Three New Karst-Dwelling *Cnemaspis* Strauch, 1887 (Squamata; Gekkonidae) from Peninsular Thailand and the Phylogenetic Placement of *C. punctatonuchalis* and *C. vandeventeri*

Perry Lee Wood Jr. Corresp. 1, L. Lee Grismer 2, Anchalee Aowphol 3, César A Aguilar 1, Micheal Cota 4, 5, Marta S. Grismer 2, Matthew L. Murdoch 2, Jack W. Sites Jr. 1

1 Department of Biology and Bean Life Science Museum, Brigham Young University, Provo, Utah, United States
2 Department of Biology, La Sierra University, Riverside, California, United States
3 Faculty of Science, Department of Zoology, Kasetsart University, Chatuchak, Bangkok, Thailand
4 Natural History Museum, National Science Museum, Thailand, Technopolis, Khlong 5, Khlong Luang, Pathum Thani, Thailand
5 Suan Sunandha Rajabhat University, Institute for Research and Development, Dusit, Bangkok, Thailand

Corresponding Author: Perry Lee Wood Jr.
Email address: pwood@byu.edu

Three new species of Rock Geckos *Cnemaspis lineogularis* sp. nov., *C. phangngaensis* sp. nov., and *C. thachanaensis* sp. nov. of the *chanthaburiensis* and *siamensis* groups are described from the Thai portion of the Thai-Malay Peninsula. These new species are distinguished from all other species in their two respective groups based on a unique combination of morphological characteristics, which is further supported by mitochondrial DNA (mtDNA) from the NADH dehydrogenase subunit 2 gene (ND2). *Cnemaspis lineogularis* sp. nov. is differentiated from all other species in the *chanthaburiensis* group by having a smaller maximum SVL 38 mm, 13 paravertebral tubercles, enlarged femoral scales, no caudal bands, and a 19.5–23.0% pairwise sequence divergence (ND2). *Cnemaspis phangngaensis* sp. nov. is differentiated from all other species in the *siamensis* group by having the unique combination of 10 infralabial scales, four continuous pore-bearing precloacal scales, paravertebral tubercles linearly arranged, lacking tubercles on the lower flanks, having ventrolateral caudal tubercles anteriorly present, caudal tubercles restricted to a single paravertebral row on each side, a single median row of keeled subcaudals, and a 8.8–25.2% pairwise sequence divergence (ND2). *Cnemaspis thachanaensis* sp. nov. is distinguished from all other species in the *siamensis* group by having 10 or 11 supralabial scales 9–11 infralabial scales, paravertebral tubercles linearly arranged, ventrolateral caudal tubercles anteriorly, caudal tubercles restricted to a single paravertebral row on each side, a single median row of keeled subcaudal scales, lacking a single enlarged subcaudal scale row, lacking postcloacal tubercles in males, the presence of an enlarged submetatarsal scale at the base if the 1st toe, and a 13.4–28.8% pairwise
sequence divergence (ND2). The new phylogenetic analyses place *C. punctatonuchalis* and *C. vandeventeri* in the siamensis group with *C. punctatonuchalis* as the sister species to *C. huaseesom* and *C. vandeventeri* as the sister species to *C. siamensis*, corroborating previous hypotheses based on morphology. The discovery of three new karst-dwelling endemics brings the total number of nominal Thai *Cnemaspis* species to 15 and underscores the need for continued field research in poorly known areas of the Thai-Malay Peninsula, especially those that are threatened and often overlooked as biodiversity hot spots.
Three new karst-dwelling *Cnemaspis* Strauch, 1887 (Squamata; Gekkonidae) from Peninsular Thailand and the phylogenetic placement of *C. punctatonuchalis* and *C. vandeventeri*

Perry L. Wood Jr.,¹ L. Lee Grismer,² Anchalee Aowphol,³ César Aguilar,¹ Micheal Cota,⁴,⁵ Marta S. Grismer,² Matthew L. Murdoch,² and Jack W. Sites Jr.¹

¹Department of Biology and Bean Life Science Museum, Brigham Young University, Provo, Utah, USA 
²Herpetology Laboratory, Department of Biology, La Sierra University, Riverwalk Parkway, Riverside, California, USA 
³Kasetsart University, Faculty of Science, Department of Zoology, Chatuchak, Bangkok, 10900, Thailand 
⁴Natural History Museum, National Science Museum, Thailand, Technopolis, Khlong 5, Khlong Luang, Pathum Thani, Thailand 
⁵Suan Sunandha Rajabhat University, Institute for Research and Development, Dusit, Bangkok, Thailand

**ABSTRACT**

Three new species of Rock Geckos *Cnemaspis lineogularis* sp. nov., *C. phangngaensis* sp. nov., and *C. thachanaensis* sp. nov. of the *chanthaburiensis* and *siamensis* groups are described from the Thai portion of the Thai-Malay Peninsula. These new species are distinguished from all other species in their two respective groups based on a unique combination of morphological characteristics, which is further supported by mitochondrial DNA (mtDNA) from the NADH dehydrogenase subunit 2 gene (ND2). *Cnemaspis lineogularis* sp. nov. is differentiated from all other species in the *chanthaburiensis* group by having a smaller maximum SVL 38 mm, 13 paravertebral tubercles, enlarged femoral scales, no caudal bands, and a 19.5–23.0% pairwise sequence divergence (ND2). *Cnemaspis phangngaensis* sp. nov. is differentiated from all other species in the *siamensis* group by having the unique combination of 10 infralabial scales, four continuous pore-bearing precloacal scales, paravertebral tubercles linearly arranged, lacking tubercles on the lower flanks, having ventrolateral caudal tubercles anteriorly present, caudal tubercles restricted to a single paraveterbral row on each side, a single median row of keeled subcaudal scales, and a 8.8–25.2% pairwise sequence divergence (ND2). *Cnemaspis thachanaensis* sp. nov. is distinguished from all other species in the *siamensis* group by having 10 or 11 supralabial scales 9–11 infralabial scales, paravertebral tubercles linearly arranged, ventrolateral caudal tubercles anteriorly, caudal tubercles restricted to a single paravertebral row on each side, a single median row of keeled subcaudal scales, lacking a single enlarged subcaudal scale row, lacking postcloacal tubercles in males, the presence of an enlarged submetatarsal scale at the base of the 1st toe, and a 13.4–28.8% pairwise sequence divergence (ND2). The new phylogenetic analyses place *C. punctatonuchalis* and *C. vandeventeri* in the *siamensis* group with *C. punctatonuchalis* as the sister species to *C. huaseesom* and *C. vandeventeri* as the sister species to *C. siamensis*, corroborating previous hypotheses based on morphology. The discovery of three new karst-dwelling endemics brings the total number of nominal Thai *Cnemaspis* species to 15 and underscores the need for continued field research in poorly known areas of the Thai-Malay Peninsula, especially those that are threatened and often over looked as biodiversity hot spots.

Keywords: *Cnemaspis*, *chanthaburiensis* group, Limestone forests, Thai-Malay Peninsula, Taxonomy, *siamensis* group
INTRODUCTION

The Thai-Malay Peninsula is a long (1,127 km) and narrow (maximum width 322 km) appendix of mainland Asia extending from Indochina in the north to its southern terminus in Singapore. The Thai-Malay Peninsula is comprised of the southern portion of Myanmar, the southwestern section of Thailand, West Malaysia, and Singapore. This region is both geologically and climatically complex and has been influenced by a number of factors. The environmental complexity of this region has helped to form two prominent biogeographic barriers, the Isthmus of Kra and the Kangar-pattani line. These biogeographic barriers serve as pivotal crossroads for faunal exchange between the Indochinese and Sundaic biota (e.g. Raes et al., 2014; de Bruyn et al., 2013; Parnell, 2013; Patou et al., 2009; Woodruff and Turner, 2009; Gorog et al., 2004; Pauwels et al., 2003; Hughes et al., 2003; Woodruff, 2003; Grismer et al., 2014d; Grismer, 2011). One feature that is often over-looked in terms of biodiversity are the myriad of limestone forests and karst formations dispersed throughout the Malay Peninsula.

