den westlichen und östlichen Annamiten vergleicht, fällt auf, dass die Artübereinstimmung bei Reptilien (38%) weit geringer als bei Amphibien (66%) ausfällt. Dies könnte andeuten, dass die Annamiten für Reptilien eine größere biogeographische Barriere bildeten als für Amphibien.

Zwei Artenpaare an Karst adaptierter, kryptischer Geckoarten (d.h. Arten die sich genetisch signifikant unterschieden, aber einen gleichen Phänotyp aufwiesen) wurden auf beiden Seiten des Gebirgszugs der Annamiten entdeckt. Nur in einem Fall waren es Schwesterarten (*Cyrtodactylus sommerladi* in Laos vs. *C. roesleri* in Vietnam), während *C. hinnamnoensis* in Laos und *C. phongnhakebangensis* in Vietnam nicht eng verwandt waren. Auf der laotischen Seite wurden weiterhin 9 endemische Geckoarten in der Hin Nam No Region nachgewiesen (*Cyrtodactylus bansocensis*, *C. calamei*, *C. darevskii*, *C. hinnamnoensis*, *C. khammouanensis*, *C. multiporus*, *C. sommerladi*, *G. boehmei*, *G. sengchanthavongi*), während auf der vietnamesischen Seite in Phong Nha - Ke Bang bislang 7 endemische Arten bekannt sind, darunter 2 Bogenfingergeckos (*Cyrtodactylus phongnhakebangensis*, *C. roesleri*), 3 Skinke

(*Lygosoma boehmei*, *Sphenomorphus tetradactylus*, *Tropidophorus noggei*), und 2 Schlangenarten (*Hebius andreae*, *Boiga bourreti*).

Die vorliegende Arbeit bestätigt damit die Funktion der nördlichen Annamiten als ein Zentrum endemischer und kryptischer Arten; insbesondere bilden die Kartsgebiete der Region ein Zentrum der Artbildung in der Gattung *Cryptodactylus*.

Die korrekte Identifikation von Arten ist eine fundamentale Voraussetzung für den Artenschutz. Insbesondere die Entdeckung von kryptischen Artkomplexen ist eine Herausforderung für die Alphataxonomie und den Artenschutz, weil die echten Verbreitungsareale von Arten viel kleiner sind als vorher angenommen.

Der Artenschutz in dieser Region von Laos sieht sich weiteren Herausforderungen gegenüber.

Neue und potenziell endemische Arten wurden auch in stark bevölkerten und gestörten Gegenden gefunden. Insbesondere der Ausbau des Ho Chi Minh Pfads in eine Hauptverbindungsstraße ermöglichte der Landbevölkerung einen leichten Zugang in vormals entlegene Waldgebiete, wodurch die rapide Zerstörung von einzigartigen Habitaten weiter zunimmt. Der südliche Hin Nam No mit seinem hohen Reichtum endemischer Arten konnte als Prioritätsgebiet für den Artenschutz identifiziert werden. Daneben wurde in Ban Soc, einem isoliert von Hin Nam No gelegenen Gebiet eine bisher unbekannte Population des stark gefährdeten Siamesischen Krokodils entdeckt. Bestrebungen diesem Gebiet einen Schutzstatus zu verleihen sind in Vorbereitung.

7. Appendix

APPENDIX 1. Current list of amphibians known from Hin Nam No (HNN) and Phong Nha - Ke Bang (PN-KB)

APPENDIX 2. Current list of reptiles known from Hin Nam No (HNN) and Phong Nha - Ke Bang (PN-KB)

APPENDIX 3. Similarities (Sørensen index) of the amphibian faunas between Hin Nam No NPA, Laos and different regions in Vietnam with similar Karst forests.

APPENDIX 4. Similarities (Sørensen index) of the reptile faunas between Hin Nam No NPA, Laos and different regions in Vietnam with similar Karst forests.

APPENDIX 5. Color plates of amphibians and reptiles from Hin Nam No NPA.

APPENDIX 1. Current list of amphibians known from Hin Nam No (HNN) and Phong Nha - Ke Bang (PN-KB)

AMPHIBIA	HNN		PN-KB
	This study	Walston & Vinton 1999	
Gymnophibia: Ichthyophidae			
<i>Ichthyophis chaloensis</i> Geissler, Poyarkov, Grismer, Nguyen, An, Neang, Kupfer, Ziegler, Böhme et Müller, 2015			1
<i>Ichthyophis</i> sp.	1		
Anura: Megophyiidae			
<i>Brachytarsophrys intermedia</i> (Smith, 1921)			1
<i>Leptobrachium chapaense</i> (Bourret, 1937)	1		1
<i>Leptobrachium</i> sp.	1		
<i>Leptolalax aereus</i> Rowley, Stuart, Richards, Phimmachak et Sivongxay, 2010	1		1
<i>Leptolalax minimus</i> (Taylor, 1962)	1	1	
<i>Ophryophryne hansii</i> Ohler, 2003	1		1
<i>Xenophrys major</i> (Boulenger, 1908)	1		1
Anura: Bufonidae			
<i>Duttaphrynus melanostictus</i> (Schneider, 1799)	1	1	1
<i>Ingerophrynus galeatus</i> (Günther, 1864)		1	1
<i>Ingerophrynus macrotis</i> (Boulenger, 1887)	1		1
Anura: Hylidae			
<i>Hyla simplex</i> Boettger, 1901			1
Anura: Microhylidae			
<i>Kalophrynus interlineatus</i> (Blyth, 1854)	1	1	1
<i>Kaloula indochinensis</i> Chan, Blackburn, Murphy, Stuart, Emmett, Ho, and Brown, 2013	1		

