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Phylogenetics, Biogeography, and Patterns of Diversification of GeckosAcross the Sunda Shelf with an Emphasis on the GenusCnemaspis (Strauch, 1887)

Perry Lee Wood

Phylogenetics, Biogeography, and Patterns of Diversification of Geckos Across the Sunda Shelf with an Emphasis on the Genus *Cnemaspis* (Strauch, 1887)

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A dissertation submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

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ABSTRACT

Phylogenetics, Biogeography, and Patterns of Diversification of Geckos Across the Sunda Shelf with an Emphasis on the Genus *Cnemaspis* (Strauch, 1887)

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Doctor of Philosophy

In my dissertation I investigate two genera of geckos (*Cyrtodactylus* and *Cnemaspis*) that are distributed across Southeast Asia with an emphasis on *Cnemaspis*. In Chapter 1 I use a multi-locus dataset, ancestral area analyses, and molecular clock dating to generate a species level time calibrated phylogeny to test the monophyly of *Cyrtodactylus* and to identify major biogeographical patterns. I identified that *Cyrtodactylus* is monophyletic only if the the Sri Lankan genus often recognized as *Geckoella* is included. The results of the Biogeographical analyses reveal a west to east pattern of diversification. Chapter 2 I use a traditional morphological dataset to describe a new species of *Cnemaspis* from Peninsular Malaysia. In Chapter 3 my colleagues and I use a multi-locus dataset and morphological characters to revise the taxonomy of all *Cnemaspis* species and put this in a phylogenetic context. This resulted in the description of eight new species and allowed us to generate hypotheses relating to parallel evolution, diversity, and biogeography. In Chapter 4 I use additional taxon sampling of *Cnemaspis* from Thailand to generate a more complete phylogeny and use an integrative taxonomic approach to describe three new species. In Chapter 5 I used high throughput sequencing of sequence capture and Ultra Conserved Elements to test for a rapid radiation in *Cnemaspis* and to investigate biogeographic hypotheses relating to the diversification and evolution of *Cnemaspis*. I determined that there was a temporal rapid radiation of *Cnemaspis* that coincides with the temporal diversification of other terrestrial vertebrates across Sundaland. The results of these studies indicate that the species diversity of *Cnemaspis* is underestimated and that both genera have experienced similar temporal and spatial diversification coinciding with major vicariant events during the Eocene and the Oligocene-Miocene transition.

Keywords: biogeography, *Cnemaspis*, *Cyrtodactylus*, evolution, Southeast Asia, taxonomy, ultra conserved elements

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Phylogeny of bent-toed geckos (*Cyrtodactylus*) reveals a west to east pattern of diversification

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ABSTRACT

The Asian/Pacific genus *Cyrtodactylus* is the most diverse and among the most widely distributed genera of geckos, and more species are continually being discovered. Major patterns in the evolutionary history of *Cyrtodactylus* have remained largely unknown because no published study has broadly sampled across the geographic range and morphological diversity of the genus. We assembled a data set including sequences from one mitochondrial and three nuclear loci for 68 *Cyrtodactylus* and 20 other gekkotan species to infer phylogenetic relationships within the genus and identify major biogeographic patterns. Our results indicate that *Cyrtodactylus* is monophyletic, but only if the Indian/Sri Lankan species sometimes recognized as *Geckoella* are included. Basal divergences divide *Cyrtodactylus* into three well-supported groups: the single species *C. tibetanus*, a clade of Myanmar/southern Himalayan species, and a large clade including all other *Cyrtodactylus* plus *Geckoella*. Within the largest major clade are several well-supported subclades, with separate subclades being most diverse in Thailand, Eastern Indochina, the Sunda region, the Papuan region, and the Philippines, respectively. The phylogenetic results, along with molecular clock and ancestral area analyses, show *Cyrtodactylus* to have originated in the circum-Himalayan region just after the Cretaceous/Paleogene boundary, with a generally west to east pattern of colonization and diversification progressing through the Cenozoic. Wallacean species are derived from within a Sundaland radiation, the Philippines were colonized from Borneo, and Australia was colonized twice, once via New Guinea and once via the Lesser Sundas. Overall, these results are consistent with past suggestions of a Palearctic origin for *Cyrtodactylus*, and highlight the key role of geography in diversification of the genus.

1. Introduction

Cyrtodactylus Gray, 1827 (bent-toed geckos), with more than 150 recognized species, is by far the most species-rich genus of gekkotan lizards (Uetz, 2012). Recently, as many as 19 new species have been described in a given year from throughout the group's broad range in Asia and the western Pacific (Fig. 1), and since the start of the 21st century, known diversity of *Cyrtodactylus* has more than doubled. Virtually all regions occupied by *Cyrtodactylus* have seen a huge increase in the number of recognized species described, including Myanmar (Bauer, 2002, 2003; Mahony, 2009), Vietnam, (Ngo, 2008; Ngo and Bauer, 2008; Nguyen et al., 2006), Sundaland (Chan and Norhayati, 2010; Grismer et al., 2010; Iskandar et al., 2011; Oliver et al., 2009), the Philippines (Welton et al., 2009, 2010a, 2010b); and Wallacea, Australia, and New Guinea (Kraus, 2008; Oliver et al., 2011; Shea et al., 2012).

Despite great activity in terms of alpha systematic studies, phylogenetic research on *Cyrtodactylus* has been relatively limited thus far. Regional phylogenies with reasonably broad taxon sampling have been generated for the bent-toed geckos of the Philippines (Siler et al., 2010; Welton et al., 2010a, 2010b), Australia and Melanesia (Shea et al., 2012), and for some Malay Peninsula and Sundaland *Cyrtodactylus* (Grismer et al., 2010). Monophyly and interrelationships of the bent-toed geckos of these and other geographic regions has yet to be established. Indeed, the composition of *Cyrtodactylus* as a whole remains unclear, especially with respect to certain taxa in Nepal, northern India, and Tibet, which have been variously assigned to *Cyrtodactylus*, *Cyrtopodion*, *Altigekko*, *Altiphylax*, *Indogekko*, and *Siwaligekko* (see Krysko et al. (2007) for a recent review). In addition, the status of *Geckoella*, a presumably monophyletic group of small, ground-dwelling bent-toed geckos (regarded as either a genus or a subgenus of *Cyrtodactylus*; Kluge, 2001; Bauer, 2002) remains uncertain.

A practical problem engendered by the lack of broader scale phylogenetic resolution in *Cyrtodactylus* is that each newly described species must be diagnosed relative to all of its congeners,

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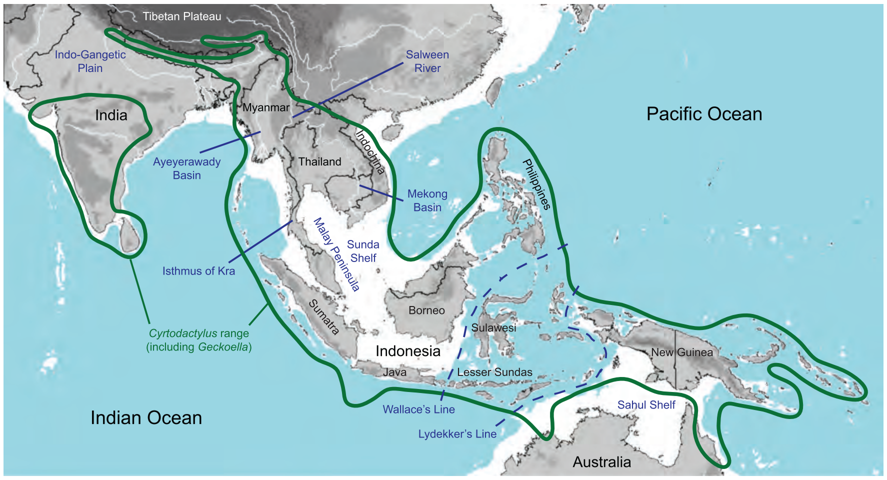

Fig. 1. Global distribution of *Cyrtodactylus*, with place names mentioned in the text listed.

or the assumption must be made that geographically coherent and morphologically similar species are monophyletic. While this appears to be the case in some instances, it is likely that not all such groups are natural, and without broad sampling monophyly cannot be conclusively demonstrated even for regional clades that do appear monophyletic (e.g., Philippines: Siler et al., 2010; Welton et al., 2010a, 2010b; Queensland: Shea et al., 2012). A phylogeny spanning the geographic distribution and morphological variation of *Cyrtodactylus* and having sufficient sampling to provide a "backbone" for the genus would make a major contribution in providing a preliminary estimate of the monophyly of as yet unevaluated presumptive clades. In addition, such a phylogeny can provide information about relevant outgroups for future regional *Cyrtodactylus* phylogenies, allow evaluation of the generic allocation of the problematic taxa that have been variously assigned to *Cyrtodactylus* or other genera, and provide a framework for comparative analyses of *Cyrtodactylus* biology, including biogeography and morphological evolution. To this end we used nucleotide sequence data from approximately 45% of recognized bent-toed gecko species, including exemplars encompassing the morphological range of variation and from across the geographic range of *Cyrtodactylus*, to erect such a backbone phylogeny for the genus. We use this data set to evaluate current taxonomy and make preliminary observations of *Cyrtodactylus* historical biogeography.

2. Materials and methods

2.1. Taxon sampling, data collection, and sequence alignment

We constructed a nucleotide sequence dataset for 68 species of *Cyrtodactylus* from throughout the range of the genus, plus two species of *Geckoella*, six *Hemidactylus*, and six genera and species of Palearctic naked-toed gecko. For purposes of establishing a timetree for the group, we included six additional gekkotan outgroups as well as *Anolis* and *Python* (Table 1). Three outgroups – *Python*, *Lialis*, and *Stenodactylus* – are composites of two closely related species. The dataset consists of the complete mitochondrial gene ND2 and flanking tRNAs (Ala, Asn, Cys, Tyr), plus portions of the nuclear genes RAG1, PDC, and MXRA5. New sequences are deposited under GenBank accession numbers JX440515–JX440726.

Liver, muscle, or tail tissue samples were derived from individuals collected in the field by the authors or donated by other researchers (see acknowledgments). When possible, specimens themselves or photographic vouchers were examined by one or more authors but in some cases we were dependent on the species identifications of collectors or other institutions. Given the rapid rate of description of *Cyrtodactylus* spp. and the break-up of "species" previously believed to be widespread (e.g. Johnson et al., 2012), it is possible that some identifications may need subsequent revision, however, all may be considered accurate to at least species group. Genomic DNA was extracted from tissue samples using Qiagen DNeasy™ tissue kits under manufacturers' protocols. All genes were amplified using a double-stranded Polymerase Chain Reaction (PCR). Included in the reaction were 2.5 μl genomic DNA, 2.5 μl light strand primer 2.5 μl heavy strand primer, 2.5 μl dinucleotide pairs, 2.5 μl 5× buffer, MgCl 10× buffer, 0.18 μl Taq polymerase, and 9.82 μl H_2O, using primers listed in Table 2. PCR reactions were executed on an Eppendorf Mastercycler gradient theromocycler 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 50–55 °C for 35 s, followed by a cycle extension at 72 °C for 35 s, for 34 cycles. All PCR products were visualized via 1.5% agarose gel electrophoresis. Successful PCR amplifications were purified using AMPure magnetic bead solution (Agencourt Bioscience). Purified PCR products were sequenced using Applied Biosystems BigDye™ Terminator v3.1 Cycle Sequencing ready reaction kit or DYEnamic™ ET Dye Terminator kit (GE Healthcare). Products were purified using a Cleanseq magnetic bead solution (Agentcourt Bioscience). Purified sequence reactions were analyzed using an ABI 3700 or ABI 3730XL automated sequencer. All sequences were analyzed from the 3′ and the 5′ ends independently to ensure congruence between the reads. The forward and the reverse sequences were imported and edited in Geneious™ version v5.4 (Drummond et al., 2011); ambiguous bases were corrected by eye. All edited sequences were aligned by eye. Protein-coding sequences were investigated in MacClade v4.08 (Maddison and Maddison, 2003) to ensure the lack of premature stop codons and to calculate the correct amino acid reading frame.