Karstic regions have been referred to as “arks” or biodiversity reservoirs that can be used as stock for repopulating degraded environments during ecosystem reassembly (Schilthuizen, 2004). In addition to serving as arks, karst formations have been known to provide natural laboratories for biogeographic, evolutionary, ecological, and taxonomic research (e.g. Ng, 1991; Grismer et al. 2014d; Schilthuizen et al., 2005; 1999; Kiew, 1991). From chemical and mechanical weathering karst formations have been molded into a unique suite of microhabitats in which a number of species have become adapted (e.g. Vermeulen and Whitten, 1999; Komo, 1998a,b; Tija, 1998). To date there has been a fair amount of research conducted on the flora of karst formations and their surrounding limestone forests, resulting in a high estimate of endemic species (Kiew, 1998; Clements et al., 2006; Chin, 1977; and references therein). In addition to the high level of floras and endemism there are also high levels of invertebrate endemism associated with karst formations (e.g. Holloway, 1986; Vermeulen and Whitten, 1999). Although these areas harbor a high degree of endemism for invertebrates and plant species they are generally not considered to hold large numbers of endemic terrestrial vertebrates (i.e. Jenkins et al., 2005; Alström et al., 2010; Woxvold et al., 2009), because most vertebrates have high dispersal capabilities. There are only a few mammals and birds that are thought to be restricted to karst formations (e.g. Latinne et al., 2011; Clements et al., 2006). In contrast recent taxonomic work in Peninsular Malaysia has uncovered an impressive amount of new microendemic karst-dwelling species of reptiles, including 14 new lizards (Grismer et al., 2008a,b; 2009; 2013b; 2012; 2014c; 2013a; 2016a; Wood et al., 2013) and two new snakes (Grismer et al., 2014b; Quah et al. in prep). However, these surveys only covered a small portion of the limestone forests and karst formations of Peninsular Malaysia continue northward up the entire Thai-Malay Peninsula into central Thailand and eastern Myanmar.

Dispersed throughout Peninsular Thailand are hundreds of unexplored isolated karst formations. From the limited number of surveys that have been conducted, a few gekkotan species have been identified and described (e.g. Grismer et al., 2012; 2015; Pauwels et al., 2013; Grismer et al., 2012; Ellis and Pauwels, 2012). A major focus of these surveys in the last two decades has lead to the discovery of at least 15 new micro-endemic karst-dwelling Bent-toed Geckos in the genus Cyrtodactylus (e.g. Ellis and Pauwels, 2012; Pauwels et al., 2013; Grismer et al., 2016a; Sacha, 2015; Wood et al., 2013) and the newly discovered representatives (Grismer et al., 2014d; Quah et al., in prep). These surveys only covered a small portion of the limestone forests and karst formations of Peninsular Malaysia continue northward up the entire Thai-Malay Peninsula into central Thailand and eastern Myanmar.

Dispersed throughout Peninsular Thailand are hundreds of unexplored isolated karst formations. From the limited number of surveys that have been conducted, a few gekkotan species have been identified and described (e.g. Grismer et al., 2012; 2015; Pauwels et al., 2013; Grismer et al., 2012; Ellis and Pauwels, 2012). A major focus of these surveys in the last two decades has lead to the discovery of at least 15 new micro-endemic karst-dwelling Bent-toed Geckos in the genus Cyrtodactylus (e.g. Ellis and Pauwels, 2012; Pauwels et al., 2013; Grismer et al., 2016a; Sacha, 2015; Wood et al., 2013) and the newly discovered representatives (Grismer et al., 2014d; Quah et al., in prep). These surveys only covered a small portion of the limestone forests and karst formations of Peninsular Malaysia continue northward up the entire Thai-Malay Peninsula into central Thailand and eastern Myanmar.

The Rock geckos of the genus Cnemaspis comprise a clade of 55 described species that are widespread throughout the Sunda Shelf, with a majority of the species being from the Thai-Malay Peninsula and their adjacent islands. Most Cnemaspis are diurnal, cryptically colored, scansorial species, however some species such as C. psychedelica Grismer, Ngo & Grismer 2010 (Grismer et al., 2014d, Figure 8) are brightly colored and a number of species dispersed throughout the phylogenetic tree are nocturnal with multiple independent transitions (Grismer et al., 2014d, Figure 5). Like Cyrtodactylus, Cnemaspis are also found on a variety of substrates (eg. granite, karst, vegetation, terrestrial and various combinations of these). Often when there are micro-endemic karst-dwelling Cyrtodactylus (nocturnal) there is usually an...
endemic diurnal karst-dwelling *Cnemaspis* occupying the same niche during different activity periods (e.g. Grismer et al. 2016a, 2012, 2014c, 2016b). From this arises a number of interesting questions about niche partitioning, behavior, and potential competition of *Cyrtodactylus* and *Cnemaspis*, however this is not the focus of this paper. Recent surveys in Phangnga, Tha Chana, Thap Sakae, Som Roi Yot, and Tham Sonk hill during the month of September 2016 resulted in the collection of *Cnemaspis punctatonuchalis*, *C. vandeventeri* and three undescribed species of *Cnemaspis* that co-occur with some of the aforementioned species of karst endemic *Cyrtodactylus*. These new populations can be placed in the genus *Cnemaspis* based on having broad, flattened heads; large somewhat forward and upwardly directed eyes with round pupils and no eyelids; flattened bodies; long, widely splayed limbs with long, inflected digits; and no femoral pores. Here we present morphological and color pattern data as evidence, for delimitation of these three new species of *Cnemaspis*, bolstered by mtDNA genetic data, and present the phylogenetic placement of *C. punctatonuchalis* and *C. vandeventeri.*

**MATERIALS AND METHODS**

**Taxon sampling**

We obtained 203 samples of *Cnemaspis* and outgroups from Grismer et al. (2014d). In combination with this dataset we added 14 new samples including two species of Thai *Cnemaspis* (*C. punctatonuchalis* and *C. vandeventeri*) that have never been sequenced, along with three undescribed species of *Cnemaspis* from peninsular Thailand (Figure 1, Table S1). Brigham Young University’s Institutional Animal Care and Use Committee (IACUC) has approved the animal use protocol for this study (protocol # 160401). The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix [http://zoobank.org/](http://zoobank.org/). The LSID for this publication is: [urn:lsid:zoobank.org:pub:987831FC-F4BA-4409-A43C-9929F913E9F9](urn:lsid:zoobank.org:pub:987831FC-F4BA-4409-A43C-9929F913E9F9). The online version of this work is archived and available from the following digital repositories: PubMed Central.

**Molecular and Phylogenetic analyses**

Genomic DNA was isolated from liver or muscle tissues stored in 95% ethanol using the animal tissue protocol in the Qiagen DNeasy<sup>TM</sup> tissue kit (Valencia, CA, USA). The mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and the flanking tRNAs (∼1335 bp) was amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions: 1.0 µl (∼10–33 µg) genomic DNA, 1.0 µl (10 µM) forward primer L4437b (5'-AAGCAGTTGGGCCCA T ACC-3'), 1.0 µl (10 µM) reverse primer H5934 (5'-AGRGTGCCAA TGTCTTTGTGR TT -3'), 1.0 µl deoxynucleotide pairs (1.5 µM), 2.0 µl 5x buffer (1.5 µM), 1.0 MgCl2 10x buffer (1.5 µM), 0.18 µl Promega Taq polymerase (5u/µl), and 7.5 µl H2O, primers are from Macey et al. (1997). All PCR reactions were executed in an Eppendorf Mastercycler gradient thermocycler under the following conditions: initial denaturation at 95°C for 2 min, followed by a second denaturation at 95°C for 35 s, annealing at 52°C for 35 s, followed by a cycle extension at 72°C for 35s, for 33 cycles. All PCR products were visualized on a 1% agarose gel electrophoresis. Successful targeted PCR products were vacuum purified using MANU 30 PCR plates Millipore plates and purified products were resuspended in DNA grade water. Purified PCR products were sequenced using the PCR primers from above and sequencing primers CyrtintF1 (5'-TAGCCYTCTCYTCACTYGGCC-3') and CyrtintR1 (5'-ATTGKTAGDTRGCYAGGSTKGG-3') from Silser et al. (2010) on the ABI Big-Dye Terminator v3.1 Cycle Sequencing Kit in an ABI GeneAmp PCR 9700 thermal cycler. Cycle sequencing reactions were purified with Sephaldex G-50 Fine (GE Healthcare) and sequenced on an ABI 3730xl DNA Analyzer at the BYU DNA Sequencing Center (DNASC). All new sequences produced from this study are deposited in GenBank under the following accession numbers KY091231–KY091244 (Table S1). All sequences were edited and aligned in Geneious v6.1.8 (Kearse et al. 2012), alignment was constructed using the Muscle plugin (Edgar 2004). Mesquite v3.02 (Maddison and Maddison 2015) was used to check for stop codons and to ensure the correct amino acid read frame.
For estimating the phylogenetic relationships we used both partitioned Maximum Likelihood (ML) and partitioned Bayesian Inference (BI) methods. The ND2 gene was partitioned by codon position and the tRNAs were treated as a single partition for both the ML and BI analyses. All models of molecular evolution were estimated in ModelTest v3.7 (Posada and Crandall, 1998), using the Bayesian Information Criterion (BIC). The best fit models of evolution are in presented in Table 1. The partitioned ML analyses was performed using RAxML HPC v7.5.4 (Stamatakis, 2006), 1000 bootstrap pseudoreplicates via therapid hill-climbing algorithm (Stamatakis et al., 2008) with 200 searches for the best tree. The Bayesian analysis was carried out in MrBayes v3.2 (Huelsenbeck et al., 2001) [Ronquist et al., 2012] using the default priors. Two simultaneous runs were performed with eight chains per run, seven hot and one cold following default priors. The analysis was run for 2 x 10^6 generations and sampled every 1000 generations from the Markov Chain Monte Carlo (MCMC). The analysis was halted after the average standard deviation split frequency was below 0.01 and we assumed convergence. We conservatively discarded the first 25% of the trees as burnin and constructed a consensus tree using the sumt command in MrBayes. Nodes having bootstrap support values (BS) greater than 70 and posterior probabilities (PP) above 0.95 were considered well supported (Huelsenbeck et al., 2001; Wilcox et al., 2002). We calculated uncorrected percent sequence divergences for ND2 in Mega v6.06 (Tamura et al., 2013).