<i>Kaloula pulchra</i> Gray, 1831	1	1	1
<i>Microhyla berdmorei</i> (Blyth, 1856)	1	1	1
<i>Microhyla butleri</i> Boulenger, 1900	1		1
<i>Microhyla fissipes</i> Boulenger, 1884	1	1	1
<i>Microhyla heymonsi</i> Vogt, 1911	1	1	1
<i>Microhyla inornata</i> (Boulenger, 1890)	1	1	1
<i>Microhyla marmorata</i> Bain et Nguyen, 2004	1		1
<i>Microhyla pulchra</i> (Hallowell, 1861)	1		1
Anura: Dicroglossidae			
<i>Fejervarya limnocharis</i> (Gravenhorst, 1829)	1	1	1
<i>Hoplobatrachus rugulosus</i> (Wiegmann, 1834)	1		1
<i>Limnonectes bannaensis</i> Je, Fei et Jiang, 2007	1		1
<i>Limnonectes gyldenstolpei</i> (and ersson, 1916)	1		1
<i>Limnonectes limborgi</i> (Sclater, 1892)	1		1
<i>Limnonectes poilani</i> (Bourret, 1942)	1	1	1
<i>Occidozyga lima</i> (Gravenhorst, 1829)	1		1
<i>Occidozyga martensii</i> (Peters, 1867)	1	1	1
Anura: Ranidae			
<i>Amolops cremnobatus</i> Inger et Kottelat, 1998			1
<i>Babina chapaensis</i> (Bourret, 1937)			1
<i>Hylarana attigua</i> (Inger, Orlov et Darevsky, 1999)	1		1
<i>Hylarana erythraea</i> (Schlegel, 1837)		1	
<i>Hylarana maosonensis</i> Bourret, 1937			1
<i>Hylarana nigrovittata</i> (Blyth, 1856)	1	1	1
<i>Hylarana taipehensis</i> (Van Denburgh, 1909)		1	1
<i>Odorrana chloronota</i> (Günther, 1876)	1	1	1

<i>Odorrana tiannanensis</i> (Yang et Li, 1980)	1		1
<i>Rana johnsi</i> Smith, 1921	1	1	1
<i>Sylvirana guentheri</i> (Boulenger, 1882)	1		1
Anura: Rhacophoridae			
<i>Feihyla vittata</i> (Boulenger, 1887)			1
<i>Gracixalus quyeti</i> (Nguyen, Hendrix, Böhme, Vu, et Ziegler, 2008)	1		1
<i>Kurixalus banaensis</i> (Bourret, 1939)	1		1
<i>Kurixalus bisacculus</i> (Taylor, 1962)	1	1	1
<i>Polypedates megacephalus</i> Hallowell, 1861	1	1	1
<i>Polypedates mutus</i> (Smith, 1940)	1		1
<i>Rhacophorus annamensis</i> Smith, 1924			1
<i>Rhacophorus dennysi</i> Blanford, 1881			1
<i>Rhacophorus exechopygus</i> Inger, Orlov et Darevsky, 1999			1
<i>Rhacophorus maximus</i> Günther, 1858	1		
<i>Rhacophorus kio</i> Ohler et Delorme, 2006	1	1	1
<i>Rhacophorus orlovi</i> Ziegler et Köhler, 2001	1		1
<i>Rhacophorus rhodopus</i> Liu et Hu, 1960	1		1
<i>Rhacophorus spelaeus</i> Orlov, Gnophanxay, Phimminith et Phomphoumy, 2010	1		
<i>Theloderma asperum</i> (Boulenger, 1886)		1	1
<i>Theloderma corticale</i> (Boulenger, 1903)			1
<i>Theloderma vietnamense</i> (Taylor, 1962)			1
Total: 59 species	43	21	51

APPENDIX 2. Current list of reptiles known from Hin Nam No (HNN) and Phong Nha - Ke Bang (PN-KB)

REPTILIA	HNN		PN-KB
	This study	Walston & Vinton (1999); Nazarov <i>et al.</i> 2014	
CROCODYLIA			
Crocodylidae			
<i>Crocodylus siamensis</i> Schneider, 1801	1		
TESTUDINES			
Platysternidae			
<i>Platysternon megacephalum</i> Gray, 1831			1
Geoemydidae			
<i>Cuora cyclornata</i> Blanck, McCord et Le, 2006			1
<i>Cuora galbinifrons</i> Bourret, 1939			1
<i>Cuora mouhotii</i> (Gray, 1862)	1	1	1
<i>Cyclemys dentata</i> (Gray, 1831)		1	
<i>Cyclemys oldhamii</i> Gray, 1863			1
<i>Heosemys annamdalii</i> (Boulenger, 1903)		1	
<i>Heosemys grandis</i> (Gray, 1860)	1		1
<i>Mauremys mutica</i> (Cantor, 1842)			1
<i>Ocadia sinensis</i> (Gray, 1834)			1
<i>Sacalia quadriocellata</i> (Siebenrock, 1903)			1

Testudinidae			
<i>Indotestudo elongata</i> (Blyth, 1854)		1	
<i>Manouria impressa</i> (Günther, 1882)	1		1
Trionychidae			
<i>Amyda cartilaginea</i> (Boddaert, 1770)		1	
<i>Palea steindachneri</i> (Siebenrock, 1906)		1	1
<i>Pelochelys cantorii</i> Gray, 1864	1		
<i>Pelodiscus cf. parviformis</i> Tang, 1997			1
SQUAMATA: SAURIA			
Gekkonidae			
<i>Cyrtodactylus calamei</i> Luu, Bonkowski, Nguyen, Le, Ngo, Schneider et Ziegler, 2016	1		
<i>Cyrtodactylus cryptus</i> Heidrich, Rösler, Vu, Böhme et Ziegler, 2007	1		1
<i>Cyrtodactylus darevskii</i> Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov et Chulisov 2014	1	1	
<i>Cyrtodactylus hinnamnoensis</i> Luu, Bonkowski, Nguyen, Le, Ngo, Schneider et Ziegler, 2016	1		
<i>Cyrtodactylus interdigitalis</i> Ulber 1993	1		
<i>Cyrtodactylus khammouanensis</i> Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov et Chulisov 2014	1	1	
<i>Cyrtodactylus multiporus</i> Nazarov, Poyarkov, Orlov, Nguyen, Milto, Martynov, Konstantinov et Chulisov 2014	1		
<i>Cyrtodactylus phongnhakebangensis</i> Ziegler, Rösler, Herrmann et Vu, 2003			1
<i>Cyrtodactylus roesleri</i> Ziegler, Nazarov, Orlov, Nguyen, Vu, Dang, Dinh et Schmitz, 2010			1
<i>Cyrtodactylus sommerladi</i> Luu, Bonkowski, Nguyen, Le, Ngo, Schneider et Ziegler, 2016	1		
<i>Dixonius</i> sp.	1		
<i>Gehyra mutilata</i> (Wiegmann, 1834)	1		1
<i>Gekko boehmei</i> Luu, Calame, Nguyen, Le et Ziegler, 2015	1		