2.2. Phylogeny reconstruction

For comparative purposes, phylogenetic reconstructions were implemented using one character-based approach, Maximum Parsimony (MP) and two model-based approaches, Maximum Likelihood (ML) and Bayesian Inference (BI). Maximum Parsimony (MP) phylogeny and bootstrap estimates for nodal support were

Table 1

Specimens used for phylogenetic analyses in this study. Identification numbers are abbreviated as follows: ACD, Arvin C. Diesmos field collection; AdS, Anslem de Silva field series (specimens pending accession at the National Museum of Sri Lanka); AMS, Australian Museum, Sydney; BPBM, Bernice P. Bishop Museum; CAS, California Academy of Sciences; CES, Center for Ecological Sciences, Indian Institute of Sciences, Bangalore; CJS, Christopher J. Schneider field series; CUMZ, Chulalongkorn University Museum of Zoology; FK, Fred Kraus field series; FMNH, Field Museum of Natural History; ID, Indraneil Das field series; IRSNB, Institute des Sciences Naturelles du Belgique, Brussels; JB, Jon Boone captive collection; JFBM, James Ford Bell Museum of Natural History (Minnesota); KU, Kansas University Museum of Natural History; LSUHC, La Sierra University Herpetological Collection; LSUMZ, Louisiana State University Museum of Zoology; MAM, Mohammed Al-Mutairi field series; MFA, M. Firoz Ahmed field series; MVZ, Museum of Vertebrate Zoology (Berkeley); RAH, Rod A. Hitchmough field series; RMBR, Rafe M. Brown field series; SP, Sabah Parks Reference Collection; TNHC, Texas Natural History Collection; USNM, United States National Museum (Smithsonian); WAM, Western Australian Museum; YPM, Yale Peabody Museum; ZRC, Zoological Reference Collection, Raffles Museum.

ID number	Species	Locality	GenBank accession numbers			
			ND2	MXRA5	PDC	RAG1
n/a	*Anolis carolinensis*	n/a	EU747728	AAWZ 02008741	AAWZ 02013979	AAWZ 02015549
n/a	*Python molurus*	n/a		AEQU 010243110	AEQU 01027927	AEQU 010344888
n/a	*Python regius*	n/a	AB177878			
FMNH 247474	*Agamura persica*	Pakistan, Balochistan, Makran district, Gwadar division	JX440515	JX440566	JX440625	JX440675
CAS 228737	*Bunopus tuberculatus*	United Arab Emirates, Sharjah			JQ945355	JX440676
MVZ 234350	*Bunopus tuberculatus*	Iran, Qeshm Island	HQ443540			
JB 127	*Cyrtopodion elongatum*	captive	JX440516	JX440567	JX440626	JX440677
CES 08022	*Hemidactylus anamallensis*	India, Tamil Nadu, Ervikulam			HM662368	HM622353
MVZ 245438	*Hemidactylus angulatus*	Ghana, Volta region, Togo Hills	EU268367		EU268336	EU268306
CAS 229633	*Hemidactylus frenatus*	Myanmar, Tanintharyi Division, Kaw Thaung District	HM559629		HM559662	HM559695
AMS R167808	*Hemidactylus frenatus*	New Caledonia, Sommet Poum		JX440568		
CAS 223286	*Hemidactylus garnotii*	Myanmar, Rakhine State, Taung Gok Township	EU268363		EU268332	EU268302
AMS R167800	*Hemidactylus garnotii*	New Caledonia, Sommet Poum		JX440569		
YPM 14798	*Hemidactylus mabouia*	USA, Florida	HM559639		HM559672	HM559705
LSUMZ H-1981	*Hemidactylus turcicus*	USA, Louisiana	EU268360		EU268329	EU268299
AMS 141027	*Lialis burtonis*	Australia, Victoria, Beulah Station		JX440570		
JFBM 8	*Lialis burtonis*	Australia			GU459742	GU459540
n/a	*Lialis jicari*	Australia	AY369025			
n/a	*Mediodactylus russowii*	captive	JX440517		JX440627	JX440678
AMS 143861	*Oedura marmorata*	Australia, Queensland	GU459951	JX440571	EF534819	EF534779
MVZ 197233	*Pygopus nigriceps*	Australia, Northern Territory	JX440518	JX440572	EF534823	EF534783
CAS 198428	*Sphaerodactylus roosevelti*	USA, Puerto Rico	JN393943	JX440573	EF534825	EF534785
JB 34	*Sphaerodactylus torrei*	Cuba	JX440519	JX440574	EF534829	EF534788
JB 35	*Stenodactylus petrii*	captive			JX440628	JX440679
MVZ 238919	*Stenodactylus petrii*	Niger, 49 km S Agadez	HQ443548			
MAM 3066	*Stenodactylus slevini*	Saudi Arabia, Ibex Reserve		JX440575		
JB 28	*Tropiocolotes steudneri*	captive	JX440520	JX440576	JX440629	JX440680
RAH 292	*Woodworthia maculata*	New Zealand, Titahi Bay	GU459852	JX440577	GU459651	GU459449
JB 7	*Cyrtodactylus* (*Geckoella*) *deccanensis*	captive (from Indian stock)	JX440521		JX440630	JX440681
AdS 35	*Cyrtodactylus* (*Geckoella*) *triedra*	Sri Lanka, Yakkunehela	JX440522	JX440578	JX440631	JX440682
n/a	*Cyrtodactylus adorus*	Australia, Northeast Queensland	HQ401166			
KU 310100	*Cyrtodactylus agusanensis*	Philippines, Dinagat Island, Municipality of Loreto	GU550818			
FMNH 265815	*Cyrtodactylus angularis*	Thailand, Sa Kaeo, Muang Sa Kaeo	JX440523	JX440579	JX440632	JQ945301
CAS 215722	*Cyrtodactylus annandalei*	Myanmar, Sagging Division, Alaung Daw Kathapa National Park, Gon Nyin Bin Camp	JX440524		JX440633	JX440683
ACD 2637	*Cyrtodactylus annulatus*	Philippines, Mindanao Island, Eastern Mindanao, Diwata Mountain Range	GU366085			
LSUHC 7286	*Cyrtodactylus aurensis*	West Malaysia, Johor, Pulau Aur, behind kg. Berhala	JX440525	JX440580		JX440684
CAS 216459	*Cyrtodactylus ayeyarwadyensis*	Myanmar, Rakhine State, Than Dawe District, Gwa Township, Rakhine Yoma Elephant Range, Elephant Camp	JX440526	JX440581	JX440634	JX440685
SP 06906	*Cyrtodactylus baluensis*	Malaysia, Borneo, Sabah, Mt. Kinabalu National Park, Headquarters	GU366080			
LSUHC 8933	*Cyrtodactylus batucolus*	West Malaysia, Melaka, Pulau Besar	JQ889178	JX440582	JX440635	JX440686
CAS 214104	*Cyrtodactylus brevidactylus*	Myanmar, Mandalay Division, Popa Mountain Park, Kyauk Pan Tawn Township	JX440527	JX440583	JX440636	JX440687
LSUHC 4056	*Cyrtodactylus cavernicolus*	East Malaysia, Sarawak, Niah Cave	JX440528			
CUMZ 2003.62	*Cyrtodactylus chanhomeae*	Thailand, Saraburi Province, Phraputthabata District, Khun Khlon Subdistrict, Thep Nimit Cave	JX440529	JX440584	JX440637	JX440688

CAS 226141	*Cyrtodactylus chrysopylos*	Myanmar, Shan State, Ywa Ngan Township, Panlaung-Pyadalin Cave Wildlife Sanctuary	JX440530	JX440585	JX440638	JX440689
LSUHC 8595	*Cyrtodactylus* cf. *condorensis*	Vietnam, Kien Giang Province, Kien Hai District, Hon Son Island	JX440531	JX440586	JX440639	JX440690
LSUHC 6546	*Cyrtodactylus consobrinus*	West Malaysia, Selangor, Kepong, FRIM	JX440532	JX440587	JX440640	JX440691
WAM R98393	*Cyrtodactylus darmandvillei*	Indonesia, Gua, 7 km NW Sumbawa Besar	JX440533	JX440588	JX440641	JX440692
LSUHC 8598	*Cyrtodactylus eisenmanae*	Vietnam, Kien Giang Province, Kien Hai District, Hon Son Island	JX440534	JX440589	JX440642	JX440693
LSUHC 6471	*Cyrtodactylus elok*	West Malaysia, Pahang, Fraser's Hill, the Gap	JQ889180	JX440590	JX440643	JX440694
BPBM 18654	*Cyrtodactylus epiroticus*	Papua New Guinea, Morobe Province, Apele, Mt. Shungol	JX440535	JX440591	JX440644	JX440695
CES 091196	*Cyrtodactylus fasciolatus*	India, Uttarkhand, Mussoorie			HM622366	HM622351
USNM 559805	*Cyrtodactylus feae*	Myanmar,Mandalay Division, Popa (village), vicinity of Popa Mountain Park	JX440536	JX440592	JX440645	JX440696
CAS 222412	*Cyrtodactylus gansi*	Myanmar, Chin State, Min Dat District, Min Dat Township, Che stream	JX440537	JX440593	JX440646	JX440697
LSUHC 8638	*Cyrtodactylus grismeri*	Vietnam, An Giang Province, Tuc Dup Hill	JX440538	JX440594	JX440647	JX440698
LSUHC 8583	*Cyrtodactylus hontreensis*	Vietnam, Kien Giang Province, Kien Hai District, Hon Tre Island	JX440539	JX440595		JX440699
n/a	*Cyrtodactylus hoskini*	Australia, Northeast Queensland	HQ401119			
FMNH 255454	*Cyrtodactylus interdigitalis*	Lao PDR, Khammouan Province, Nakai District	JQ889181	JX440596	JX440648	JX440700
FMNH 265812	*Cyrtodactylus intermedius*	Thailand, Sa Kaeo, Muang Sa Kaeo	JQ889182	JX440597	JX440649	JX440701
FMNH 258697	*Cyrtodactylus irregularis*	Lao PDR, Champasak Province, Pakxong District	JX440540	JX440598	JX440650	JQ945302
KU 314793	*Cyrtodactylus jambangan*	Philippines, Mindanao Island, Zamboanga del Sur Prov., Municipality of Pasonanca, Pasonanca Natural Park, Tumaga River	GU366100			
FMNH 255472	*Cyrtodactylus jarujini*	Lao PDR, Bolikhamxay Province, Thaphabat District	JX440541	JX440599	JX440651	JQ945303
MVZ 239337	*Cyrtodactylus jellesmae*	Indonesia, Sulawesi Island, Propinsi Sulawesi Selatan, Kabupaten Luwu Utara, Kecematan Malili, ca. 4 km N of Malili	JX440542	JX440600	JX440652	JX440702
MFA 50083	*Cyrtodactylus khasiensis*	India, Assam, Kaziranga, Kohora, Haldhibari	JX440543			
WAM R164144	*Cyrtodactylus kimberleyensis*	Australia, Western Australia, East Montalivet Island	JX440544	JX440601	JX440653	JX440703
n/a	*Cyrtodactylus klugei*	Papua New Guinea, Sudest Island	HQ401198			
FK 7709	*Cyrtodactylus loriae*	Papua New Guinea, Milne Bay Prov., Bunisi, N slope Mt. Simpson	EU268350	JX440602	EU268319	EU268289
n/a	*Cyrtodactylus louisiadensis*	Papua New Guinea, Sudest Island	HQ401190			
LSUHC 7532	*Cyrtodactylus macrotuberculatus*	Malaysia, Kedah, Pulau Langkawi, Gunung Raya	JX440545	JX440603	JX440654	JX440704
ID 8424	*Cyrtodactylus malayanus*	Malaysia, Sarawak, Gunung Mulu National Park			JX440655	JX440705
RMBR 00866	*Cyrtodactylus malayanus*	Indonesia, Borneo, Kalimantan, Bukit Baka Bukit Raya National Park	GU550732			
ABTC 48075	*Cyrtodactylus marmoratus*	Indonesia, Java	GQ257747			
TNHC 59549	*Cyrtodactylus "marmoratus"*	Indonesia, Propinsi Maluku, Buru Island, Dusun Labuan	JX440546	JX440604	JX440656	JX440706
n/a	*Cyrtodactylus mcdonaldi*	Australia, Northeast Queensland	HQ401150			
BPBM 23316	*Cyrtodactylus novaeguineae*	Papua New Guinea, West Sepik Prov., Parkop, Toricelli Mts.	JX440547	JX440605	HQ426185	HQ426274
JB 126	*Cyrtodactylus oldhami*	captive	JX440548	JX440606	JX440657	JX440707
LSUHC 8906	*Cyrtodactylus pantiensis*	West Malaysia, Johor, Gunung Panti FR, Bunker Trail	JQ889185	JX440607	JX440658	JX440708
LSUHC 8672	*Cyrtodactylus paradoxus*	Vietnam, Hon Nghe Island	JX440549	JX440608	JX440659	JX440709
CUMZ R2005.07.30.54	*Cyrtodactylus peguensis*	Thailand, Khao Luang National Park	GU550727			
FMNH 236073	*Cyrtodactylus philippinicus*	Philippines, Romblon Island	JX440550	JX440609	JX440660	JQ945304
n/a	*Cyrtodactylus pronarus*	Australia, Northeast Queensland	HQ401163			
LSUHC 4069	*Cyrtodactylus pubisulcus*	East Malaysia, Sarawak, Niah Cave	JX4405510	JX440610	JX440661	JX440710
LSUHC 6637	*Cyrtodactylus pulchellus*	West Malaysia, Selangor, Genting Highlands				JX440711
LSUHC 6729	*Cyrtodactylus pulchellus*	West Malaysia, Penang, Pulau Penang, Moongate Trail	JX440552	JX440611	JX440662	
LSUHC 4813	*Cyrtodactylus quadrivirgatus*	West Malaysia, Pahang, Pulau Tioman, Tekek-Juara Trail	JX440553	JX440612	JX440663	JX440712
KU 309330	*Cyrtodactylus redimiculus*	Philippines, Palawan Island, Municipality of Brooke's Point	GU550740			
BPBM 19731	*Cyrtodactylus robustus*	Papua New Guinea, Sudest Island	JX440554	JX440613	JX440664	JX440713
CAS 226137	*Cyrtodactylus russelli*	Myanmar, Sagaing Division, Hkamti Township, Htamanthi Wildlife Sanctuary, upper Nat E-Su stream	JX440555	JX440614		JX440714
AMS R134930	*Cyrtodactylus salomonensis*	Solomon Islands, New Georgia I., Mt Javi, 5 km N Tatutiva Village, Marovoa	JX440556	JX440615	JX440665	JX440715