Morphological analyses

Morphological and color pattern characteristics follow Grismer et al., (2014d). Color pattern characters were taken from digital images of living specimens cataloged in the La Sierra University Digital Photo Collection (LSUDPC) and from living specimens in the field. The following measurements on the type series were taken by PL WJ with a electronic digital caliper to the nearest 0.1 mm, under a Lica WILD M10 dissecting microscope on the left side of the body where appropriate: snout-vent length (SVL), taken from the tip of snout to the vent; tail length (TL), taken from the vent to the tip of the tail, original or regenerated; tail width (TW), taken at the base of the tail immediately posterior to the postcloacal swelling; forearm length (FL), taken on the dorsal surface from the posterior margin of the elbow while flexed 90° to the inflection of the flexed wrist; tibia length (TBL), taken on the ventral surface from the posterior surface of the knee while flexed 90° to the base of the heel; axilla to groin length (AG), taken from the posterior margin of the forelimb at its insertion point on the body to the anterior margin of the hind limb at its insertion point on the body; head length (HL), the distance from the posterior margin of the retroarticular process of the lower jaw to the tip of the snout; head width (HW), measured at the angle of the jaws; head depth (HD), the maximum height of head from the occiput to the throat; eye diameter (ED), the greatest horizontal diameter of the eyeball; eye to ear distance (EE), measured from the anterior edge of the ear opening to the posterior edge of the eyeball; eye to snout distance (ES), measured from anteriormost margin of the eyeball to the tip of snout; eye to nostril distance (EN), measured from the anteriormost margin of the eyeball to the posterior margin of the external nares; inner orbital distance (IO), the width of the frontal bone at the level of the anterior edges of the orbit; ear length (EL), the greatest vertical distance of the ear opening; and internarial distance (IN), measured between the medial margins of the nares across the rostrum. Additional character states evaluated were numbers of supralabial and infralabial scales counted from below the middle of the orbit to the rostral and mental scales, respectively; the texture of the scales on the anterior margin of the forearm; the number of paravertebral tubercles between limb insertions counted in a straight line immediately left of the vertebral column (where applicable); the presence or absence of a row of enlarged, widely spaced, tubercles along the ventrolateral edge of the body (flank) between the limb insertions; the general size (i.e., strong, moderate, weak) and arrangement (i.e., random or linear) of the dorsal body tubercles; the number of subdigital lamellae beneath the fourth toe counted from the base of the first phalanx to the claw; the distribution of transverse and granular subdigital lamellae on the fourth toe; the total number of precloacal pores, their orientation and shape; the number of precloacal scales lacking pores separating the left and right series of pore-bearing precloacal scales; the degree and arrangement of body and tail tuberculation; the relative size and morphology of the subcaudal scales, subtibial scales, and submetatarsal scales beneath the first metatarsal; and the number of postcloacal tubercles on each side of the tail base. Longitudinal rows of caudal tubercles on the non-regenerated portion of the tail are quite variable between species and useful in differentiating several taxa. Up to five pairs of the following rows may be present in varying combinations: paravertebral row—the dorsal row adjacent to the middorsal, caudal furrow; dorsolateral row—the row between the
RESULTS

The phylogenetic analyses place both *C. punctatonuchalis* and *C. vandeventeri* in the *siamensis* group (Figure 2). *Cnemaspis punctatonuchalis* is strongly recovered for the ML analysis (100 BS) but not the BI (0.87 PP) as the sister species to *C. huaseesom*. *Cnemaspis vandeventeri* is strongly supported (100 BS and 0.99 PP) as the sister lineage to *C. siamensis*. Phylogenetic analyses of the three new populations sampled from Som Roi Yot, Phangnga, and Tha Chana represent well-supported independent lineages (100 BS, 1.0 PP; 100 BS, 1.0 PP; 100 BS, 1.0 PP, respectively). The samples from Wat Khao Daeng are well-supported (100 BS, 1.0 PP) as the sister lineage to the *chanthaburiensis* group (Figure 2A) and demonstrate a 19.5–23% mtDNA pairwise sequence divergence from all of the other species in this group (Table 2). Both the Phangnga and the Tha Chana populations are nested within the *siamensis* group (Figure 2B). The Phangnga population is well-supported for ML (99 BS) but lacks support from the BI (0.56 PP) as the sister lineage to a clade composed of *C. omari* and *C. roticani* and demonstrate a 8.8–25.2% mtDNA pairwise sequence divergence from all of the other species in the *siamensis* group (Table 3). The population from Tha Chana forms a well-support lineage (100 BS and 1.0 PP) and is strongly (100 BS and 1.0 PP) placed as the sister lineage to a clade composed of *C. siamensis* and *C. vandeventeri* and shares a 13.4–28% mtDNA pairwise sequence divergence form all of the other species in the *siamensis* group (Table 3). Given that these new populations form well-supported independent lineages (Figs. 2A, B) coupled with high genetic distances and a unique set of morphological and color pattern characteristics that separate them from all members of their respective groups, we describe these three populations below as new species.

Systematics

*Cnemaspis lineogularis* sp. nov. urn:lsid:zoobank.org:act:8E3B21A4-93BF-4D08-B8D1-0A3EEF6BE44F

Common name: Striped Throated Rock Gecko

(Figs. 3–5)

**Holotype.** BYU 62535 adult male, collected near Wat Khao Daeng, Kui Buri, Prachuap Khiri Khan, Thiland (12.134620°N, 99.961078°E; 12 m a.s.l.), 31 July 2016, by PLW, LLG, CA, MC, MSG, MLM.

**Paratopotypes.** BYU 62536 adult male and ZMKU R 00728 adult female paratypes bear the same collection and data as the holotype.

**Diagnosis.** *Cnemaspis lineogularis* is distinguished from all other species of *Cnemaspis* in the *chanthaburiensis* group by the combination of the following morphological and color pattern characters: maximum SVL 38 mm; nine supralabials; eight infralabials; ventral scales smooth; no precloacal pores; 13 paravertebral tubercles linearly arranged; no tubercles on the lower flanks; lateral caudal furrows present; no caudal tubercles in the lateral furrows; ventrolateral caudal tubercles anteriorly; caudal tubercles not encircling tail; subcaudals smooth bearing a single median row of enlarged smooth scales; lateral caudal tubercle row absent; shield-like subtibial scales absent; one post cloacal tubercle in males; no enlarged femoral or submetatarsal scales; enlarged femoral scales; subtibials smooth; 27–29 subdigital fourth toe lamellae; sexually dimorphic for dorsal color pattern; gular region yellow-orange, thick, black lineate markings in males, absent in females; subcaudal whitish (Tables 4–6).

**Description of the holotype.** Adult male; SVL 38 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.25), somewhat narrow (HW/SVL 0.16), flattened (HD/HL 0.38), head distinct from neck; snout moderate (ES/HL 0.52), snout slightly concave in lateral view; postnasal region concave medially; scales on rostrum smooth becoming keeled posteriorly, raised, larger than conical scales on occiput; weak to absent supra ocular ridges; frontalrostralis sulcus deep; canthus rostralis nearly absent, smoothly rounded; eye large (ED/HL 0.26); extra-brillar, fringe scales largest anteriorly; pupil round; ear opening more round than oval; rostral slightly concave, dorsal 80% divided by longitudinal median groove; rostral...
bounded posteriorly by supra nasals and one small azygous scale and laterally by first supralabials; 9,9 (R.L) slightly raised supralabials decreasing in size posteriorly; 8,8 (R.L) infralabials decreasing in size posteriorly; nostrils elliptical, oriented dorsoposteriorly; bordered by small postnasal scales; mental large, triangular, concave, bordered posteriorly by three postmentals; gular and throat scales raised, smooth, small and round.