<i>Gekko palmatus</i> Boulenger, 1907			1
<i>Gekko</i> cf. <i>reevesii</i> (Gray, 1831)	1	1	1
<i>Gekko sengchanthavongi</i> Luu, Calame, Nguyen, Le et Ziegler, 2015	1		
<i>Gekko scientiadventura</i> Rösler, Ziegler, Vu, Herrmann et Böhme, 2004	1		1
<i>Hemidactylus frenatus</i> Dumérilet Bibron, 1836	1		1
<i>Ptychozoon lionotum</i> Annandale, 1905	1		1
Agamidae			
<i>Acanthosaura lepidogaster</i> (Cuvier, 1829)	1	1	1
<i>Calotes emma</i> Gray, 1845	1	1	1
<i>Calotes</i> sp.	1		
<i>Calotes versicolor</i> (Daudin, 1802)	1	1	1
<i>Draco maculatus</i> (Gray, 1845)	1	1	
<i>Physignathus cocincinus</i> Cuvier, 1829	1	1	1
Anguidae			
<i>Dopasia gracilis</i> Gray, 1845			1
Varanidae			
<i>Varanus nebulosus</i> (Gray, 1831)	1		
<i>Varanus salvator</i> (Laurenti, 1768)			1
Lacertidae			
<i>Takydromus hani</i> Chou, Nguyen et Pauwels, 2001			1
<i>Takydromus kuehnei</i> van Denburgh, 1909			1
<i>Takydromus sexlineatus</i> Daudin, 1802			1
Scincidae			
<i>Eutropis longicaudatus</i> (Hallowell, 1856)	1	1	1
<i>Eutropis macularius</i> (Blyth, 1853)	1	1	1
<i>Eutropis multifasciatus</i> (Kuhl, 1820)	1	1	1

<i>Lygosoma boehmei</i> Ziegler, Schmitz, Heidrich, Vu et Nguyen, 2007			1
<i>Lygosoma quadrupes</i> (Linnaeus, 1766)			1
<i>Plestiodon elegans</i> (Boulenger, 1887)			1
<i>Plestiodon quadrilineatus</i> Blyth, 1853			1
<i>Scincella melanosticta</i> (Boulenger, 1887)			1
<i>Scincella rufocaudata</i> (Darevsky et Nguyen, 1983)	1	1	1
<i>Sphenomorphus indicus</i> (Gray, 1853)	1	1	1
<i>Sphenomorphus maculatus</i> (Blyth, 1853)	1	1	
<i>Sphenomorphus tetradactylus</i> (Darevsky et Orlov, 2005)			1
<i>Tropidophorus cocincinensis</i> Duméril et Bibron, 1839	1		1
<i>Tropidophorus noggei</i> Ziegler, Vu et Bui, 2005			1
SQUAMATA: SERPENTES			
Typhlopidae			
<i>Ramphotyphlops braminus</i> (Daudin, 1803)			1
Xenopeltidae			
<i>Xenopeltis hainanensis</i> Hu et Zhao, 1972			1
<i>Xenopeltis unicolor</i> Boie, 1827			1
Boidae			
<i>Broghammerus reticulatus</i> (Schneider, 1801)			1
<i>Python molurus</i> (Linnaeus, 1758)			1
Xenodermatidae			
<i>Fimbrios smithi</i> Ziegler, David, Miralles, Doan et Nguyen, 2008			1
Colubridae			
<i>Ahaetulla prasina</i> (Boie, 1827)	1		1
<i>Boiga bourreti</i> Tillack, Ziegler et Le, 2004			1
<i>Boiga cyanea</i> (Duméril, Bibron et Duméril, 1854)	1	1	

<i>Boiga guangxiensis</i> Wen, 1998			1
<i>Boiga multomaculata</i> (Boie, 1827)	1		1
<i>Calamaria thanhi</i> Ziegler et Le, 2005			1
<i>Chrysopelea ornata</i> (Shaw, 1802)	1	1	1
<i>Coelognathus radiatus</i> (Boie, 1827)	1		1
<i>Cyclophiops major</i> (Günther, 1858)	1		1
<i>Cyclophiops multicinctus</i> (Roux, 1907)			1
<i>Dendrelaphis pictus</i> (Gmelin, 1789)	1	1	
<i>Dendrelaphis ngansonensis</i> (Bourret, 1935)			1
<i>Dryocalamus davisonii</i> (Blanford, 1878)	1	1	1
<i>Gonyosoma boulengeri</i> Mocquard, 1897			1
<i>Gonyosoma prasinus</i> (Blyth, 1854)	1	1	1
<i>Liopeltis frenatus</i> (Günther, 1858)			1
<i>Lycodon capucinus</i> (Boie, 1827)	1		
<i>Lycodon fasciatus</i> (Anderson, 1897)			1
<i>Lycodon futsingensis</i> (Pope, 1928)	1		1
<i>Lycodon paucifasciatus</i> Rendahl, 1943			1
<i>Lycodon</i> cf. <i>rufozonatum</i> Cantor, 1842			1
<i>Lycodon ruhstrati</i> (Fischer, 1886)	1		1
<i>Lycodon</i> cf. <i>subcinctus</i> Boie, 1827	1		
<i>Lycodon</i> sp.	1		
<i>Oligodon chinensis</i> (Günther, 1888)	1		1
<i>Oligodon</i> cf. <i>cinereus</i> (Günther, 1864)	1		1
<i>Oreocryptophis porphyraceus</i> (Cantor, 1839)			1
<i>Orthriophis taeniurus</i> Cope, 1861			1
<i>Ptyas korros</i> (Schlegel, 1837)	1		1

<i>Ptyas mucosa</i> (Linnaeus, 1758)			1
Elapidae			
<i>Bungarus candidus</i> (Linnaeus, 1758)	1	1	1
<i>Bungarus fasciatus</i> (Schneider, 1801)	1		1
<i>Naja cf. atra</i> Cantor, 1842			1
<i>Ophiophagus hannah</i> (Cantor, 1836)			1
<i>Sinomicrurus macclellandii</i> (Reinhardt, 1844)			1
Homalopsidae			
<i>Enhydris plumbea</i> (Boie, 1827)	1	1	1
Lamprophiidae			
<i>Psammodynastes pulverulentus</i> (Boie, 1827)			1
Natricidae			
<i>Amphiesma boulengeri</i> (Gressitt, 1937)			1
<i>Amphiesma leucomystax</i> David, Bain, Nguyen, Orlov, Vogel, Vu et Ziegler, 2007	1		1
<i>Amphiesma stolatum</i> (Linnaeus, 1758)	1		1
<i>Hebius andreae</i> (Ziegler et Le, 2006)			1
<i>Parahelicops annamensis</i> Bourret, 1934			1
<i>Rhabdophis chrysargos</i> (Schlegel, 1837)	1		1
<i>Rhabdophis nigrocinctus</i> (Blyth, 1856)	1	1	
<i>Rhabdophis subminiatus</i> (Schlegel, 1837)	1		1
<i>Sinonatrix percarinata</i> (Boulenger, 1899)			1
<i>Xenochrophis flavipunctatus</i> (Hallowell, 1860)			1
Pareatidae			
<i>Pareas carinatus</i> Wagler, 1830	1		1
<i>Pareas hamptoni</i> (Boulenger, 1905)	1		1
<i>Pareas macularius</i> Blyth, 1868	1		1