(*continued on next page*)

Table 1 (*continued*)

ID number	Species	Locality	GenBank accession numbers			
			ND2	MXRA5	PDC	RAG1
LSUHC 8900	*Cyrtodactylus semenanjungensis*	West Malaysia, Johor, Gunung Panti FR, Bunker Trail	JQ889177	JX440616	JX440666	JX440716
LSUHC 6348	*Cyrtodactylus seribuatensis*	West Malaysia, Johor, Pulau Mentigi	JX440557	JX440617	JX440667	JX440717
BPBM 23317	*Cyrtodactylus sermowaiensis*	Papua New Guinea, West Sepik Prov., Parkop, Toricelli Mts.	JX440558	JX440618	JX440668	JX440718
CAS 210205	*Cyrtodactylus slowinskii*	Myanmar, Sagaing Division, Alaungdaw Kathapa National Park, Sunthaik Chaung (tributary to Hkaungdin Chaung)	JX440559	JX440619		JX440719
USNM 579045	*Cyrtodactylus* sp. "Timor"	Timor L'Est, Manufahi District, Same, Trilolo River	JX440560	JX440620	JX440669	JX440720
LSUHC 7685	*Cyrtodactylus sworderi*	Malaysia, Johor, Endau-Rompin, Peta, Sungai Kawal	JQ889189	JX440621	JX440670	JX440721
KU 309319	*Cyrtodactylus tautbatorum*	Philippines, Palawan Island, Palawan Province, Municipality of Brooke's Point	GU366083			
MVZ 233251	*Cyrtodactylus tibetanus*	China, Tibet Autonomous Region, Lhasa, 3 km WNW of Potala Palace	JX440561			JX440722
IRSNB 2380	*Cyrtodactylus tigroides*	Thailand, Kanchanaburi Province, Sai-Yok District, Ban Tha Sao	JX440562		JX440671	JX440723
LSUHC 6251	*Cyrtodactylus tiomanensis*	West Malaysia, Pahang, Pulau Tioman, Tekek-Juara Trail	JX440563	JX440622	JX440672	JX440724
n/a	*Cyrtodactylus tripartitus*	Papua New Guinea, Misima Island	HQ401203			
CJS 833	*Cyrtodactylus tuberculatus*	Australia, Northeast Queensland	JX440564		JX440673	JX440725
USNMFS 36138	*Cyrtodactylus tuberculatus*	Australia, Northeast Queensland		JX440623		
ZRC 2.4851	*Cyrtodactylus yoshii*	Malaysia, Sabah, Poring, Sungai Kipungit trail	JX440565	JX440624	JX440674	JX440726

implemented in PAUP∗ v4.0 (Swofford, 2002). A thousand bootstrap replicates for each heuristic search were run with ten random sequence replicates using TBR branch swapping. The 1000 bootstrap replicates were summarized as a strict consensus tree.

For ML and Bayesian analyses, the data were divided into 13 partitions, 12 corresponding to each codon position of the protein-coding genes and the 13th grouping the tRNA sequences. A 5-partition scheme dividing the analyses among genes was also employed; the resulting ML and Bayesian trees had no significant differences from the 13-partition scheme, so we report only the results from the 13-partition scheme. Partitioned ML analyses were performed using RAxML HPC v7.2.3 (Stamatakis, 2006) on the concatenated dataset. Best fit evolutionary models were estimated in ModelTest v3.7 (Posada and Crandall, 1998) under the Akaike information criterion (Table 3). The analyses were performed using the more complex model (GTR + I + Γ) applied to all partitions due to computer programming limitations (see Table 3 for selected models). Maximum likelihood inferences were performed for 200 replicates and each inference was initiated with a random starting tree. Gaps were treated as missing data and clade confidence was assessed using 1000 bootstrap pseudoreplicates employing the rapid hill-climbing algorithm (Stamatakis et al., 2008).

Partitioned Bayesian analyses were carried out in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003) using default priors, with models of nucleotide substitution determined in ModelTest v3.7 (Posada and Crandall, 1998) (Table 3). Two simultaneous parallel runs were performed with eight chains per run, seven hot and one cold. The analysis was run for 20,000,000 generations and sampled every 2000 generations, by which time the chains had long since reached a stationary position and the average standard deviation split frequency fallen below 0.01. The program Are We There Yet? (AWTY) (Nylander et al., 2008) was employed to plot the log likelihood scores against the number of generations to assess convergence and to determine the appropriate number of burn-in trees. We conservatively discarded the first 25% of the trees as burn-in. Nodal support of 0.95 or higher was considered strongly supported.

In addition to analyzing the complete dataset, we also performed separate ML analyses of each individual locus to ensure that there were no strongly conflicting patterns among the loci. These analyses were performed in RAxML 7.2.3 under conditions similar to the combined analysis: data were partitioned by codon position (for mitochondrial data, tRNAs constituted a fourth partition), the GTR + I + Γ model was employed, each initial analysis was repeated for 200 replicates, and 1000 rapid bootstraps were used to assess branch support.

2.3. Divergence timing and ancestral area analyses

A timescale of evolution in *Cyrtodactylus* was estimated in BEAST 1.6.1 (Drummond and Rambaut, 2007). As in the preceding analyses, two separate partitioning schemes were employed. However, the 13-partition analysis was terminated after 150 million generations after failing to reach convergence. Therefore, we report results of the 5-partition analysis. The analysis used a random starting tree, and employed Yule tree priors and a relaxed uncorrelated lognormal clock. The analysis was run for 300 million generations, sampling every 10,000 generations, with the first ten percent of generations discarded as burn-in. Estimated sample sizes (>200 for all parameters) were consulted in Tracer 1.5 (Rambaut and Drummond, 2007) to ensure adequate chain length, and 95% highest posterior densities were calculated to provide credible ranges of nodal divergence dates.

Three previously-used calibrations (Heinicke et al., 2011) were employed to date the tree. The divergence between *S. roosevelti*

Table 2
Primers used for PCR amplification and sequencing.

Gene	Primer name	Primer reference	Sequence
ND2	L4437b	Macey and Schulte (1999)	5′-AAGCAGTTGGGCCCATACC-3′
	L5002	Macey and Schulte (1999)	5′-AACCAAACCCAACTACGAAAAAT-3′
PDC	PHOF1	Bauer et al. (2007)	5′-AGATGAGCATGCAGGAGTATGA-3′
	PHOR1	Bauer et al. (2007)	5′-TCCACATCCACAGCAAAAAACTCCT-3′
RAG1	R13	Groth and Barrowclough (1999)	5′-TCTGAATGGAAATTCAAGCTGTT-3′
	R18	Groth and Barrowclough (1999)	5′-GATGCTGCCTCGGTCGGCCACCTTT-3′
	RAG1F700	Bauer et al. (2007)	5′-GGAGACATGGACACAATCCATCCTAC-3′
	RAG1R700	Bauer et al. (2007)	5′-TTTGTACTGAGATGGATCTTTTTGCA-3′
MXRA5	MXRA5F2	Portik et al. (2012)	5′-KGCTGAGCCTKCCTGGGTGA-3′
	MXRA5R2	Portik et al. (2012)	5′-YCTMCGGCCYTCTGCAACATTK-3′

Table 3
Best-fit models for data partitions as determined by AIC, and similar models chosen for phylogenetic analyses.

Gene	Model selected	Model applied
ND2		
1st pos	GTR + I + Γ	GTR + I + Γ
2nd pos	TVM + I + Γ	GTR + I + Γ
3rd pos	GTR + Γ	GTR + Γ
tRNAs	HKY + Γ	HKY + Γ
PDC		
1st pos	K81uf + Γ	GTR + Γ
2nd pos	HKY + Γ	HKY + Γ
3rd pos	TIMef + Γ	GTR + Γ
RAG1		
1st pos	HKY + Γ	HKY + Γ
2nd pos	TRN + Γ	GTR + Γ
3rd pos	K81uf + Γ	GTR + Γ
MXRA5		
1st pos	TrN + I + Γ	GTR + I + Γ
2nd pos	TVM + I	GTR + I
3rd pos	HKY + Γ	HKY + Γ

and *S. torrei* was calibrated (exponential, mean = 3, offset = 15) based on an amber-preserved fossil *Sphaerodactylus* from Hispaniola dated 15–20 Ma (Iturralde-Vinent and MacPhee, 1996). The divergence between *Oedura* and *Woodworthia* was calibrated (exponential, mean = 17, offset = 16) based on fossil New Zealand "*Hoplodactylus*" dated to 16–19 Ma (Lee et al., 2008). The divergence between *Pygopus* and *Lialis* was calibrated (exponential, mean = 10, offset = 20) based on fossil *Pygopus* dated to 20–22 Ma (Hutchinson, 1998). Root height was calibrated (normal, mean = 200, S.D. = 13) based on estimated times of divergence of gekkotans from other squamates (Hugall et al., 2007; Jonniaux and Kumazawa, 2008; Vidal and Hedges, 2005).

When the final timetree was obtained, ancestral biogeographic regions occupied by *Cyrtodactylus* were estimated in Mesquite 2.74 (Maddison and Waddison, 2011) under both MP and ML (Mk1 model) criteria. Areas were treated as unordered categorical variables, dividing the range of *Cyrtodactylus* into eight regions: Tibet, India/Sri Lanka, West Indochina, Thailand, Indochina, Sunda/Wallacea, Philippines, and Papua. Regions correspond to *Cyrtodactylus* faunal breaks rather than political borders, in some cases enlarged from traditional definitions, and are defined as follows. Tibet includes all areas to the north of the Himalayas inhabited by *Cyrtodactylus*. India/Sri Lanka includes those parts of India south of the Indo-Gangetic plain as well as the island of Sri Lanka. West Indochina largely corresponds to Assam and Myanmar, and is defined as the part of mainland Southeast Asia west of the Salween River, as well as the southern slopes of the Himalayas. Central Indochina largely corresponds to Thailand, and is defined as the region east of the Salween River, north of the Isthmus of Kra, and west of the Mekong River, except that those parts of southern Vietnam west of the Mekong River (the greater Mekong Delta region) are excluded. Eastern Indochina is defined as all of Vietnam plus those parts of Cambodia and Laos east of the Mekong River. The Sunda/Wallacea region includes both Sundaland (peninsular Malaysia and islands of the Malay Archipelago east to Wallace's Line) and Wallacea (islands between Wallace's Line and Lydekker's Line). The Philippines include the entire Philippine Archipelago. The Papuan Region includes New Guinea, adjacent Indonesian islands east of Lydekker's Line, those parts of Melanesia inhabited by *Cyrtodactylus* (Bismarck Archipelago, Solomon Islands), and northeast Queensland, Australia. Several sampled taxa occur in more than one region as defined above; these were coded as occurring in C. Indochina (*intermedius*, *jarujini*, *oldhami*, *peguensis*) and E. Indochina (*interdigitalis*), respectively, based on main areas of occurrence plus distributions of their closest relatives.