Body slender, elongate (AG/SVL 0.46); small, keeled, dorsal scales equal in size throughout body, intermixed with several large, multicarinate conical tubercles more or less randomly arranged; tubercles extend from the occiput to base of the tail; no tubercles on flanks; pectoral and abdominal scales smooth, not larger posteriorly; abdominal scales slightly larger than dorsals; no pore-bearing, precloacal scales or precloacal depressions; forelimbs moderately long, slender; dorsal scales slightly raised, multicarinate; ventral scales of brachia smooth, raised, juxtaposed; scales beneath forearm smooth, raised, subimbricate; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; claws recurved; sub digital lamellae unnotched; lamellae beneath first phalanges granular proximally, widened distally; lamellae beneath phalanx immediately following inflection granular, lamellae of distal phalanges wide; interdigital webbing absent; fingers increase in length from first to fourth with fourth and fifth equal in length; hind limbs slightly longer and thicker than forelimbs; dorsal scales raised, multicarinate, juxtaposed; dorsal scales on anterior margin of thighs enlarged, multicarinate, becoming smaller posteriorly; ventral scales of thigh smooth; subtitial scales smooth, flat, imbricate, with no enlarged anterior row; plantar scales smooth, juxtaposed, raised; no enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected jointed; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges granular proximally, widened distally; lamellae beneath phalanx immediately following inflection granular, lamellae of distal phalanges wide; interdigital webbing absent; toes increase in length from first to fourth with fourth and fifth equal in length; 29,28 (R.L) subdigital lamellae on fourth toe; caudal scales similar to dorsal scale size, enlarge caudal tubercles arranged in segmented whorls, no encircling tail; caudal scales keeled, juxtaposed anteriorly; shallow, middorsal furrow; deeper, single, lateral furrow; enlarged, median, subcaudal scales; subcaudals smooth; median row of enlarged, keeled, subcaudal scales; transverse, tubercle rows do not encircle tail; caudal tubercles absent from lateral furrow; 2,1 (R.L) enlarged, postcloacal tubercles on lateral surface of hemipenal swellings at base of tail; posterior 30% of tail regenerated.

Coloration. In life, dorsal ground color of head light beige-green, that of the body, limbs and tail slightly lighter than head; top of the head bearing, small black and light green markings; thin diffuse broken dark-brown to black postorbital stripe, extending to the nape; two dark lines radiating distally from orbit; dark paravertebral markings extend from nape to anterior fourth of tail where they transform into diffuse incomplete bands, intermixed with sage colored paravertebral blotches; single dark prescapular blotch dorsoanteriorly of forelimb insertion; limbs slightly lighter than dorsal ground color with randomly placed, diffuse dark blotches; all ventral surfaces grayish white, except gular region and anterior-most portion of throat orange with black midgular stripe and adjacent black stripes along the mandibular margin; posterior margin of orange gular coloration edged with black, transverse markings (Figures 3–5).

Variation. Paratypes approximate the holotype (BYU 62535) in general aspects of coloration except that the female paratype (ZMKU R 00728) lacks the black markings in the gular region and the yellowish-orange gular coloration is less prominent, additionally the dorsal coloration is much lighter. Selected body measurements and variation in squamation are presented in Table 4.

Etymology. The specific epithet *lineogularis* is derived from the Latin adjective *lineus* for the word “line” and the nominative form of the Latin word *gulare* meaning “throat” and is in reference to the multiple dark gular lines present in the males of this species.

Distribution. Only known from the type locality but we hypothesize it will be found in nearby karst formations (Figures 1 and 6).

Natural history. The type series and several other individuals were active during the day in shaded areas and would rapidly retreat to nearby cracks and crevices at the slightest provocation. We hypothesize this may be due to high predation as we found *Trimeresurus fucatus* in an ambush posture in the same microhabitat. No individuals were seen deep within the caves and from our observations, it appears this species primarily inhabits the more exterior surfaces of the karst tower (Figure 6). The karst formations in this area are extensive and we assume this species has a much wider distribution than that reported here.
We hypothesize that diurnality in this species is to avoid competition with and predation from the much larger *Cyrtodactylus lineogularis* with which it is syntopic. This is a commonly observed pattern among syntopic pars of *Cnemaspis* and *Cyrtodactylus* throughout their distributions in Southeast Asia (Grismer et al., 2014d and references therein).

**Comparisons.** *Cnemaspis lineogularis* sp. nov. can be differentiated for all other species in the *chanthaburiensis* group based on the following morphological and color pattern characteristics (see Tables 5, 6 for additional comparisons). *Cnemaspis lineogularis* sp. nov. differs from *C. chanthaburiensis*, *C. neangthyi*, *C. laoensis*, *C. aurantiacopes*, *C. caudanivea*, *C. nuicamensis*, and *C. tucdupensis* by having a smaller maximum SVL (38 mm vs. 42.2 mm, 54.0 mm, 40.9 mm, 58.4 mm, 47.2 mm, 48.2 mm, and 51.0 mm, respectively), by having less paravertebral tubercles (13 vs. 21–25, 20–26, 22, 23–31, 20–24, 16–21, and 16–22 respectively), and by having enlarged femoral scales. *Cnemaspis lineogularis* sp. nov. is further differentiated from *C. neangthyi* by having less supralabial scales (9 vs. 11–13).

*Cnemaspis lineogularis* sp. nov. differs from *C. neangthyi* by having less infralabial scales (8 vs. 10–12) and from *C. nuicamensis* by having more infralabial scales (8 vs. 6–7). It is further differentiated from *C. chanthaburiensis*, *C. neangthyi*, *C. aurantiacopes*, *C. caudanivea*, and *C. nuicamensis* by lacking precloacal pores. From *C. laoensis*, *C. lineogularis* sp. nov. differs by having linearly arranged tubercles versus randomly arranged tubercles. *Cnemaspis lineogularis* sp. nov. differs from *C. chanthaburiensis*, *C. neangthyi*, *C. laoensis*, *C. aurantiacopes*, *C. nuicamensis*, and *C. tucdupensis* by lacking tubercles on the lower flanks. *Cnemaspis lineogularis* sp. nov. differs from *C. chanthaburiensis*, *C. neangthyi*, *C. laoensis*, by lacking caudal tubercles in the lateral furrow. *Cnemaspis lineogularis* sp. nov. has ventrolateral caudal tubercles anteriorly which separates it from *C. chanthaburiensis* and *C. laoensis* which lack this character. *Cnemaspis lineogularis* sp. nov. differs from *C. laoensis*, *C. caudanivea*, *C. nuicamensis*, and *C. tucdupensis* by the presence of a lateral caudal tubercle row. From *C. chanthaburiensis*, *C. laoensis*, *C. caudanivea*, and *C. tucdupensis*, *C. lineogularis* sp. nov. differs by having an enlarged median subcaudal scale row. *C. lineogularis* sp. nov. differs from *C. laoensis* and *C. nuicamensis* by having one postcloacal tubercle in males versus 2,3 and 2–4 respectively. *C. lineogularis* sp. nov. is further differentiated from *C. caudanivea* by lacking shield-like subtibial scales. *Cnemaspis lineogularis* sp. nov. differs from *C. neangthyi*, *C. laoensis*, and *C. aurantiacopes* by lacking keeled subtibial scales. *Cnemaspis lineogularis* sp. nov. differs from *C. aurantiacopes* and *C. tucdupensis* by lacking an enlarged submetatarsal scale on the 1st toe. *Cnemaspis lineogularis* sp. nov. is further differentiated from *C. neangthyi* by having more 4th toe lamellae (27–29 vs. 22–25). *Cnemaspis lineogularis* sp. nov. is further differentiated from all other species in the *chanthaburiensis* group based on squamation and color pattern characteristics (Tables 5 and 6).

*Cnemaspis phangngaensis* sp. nov. urn:lsid:zoobank.org:act:6053C709-A409-4F65-B15C-8C647D7EDF1C
Common name: The Phangnga Rock Gecko (Figs. 7–9)

**Holotype.** BYU 62538 adult male, collected at Phung Chang Cave, Phangnga, Mueang Phangnga, Thailand (8.442344°N, 98.514869°E; 12 m a.s.l.), 26 July 2016, by PLW, LLG, CA, MC, MSG, MLM.

**Paratopotype.** BYU 62537 adult female paratype bears all the same collection and locality information as the holotype.

**Diagnosis.** *Cnemaspis phangngaensis* sp. nov. is distinguished from all other species of *Cnemaspis* in the *siamensis* group by the combination of the following morphological and color pattern characteristics: maximum SVL 42 mm; 10 supralabials; 10 infralabials; ventral scales keeled; four continuous precloacal scales bearing a single round pore in males; 22 paravertebral tubercles linearly arranged; no tubercles on the lower flanks; lateral caudal furrows present; no caudal tubercles in the lateral furrows; lateral caudal tubercle row present; ventrolateral caudal tubercles anteriorly; caudal tubercles not encircling tail; caudal tubercles restricted to a single paravertebral row; subcaudals keeled bearing a single median row of enlarged keeled scales; two post cloacal tubercle in males; no enlarged femoral, tibial, or sub metatarsal scales; subtibials keeled; no enlarged median subcaudal scale row; no submetatarsal scale on first toe; 29 subdigital fourth toe lamellae; no enlarged median subcaudal scale row; dorsal and ventral color pattern sexually dimorphic; yellow or white bars present on flanks; prescapular marking present; anterior gular
region dark yellowish, no dark lineate markings in males or females, and no mid-gular marking; posterior
gular region and pectoral region whitish in males; abdomen yellow; subcaudal region yellow (Table 5–7).