<i>Pareas margaritophorus</i> (Jan, 1866)	1		1
Pseudoxenodontidae			
<i>Pseudoxenodon macrops</i> (Blyth, 1854)			1
Viperidae			
<i>Protobothrops cornutus</i> (Smith, 1930)			1
<i>Protobothrops mucrosquamatus</i> (Cantor, 1839)		1	1
<i>Protobothrops sieversorum</i> (Ziegler, Herrmann, David, Orlov et Pauwels, 2000)	1		1
<i>Trimeresurus albolabris</i> (Gray, 1842)	1	1	1
<i>Trimeresurus macrops</i> Kramer, 1977	1		
<i>Trimeresurus</i> cf. <i>truongsonensis</i> (Orlov, Ryabov, Bui et Ho, 2004)	1		1
<i>Trimeresurus vogeli</i> (David, Vidal et Pauwels, 2001)	1		1
Total: 128 species	69	30	101

APPENDIX 3. Similarities (Sørensen index) of the amphibian faunas between Hin Nam No NPA, Laos and different regions in Vietnam with similar Karst forests.

	Hin Nam No NPA	Ba Be NP	Cat Ba NP	Du Gia Nature Reserve (NR)	Kim Hy NR	Phong Nha - Ke Bang NP	Tay Con Linh NR
Hin Nam No NPA	–						
Ba Be NP	0.38889	–					
Cat Ba NP	0.25	0.41176	–				
Du Gia NR	0.31884	0.46809	0.3871	–			
Kim Hy NR	0.42857	0.54167	0.375	0.44444	–		
Phong Nha - Ke Bang NP	0.78788	0.38961	0.2623	0.2973	0.45333	–	
Tay Con Linh NR	0.31707	0.4	0.4	0.66667	0.37931	0.32184	–

APPENDIX 4. Similarities (Sørensen index) of the reptile faunas between Hin Nam No NPA, Laos and different regions in Vietnam with similar Karst forests.

	Hin Nam No NPA	Ba Be NP	Cat Ba NP	Du Gia NR	Kim Hy NR	Phong Nha-Ke Bang NP	Tay Con Linh NR
Hin Nam No NPA	–						
Ba Be NP	0.31481	–					
Cat Ba NP	0.28333	0.51282	–				
Du Gia NR	0.21739	0.36	0.35484	–			
Kim Hy NR	0.29412	0.46667	0.55556	0.40909	–		
Phong Nha-Ke Bang NP	0.54237	0.35556	0.39456	0.18487	0.34109	–	
Tay Con Linh NR	0.20833	0.51852	0.42424	0.42105	0.33333	0.22764	–

APPENDIX 5. Color plates of amphibians and reptiles from Hin Nam No NPA.



A) *Ichthyophis* sp.; B) *Leptobrachium chapaense*; C) *Leptobrachium* sp.; D) *Leptolalax aereus*; E) *Leptolalax minimus*; and F) *Xenophrys major*. Photos: V. Q. Luu



A) *Ingerophrynus macrotis*; B) *Kalophrynus interlineatus*; C) *Kaloula indochinensis*; D) *Kaloula pulchra*; E) *Microhyla berdmorei*; and F) *Microhyla fissipes*. Photos: V. Q. Luu



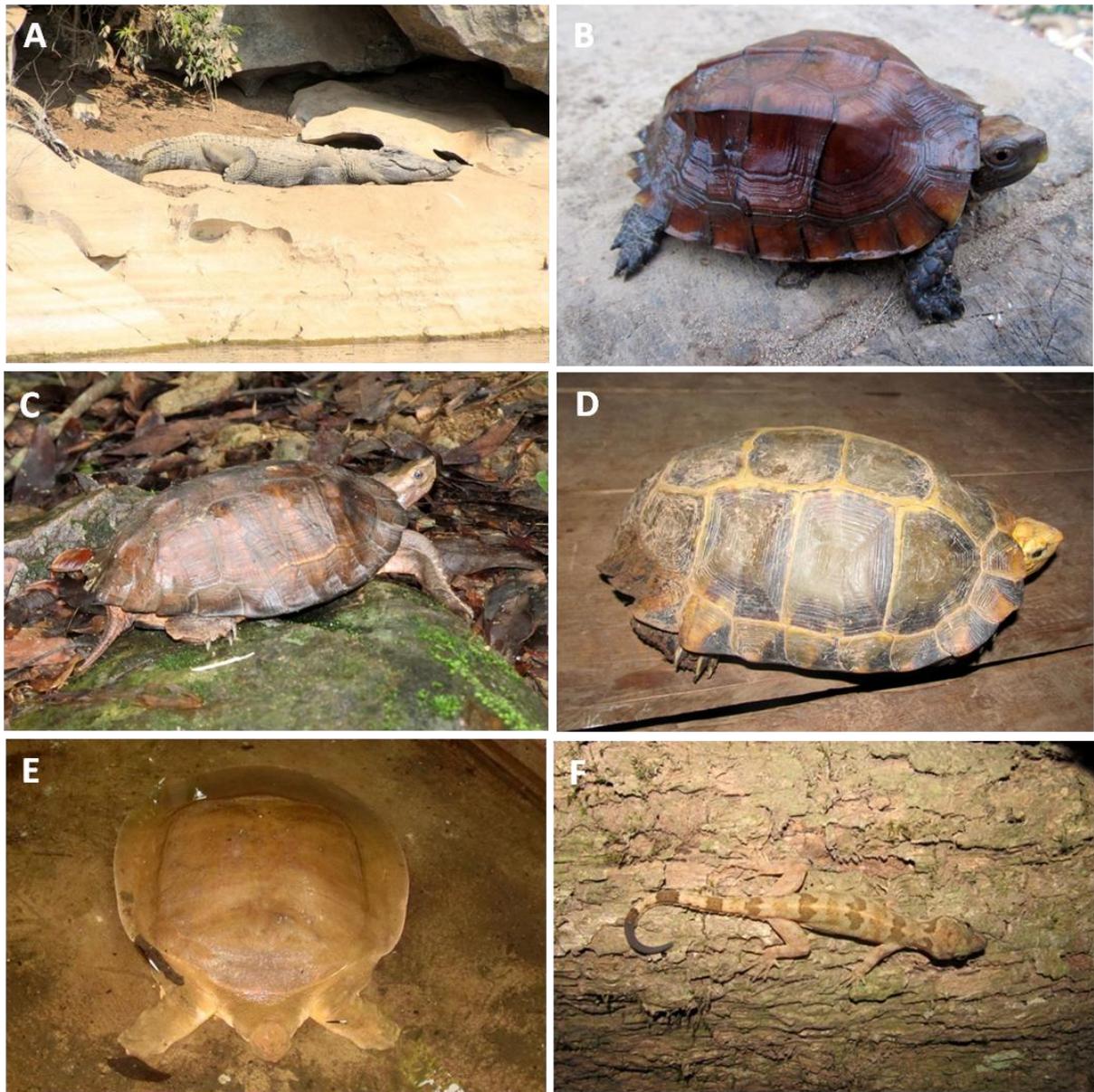
A) *Microhyla heymonsi*; B) *Microhyla inornata*; C) *Microhyla marmorata*; D) *Fejervarya limnocharis*; E) *Hoplobatrachus rugulosus*; and F) *Limnonectes bannaensis*. Photos: V. Q. Luu