3. Results

The final combined dataset includes 3786 bp, of which 1808 sites are variable and 1251 are parsimony-informative. Bayesian, ML, and MP analyses of the combined dataset recover highly concordant phylogenies (Fig. 2). Our analyses moderately support (Bayesian PP/ML bootstrap/MP bootstrap = 0.74/78/37) the monophyly of *Cyrtodactylus* with one exception – the peninsular India/Sri Lanka endemic genus *Geckoella* is embedded within *Cyrtodactylus*. None of the included Palearctic bent-toed gecko genera that have long been associated and confused with *Cyrtodactylus*, especially *Cyrtopodion* and *Mediodactylus*, are part of the *Cyrtodactylus* + *Geckoella* clade (hereafter referred to *Cyrtodactylus sensu lato*). However, the species *C. tibetanus*, which occurs north of the Himalayas and has occasionally been considered allied to some Palearctic bent-toed geckos (e.g. Szczerbak and Golubev, 1986; Szcerback and Golubev, 1996), is confirmed as a member of *Cyrtodactylus* (Shi and Zhao, 2010).

Basal divergences divide *Cyrtodactylus sensu lato* into three well-supported monophyletic, geographically-circumscribed groupings: (1) *C. tibetanus* (Clade A in Fig. 2) of the Tibetan Plateau and the northern slopes of the Himalayas; (2) a "Myanmar Clade" (Clade B in Fig. 2) that includes all ten sampled *Cyrtodactylus* species of diverse habits, size, and body form from Myanmar and the southern flank of the Himalayas, and probably additional unsampled *Cyrtodactylus* from this region; and (3) a clade that includes all *Geckoella* plus *Cyrtodactylus* from Thailand, Indochina, the Malay Peninsula, Indonesia, the Philippines, Australia, and Melanesia, representing about 134 species (Clades C–M in Fig. 2). There is strong support from our analyses that *C. tibetanus* is outside all remaining *Cyrtodactylus* + *Geckoella* (Bayesian PP/ML bootstrap/MP bootstrap = 1.00/98/78).

Within the large third grouping, several additional geographically and morphologically cohesive clades can be identified.

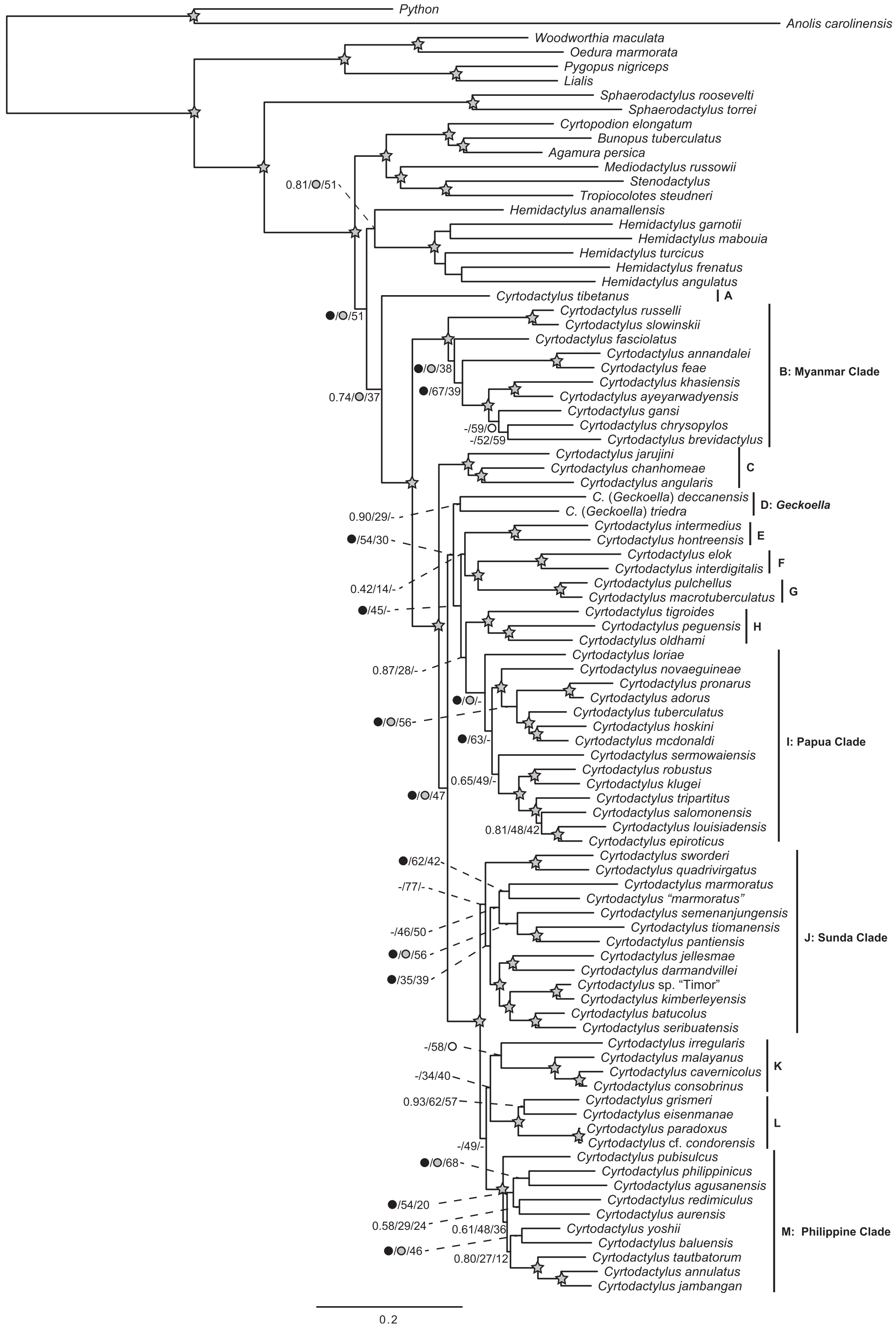

Fig. 2. Maximum likelihood phylogeny of *Cyrtodactylus*, under the 13-partition scheme (−ln L 71587.112627). Nodes supported by all analyses (Bayesian PP > 0.95, ML and MP bootstrap > 70) are indicated by stars. For nodes not supported by all analyses, support from individual analyses is indicated by black (Bayesian), gray (ML), or white (MP) circles, respectively, or support values are reported when less than 0.95 (Bayesian PP) or 70 (ML and MP bootstrap).

Geckoella (Clade D) is recovered as monophyletic, but with poor support (Bayesian PP/ML bootstrap/MP bootstrap = 0.9/29/–). A significantly-supported grouping includes all sampled large-bodied species from New Guinea, adjacent island groups in Indonesia and Melanesia, and the Cape York Peninsula of Australia ("Papua Clade"; Clade I). A large, well-supported group of mainly medium-sized *Cyrtodactylus* (Clades J–M) includes species ranging from mainland Southeast Asia to the Philippines and northwestern Australia, including one subset of species in northern Borneo and the Philippines ("Philippine Clade"; Clade M) and another subset of species from the Malay Peninsula, Greater Sundas, Sulawesi, the Lesser Sundas, and the northwestern coast of Australia ("Sunda Clade"; Clade J).

Separate analyses of individual loci show little significant conflict with one another or the phylogenies generated using the combined dataset, suggesting that lineage sorting or other coalescent processes have no effect on phylogeny estimates within *Cyrtodactylus sensu lato*. Of the clades described in the preceding paragraphs, most are recovered by either three or all four single-locus analyses. The only exceptions are *Geckoella* (poor support in combined analysis; not recovered in any single-locus analysis) and Clade J (not recovered in the PDC or ND2 analyses), though all Clade J species are still recovered as relatively close relatives. Additionally, in comparing among the four single-locus trees, there are only four instances of conflict among loci, where conflict is defined as a clade receiving ML bootstrap support >70 in one single-locus analysis being incompatible with a clade receiving ML bootstrap support >70 in another single-locus analysis. Specifically, in one analysis *C. pantiensis* is recovered as most closely related to *C. semenanjungensis* (PDC, bootstrap support = 87), rather than *C. tiomanensis* (other loci, bootstrap support = 81–90); in one analysis *C. novaeguineae* is recovered as most closely related to *C. loriae* (PDC, bootstrap support = 83), rather than Queensland *Cyrtodactylus* (other loci, bootstrap support = 86–89); in one analysis *C. ayeyarwadyensis* is outside a *brevidactylus*/*chrysopylos*/*gansi* clade (ND2, bootstrap support = 88), rather than within this clade (other loci, bootstrap support = 71–75); in one analysis *C. darmandvillei* is recovered as most closely related to *C. batucolus* plus *C. seribuatensis* (ND2, bootstrap support = 76), rather than *C. jellesmae* (MXRA5, bootstrap support = 89). In each of these cases, conflicts are within geographically-coherent clades and do not affect biogeographic interpretations.

The Bayesian relaxed-clock timing analysis also recovered a phylogeny that is largely concordant with the combined ML, MP, and BI phylogenies, differing in branching pattern only at a couple poorly-supported short internal nodes. The analysis shows that *Cyrtodactylus* diverged from *Hemidactylus* sometime near the Cretaceous–Paleogene boundary, and that *Cyrtodactylus sensu lato* has diversified throughout the Cenozoic Era (Fig. 3). Ancestral biogeographic analyses depict a generally southeastward pattern of colonization, with *Cyrtodactylus* originating in the Palearctic and sequentially colonizing the W. Indochina region, the C. Indochina region, and the E. Indochina and Sunda/Wallacea regions; radiations in Wallacea, the Philippines, and the Papua region (including Melanesia and northeastern Queensland) all trace to Sundaland ancestors. The divergence between the Palearctic species *C. tibetanus* and other *Cyrtodactylus* occurred approximately 52 (65–40) Ma (Fig. 3), approximately contemporaneous with the timing of the collision of the Indian and Eurasian tectonic plates (Rowley, 1996). The Myanmar Clade diversified starting 32 (39–23) Ma, the divergence between the two sampled *Geckoella* occurred 31 (38–24) Ma, and the earliest divergences in the Papuan, Sunda, and Philippine Clades were approximately contemporaneous, about 22 (28–15) Ma. The Australian species C. *kimberleyensis* and those in the Queensland radiation (*C. tuberculatus*, *C. hoskini*, *C. mcdonaldi*, *C. adorus*, *C. pronarus*) diverged from their closest relatives in Timor and New Guinea approximately 3 (5–2) Ma and 13 (18–9) Ma, respectively.

4. Discussion

4.1. Phylogeny

Our results support the general supposition that geographically coherent groups of *Cyrtodactylus* also represent monophyletic groups. The basalmost lineage is represented in this study by only *C. tibetanus*. It is possible that the other Tibetan/northern Himalayan species (e.g. *C. medogense*, *C. zhaoermii*; Shi and Zhao, 2010) are also members of this clade. Members of this group have been problematic with respect to generic allocation and have variously been placed in *Tenuidactylus* (Szczerbak and Golubev, 1986; Szcerback and Golubev, 1996), *Cyrtopodion* (Zhao and Li, 1987), and *Siwaligekko* (Khan, 2003) and some species possess characteristics that are distinctive relative most other *Cyrtodactylus*, including small body size, a clearly segmented, strongly tuberculate tail (in some species), and large dorsal tubercles. It is possible that some unsampled Himalayan geckos currently assigned to the genera *Altigekko* or *Indogekko* also belong to this group, but each of these have putatively diagnostic morphological differences from *Cyrtodactylus* (Khan, 2003).