Description of the holotype. Adult male; SVL 42 mm; head oblong in dorsal profile, moderate in
size (HL/SVL 0.27), somewhat narrow (HW/SVL 0.16), flattened (HD/HL 0.35), head distinct from
neck; snout moderate (ES/HL 0.44), slightly concave in lateral view; postnasal region concave medially;
scales on rostrum smooth becoming keeled posteriorly, raised, larger than conical scales on occiput; weak
to absent supra ocular ridges; frontalrostralis sulcus shallow; canthus rostralis nearly absent, smoothly
rounded; eye large (ED/HL 0.20); extra-brillar, fringe scales largest anteriorly; pupil round; ear opening
more oval, taller than wide; rostral slightly concave, dorsal 80% divided by longitudinal median groove;
rostral bordered posteriorly by supra nasals and one small azygous scale and laterally by first supralabials;
10, 10 (R,L) slightly raised supralabials decreasing in size posteriorly; 10, 10 (R,L) infralabials decreasing
in size posteriorly; nostrils elliptical, oriented dorsoanteriorly; bordered by small postnasal scales; mental
large, triangular, concave, bordered posteriorly by three postmentals; gular and throat scales raised, keeled,
small and round.

Body slender, elongate (AG/SVL 0.45); small, raised, keeled, dorsal scales equal in size throughout
body, intermixed with several large, multicarinate conical tubercles more or less randomly arranged;
tubercles extend from the occiput to base of the tail; no tubercles on flanks; pectoral and abdominal
scales keeled, not larger posteriorly; abdominal scales slightly larger than dorsals; two pore-bearing,
continuous, precloacal pores on each side; forelimbs moderately long, slender; dorsal scales slightly
raised, keeled; ventral scales of brachia smooth, raised, juxta posed; scales beneath forearm smooth,
slightly raised, subimbricate; palmar scales smooth, juxta posed, raised; digits long with an inflected joint;
claw recurved; sub digital lamellae unnotched; lamellae beneath first phalanges granular proximally,
widened distally; lamellae beneath phalax immediately following inflection granular, lamellae of distal
phalanges wide; interdigital webbing absent; fingers increase in length from first to fourth with fourth
and fifth equal in length; hind limbs slightly longer and thicker than forelimbs; dorsal scales raised,
multicarinate, juxta posed; ventral scales of thigh, slightly raised, conical, keeled; subtibial scales keeled,
flat, imbricate, with no enlarged anterior row; plantar scales smooth, juxta posed, raised; no enlarged
submetatarsal scales beneath first metatarsal; digits elongate with an inflected jointed; claws recurved;
subdigital lamellae unnotched; lamellae beneath first phalanges granular proximally, widened distally;
lamellae beneath phalax immediately following inflection granular, lamellae of distal phalanges wide;
interdigital webbing absent; toes increase in length from first to fourth with fourth and fifth equal in length;
29, 29 (R,L) subdigital lamellae on fourth toe; caudal scales similar to dorsal scale size, enlarge caudal
tubercles arranged in segmented whors, not encircling tail; caudal scales keeled, juxta posed anteriorly;
shallow, middorsal furrow; deeper, single, lateral furrow; enlarged, median, subcaudal scales; subcaudals
keeled; median row of enlarged, keeled, subcaudal scales; transverse, tubercle rows do not encircle tail;
caudal tubercles absent from lateral furrow; 1, 1 (R,L) enlarged flat, postcloacal tubercle on lateral surface
of hemipenal swellings at base of tail; posterior ~30% of tail missing.

Coloration. In life dorsal ground color of head light beige, that of the body, limbs and tail slightly darker
than the head with dark irregular blotches; top of the head bearing, small black and sage markings; thin
diffuse broken dark brown to black postorbital stripe, extending to the nape, not complete; light sage
vertebral blotches extending form the nape to tail where they transform into diffuse near complete irregular
bands; intermixed with light sage blotches; single light-yellowish prescapular crescent dorsoanteriorly
of forelimb insertion; flanks with irregular incomplete sage to yellowish-orange bars becoming more
orange distally; limbs slightly darker than dorsal ground color with randomly placed, diffuse dark and
sage colored blotches; all ventral surfaces grayish-white, except gular, abdominal, and subcaudal regions
are yellowish-orange, with more pronounced darker yellow stippling (Figs. 7–9).

Variation in the type series. The female paratype (BYU 62537) approximates the holotype in general
aspects of coloration except the overall dorsal coloration is lighter and the ventral coloration is a uniform
light yellow and is not as prominent in the gular and abdominal regions. Select body measurements and
variation in squamation are presented in Table 7.

Etymology. The specific epithet phangngaensis is a noun in apposition to the type locality where this
species is found.
Distribution. Only known from the karst formation in which it is found the Phung Chang Cave, Phangnga, Mueang Phangnga, Thailand. We hypothesize that this species will be found on nearby contiguous karst formations.

Natural history. Cnemaspis phangngaensis inhabits a karst formation in a lowland limestone forest (Fig. 10) surrounded by highly disturbed, urbanized habitat. The male holotype was collected at night on the karst approximately 15 m above the ground on the exterior surface of the tower and the female was collected at night sleeping on a leaf approximately 1.2 meters above the limestone forest floor adjacent to the nearby karst formation. Individuals were also observed active during the day, but avoided being captured by retreating into the rock crevices. We hypothesize that these are diurnal karst dwellers that use the vegetation at night for refuge. We hypothesize that diurnality in this species is to avoid competition with and predation from the much larger Cyrtodactylus lekaguli with which it is syntopic.

Comparisons. The phylogenetic analysis recovers the chanardi group and C. phangngaensis sp. nov. as the sister species to a clade containing C. omari and C. roticanai (Figure 2). This relationship is further supported by the following derived morphological characters (sensu Grismer et al., 2014d), prescapular crescent present, yellow abdomen, yellow ventral surfaces of the hind limbs and tail being yellow and numerous other morphological and color pattern characteristics (Tables 5 and 9). C. phangngaensis sp. nov. differs from C. chanardi, C. omari, and C. roticanai by having: more infralabial scales (10 vs. 6–8, 7,8, and 7,8, respectively); continuous precloacal pores; paravertebral tubercles linearly arranged; lacking tubercles on the lower flank; ventrolateral caudal tubercles anteriorly; caudal tubercles restricted to a single paravertebral row on each side; a single median row of keeled subcaudals. Cnemaspis phangngaensis sp. nov. is further differentiated from C. chanardi and C. omari by having a larger maximum SVL (42 mm vs. 40.1 mm and 41.3 mm, respectively). Cnemaspis phangngaensis sp. nov. differs from C. omari, and roticanai by having more supralabial scales (10 vs. 8, 9, and 8, 9, respectively). C. phangngaensis sp. nov. nov. differs from C. chanardi by having fewer precloacal pores (4 vs. 6–8). Cnemaspis phangngaensis sp. nov. differs from C. roticanai by having fewer paravertebral tubercles (22 vs. 25–27). From C. roticanai, C. phangngaensis sp. nov. differs by lacking caudal tubercles in the lateral furrow and by having a lateral caudal tubercle row present. Cnemaspis phangngaensis sp. nov. differs from C. omari by lacking caudal tubercles encircling the tail and by having more lamellae under the 4th toe (29 vs. 25–28). Cnemaspis phangngaensis sp. nov. is further differentiated from C. chanardi by lacking an enlarged median subcaudal scale row. From C. chanardi and C. omari, C. phangngaensis differs by have two postcloacal tubercles in males versus one. Cnemaspis phangngaensis is further differentiated from all other species in the siamensis group based on squamation and color pattern characteristics (Table 5 and 9).

Cnemaspis thachanaensis sp. nov. urn:lsid:zoobank.org:act:3581C94E-6170-4F42-9159-E2B564B576F1

Common name: The  Tha Chana Rock Gecko (Figs. 11–13)

Cnemaspis kamolnorranathi (Grismer et al., 2010) pg. 29
Cnemaspis kamolnorranathi (Grismer et al., 2014d) pg. 130

Holotype. BYU 62544 adult male, collected at Tham Khao Sonk hill, Tha Chana District, Changwat Surat Thani, Thailand (9.549878°N, 99.175544°E; 107 m a.s.l.), 30 July 2016, by PLW, LLG, CA, MC, MSG, MLM.