A) *Limnonectes gyldenstolpei*; B) *Limnonectes poilani*; C) *Hylarana nigrovittata*;
D) *Odorrana chloronota*; E) *Odorrana tiannanensis*; and F) *Rana johnsi*. Photos: V. Q. Luu



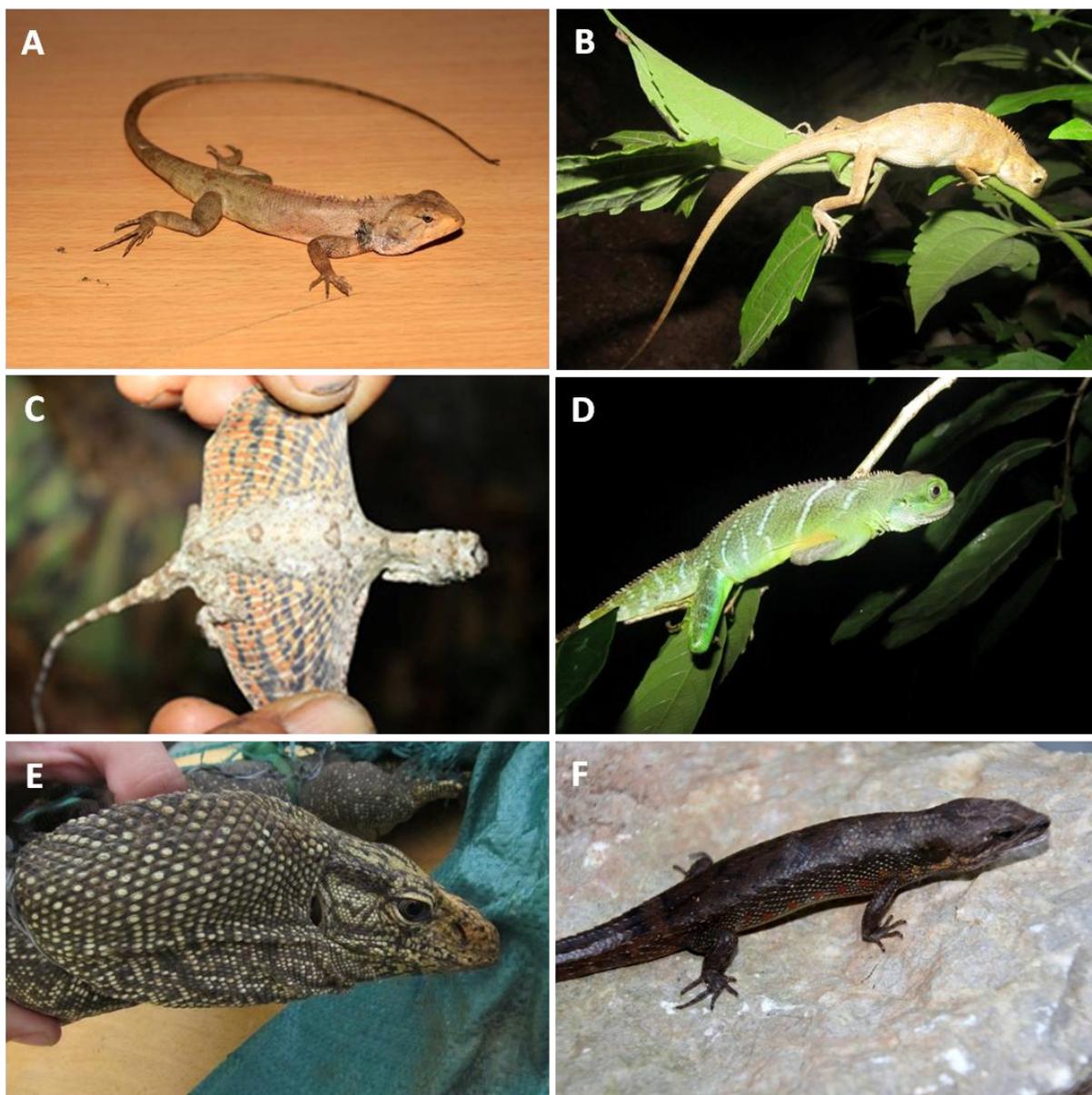
A) *Gracixalus quyeti*; B) *Rhacophorus maximus*; C) *Rhacophorus kio*; D) *Rhacophorus orlovi*; E) *Rhacophorus rhodopus*; and F) *Rhacophorus spelaeus*. Photos: V. Q. Luu