Monophyly of the Myanmar Clade is strongly supported. Sampling in this clade is especially good and even the most aberrant member of this geographic region, *C. brevidactylus*—originally considered as possibly allied to *Geckoella* based on morphological grounds (Bauer, 2002)—is embedded well within this clade. One species included in our phylogeny, *C. fasciolatus*, belongs to this group as well and extends the range of the group west along the southern flanks of the Himalayas to northwest India. At least two species, *C. oldhami* and *C. peguensis*, occur peripherally in Myanmar but are not members of this clade. The ranges of both species are east of the Ayeyarwady and Salween Basins and extend deep into Thailand; their relationships are, not surprisingly, with Thai species.

The remaining large clade of geckos includes many other geographic groupings, some of which are exclusive. For example, all Philippine *Cyrtodactylus* fall in a single clade (intermixed with Borneo species) as do the sampled *Geckoella*, and all of the Papuan and Queensland species (although at least one other Papuan species is not a member of this clade, Oliver et al., pers. comm.). Central Indochina, Eastern Indochina, and the Sunda region all harbor multiple lineages. One Central Indochinese clade (Clade C: *C. jarujini*, *C. angularis*, *C. chanhomeae*) is sister to all remaining taxa, but another C. Indochinese clade occurs elsewhere in the tree (Clade H: *C. tigroides*, *C. oldhami*, *C. peguensis*), and *C. interdigitalis* is sister to the Sundaland species *C. elok* (Clade F). Eastern Indochinese *Cyrtodactylus* are likewise distributed in multiple clades (Clades E, F, and L, as well as *C. irregularis*, which is in Clade K (Fig. 2) but apparently not closely related to "core" Clade K), each deeply divergent from their respective sister taxa. Borneo supports two lineages, with three species clustering with the Philippine taxa (Clade M), and three others appearing elsewhere (Clade K). Sri Lanka is represented in or sample only by one species of *Geckoella*, with its sister taxa in peninsular India. However, Sri Lanka supports five species in the *C. fraenatus* group, which on morphological grounds appears to be a distinct lineage, perhaps allied to the larger-bodied Myanmar taxa.

The largest clade of Sunda/Wallacea species (Clade J) is that sister to the main Vietnamese + Borneo/Philippine clades. This includes a subgroup endemic to the Malay Peninsula and its offshore islands. This in turn is sister to *C. marmoratus* from Bali and Java, and these are sister to a subgroup including two Malaysian species, one from Sulawesi, two from the Lesser Sundas (including Timor) and a newly discovered species from East Montalivet Island off

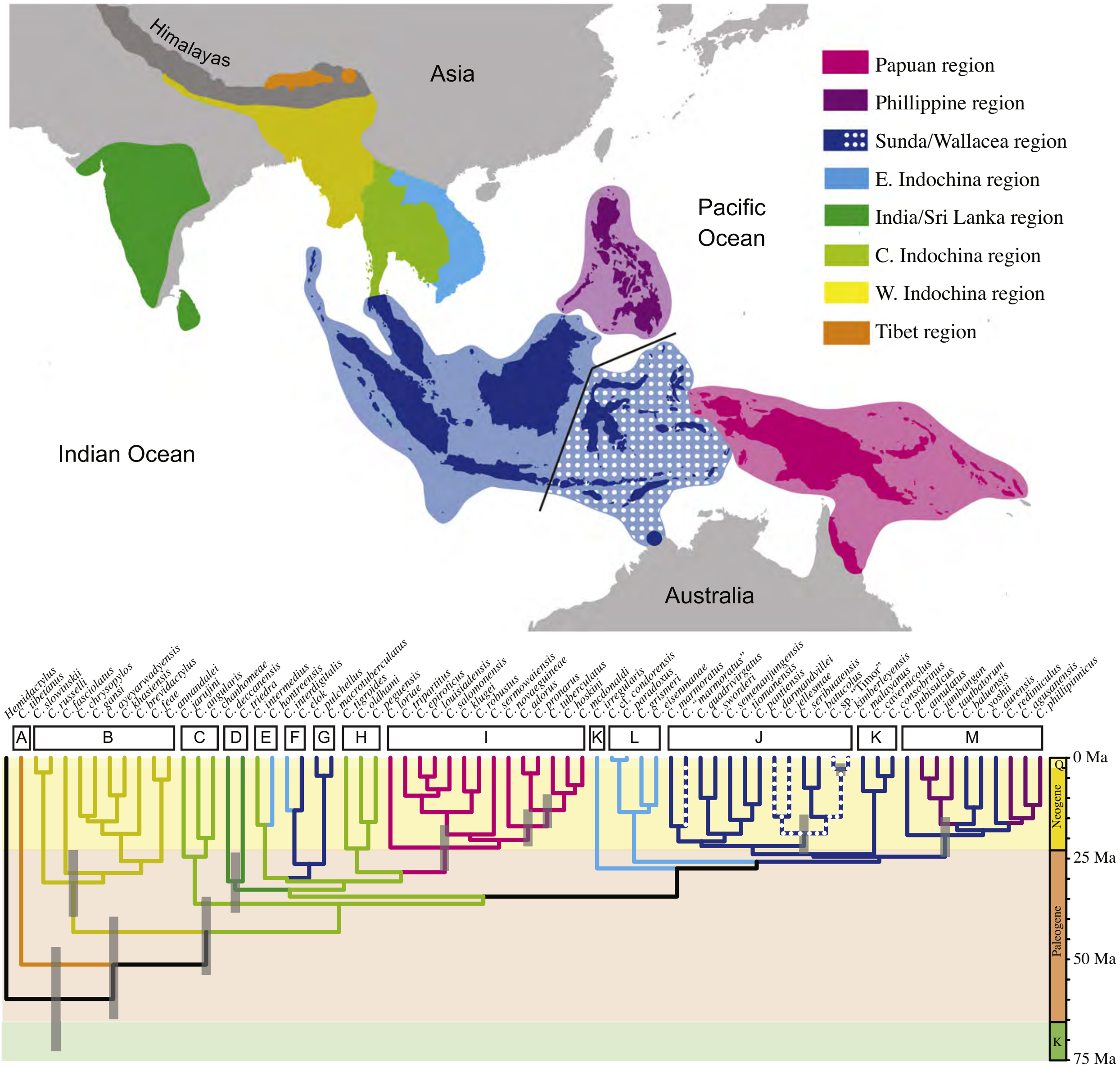

Fig. 3. Historical biogeography of *Cyrtodactylus*. The phylogeny is a Bayesian timetree of *Cyrtodactylus*, with 95% HPD intervals depicted at key nodes. Branches are colored according to the results of the ML ancestral area reconstruction. Branches where no one inferred area received at least twice as much support as the next most likely area were considered equivocal and are colored black. Other colors correspond to the map, which depicts major distributional regions of *Cyrtodactylus*.

the coast of the Kimberley region of Western Australia (Bauer and Doughty, 2012). Remaining Sundaland species (Clade G) are more closely related to the Papuan Clade and some Indochinese species.

4.2. Biogeography

Our results depicting a Palearctic origin of *Cyrtodactylus* are in general agreement with biogeographic interpretations that have been made under the assumption that Himalayan bent-toed geckos (including *C. tibetanus* and the unsampled genera *Siwaligekko*, *Altigekko*, and *Indogekko*) represent a "transition" between Palearctic naked-toed geckos such as *Cyrtopodion* on one hand, and more typical Indo-Australian *Cyrtodactylus* on the other (e.g., Khan, 2009; Shi and Zhao, 2010; Szcerback and Golubev, 1996). Not sampling *Siwaligekko*, *Altigekko*, or *Indogekko* has little impact on this biogeographic interpretation, as on morphological grounds they are certainly not embedded in core *Cyrtodactylus* (Clades B–M), and any placement for these genera still would recover a Palearctic origin for *Cyrtodactylus*. The subsequent spread of *Cyrtodactylus* to the east superficially resembles the pattern evident in other gekkonid geckos with similar distributions, such as *Gehyra*, which originated in Asia and colonized the southwest Pacific (Heinicke et al., 2011). However, *Cyrtodactylus* is significantly more diverse in both mainland Asia and Indonesia, and species of *Cyrtodactylus* tend to have limited ranges, whereas most Asian and Indonesian *Gehyra* species are more widespread.

A number of fine-scale biogeographic patterns within *Cyrtodactylus* deserve comment. Our data cannot conclusively resolve the colonization route of the peninsular Indian/Sri Lankan species in *Geckoella*, as basal relationships within core *Cyrtodactylus* are not fully resolved. The time of divergence post-dates the Indian/Eurasian plate collision (Rowley, 1996), so an overland route from Myanmar was available. However, *Geckoella* is in a more derived position in the phylogeny than are the Myanmar taxa, and the ancestral area analysis does suggest it is most likely that the ancestor of *Geckoella* + *Cyrtodactylus* Clades E–M occupied Central Indochina. Thus, *Geckoella* may have originated via a cross-Bay of Bengal dispersal event, which would also explain the range gap between *Geckoella* and other *Cyrtodactylus*.

In mainland Southeast Asia, the strong geographic segregation of separate *Cyrtodactylus* clades in Myanmar, Thailand, Eastern Indochina, and the Malay Peninsula hints at the importance of long-term geographic barriers in promoting regional endemism (see Fig. 1 for locations of potential barriers). The Isthmus of Kra, separating the Thailand region from the Sunda region (which includes the Malay Peninsula), has long been recognized as such a barrier both currently as the location of an abrupt ecological transition from evergreen rainforest to tropical deciduous forest and historically as a zone affected by marine transgressions through much of the Paleogene (Hughes et al., 2003; Woodruff, 2003; Woodruff and Turner, 2009). These transgressions could have isolated Thai and Sunda *Cyrtodactylus* radiations from one another as they diversified in the mid-Cenozoic. Members of the Myanmar clade occur west of the Ayeyarwady River or in isolated highland regions between the Ayeyarwady and Salween Rivers. These river valleys have likely acted as dispersal barriers due to a lack of suitable habitat (most mainland *Cyrtodactylus* prefer karstic or otherwise rocky terrain). Likewise, the Mekong valley may serve as a barrier between Thai and Indochinese *Cyrtodactylus*. An analysis of the entire Indochinese herpetofauna suggests the Mekong is not a major herpetofaunal biogeographic barrier (Bain and Hurley, 2011). However, it does serve as a barrier for other groups (Meijaard and Groves, 2006) and a preference for rocky terrain separates *Cyrtodactylus* from many other reptile and amphibian groups – the only *Cyrtodactylus* known from the Mekong valley occur in isolated rocky portions of the Mekong Delta (Bain and Hurley, 2011). Our sampling of the relatively species-rich *Cyrtodactylus* faunas of Thailand, Cambodia, Laos, and Vietnam is quite limited, however, so we cannot discount the possibility that there is extensive geographic overlap between mainland Southeast Asian *Cyrtodactylus* clades that our dataset did not capture.

In the Malay Archipelago, our analyses clearly indicate that all Philippine *Cyrtodactylus* species are closely related to species in Borneo. Unlike previous studies that have recovered a monophyletic Philippine radiation (Siler et al., 2010; Welton et al., 2010a, 2010b), our tree indicates two Borneo to Philippines colonization events in the early Neogene, about 10–20 Ma. However, support values for some of the branches in the larger Philippine/Borneo group are not significant, so it is possible that a larger data set would recover a monophyletic set of Philippine species. Within the Philippines, there is a pattern of south to north colonization, in agreement with previous studies. This overall pattern is in contrast to that inferred in another major Philippine gekkonid radiation, *Gekko*. Philippine *Gekko* species are monophyletic, but do not have close relatives in Borneo (Rösler et al., 2011). Instead, based on molecular clock dates, Philippine *Gekko* most likely rafted on Palawan after rifting from the Asian mainland about 30 Ma (Siler et al., 2012). A similar scenario has been proposed in frogs, with Borneo being colonized from Palawan (Blackburn et al., 2010). While such a scenario is not compatible with the topology and divergence dates we infer for *Cyrtodactylus*, we cannot wholly discount this possibility based on low support values for some of these branches. One species in the Philippine/Borneo clade, *C. aurensis*, occurs in the Seribuat Archipelago east of peninsular Malaysia. Two other sampled species, *C. seribuatensis* and *C. tiomanensis*, are also endemic to this archipelago. Interestingly, none of these species are closely related to one another, clearly indicating that the South China Sea has not been a major barrier to dispersal in *Cyrtodactylus*.