Paratopotypes. All paratypes (BYU 62542–62543, ZMKU R 00729–00731) bear the same collection and locality data as the holotype.

Diagnosis. Cnemaspis thachanaensis sp. nov. is distinguished from all other species of Cnemaspis in the siamensis group by the combination of the following morphological and color pattern characteristics: maximum SVL 39 mm; 10 or 11 supralabials; 9–11 infralabials; ventral scales keeled; no precloacal pores in males; 15–19 paravertebral tubercles linearly arranged; tubercles generally present on the lower flanks; lateral caudal furrows present; no caudal tubercles in the lateral furrows; ventrolateral caudal tubercles anteriorly; presence of lateral caudal tubercle row; caudal tubercles not encircling tail; caudal tubercles restricted to a single paravertebral row; subcaudals keeled bearing a single median row of enlarged keeled scales; one or two post cloacal tubercles in males; no enlarged femoral or tibial scales; subtibials keeled;
enlarged submetatarsal scale on first toe; 23–25 subdigital fourth toe lamellae; sexually dimorphic for ventral and dorsal coloration; yellow or white bars present on flanks; prescapular marking present; gular region yellowish-orange, dark incomplete lineate markings in males, less prominent in females; abdomen, limbs and subcaudal region whitish (Table 8).

**Description of the holotype.** Adult male; SVL 33 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.29), somewhat narrow (HW/SVL 0.16), flattened (HD/HL 0.37), head distinct from neck; snout moderate (ES/HL 0.44), snout slightly concave in lateral view; postnasal region concave medially; scales on rostrum smooth becoming keeled posteriorly, raised, larger than conical scales on occiput; weak to absent supra ocular ridges; frontal rostralis sulcus shallow; canthus rostralis nearly absent, smoothly rounded; eye large (ED/HL 0.22); extra-ocular, fringe scales largest anteriorly; pupil round; ear opening more oval than round, taller than wide; rostral slightly concave, dorsal 80% divided by longitudinal median groove; rostral bordered posteriorly by supra nasals and one small azygous scale and laterally by first supralabials; 11, 11 (R,L) slightly raised supralabials decreasing in size posteriorly; 10, 10 (R,L) infralabials decreasing in size posteriorly; nostrils elliptical, oriented dorsolaterally; bordered by small postnasal scales; mental large, triangular, concave, bordered posteriorly by three postmentals; gular scales small, smooth, raised and round; throat scales subimbricate, keeled, small and round.

Body slender, elongate (AG/SVL 0.44); small, raised, keeled, dorsal scales equal in size throughout body, intermixed with several large, multicarinate conical tubercles more or less randomly arranged; tubercles extend from the occiput to base of the tail; enlarged multicarinate conical tubercles on flanks; pectoral and abdominal scales keeled, not larger posteriorly; abdominal scales slightly larger than dorsals; no pore-bearing, precloacal pores on either side; forelimbs moderately long, slender; dorsal scales slightly raised, keeled; ventral scales of brachia smooth, raised, juxtaposed; scales beneath forearm smooth, slightly raised, subimbricate; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; claws recurved; sub digital lamellae unnotched; lamellae beneath first phalanges granular proximally, widened distally; lamellae beneath phalanx immediately following inflection granular, lamellae of distal phalanges wide; interdigital webbing absent; fingers increase in length from first to fourth with fourth and fifth equal in length; hind limbs slightly longer and thicker than forelimbs; dorsal scales raised, multicarinate, juxtaposed; ventral scales of thigh, slightly raised, conical, keeled; subdigital scales keeled, flat, imbricate, with no enlarged anterior row; plantar scales smooth, juxtaposed, raised; enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected jointed; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges granular proximally, widened distally; lamellae beneath phalanx immediately following inflection granular, lamellae of distal phalanges wide; interdigital webbing absent; toes increase in length from first to fourth with fourth and fifth equal in length; 24,24 (R,L) subdigital lamellae on fourth toe; caudal scales similar to dorsal scale size, enlarge caudal tubercles arranged in segmented whorls, not encircling tail; caudal scales keeled, juxtaposed anteriorly; shallow, middorsal furrow; deeper, single, lateral furrow; enlarged, median, subcaudal scales; subcaudals keeled; median row of enlarged, keeled, subcaudal scales on last 2/3 of tail; transverse, tubercle rows do not encircle tail; caudal tubercles absent from lateral furrow; 1,1 (R,L) enlarged flat, postcloacal tubercle on lateral surface of hemipenal swellings at base of tail.

**Coloration.** In life dorsal ground color of head light-brown, that of the body, limbs and tail slightly darker than the head with even darker irregular blotches; top of the head bearing, small dark-brown and light-green markings; thin diffuse broken dark brown to black postorbital stripe, extending to the nape, not complete; light-green vertebral blotches extending form the nape to the tail where they transform into diffuse near complete irregular bands intermixed with dark brown blotches turning into bands posteriorly; flanks with irregular incomplete small light-green colored blotches to yellow-orange bars becoming smaller posterior; limbs much lighter than dorsal ground color, limbs grayish-white and dark brown incomplete irregular bands; all ventral surfaces grayish-white, except gular and throat regions are yellow-orange not restricted to the gular region and extend onto the throat and the anterior region of the pectoral region in males, incomplete transverse markings in the gular region in male and is less prominent in females (Figures 11–13).

**Variation.** The paratypes approximate the holotype (BYU 62544) in general aspects of morphology except that the female paratypes lack precloacal pores and yellow-orange gular regions. Paratypes ZMKU R 00731, BYU 62542, and BYU 62541 have more paravertebral tubercles (19, 17, 16 respectively vs. 15), dark irregular gular spots not as prominent in females (Figure 12). Select body measurements and...
additional variation in squamation are presented in Table 8.

**Etymology.** The specific epithet *thachanaensis* is a noun in apposition to the type locality where this species is found.

**Distribution.** This species is only known from the type locality Thom Sonk Hill, Tha Chana District, Surat Thani Province, Thailand and we expect that it will be found on nearby adjacent karst formations (Figure 14).

**Natural history.** *Cnemaspis thachanaensis* inhabits a karst tower embedded within a highly disturbed lowland limestone forest. One male individual was observed during the day situated upside down on a karst overhang displaying its yellow-orange throat by doing push-ups. All other specimens were found active during the day on the karst and we hypothesize that these are diurnal karst dwellers. No specimens were observed at night. Grismer et al. (2010) noted that one specimen (CUMZ-R 2009,624-3) was collected on a vine near the adjacent limestone. Karst dwelling species of *Cnemaspis* have been known to sleep on vegetation at night (Grismer et al. 2010, 2014d) Wood, pers. obs.). This species may use the vegetation at night for refuge to avoid *Cyrtodactylus thirakaputhi* which is nocturnal and maybe a potential predator.

**Remarks.** Specimen CUMZ-R 2009,6,24-3 was collected from Thom Sonk Hill, Tha Chana District, Surat Thani Province and was described as *C. kamolnorranathi* in Grismer et al. (2010). Grismer et al. (2010) noted that the relatively wide separation (~110 km) between the type locality of *C. kamolnorranathi* (Petchphanomwat Waterfall, Tai Rom Yen National Park, Ban Nasan District, Surat Thai Province) and the locality of the paratype CUMZ-R 2009,6,24-3 from Thom Sonk Hill, Tha Chana District, Surat Thani Province and suggested that there are probably undiscovered, geographically intervening populations in the appropriate habitat separating these two localities (Grismer et al. 2014d, Grismer et al. 2010) and Grismer et al. (2014d) noted that there is exceptional intrapopulational variation in the degree of keeling of the ventral and the subtibial scales in *C. kamolnorranathi* suggesting the possibility that *C. kamolnorranathi* may be composed of multiple species. After examining additional specimens from Thom Sonk Hill, Tha Chana District, Surat Thani Province (BYU 62542, ZMKU R 00729–00731 and the paratype CUMZ-R 2009,6,24-3) we determined that CUMZ-R 2009,6,24-3 is not conspecific with *C. kamolnorranathi* and with additional specimens it can be diagnosed as a new species (see comparisons below for details). Here we remove CUMZ-R 2009,6,24-3 from *C. kamolnorranathi* and place it in *C. thachanaensis* restricting *C. kamolnorranathi* to the Petchphanomwat Waterfall, Tai Rom Yen National Park, Ban Nasan District, Surat Thai Province. There are no genetic samples of *C. kamolnorranathi* available to further test this hypotheses, however we present strong morphological evidence separating these species.