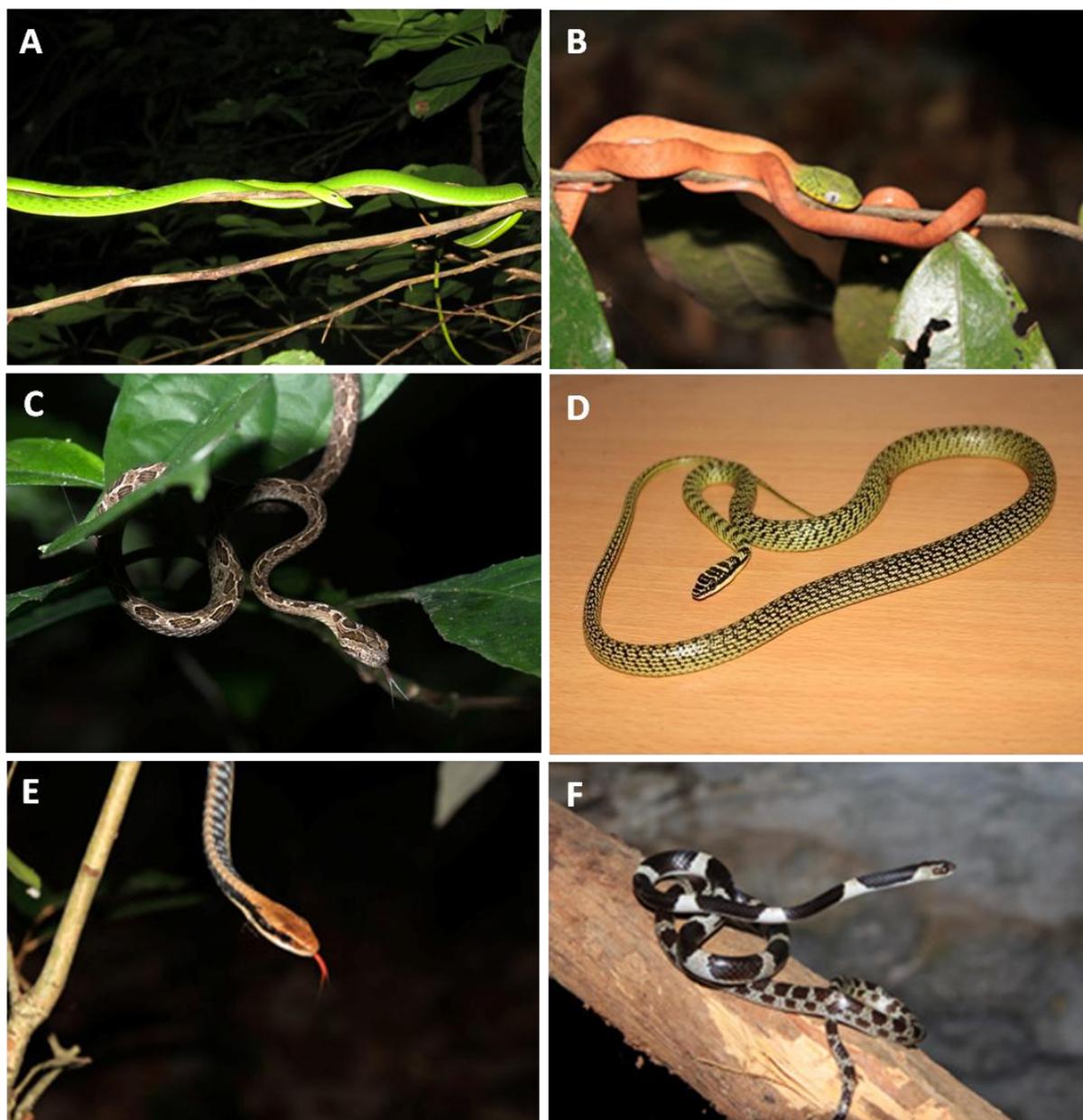
A) *Crocodylus siamensis*; B) *Cuora mouhotii*; C) *Heosemys grandis*; D) *Manouria impressa*; E) *Pelochelys cantorii*; and F) *Cyrtodactylus interdigitalis*. Photos: V. Q. Luu



A) *Cyrtodactylus multiporus*; B) *Gekko* cf. *reevesii*; C) *Gekko scientiadventura*; D) *Ptychozoon lionotum*; E) *Acanthosaura lepidogaster*; and F) *Calotes emma*. Photos: V. Q. Luu



A) *Calotes* sp.; B) *Calotes versicolor*; C) *Draco maculatus*; D) *Physignathus cocincinus*; E) *Varanus nebulosus*; and F) *Tropidophorus cocincinensis*. Photos: V. Q. Luu



A) *Ahaetulla prasina*; B) *Boiga cyanea*; C) *Boiga multomaculata*; D) *Chrysopelea ornata*; E) *Dendrelaphis pictus*; and F) *Dryocalamus davisonii*. Photos: V. Q. Luu & T. Calame (C)



A) *Gonyosoma prasinus*; B) *Lycodon capucinus*; C) *Lycodon* cf. *subcinctus*; D) *Lycodon* sp.; E) *Bungarus candidus*; and F) *Bungarus fasciatus*. Photos: V. Q. Luu



A) *Enhydris plumbea*; B) *Amphiesma leucomystax*; C) *Amphiesma stolatum*; D) *Rhabdophis chrysargos*; E) *Rhabdophis nigrocinctus*; and F) *Rhabdophis subminiatus*. Photos: V. Q. Luu



A) *Pareas carinatus*; B) *Pareas hamptoni*; C) *Protobothrops sieversorum*; D) *Trimeresurus albolabris*; E) *Trimeresurus* cf. *truongsonensis*; and F) *Trimeresurus vogeli*. Photos: V. Q. Luu

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Finally, I would like to thank all the people whose direct and indirect support helped me complete my thesis in time.

9. Declaration of Contribution as Author and Co-Author

I am first author and contributed mainly in all publications submitted for the doctoral dissertation including:

- Field survey design
- Data and samples gathering
- Morphological examination of specimens
- Data handling and processing
- Statistical analyses
- Interpretation of data
- Manuscript writing
- Submission process and correspondence together with supervisors to editors and/or reviewers

In addition, I am second co-author in one publication. Here, I contributed in the following contents:

- Designing field survey
- Collecting data and samples
- Supporting data and figures
- Revising manuscript

Dissertation Title: The taxonomy, zoogeography and ecology of amphibians and reptiles of Hin Nam No National Protected Area (Laos) in comparison with data from Phong Nha – Ke Bang National Park (Vietnam).

The degree of dissertation author's contribution according to categories:

- A. has contributed to the collaboration (0-33%);
- B. has contributed substantially (34-66%);
- C. has to a high degree carried out the work independently (67-100%)

Declaration of Contribution as Author and Co-Author

Publication 1

Luu, V.Q., Nguyen, T.Q., Pham, C.T., Dang, K.N., Vu, T.N., Miskovic, S., Bonkowski, M., Ziegler, T. (2013) No end in sight? Further new records of amphibians and reptiles from Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam. *Biodiversity Journal*, 4 (2), 285–300.