In Australia, the close relationship between *C. kimberleyensis* and an undescribed Timorese species suggests that Western Australia was colonized over water from the Lesser Sundas. Unsampled species from the Lesser Sundas (including *C. laevigatus*, *C. wetariensis* and several undescribed species) are similarly small (maximum 73 mm SVL) and similar in general morphology, suggesting that there is a regional radiation. Not surprisingly, given the single species in Western Australia and its very marginal distribution, this colonization of Australia is much younger than that that came via New Guinea and is represented by a group of Queensland taxa (including *C. tuberculatus*), most only recently recognized (Shea et al., 2012). Each of these Australian colonization events may have been facilitated by expansion of exposed land during periods of low sea level. Another Lesser Sunda species, *C. darmandvillei*, is related to the single species sampled from Sulawesi, *C. jellesmae*. Sulawesi supports four additional named species and many more remain to be described (D. Iskandar, pers. comm.). The composite geological nature of Sulawesi raises the possibility that it may have a compound fauna of bent-toed geckos, and several animal clades are known to have colonized Sulawesi multiple times (Stelbrink et al., 2012). Based on morphological traits, it has already been suggested that the Sulawesi *Cyrtodactylus* fauna is comprised of multiple distinct lineages (Iskandar et al., 2011).

Divergence times obtained in this study are quite similar to dates recovered for some *Cyrtodactylus* species by Siler et al. (2012), even though our studies differ in calibration choice (Siler et al. calibrated the divergence between *Cyrtodactylus* and *Gekko*) and overall taxon sampling (Siler et al. included six *Cyrtodactylus* species). For example, we estimate that the lineage leading to *C. philippinicus* diverged from that leading to *C. baluensis* 18 (23–13) Ma, compared to an estimate of 20 (25–15) Ma in Siler et al. (2012). Estimated mean rates of molecular evolution are also similar to those estimated for other gekkonids. For example, the estimated mean rate of molecular evolution for RAG1 in our study was 7.1×10^{-4} substitutions per site per million years, compared to 6.5×10^{-4} estimated for the genus *Gehyra* in a previous study (Heinicke et al., 2011).

4.3. Taxonomy

It may be argued that *Cyrtodactylus* is a large and still growing genus that has already become unwieldy to systematists. This phylogenetic analysis then could provide an opportunity to dismantle the genus in a way consistent with the well-supported monophyletic groups hypothesized. It is clear that *Geckoella* is embedded within other *Cyrtodactylus* and that the recognition of former as a valid genus would render the latter paraphyletic. *Geckoella* are indeed morphologically distinctive, with small, relatively stout bodies, short tails, and noticeably large dorsal scales, and also geographically separated from most other *Cyrtodactylus*, being restricted to South Asia. However, *C. brevidactylus*, a member of the Myanmar clade, is morphologically very similar to *Geckoella*. To be consistent with our tree topology recognition of *Geckoella* would imply the recognition of at least four new genera, one for *C. tibetanus* (clade A), one for the Myanmar clade (Clade B), one for some Thai species (Clade C), and one for Clades J–M. Our results support that *C. tibetanus* is more closely related to typical *Cyrtodactylus* than to the Palearctic naked-toed clade. However, we do not know which, if any, other Tibetan/Himalayan geckos might belong in this group (Khan, 2003, 2009; Shi and Zhao, 2010; Szcerback and Golubev, 1996). Further, the position of *C. tibetanus* as sister to all other *Cyrtodactylus* does not receive more than moderate support in any of the analyses. The Myanmar clade receives the highest level of support of any clade in the genus. However, morphologically, the members of this clade span almost the entire range of morphological variation in the genus, including very large species, miniaturized species, short-fingered ground dwellers, and ''average-sized'' climbing species.

Because of these issues we advocate continued recognition of the entire bent-toed clade as a single genus for the time being, although more detailed morphological studies that may reveal unambiguous synapomorphies of each of the major lineages might prompt the future dismantling of *Cyrtodactylus*. With respect to *Geckoella* we recommend the use of this name at the subgeneric level to recognize this distinctive monophyletic lineage within *Cyrtodactylus*. *Geckoella* has been regularly employed as a subgeneric name in the past, so such a change is minimally disruptive (Bauer, 2002, 2003; Rösler, 2000; Ulber and Gericke, 1988). There are two other available genus-group names currently in the synonymy of *Cyrtodactylus*: *Puellula* Blyth 1861 (type species *Puellula rubida* Blyth 1861) and *Quantasia* Wells and Wellington 1985 (type species *Hoplodactylus tuberculatus* Lucas and Frost 1900). As we did not sample *C. rubidus*, a species endemic to the Andaman Islands and adjacent Cocos Islands in the Bay of Bengal, it is unclear to which clade that name would apply. *Quantasia* could be used for the Papuan clade (Clade I), but we do not recommend such usage at this time.

4.4. Conclusions

The phylogeny we present in this study does offer a guide to search for synapomorphies or potential diagnostic differences among clades. When such diagnostic traits are identified, the generic- and subgeneric-level taxonomy of *Cyrtodactylus* can be re-evaluated. In addition, it provides a scheme for outgroup selection for regionally focused studies and a guide for making appropriate comparisons for new species descriptions. Finally, the phylogeny we present also opens the possibility of analyzing the biogeography, ecomorphology, and other evolutionary aspects of *Cyrtodactylus* biology in a phylogenetic, hypothesis-driven context. For example, long-limbed, flat-bodied cave-dwelling species occur in multiple places in the phylogeny, and the strong geographic signal in the phylogeny suggests that convergence in other traits could be similarly widespread in *Cyrtodactylus*.

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Chapter 2: A new species of lowland karst dwelling *Cnemaspis* Strauch, 1887 (Squamata: Gekkonidae) from northwestern Peninsular Malaysia

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A new species of lowland karst dwelling *Cnemaspis* Strauch 1887 (Squamata: Gekkonidae) from northwestern Peninsular Malaysia

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Abstract

A new species of lowland karst dwelling *Cnemaspis* Strauch 1887, *C. grismeri* **sp. nov.** is described from the southeastern base of the Banjaran Bintang in northern Peninsular Malaysia. It is differentiated from its congeners by a unique combination of characters including size, coloration and scalation. *Cnemapis grismeri* **sp. nov.** is most closely related to *C. mcguirei*, an upland species endemic to the Banjaran Bintang. This phylogeographic pattern is also seen in the upland and lowland Banjaran Bintang species of *Cyrtodactylus bintangtinggi* and *C. bintangrendah*, respectively (Grismer *et al*. 2012). The discovery of yet another endemic gekkonid in the poorly explored karst regions of Peninsular Malaysia underscores the necessity for concentrated collecting efforts in these unique landscapes.

Key words: new species, taxonomy, karst, *Cnemaspis grismeri*, Gekkonidae, herpetofauna, Malaysia

Introduction

The gekkonid genus *Cnemaspis* Strauch 1887 currently contains 103 species from three non-monophyletic groups (Africa, South-Asia, and Southeast Asian [see Gamble *et al*. 2012; Uetz 2013]). The Southeast Asian clade (*sensu* Grismer *et al*. 2010a,b,c) comprises a group of scansorial forest dwelling lizards with numerous adaptations for moving about on flat surfaces (vegetation and rocks) during low levels of illumination. In the past, this conserved morphology and behavior lead to considerable taxonomic confusion that was ultimately disentangled with a morphological review of the entire genus and a series of new, reliable diagnostic characters (Grismer *et al*. 2010a,b,c). This has, in part, resulted in a rapid increase in the number of species in this genus (surpassed only by the genera *Cyrtodactylus* ~170 spp. and *Hemidactylus* ~114 spp. [Uetz 2013]) with 23 of the currently recognized 34 species having been described in the last 11 years (Chan & Grismer 2008; Chan *et al*. 2010; Das & Grismer 2003; Grismer 2010; Grismer & Chan 2008, 2009, 2010; Grismer & Das 2006; Grismer & Ngo 2007; Grismer *et al*. 2008a,b; 2009; 2010a,b,c; J. Grismer *et al*. 2010). Many of these new species were discovered during expeditions into previously unexplored karst forests or karst outcroppings, resulting in the acquisition of a number of new specialized lineages with highly restrictive substrate specificity, namely limestone (Grismer & Chan 2009; Grismer *et al*. 2008a,b, 2009, 2010a; J. Grismer *et al*. 2010). We report here another new lowland karst-adapted species of gecko from the limestone forests of the Lenggong Valley, Perak, in northern Peninsular Malaysia (Fig. 1). We assign the individuals of this population to the genus *Cnemaspis* in that they all have the unique combination of broad, flattened heads; large, somewhat forward and upwardly directed eyes with round pupils; dorsoventrally compressed bodies; and long, widely splayed limbs bearing long, inflected digits—adaptations for climbing on flat surfaces in all planes or orientations. A molecular analysis using the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) indicates they have a 7.3–11.7% sequence divergence from their closest upland relative *C. mcguirei* (L. Grismer *et al*. unpublished). Additionally, they have a unique combination of color pattern and scale characteristics that differentiate them from all other known species of *Cnemaspis*. Therefore, this population is described below as a new species.

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FIGURE 1. Distribution map showing the location of the type locality of *Cnemaspis grismeri* **sp. nov.** in the Lenggong Valley, Perak.

Materials and methods

Color characters were taken from digital images of living specimens cataloged in the La Sierra University Digital Photo Collection (LSUDPC) and in some cases, from living specimens. The following measurements on the type series were taken with Mitutoyo dial calipers to the nearest 0.1 mm under a Nikon SMZ 1500 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 90º to the inflection of the flexed wrist; tibia length (TBL), taken on the ventral surface from the posterior surface of the knee while flexed 90º 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 eye-ball; eye to ear distance (EE), measured from the anterior edge of the ear opening to the posterior edge of the eye-ball; eye to snout distance (ES), measured from anteriormost margin of the eye-ball to the tip of snout; eye to nostril distance (EN), measured from the anterior margin of the eye-ball to the posterior margin of the external nares; inner orbital distance (IO), measured between the anterior edges of the orbit; ear length (EL), the greatest horizontal distance of the ear opening; and internarial distance (IN), measured between 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; size and number of postmental scales contacting the mental; 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 between the limb insertions; the number of subdigital lamellae beneath the fourth toe counted from the base of the first phalanx to the claw; the total number of precloacal pores, their orientation, shape, and degree of separation; 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 precloacal 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 paravertebral row and the lateral, caudal furrow on the dorsolateral margin of the tail; lateral row — the row immediately below the lateral, caudal furrow; and ventrolateral row — the row below the lateral row on the ventrolateral margin of the tail. When present, this row is usually restricted to the anterior 25% (or less) of the tail. Rarely there may be a row of tubercles within the lateral, caudal furrow. Various color pattern characteristics were also evaluated (see description). Some meristic data were statistically analyzed using a one-tailed *t*-test with a 0.95 confidence limit on Excel 14.1.3 to test for significant differences between population means.

A 1335 aligned base pair fragment of the mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and its flanking t-RNAs (t-RNA-Trp, t-RNA-Ala, t-RNA-Asn, and t-RNA-Cys) was amplified using the following primers L4437b 5'-AAGCAGTTGGGCCCATACC-3' and L5002 5'-AACCAAACCCAACTACGAAAAAT-3' (Macey & Schulte 1999) and sequenced for nearly all species of *Cnemaspis* (see L. Grismer *et al*. unpublished). Uncorrected pairwise sequence divergences were calculated in PAUP* v4.0 (Swofford 2002) for the undescribed species (five specimens: LSUHC 9730, 9732, 9733, 9969–70) and its sister taxon (three specimens: LSUHC 8853–8855).