**Comparisons.** *Cnemaspis thachanaensis* sp. nov. is the sister species to a clade containing *C. siamensis* and *C. vandeventeri* (Figure 2). Although we were not able to obtain genetic material for *C. kamolnorranathi* we compare it here using morphology to demonstrate that the paratype (CUMZ-R 2009,6,24-3, MS101) is conspecific with *C. thachanaensis* sp. nov. *Cnemaspis thachanaensis* sp. nov. differs from *C. siamensis* and *C. vandeventeri* by having a smaller SVL (39 mm, vs. 39.7 mm and 44.7 mm) and by having a larger maximum SVL from *C. kamolnorranathi* (39 mm vs. 37.8 mm). *C. thachanaensis* sp. nov. differs from *C. siamensis*, *C. vandeventeri*, and *C. kamolnorranathi* by: having more supralabial scales (10–11 vs. 8–9, 8–9, 8–9, respectively); having more infralabials (9–11 vs. 6–8, 7–9, and 7–8, respectively); having paravertebral tubercles linearly arranged; having ventrolateral caudal tubercles anteriorly; having keeled subcaudal scales; lacking a single enlarged subcaudal scale row; lacking postcloacal tubercles in males; the presence of an enlarged submetatarsal scale on the 1st toe. *Cnemaspis thachanaensis* sp. nov. is further differentiated from *C. kamolnorranathi* by having keeled ventral scales. *Cnemaspis thachanaensis* sp. nov. differs from *C. vandeventeri* and *C. kamolnorranathi* by lacking precloacal pores. We can further differentiate *C. thachanaensis* sp. nov. from *C. vandeventeri* by having less paravertebral tubercles (15–19 vs. 25–29). *Cnemaspis thachanaensis* sp. nov. differs from *C. kamolnorranathi* by lacking tubercles in the lateral furrow. *Cnemaspis thachanaensis* sp. nov. is further differentiated the more distantly related species *C. huaseesom* and *C. punctatonuchalis* in the *siamensis* group by having a smaller maximum SVL (39 mm vs. 43.5 mm and 49.6 mm, respectively); having more supralabials 10,11 vs. 6–8; having caudal tubercles restricted to a single paravertebral row; having keeled ventral scales; single median row
of keeled subcaudals; lacking enlarged median subcaudal scale row; by lacking postcloacal tubercles in males. *Cnemaspis thachanaensis* sp. nov. differs by having more infralabials 9–11 vs. 7, 8 in *C. punctatonuchalis*. *Cnemaspis thachanaensis* sp. nov. differs from *C. huaseesom* by lacking precloacal pores. From *C. huaseesom*, *C. thachanaensis* sp. nov. differs by having ventrolateral caudal tubercles anteriorly and the presence of a lateral caudal tubercle row. *Cnemaspis thachanaensis* sp. nov. differs from *C. punctatonuchalis* by having keeled subcaudal scales. *Cnemaspis thachanaensis* sp. nov. differs from *C. huaseesom* by having keeled subtibial scales an an enlarged submetatarsal scale on the first toe. From *C. punctatonuchalis*, *C. thachanaensis* sp. nov. differs by having less fourth toe lamellae, 24 vs. 29–31. *Cnemaspis thachanaensis* sp. nov. is differentiated from all other species in the *siamensis* group based on squamation and color pattern characteristics (Table 5 and 9).

**DISCUSSION**

The discovery of three new species of karst-dwelling *Cnemaspis* from Peninsular Thailand is not surprising, given the nature of the vastly unexplored karst and limestone forests dispersed throughout this area. Peninsular Malaysia received considerable attention with respect to herpetofaunal surveys, yet new karst-dwelling species are being discovered and described every year (see Grismer et al. [2016a] for a summary). The results of these surveys have resulted in the discovery of 14 species of geckos (including *Cnemaspis* and *Cyrtodactylus* as well as two snakes [Grismer et al. 2016a]). In comparison, Peninsular Thailand has received little attention with most of the focus on the genus *Cyrtodactylus* resulting in the discovery and description of 15 species in the last 55 years, with 14 of these being described in the last 15 years (see Table 6 in Grismer et al. [2016a]). However, there has been limited field research on the Thai karst-dwelling *Cnemaspis* from these areas (Grismer et al. [2010]). With the small amount of time spent in Phangnga, Tha Chana, and Prachuap Khiri Khan, we were able to discover three new species (*C. lineogularis* sp. nov., *C. phangngaensis* sp. nov., *C. thachanaensis* sp. nov.) and successfully collect genetic samples of *C. punctatonuchalis* and *C. vandeventeri*. We expect that as more time is focused collecting specimens from the unexplored karst formations additional new species will be discovered.

From the fieldwork that has been conducted on the Thai and Malaysian karst formations a fair amount of *Cyrtodactylus* and *Cnemaspis* have been discovered and described. On some of these formations both the nocturnal *Cyrtodactylus* and diurnal *Cnemaspis* occur syntopically. For example both *Cyrtodactylus lekaguli* and *Cnemaspis phangngaensis* sp. nov. at Phung Chang Cave, Phangnga, Thailand, both *Cyrtodactylus astrum* and *Cnemaspis omari* in Perlis, Malaysia, and both *Cyrtodactylus langkawiensis* and *Cnemaspis roticanai* on Pulau Langkawi, Malaysia. Comparing the phylogenetic relationships of these *Cyrtodactylus* with the *Cnemaspis* reveals an identical phylogeographic pattern (Phangnga (Perlis, Pulau Langkawi)). Corroborating these relationships are the calculated average mean pairwise sequence divergence with in the respective genera (*Cyrtodactylus* 9.4% [Grismer et al. 2016b] and *Cnemaspis* 9.6% [this study]). From these preliminary analyses we hypothesize that the formation of these karst formations may have been the resulting factor for simultaneous speciation events within these two respective genera. With additional fieldwork and data collection in these areas more detailed analyses with divergence times can be estimated to investigate the timing of these divergence events.

The inclusion of *C. punctatonuchalis* and *C. vandeventeri* in the phylogenetic analyses helps test previous morphological hypotheses set forth by Grismer et al. [2010] [2014d], and has also contributed towards a more complete phylogeny of the genus *Cnemaspis* (49 of the 55 named species including the three new species described herein). *Cnemaspis punctatonuchalis* was nested within the *siamensis* group confirming the placement solely based on morphological and color pattern characteristics by Grismer et al. [2014d], which was also hypothesized to be more closely related to the other northern species (north of the Isthmus of Kra, *C. huaseesom* and *C. siamensis*). This is further supported here as the sister species to *C. huaseesom* (Figure 2). *Cnemaspis vandeventeri* was hypothesized based on its distribution that it should align with the *siamensis* group, however Grismer et al. [2014d] also suggested that the presence of a light prescapular crescent that diagnoses a monophyletic group composed of *C. chanardi*, *C. phangngaensis*, *C. omari* and *C. roticanai* may suggest that it is more closely related to this group. The phylogenetic placement of *C. vandeventeri* is well nested in the *siamensis* group confirming the placement based on its distribution of Grismer et al. [2010] [2014d], however the hypothesis that it may be more closely related to the group with the prescapular crest is not supported by our phylogenetic hypothesis and could represent an instance of convergent evolution of the prescapular crescent. This is not surprising based on the well
documented parallel/convergent evolution present in the genus *Cnemaspis* (Grismer et al., 2014d), and further analyses to address hypotheses pertaining to parallel/convergent evolution of multiple traits are in preparation (Wood et al. in prep).

The phylogenetic position of *C. lineogularis* as the sister taxon to the entire *chanthaburiensis* group, indicates a trans-Gulf of Thailand relationship with other species from southern Indochina. This is not a novel biogeographic pattern and the close relationship between Indochinese and Malaysian lineages has been observed in Butterfly lizards in the genus *Leiolepis* (Grismer et al., 2014a), and in some species of *Cyrtodactylus* (Grismer et al., 2015). However, the previous documented cases of this pattern are much further south on the peninsula. This pattern could easily be explained by previous cyclic sea level fluctuations that exposed the Sunda Shelf providing multiple dispersal corridors between the Thai-Malay Peninsula and Indochina (e.g. Voris [2000] Sathiamurthy and Voris [2006] Woodruff [2010]). Further investigation into the biogeographic patterns for *Cnemaspis* are in preparation (Wood et al. in prep), and with the continued discovery of new species of *Cnemaspis* in the area, these broader studies will contribute to the understanding of the complex biogeography patterns on the Thai-Malay Peninsula. The discovery of three new species of *Cnemaspis* described here underscores the need for additional fieldwork in the karst towers of the Thai-Malay Peninsula and the surrounding areas to aid in conservation efforts, document the herpetofauna diversity, and provide data for biogeographic studies.