Declaration in each element	A, B, or C
1. Formulating the scientific idea based on theoretical assumptions to be clarified, including formulation of the question to be answered through analytical work and research plans.	B
2. Planning of experiments and analyses, design of the experimental methods in a way that the questions asked under point 1 can be expected to be answered.	C
3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	C
4. Presentation, interpretation and discussion of the results.	B

Publication 2

Luu, V.Q., Nguyen, T.Q., Calame, T., Hoang, T.T., Southichack, S., Bonkowski, M. & Ziegler, T. (2013) New country records of reptiles from Laos. *Biodiversity Data Journal*, 1, e1015. DOI: 10.3897/BDJ.1.e1015.

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4. Presentation, interpretation and discussion of the results.	B

Declaration of Contribution as Author and Co-Author

Publication 3

Luu, V.Q., Calame, T., Nguyen, T.Q., Ohler, A., Bonkowski, M., & Ziegler, T. (2014) First records of *Gracixalus supercornutus* (Orlov, Ho & Nguyen, 2004) and *Rhacophorus maximus* Günther, 1858 from Laos. *Herpetology Notes*, 7, 419–423.

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3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	C
4. Presentation, interpretation and discussion of the results.	C

Publication 4

Luu, V.Q., Calame, T., Bonkowski, M., Nguyen, T.Q. & Ziegler, T. (2014) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from Khammouane Province, Laos. *Zootaxa*, 3760 (1), 54–66. <http://dx.doi.org/10.11646/zootaxa.3760.1.3>

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3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	C
4. Presentation, interpretation and discussion of the results.	C

Publication 5

Luu, V.Q., Calame, T., Nguyen, T.Q., Le, M.D., Bonkowski, M. & Ziegler, T. (2014) A new species of the *Gekko japonicus* group (Squamata: Gekkonidae) from central Laos. *Zootaxa*, 3895 (1), 73–88. <http://dx.doi.org/10.11646/zootaxa.3895.1.4>

Declaration in each element	A, B, or C
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3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	B
4. Presentation, interpretation and discussion of the results.	B

Publication 6

Luu, V.Q., Calame, T., Nguyen, T.Q., Le, M.D. & Ziegler, T. (2015) Morphological and molecular review of the *Gekko* diversity of Laos with descriptions of three new species. *Zootaxa*, 3986 (3), 279–306. <http://dx.doi.org/10.11646/zootaxa.3986.3.2>

Declaration in each element	A, B, or C
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3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	B
4. Presentation, interpretation and discussion of the results.	B

Declaration of Contribution as Author and Co-Author

Publication 7

Ziegler, T., **Luu, V.Q.**, Soudthichak, S. & Nguyen, T.Q. (2015) Rediscovery of the Siamese crocodile (*Crocodylus siamensis*) in Khammouane Province, central Lao PDR. *Crocodile Specialist Newsletter*, 34 (3), 11–13.

Declaration in each element	A, B, or C
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3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	C
4. Presentation, interpretation and discussion of the results.	B

Publication 8

Luu, V.Q., Calame, T., Nguyen, T.Q., Bonkowski, M. & Ziegler, T. (2015) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from limestone forest, Khammouane Province, central Laos. *Zootaxa*, 4058 (3), 388–402. <http://dx.doi.org/10.11646/zootaxa.4058.3.6>

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4. Presentation, interpretation and discussion of the results.	C

Publication 9

Luu, V.Q., Calame, T., Nguyen, T.Q., Le, M.D., Bonkowski, M. & Ziegler, T. (2016) *Cyrtodactylus rufford*, a new cave-dwelling bent-toed gecko (Squamata: Gekkonidae) from Khammouane Province, central Laos. *Zootaxa*, 4067 (2), 185–199. <http://doi.org/10.11646/zootaxa.4067.2.4>

Declaration in each element	A, B, or C
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2. Planning of experiments and analyses, design of the experimental methods in a way that the questions asked under point 1 can be expected to be answered.	C
3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	B
4. Presentation, interpretation and discussion of the results.	C

Publication 10

Luu, V.Q., Nguyen, T.Q., Le, M.D., Bonkowski, M. & Ziegler, T. (2016) A new species of karst-dwelling bent-toed gecko (Squamata: Gekkonidae) from Khammouane Province, central Laos. *Zootaxa*, 4079 (1), 087–102. <http://doi.org/10.11646/zootaxa.4079.1.6>

Declaration in each element	A, B, or C
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4. Presentation, interpretation and discussion of the results.	C

Publication 11

Luu, V.Q., Bonkowski, M., Nguyen, T.Q., Le, M.D., Ngo, H.T, Schneider N. & Ziegler, T. (2016) 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. *Zootaxa*, 4107 (2), 101–140. <http://doi.org/10.11646/zootaxa.4107.2.1>

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4. Presentation, interpretation and discussion of the results.	B

Publication 12

Luu, V.Q., Bonkowski, M., Nguyen, T.Q., Le, M.D., Calame, T. & Ziegler, T. (in review) A new species of the genus *Lycodon* Boie, 1826 (Serpentes: Colubridae) from Khammouane Province, central Laos. *Zootaxa*.

Declaration in each element	A, B, or C
1. Formulating the scientific idea based on theoretical assumptions to be clarified, including formulation of the question to be answered through analytical work and research plans.	C
2. Planning of experiments and analyses, design of the experimental methods in a way that the questions asked under point 1 can be expected to be answered.	C
3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	B
4. Presentation, interpretation and discussion of the results.	B

Declaration of Contribution as Author and Co-Author

Publication 13

Egert, J., **Luu, V.Q.**, Nguyen, T.Q., Le, M.D., Bonkowski, M. & Ziegler, T. (in review) First record of *Gracixalus quyeti* (Amphibia: Anura: Rhacophoridae) from Laos: molecular consistency versus morphological divergence between populations on both sides of the Truong Son range. *Revue Suisse de Zoologie*.

Declaration in each element	A, B, or C
1. Formulating the scientific idea based on theoretical assumptions to be clarified, including formulation of the question to be answered through analytical work and research plans.	B
2. Planning of experiments and analyses, design of the experimental methods in a way that the questions asked under point 1 can be expected to be answered.	B
3. Involvement in analytical work with respect to the concrete experimental studies and investigations.	B
4. Presentation, interpretation and discussion of the results.	B

Dissertation author's signature

Köln, 30.04.2016

(Vinh Quang Luu)

10. Statutory Declaration and Statement (Erklärung)

I declare that I have authored this doctoral dissertation independently, that I have not used other than the declared sources, and that I have explicitly marked all material which has been quoted either literally or by content from the used sources.