Specimens examined are listed in the appendix. Institutional abbreviations follow Leviton *et al*. (1985), except we retain ZRC (Zoological Reference Collection, Raffles Museum) for USDZ, following conventional usage. DWNP refers to the Department of Wildlife and National Parks Collection, Krau, Pahang, Peninsular Malaysia; LSUHC refers to the La Sierra University Herpetological Collection, La Sierra University, Riverside, California, USA; HC refers to the Herpetological Collection of the Universiti Kebangsaan Malaysia, Bangi, Selangor; THNHM refers to the Thailand Natural History Museum, National Science Museum, Khlong Luang, Pathum Thani, Bangkok; CUMZ refers to the Chulalongkorn University Museum of Zoology, Bangkok, Thailand; PSUZC refers to the Prince of Songkhla University Zoological Collection, Songkhla, Thailand; ZMKU refers to the Zoological Museum of the Kasetsart University, Bangkok, Thailand; KZM refers to the Nakhon Ratchasima Zoo Museum, ZPO, Nakhon Ratchasima, Thailand; MS refers to the collection of Montri Sumontha at the Ranong Marine Fisheries Station, Paknam, Ranong, Thailand; and UNS refers to the University of Natural Sciences, Ho Chi Minh City, Vietnam.

Systematics

Cnemaspis grismeri sp. nov.

Grismer's Rock Gecko
Malaysian name: Cicak Batu Grismer
Figures 2–3

Cnemaspis mcguirei Grismer, 2011:349.

Holotype. Adult male (ZRC 2.6989) collected on 7 October 2012 at Gua Asar, Bukit Kepala Gajah limestone massif, Lenggong, Perak, Malaysia (5°07.53'N, 100°58.82'E) at 78 m a.s.l. by Evan S.H. Quah and Shahrul Anuar Mohd Sah.

Paratypes. ZRC 2.6990, LSUHC 9969, 9970, 9972 and 9973 were collected on 5 November 2010 from the same locality as the holotype by Evan S.H. Quah, Shahrul Anuar Mohd Sah and Mohd Abdul Muin. LSUHC 10941–10944 were collected on 7 July 2012 by the same collectors at the same locality.

Diagnosis. *Cnemaspis grismeri* **sp. nov.** differs from all other Southeast Asia species of *Cnemaspis* in having the unique combination of adult males reaching 48.8 mm SVL, adult females reaching 50.6 mm SVL; 8–9 supralabials; 7–9 infralabials; large, lateral postmentals separated at midline by one or two smaller postmentals; forearm, subtibials, ventrals, subcaudals, and dorsal tubercles keeled; 27–32 paravertebral tubercles; tubercles on flanks, relatively small and not linearly arranged; tubercles within lateral caudal furrow; ventrolateral caudal tubercles present anteriorly; median subcaudal row not enlarged; no keeled, median subcaudal row of enlarged scales; two or three postcloacal tubercles; continuous row of eight to ten precloacal pores; subtibial scales not shield-like; no enlarged submetatarsal scales; 25–31 subdigital lamellae on fourth toe; no distinct, large, dark spots on neck; dark shoulder patch enclosing two white to yellow ocelli; prominent, wide, yellow to white, postscapular band; yellowish bars on flanks; distinct, dark, caudal bands present posteriorly; subcaudal region pigmented, not immaculate. Scalation and body size differences are summarized across all Southeast Asian species in TABLE 1.

Description of holotype. Adult male; SVL 47.7 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.26), somewhat narrow (HW/SVL 0.18), flattened (HD/HL 0.44), distinct from neck; snout short (ES/HL 0.49), slightly concave in lateral profile; postnasal region constricted medially, flat; scales of rostrum keeled, raised, larger than conical scales on occiput; prominent, supraorbital ridges; shallow frontorostral sulcus; canthus rostralis nearly absent, smoothly rounded; eye large (ED/HL 0.21); extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral slightly concave, dorsal 80% divided by longitudinal groove; rostral bordered posteriorly by supranasals and one small, azygous scale and laterally by first supralabials; eight (R,L) raised supralabials of similar size; eight (R,L) infralabials, decreasing in size posteriorly; nostrils elliptical, oriented posterodorsally; bordered posteriorly by small, granular, postnasal scales; mental large, subtriangular, bordered posteriorly by three postmentals, outer two largest; gular scales raised; throat scales larger and conical.

Body slender, elongate; small, keeled, dorsal scales equal in size throughout body, intermixed with several large, multicarinate tubercles more or less randomly arranged; tubercles extend from occiput to base of tail; tubercles on flanks not enlarged, moderate in size; pectoral and abdominal scales strongly keeled, raised, slightly elongate, slightly larger posteriorly; abdominal scales slightly larger than dorsals; ten continuous precloacal pores arranged in a chevron separated anteriorly by a single, non-pore bearing scale; precloacal depression present; forelimbs moderately long, slender; dorsal scales of brachium raised, keeled; dorsal scales of forearm same as brachials; ventral scales of brachium weakly keeled, raised, juxtaposed; scales beneath forearm, weakly keeled, raised; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; 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 weak; 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 of thigh keeled, raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh keeled; subtibial scales keeled, 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 present; toes increase in length from first to fourth with fourth and fifth equal in length; 29 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; caudal scales raised, keeled, juxtaposed anteriorly; shallow middorsal furrow; deeper, single lateral furrow; no enlarged, median subcaudal scales; subcaudals keeled; no median row of enlarged keeled subcaudal scales; transverse tubercle rows do not encircle tail; caudal tubercles present in lateral furrow; three enlarged postcloacal tubercles on lateral surface of hemipenal swellings at base of tail; tail 1.45% of SVL.

FIGURE 2. Upper left: adult female *Cnemaspis grismeri* **sp. nov.** paratype LSUHC 9973 in dark daytime coloration. Upper right: adult male *C. mcguirei* LSUDPC 5175. Lower left: adult male *C. grismeri* (uncataloged) sleeping on a leaf in its light, nighttime color phase. Lower right: adult male *C. grismeri* **sp. nov.** LSUHC 9972 in dark daytime coloration.

Coloration (in life). Dorsal ground color grey to brown; head and body overlain with irregularly shaped, small, dark and yellowish flecks giving an overall mossy appearance; cream to yellowish markings on top of head; thin dark postorbital stripe extending onto nape; paired, elongate, medial, yellowish markings on nape followed by small, indistinct, black shoulder patches enclosing two yellow ocelli; ocellus dorsal to forelimb insertion distinct and another anterior to forelimb insertion very weak; shoulder patch edged posteriorly by wide, postscapular band that is yellow laterally and white medially; irregularly shaped, offset, paravertebral, yellowish markings on dorsum extend to base of tail; distinct, transversely elongate, yellow bars on flanks; diffuse brown and dull yellow bands encircle tail anteriorly; posterior portion of tail with dark brown and off-white bands ; irregularly shaped yellowish to dull white markings on limbs; dark and light diffuse bands encircling digits; ventral surfaces of head, body, and limbs dull beige, immaculate, darkening laterally; subcaudal region suffused with pigment, not immaculate.

Variation (Fig. 2,3). The overall general color pattern of the paratypes closely approaches that of the holotype. The postscapular band in the paratype LSUHC 9972 is offset. The light dorsal markings in ZRC 2.6990, LSUHC 9969 and 9973 appear more as transverse bands than paravertebral blotches. The black shoulder patch and postscapular bar in females is not nearly as well developed as it is in males (Fig. 3). LSUHC 10943 is missing a tail and the tails of LSUHC 9969–70 are mostly or entirely regenerated. Meristic differences are presented in TABLE 2. During the evening, the color pattern lightens considerably (Fig. 2).

FIGURE 3. Differences between male and female *Cnemaspis grismeri* **sp. nov.** in the development of the dark shoulder patch. Upper: uncataloged adult female. Lower: adult male holotype ZRC 2.6989.

TABLE 1. Diagnostic characters of Southeast Asian species of *Cnemaspis*. /=Character not applicable. Ant=anteriorly only. Highlighted values are discretely diagnostic and differ from those values in *C. grismeri* sp. nov.

	affinis	*argus*	*aurantiacopes*	*baueri*	*bayuensis*	*biocellata*	*boulengeri*	*caudanivea*	*chanardi*	*chanthaburiensis*
Maximum SVL	**48**	**65.2**	56.6	**64.9**	46.1	**40.1**	**69**	47.1	**40.1**	**42.1**
Supralabials	9–13	8	9–11	**11–13**	9,10	6–10	8,9	8,9	7–10	8–10
Infralabials	8–10	8	8–10	**10–12**	8,9	5–7	6,7	7,8	4–8	7–9
Ventral scales keeled (1) or not (0)	**0**	1	**0**	1	1	1	**0**	**0**	1	**0**
No. of precloacal pores	**5,6**	8–10	0	0	5–9	8–12	**0**	**0–3**	6–8	7–9
Precloacal pores continuous (1) or separated (0)	0	0,1	/	/	0	**1**	/	0	0	**1**
Precloacal pores elongate (1) or round (0)	0	0	/	/	0	0	/	0	0	0
No. of paravertebral tubercles	**20–28**	28–32	23–29	18–27	23–30	**21–23**	32–38	20–27	20–30	**23–25**
Tubercles of ventralmost row on flank linearly arranged and in contact or nearly so (1) or tubercles on flank widely spaced and more randomly distributed (0)	0	0	**1**	0	0	0	**1**	0	0	0
Tubercles present (1) or absent (0) on flanks	1	1	1	1	1	1	**0**	weak	1	1
Caudal tubercles in lateral furrow (1) or not (0)	**0**	**0**	**0**	**0**	**0**	/	/	**0**	**0**	1

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TABLE 1. (Continued)

	affinis	*argus*	*aurantiacopes*	*baueri*	*bayuensis*	*biocellata*	*boulengeri*	*caudanivea*	*chanardi*	*chanthaburiensis*
Ventrolateral caudal tubercles anteriorly (1) or not (0)	**0**	**0**	1	1	0	0	0	0	**0**	0
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	1	1	1	**0**	1	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	0	**1**	0	0	0
Subcaudals keeled (1) or not (0)	1	1	**0**	**0**	1	**0**	**0**	**0**	1	**0**
Single median row of keeled subcaudals (1) or not (0)	0	0	**1**	0	0	0	0	0	**weak**	0
Caudal tubercles encircle tail (1) or not (0)	0	0	0	**1**	0	0	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	0	**1**	0	0	**1**	**1**	0	**1**	0
No. of postcloacal tubercles	2	1–4	2	2	2	**1**	**1**	1,2	**1**	1–3
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	**1**	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	**1**	**1**	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	1	**0**	**0**	**0**	1	**0**
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	**1**	0	0	0	**1**	**1**	0	0
No. of 4th toe lamellae	**17–20**	**32–35**	27–30	26–27	27–30	29–37	29–32	23–30	25–30	25–29

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TABLE 1. (Continued)

	dringi	*flavigaster*	*flavolineata*	*harimau*	*kamolnorranathi*	*karsticola*	*kendallii*	*kumpoli*	*laoensis*	*limi*
Maximum SVL	46.4	50.1	46.7	40.7	**37.8**	48.1	**58**	**63**	40.9	**88.2**
Supralabials	**11**	9,10	8–10	9,10	8,9	7,8	**10–12**	7,8	9	8–11
Infralabials	9	8–10	8–10	9,10	7,8	6,7	7–9	6–8	7	7–9
Ventral scales keeled (1) or not (0)	1	**0**	1	1	0-weak	1	1	**0**	**0**	1
No. of precloacal pores	**5,6**	7,8	7	4	**6,7**	7,8	**0**	7,8	/	**0**
Precloacal pores continuous (1) or separated (0)	0	**1**	**1**	0	**1**	**1**	/	0	/	/
Precloacal pores elongate (1) or round (0)	0	0	0	0	**1**	0	/	0	/	/
No. of paravertebral tubercles	25–27	**21–24**	**22–24**	**18–20**	**19–24**	**17–19**	**20–26**	29–35	22	25–33
Tubercles of ventralmost row on flank linearly arranged and in contact or nearly so (1) or tubercles on flank widely spaced and more randomly distributed (0)	0	0	0	0	0	0	0	0	0	0
Tubercles present (1) or absent (0) on flanks	**0**	1	1	1	1	1	weak	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	**0**	**0**	1	0	**0**	**0**	**0**	**0**	1	**0**