ACKNOWLEDGMENTS

We are thankful for general discussions and logistical conversations with Attapol Rujirawan (aka Bank), Siriporn Yodthong, Natee Ampai, Korkhwan Termprayoon, Piyawan Phuanprapai, and Sengvilay Seateun. We would also like to thank Todd R. Jackman, Angelica Crottini, and D. James Harris for providing feedback that greatly improved the quality of the manuscript.
Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, J., Jenkins, P. D., Kilpatrick, C. W., Robinson, M. F., and Timmins, R. J. (2005). Morphological and molecular

Hughes, J. B., Round, P. D., and Woodruff, D. S. (2003). The Indochinese–Sundaic faunal transition at

Huelsenbeck, J. P., Ronquist, F., Nielsen, R., and Bollback, J. P. (2001). Bayesian inference of phylogeny

High Altitude Tropical Biogeography

Holloway, J. (1986). *High Altitude Tropical Biogeography*, chapter Origins of lepidopteran faunas in high mountains of the Indo-Australian tropics, pages 533–566. Oxford University Press.

Huelsnbecker, J. P., Ronquist, F., Nielsen, R., and Bollback, J. P. (2001). Bayesian inference of phylogeny and its impact on evolutionary biology. *Science*, 294(5550):2310–2314.

Hughes, J. B., Round, P. D., and Woodruff, D. S. (2003). The Indochinese–Sundaic faunal transition at the Isthmus of Kra: an analysis of resident forest bird species distributions. *Journal of Biogeography*, 30(4):569–580.

Jenkins, P. D., Kilpatrick, C. W., Robinson, M. F., and Timmins, R. J. (2005). Morphological and molecular investigations of a new family, genus and species of rodent (Mammalia: Rodentia: Hystricognatha) from Lao PDR. *Systematics and Biodiversity*, 2(4):419–454.

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T and Ashton, B., Mentlles, P., and Drummond, A. (2012). *Geneious basic*: an integrated and extendable desktop software platform for the organization and analysis of biological sequence data.
analysis of sequence data. *Bioinformatics*, 28(12):1647–1649.

Kiew, R. (1991). The limestone flora. *The State of Nature Conservation in Malaysia, Malaysian Nature Society*, pages 42–50.

Kiew, R. (1998). *The Encyclopedia of Malaysia: Plants*, chapter Limestone, Quartzite and Ultramafic Vegetation, pages 26–27. Editions Didier Miller, Singapore.

Komo, I. (1998a). *The Encyclopedia of Malaysia: The Environment*, chapter The Karst Morphology of Langkawi, pages 40–41. Editions Didier Miller, Singapore.

Komo, I. (1998b). *The Encyclopedia of Malaysia: The Environment*, chapter Caves and cave Systems: The Mulu Caves, pages 42–43. Editions Didier Miller, Singapore.

Latinne, A., Waengo, S., Herbreteau, V., and Michaux, J. R. (2011). Evidence of complex phylogeographic structure for the threatened rodent *Leopoldamys neilli*, in Southeast Asia. *Conservation genetics*, 12(6):1495–1511.

Macey, J. R., Larson, A., Ananjeva, N. B., Fang, Z., and Papenfuss, T. J. (1997). Two novel gene orders and the role of light-strand replication in rearrangement of the vertebrate mitochondrial genome. *Molecular Biology and Evolution*, 14(1):91–104.

Maddison, W. and Maddison, D. (2015). Mesquite: a modular system for evolutionary analysis. version 3.04. 2015. URL http://mesquiteproject.org.

Ng, P. (1991). *Cancroceca xenomorpha*, new genus and species, a blind troglobitic freshwater hymenosomatid (Crustacea: Decapoda: Brachyura) from Sulawesi, Indonesia. *Raffles Bulletin of Zoology*, 39(1):59–73.

Parnell, J. (2013). The biogeography of the Isthmus of Kra region: a review. *Nordic Journal of Botany*, 31(1):001–015.

Patou, M.-L., Chen, J., Cosson, L., Andersen, D., Cruaud, C., Couloux, A., Randi, E., Zhang, S., and Veron, G. (2009). Low genetic diversity in the masked palm civet *Paguma larvata* (Viverridae). *Journal of Zoology*, 278(3):218–230.

Pauwels, O., David, P., Chimsunchart, C., and Thirakhupt, K. (2003). Reptiles of Phetchaburi Province, Western Thailand: a list of species, with natural history notes, and a discussion on the biogeography at the Isthmus of Kra. *The Natural History Journal of Chulalongkorn University*, 3(1):23–53.

Pauwels, O. S., Sumontha, M., Latinne, A., and Grismer, L. L. (2013). *Cyrtodactylus sanook* (Squamata: Gekkonidae), a new cave-dwelling gecko from Chumphon Province, southern Thailand. *Zootaxa*, 3635(3):275–285.

Posada, D. and Crandall, K. A. (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14(9):817–818.

Raes, N., Cannon, C. H., Hijmans, R. J., Piessens, T., Saw, L. G., and Slik, J. F. (2014). Historical distribution of Sundaland’s Dipterocarp rainforests at Quaternary glacial maxima. *Proceedings of the National Academy of Sciences*, 111(47):16790–16795.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., and Huelsenbeck, J. P. (2012). Mrbayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic biology*, 61(3):539–542.

Sacha, M. (2015). Herpetoreisen in Thailand: Erste Eindrücke aus Krabi. *Sauria*, 37(3):43–55.

Sathiamurthy, E. and Voris, H. K. (2006). Maps of Holocene sea level transgression and submerged lakes on the Sunda Shelf. *The Natural History Journal of Chulalongkorn University, Supplement*, 2:1–43.

Schilthuizen, M. (2004). Land snail conservation in Borneo: Limestone outcrops act as arks. *Journal of Conchylogie Special Publication*, 3:149–154.

Schilthuizen, M., Liew, T.-S., Elahan, B. B., and Lackman-Ancrenaz, I. (2005). Effects of karst forest degradation on pulmonate and prosobranch land snail communities in Sabah, Malaysian Borneo. *Conservation Biology*, 19(3):949–954.

Schilthuizen, M., Vermeulen, J., Davison, G., and Gittenberger, E. (1999). Population structure in a snail species from isolated Malaysian limestone hills, inferred from ribosomal DNA sequences. *Malacologia*, 41:271–284.

Siler, C. D., Oaks, J. R., Esselstyn, J. A., Diesmos, A. C., and Brown, R. M. (2010). Phylogeeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodactylus*) contradict a prevailing model of Pleistocene diversification. *Molecular Phylogenetics and Evolution*, 55(2):699–710.

Stamatakis, A. (2006). *Raxml-vi-hpc*: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22(21):2688–2690.
Stamatakis, A., Hoover, P., and Rougemont, J. (2008). A rapid bootstrap algorithm for the raxml web servers. *Systematic Biology*, 57(5):758–771.

Tamura, K., Stecher, G., Peterson, D., Filipski, A., and Kumar, S. (2013). MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution*, 30(12):2725–2729.

Tija, H. D. (1998). *The Encyclopedia of Malaysia: The Environment*, chapter Limestone and Karst Morphology, pages 38–39. Editions Didier Miller, Singapore.

Uetz, P., Freed, P., and Hošek, J. (2016). The Reptile Database.

Vermeulen, J. and Whitten, T. (1999). Biodiversity and cultural property in the management of limestone resources. *World Bank, Washington, DC*, 120.

Voris, H. K. (2000). Maps of pleistocene sea levels in southeast asia: shorelines, river systems and time durations. *Journal of Biogeography*, 27(5):1153–1167.

Wilcox, T. P., Zwickl, D. J., Heath, T. A., and Hillis, D. M. (2002). Phylogenetic relationships of the dwarf boas and a comparison of bayesian and bootstrap measures of phylogenetic support. *Molecular Phylogenetics and Evolution*, 25(2):361–371.

Wood, Jr., P. L., Heinicke, M. P., Jackman, T. R., and Bauer, A. M. (2012). Phylogeny of bent-toed geckos (*Cyrtodactylus*) reveals a west to east pattern of diversification. *Molecular Phylogenetics and Evolution*, 65(3):992–1003.

Wood, Jr, P. L., Quah, E. S., Anuar, S., and Muin, M. A. (2013). A new species of lowland karst dwelling *Cnemaspis Strauch 1887* (Squamata: Gekkonidae) from northwestern Peninsular Malaysia. *Zootaxa*, 3691(5):538–558.

Woodruff, D. S. (2003). Neogene marine transgressions, palaeogeography and biogeographic transitions on the Thai–Malay Peninsula. *Journal of Biogeography*, 30(4):551–567.

Woodruff, D. S. (2010). Biogeography and conservation in southeast asia: how 2.7 million years of repeated environmental fluctuations affect today’s patterns and the future of the remaining refugial-phase biodiversity. *Biodiversity and Conservation*, 19(4):919–941.

Woodruff, D. S. and Turner, L. M. (2009). The Indochinese–Sundaic zoogeographic transition: a description and analysis of terrestrial mammal species distributions. *Journal of Biogeography*, 36(5):803–821.

Woxvold, I., Duckworth, J., and Timmins, R. (2009). An unusual new bulbul (Passeriformes: Pycnonotidae) from the limestone karst of Lao PDR. *Forktail*, 25:1–12.