My dissertation was supervised by Prof. Dr. Michael Bonkowski and Associate Professor Dr. Thomas Ziegler.

Publications:

1. **Luu, V.Q.**, Nguyen, T.Q., Pham, C.T., Dang, K.N., Vu, T.N., Miskovic, S., Bonkowski, M., Ziegler, T. (2013) No end in sight? Further new records of amphibians and reptiles from Phong Nha - Ke Bang National Park, Quang Binh Province, Vietnam. *Biodiversity Journal*, 4 (2), 285–300.
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4. **Luu, V.Q.**, Calame, T., Bonkowski, M., Nguyen, T.Q. & Ziegler, T. (2014) A new species of *Cyrtodactylus* (Squamata: Gekkonidae) from Khammouane Province, Laos. *Zootaxa*, 3760 (1), 54–66. <http://dx.doi.org/10.11646/zootaxa.3760.1.3>
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11. **Luu, V.Q.**, Bonkowski, M., Nguyen, T.Q., Le, M.D., Schneider, N., Ngo, H.T & Ziegler, T. (2016) 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. *Zootaxa*, 4107 (2), 101–140. <http://doi.org/10.11646/zootaxa.4107.2.1>
12. **Luu, V.Q.**, Bonkowski, M., Nguyen, T.Q., Le, M.D., Calame, T. & Ziegler, T. (in review) A new species of the genus *Lycodon* Boie, 1826 (Serpentes: Colubridae) from Khammouane Province, central Laos. *Zootaxa*.
13. Egert, J., **Luu, V.Q.**, Nguyen, T.Q., Le, M.D., Bonkowski, M. & Ziegler, T. (in review) First record of *Gracixalus quyeti* (Amphibia: Anura: Rhacophoridae) from Laos: molecular consistency versus morphological divergence between populations on both sides of the Truong Son range. *Revue Suisse de Zoologie*.

Köln, 30.04.2016

(Vinh Quang Luu)

11. Curriculum Vitae

1. Personal and contact details

Name **VINH QUANG LUU**
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2. Professional and educational history

(a) Education

- Since 10/2012 Doctoral student at the Institute of Zoology, University of Cologne, Germany, with the topic “The taxonomy, zoogeography and ecology of amphibians and reptiles of Hin Nam No National Protected Area (Laos) in comparison with data from Phong Nha – Ke Bang National Park (Vietnam)”.
- 2006 - 2009 Master degree at the Faculty of Forest Resources Protection and Management, Forestry University of Vietnam, with the topic “Research on amphibian fauna of Thuong Tien Nature Reserve, Hoa Binh Province, Vietnam”.
- 1998 - 2002 Bachelor degree at the Faculty of Forest Resources Protection and Management, Forestry University of Vietnam, with the topic “Potential resources and status of ecotourism development in Ba Vi National Park, Hanoi, Vietnam”.

(b) Employment & experiences

- Since 12/2002 Lecturer at the Faculty of Forest Resources and Environmental Management, Vietnam Forestry University. *Teaching subjects:* Wildlife Identification, Wildlife Ecology and Management, Biodiversity Conservation, Landscape Ecology Planning and Eco-tourism. *Research interests:* Systematics, zoogeography, ecology, and conservation of amphibians and reptiles in Vietnam and Laos.
- 01/2013-12/2013 Biodiversity investigation towards the establishment of ecotourism types in combination with biodiversity conservation in Ba Be National Park and Kim Hy Nature Reserve, supported Bac Kan Pro-Poor Partnerships for Agro-Forestry Development (3PAD) Project in Bac Kan Province, Project Leader.
- 10/2012 Survey and monitoring on amphibians and reptiles in Ba Be National Park, Vietnam Conservation Fund (VCF), Team Leader.

- 09/2012 Research on herpetofauna in Kim Hy Nature Reserve, Bac Kan, Provincial Project, Team Leader.
- 07/2012 Survey and observation of amphibians and reptiles in Van Ban – Hoang Lien Nature Reserve, VCF, Team Leader.
- 06/ 2012 Research on herpetofauna in Ta Dung Nature Reserve, Dak Nong, Provincial Project, Team Leader.
- 05/2012 Training course for staff and local people on survey and monitoring biodiversity in Ben En National Park, VCF, Lecturer.
- 06/2010 - Status of Yellow-cheeked crested gibbon (*Nomasus gabriellae*) populations in
03/2011 Kon Cha Rang Nature Reserve, Conservation Internatinal (CI), Project Leader.
- 05/2009 Training course on survey and observation biodiversity, VFU, VCF, Lecturer.
- 12/2007 - A preliminary survey of the amphibian fauna of Ngoc Son-Ngo Luong Nature
01/2008 Reserve, Hoa Binh Province, Viet Nam, FFI, Researcher
- 12/2007 Conservation planning and development wildlife in Vietnam, Vietnam Ranger
- VFU, Researcher.

3. Scientific Awards, Fellowships and Grants

- 10/2012- Doctoral dissertation project in Germany funded by the Ministry of Education
06/2016 and Training of Vietnam (MOET, Project 911) and the German Academic Exchange Service (DAAD).
- 2015 A Booster Grant of the Rufford Small Grants for my doctoral dissertation with the project “The Annamite Mountain Range: An Evolutionary Barrier for Herpetofauna? A Case Study in The Karst Forest of the Hin Nam No National Protected Area, Central Laos”.
- 2014 Grant of the Idea Wild Organirasion, United State for my doctoral dissertation with the project “Exploration of the amphibian diversity in karst forests of the Hin Nam No National Protected Area, central Laos”.
- 2014 The Second Grant of the Rufford Small Grants for my doctoral dissertation with the project “Exploration of the herpetofaunal diversity in karst forests of the Hin Nam No National Protected Area and surrounding areas, central Laos”.
- 2013 The First Grant of the Rufford Small Grants for my doctoral dissertation with the project “The diversity of the reptile fauna of Hin Nam No National Biodiversity Conservation Area (Laos)”.
- 2008 Grant of the Idea Wild Organirasion, United State for my master thesis with the project “Research on amphibian fauna of Thuong Tien Nature Reserve, Hoa Binh Province, Vietnam”.

4. Scientific Association and Voluntary Service

- Since 4.2016 Member of Society for the Study of Amphibians and Reptiles (SSAR)
- Reviewer for Zootaxa

Signature:

Date: 30.4.2016