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TABLE 1. (Continued)

	dringi	*flavigaster*	*flavolineata*	*harimau*	*kamolnorranathi*	*karsticola*	*kendallii*	*kumpoli*	*laoensis*	*limi*
Ventrolateral caudal tubercles anteriorly (1) or not (0)	0	**0**	**0**	**0**	**0**	**0**	1	**0**	**0**	**0**
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	1	1	1	1	**0**	**0**	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	0	0	0	0	0
Subcaudals keeled (1) or not (0)	1	**0**	1	1	weak	1	1	**0**	**0**	**0**
Single median row of keeled subcaudals (1) or not (0)	1	0	0	0	**weak**	0	**1**	0	0	0
Caudal tubercles encircle tail (1) or not (0)	0	0	**1**	**1**	0	0	**1**	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	**1**	0	0	/	**1**	0	*1*	0	1	**weak**
No. of postcloacal tubercles	2	1,2	2,3	0	1,2	2,3	1,3	2,3	2,3	1,2
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0	0	/	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0	0	1	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	0-weak	1	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	**1**	0	0	0	0	0	0	0	0
No. of 4th toe lamellae	32–35	29–34	23–26	25–30	24–28	27–30	23–36	**34–41**	**29**	30–35

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TABLE 1. (Continued)

	mcguirei	*monachorum*	*neangthyi*	*nigridia*	*niyomwanae*	*nuicamensis*	*paripari*	*pemanggilensis*	*perhentianensis*	*pseudomcguirei*
Maximum SVL	**65**	**32.9**	**54**	**75.5**	**56.8**	47.5	50.7	**76**	47	**42.5**
Supralabials	7–9	7,8	11–13	**10,11**	**8–11**	7–9	**12**	**10–13**	8–10	9
Infralabials	7,8	5–7	11–12	9–11	6–8	6–7	**10,11**	**10–14**	7–8	8,9
Ventral scales keeled (1) or not (0)	1	**0**	1	1	0	**0**	1	1	0,1	1
No. of precloacal pores	5–10	**3**	**2**	**12–14**	**3**	**4–6**	**2–6**	**0**	6–8	**1–5**
Precloacal pores continuous (1) or separated (0)	0	**1**	/	0	1,0	0	0	/	**1**	**1**
Precloacal pores elongate (1) or round (0)	0	0	/	0	0	0	0	/	0	0
No. of paravertebral tubercles	26–32	**11–19**	/	**39–43**	**26–31**	**20–22**	26–31	30–37	22–27	26–32
Tubercles of ventralmost row on flank linearly arranged and in contact or nearly so (1) or tubercles on flank widely space and more randomly distributed (0)	0	0	1	0	0	**1**	0	0	0	0
Tubercles present (1) or absent (0) on flanks	1	**0**	/	**0**	**0**	1	**0**	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	1	**0**	/	**0**	**0**	**0**	**0**	**0**	**0**	1
Ventrolateral caudal tubercles anteriorly (1) or not (0)	**0**	**0**	1	1	0	1	**0**	1	**0**	**0**
Lateral caudal tubercle row present (1) or absent (0)	1	ant	1	1	0	1	1	1	1	ant

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TABLE 1. (Continued)

	mcguirei	*monachorum*	*neangthyi*	*nigridia*	*niyomwanae*	*nuicamensis*	*paripari*	*pemanggilensis*	*perhentianensis*	*pseudomcguirei*
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	1	0	0	0	0	0
Subcaudals keeled (1) or not (0)	1	**0**	**0**	**0**	0	**0**	1	1	1	1
Single median row of keeled subcaudals (1) or not (0)	0	0	0	0	0	**weak**	0	**1**	0	0
Caudal tubercles encircle tail (1) or not (0)	0	0	1	0	0	0	0	**1**	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	**1**	**1**	**1**	1	**1**	**1**	**1**	0	0
No. of postcloacal tubercles	2,3	1,2	/	2–4	1,2	2–4	2	2	3–4	2,3
Enlarged femoral scales present (1) or absent (0)	0	0	/	0	0	**weak**	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	1	0	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	**0**	**0**	1	0	**0**	1	**0**	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0	**1**	0	0	**1**	0	0	**0,1**
No. of 4th toe lamellae	30–35	25–27	22–25	28,29	31–34	29–33	26–31	27–31	28–31	23–25

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TABLE 1. (Continued)

	psychedelica	*roticanai*	*shahruli*	*siamensis*	*tucdupensis*	*vandeventeri*	*narathiwatensis*	*huaseesom*	*punctatonuchalis*	*grismeri*
Maximum SVL	**75.3**	47	36.5	**39.7**	51	44.7	**43.2**	**37.9**	49.6	50.6
Supralabials	7,8	8,9	10,11	8,9	8–10	8,9	9,10	7–9	8	8,9
Infralabials	5–7	7,8	8–10	6–8	7,8	7–9	7–9	6–8	7,8	7–9
Ventral scales keeled (1) or not (0)	**0**	1	1	1	**0**	1	1	**0**	**0**	1
No. of precloacal pores	**0**	**3–6**	0	**0**	**0**	**4**	**3–6**	**5,6**	**0**	8–10
Precloacal pores continuous (1) or separated (0)	/	0	/	/	/	0	0	**1**	/	0
Precloacal pores elongate (1) or round (0)	/	0	/	/	/	0	0	0	/	0
No. of paravertebral tubercles	**34–48**	25–27	19–23	**19–25**	**18–21**	25–29	28,29	**18–24**	24–27	27–32
Tubercles of ventralmost row on flank linearly arranged and in contact or nearly so (1) or tubercles on flank widely space and more randomly distributed (0)	0	0	0	0	**1**	0	0	0	0	0
Tubercles present (1) or absent (0) on flanks	**0**	1	1	1	1	**0**	1	1	1	1
Lateral caudal tubercle row present (1) or absent (0)	**0**	1	/	**0**	**0**	**0**	1	1	ant	1
Caudal tubercles in lateral furrow (1) or not (0)	**0**	**0**	1	**0**	1	**0**	1	**0**	**0**	1
Ventrolateral caudal tubercles anteriorly (1) or not (0)	**0**	**0**	**0**	1	**0**	1	**0**	**0**	1	1

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TABLE 1. (Continued)

	psychedelica	*roticanai*	*shahruli*	*siamensis*	*tucdupensis*	*vandeventeri*	*narathiwatensis*	*huaseesom*	*punctatonuchalis*	*grismeri*
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	**1**	0	0	0	**1**	0	0	0	**1**	0
Subcaudals keeled (1) or not (0)	**0**	1	1	1	**0**	1	1	**0**	**0**	1
Single median row of keeled subcaudals (1) or not (0)	**1**	**1**	0	**weak**	**1**	**weak**	0	0	0	0
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	0	0	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	**1**	**weak**	**0**	**1**	**1**	**1**	0	0	**1**	0
No. of postcloacal tubercles	1,2	1,2	1–3	1,2	0–3	1–3	2,3	1,2	1,3	2,3
Enlarged femoral scales present (1) or absent (0)	1	0	0	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	**1**	0	0	0	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	**0**	1	1	1	**0**	1	1	**0**	**0**	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	**1**	0	0	0	1	0	0	0	0	0
No. of 4th toe lamellae	25–28	26–29	21–30	24–26	27–30	24–28	24–26	21–31	29	25–31

TABLE 2. Morphological data taken for the type series. BT=broken tail; r=regenerated tail; /=unable to assess. See Materials and methods for character abbreviations.

Cnemaspis grismeri	ZRC 2.6989 holotype	LSUHC 9969 paratype	LSUHC 9970 paratype	ZRC 2.6990 paratype	LSUHC 9972 paratype	LSUHC 9973 paratype	LSUHC 10941 paratype	LSUHC 10942 paratype	LSUHC 10943 paratype	LSUHC 10944 paratype
Sex	M	F	F	F	M	F	M	F	F	F
Supralabials	8	8	9	9	9	8	8	8	9	9
Infralabials	8	7	8	7	8	7	8	8	9	8
Ventral scales keeled (1) or smooth (0)	1	1	1	1	1	1	1	1	1	1
No. of precloacal pores	10	/	/	/	8	/	9	/	/	/
Precloacal pores in a continuous row (1) or separated medially (0)	0	/	/	/	0	/	0	/	/	/
Precloacal pores elongate (1) or round (0)	0	/	/	/	0	/	0	/	/	/
No. paravertebral tubercles	27	31	27	30	32	27	28	30	30	31
Tubercles present (1) or absent (0) on flanks	1	1	1	1	1	1	1	1	1	1
Tubercles of ventral most row on flank linearly arranged and in contact or nearly so (1) or tubercles on flank widely space and more randomly distributed (0)	0	0	0	0	0	0	0	0	0	0
Caudal tubercles in lateral caudal furrow (1) or not (0)	1	1	/	1	1	1	1	1	/	1
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	1	/	1	1	1	1	1	/	1
Lateral caudal tubercles present (1) or not (0)	1	1	/	1	1	1	1	1	/	1

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TABLE 2. (Continued)

	ZRC 2.6989 holotype	LSUHC 9969 paratype	LSUHC 9970 paratype	ZRC 2.6990 paratype	LSUHC 9972 paratype	LSUHC 9973 paratype	LSUHC 10941 paratype	LSUHC 10942 paratype	LSUHC 10943 paratype	LSUHC 10944 paratype
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	/	0	0	0	0	0	/	0
Subcaudals keeled (1) or not (0)	1	1	/	1	1	1	1	1	/	1
Single median row of keeled subcaudals (1) or not (0)	0	0	/	0	0	0	0	0	/	0
Caudal tubercles encircle tail (1) or not (0)	0	0	/	0	0	0	0	0	/	0
Enlarged median subcaudal scale row (1) or not (0)	0	0	/	0	0	0	0	0	/	0
No. of postcloacal tubercles	3	2	2	2	3	3	3	2	3	2
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	1	1	1	1	1	1
Enlarged submetatarsal scales on first toe (1) or not (0)	0	0	0	0	0	0	0	0	0	0
No. of 4th toe lamellae	29	30	29	29	30	28	25	30	27	31
Dark, longitudinal, gular markings present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0
Head and tail yellow in males (1) or not (0)	0	0	0	0	0	0	0	0	0	0
White to yellow crescent anterior to forelimb (1) or not (0)	0	0	0	0	0	0	0	0	0	0
Black shoulder patch enclosing yellow to white ocelli (1) or not (0)	1	1	1	1	1	1	1	1	1	1
Distinct, large, isolated, dark spots on neck (1) or not (0)	0	0	0	0	0	0	0	0	0	0
Distinct, dark and light caudal bands present (1) or absent (0)	1	0	0	0	0	0	0	0	0	0

……*continued on the next page*

TABLE 2. (Continued)

	ZRC 2.6989 holotype	LSUHC 9969 paratype	LSUHC 9970 paratype	ZRC 2.6990 paratype	LSUHC 9972 paratype	LSUHC 9973 paratype	LSUHC 10941 paratype	LSUHC 10942 paratype	LSUHC 10943 paratype	LSUHC 10944 paratype
SVL	47.7	50.6	48.6	43.5	48.8	45.5	45.7	48.5	44.4	48.2
TL	69.3	54.2r	49r	21.2b	47.9	64	61.1	70.1	BT	68.1
TW	4.9	5.4	4.8	4.5	5.2	4.8	5.2	5.4	4.8	5.2
FL	7.7	8.2	8.7	7.1	8.4	7.7	7.7	8.1	7.2	8.1
TBL	10.1	10.6	9.8	9.7	10.6	9.7	10.1	10.1	9.4	10.1
AG	20.1	21.2	20.2	19	24.3	20.1	20.3	22.7	20.1	22.1
HL	12.4	13.1	12.7	12.1	13	12.4	12.6	12.6	11.8	12.6
HW	8.5	8.2	8.3	7.3	8.5	7.7	8.1	8.1	8.1	8.1
HD	5.4	5.9	5.4	4.8	5.3	5.1	5.7	5.1	5.1	5.3
ED	2.6	2.3	2.8	2.7	2.7	2.5	2.6	2.5	2.5	2.5
EE	3.4	3.7	3.7	3.5	3.6	3.4	3.4	3.6	3.6	3.5
ES	6.1	6.6	6.4	6	6.6	6.1	6.1	6.1	6.1	6.1
EN	4.3	5	5.1	4.5	4.9	4.6	5.8	4.5	4.5	4.9
IO	3.8	3.1	2.6	2.8	3.5	2.5	2.7	2.6	2.9	2.9
EL	1.1	1.3	1.2	1.2	1.3	1.2	1.1	1.1	1.1	1.2
IN	1.2	1.3	1.3	1.1	1.2	1.2	1.2	1.3	1.3	1.5
									gravid	gravid

Distribution. *Cnemaspis grismeri* **sp. nov.** is known from Gua Asar at the Bukit Kepala Gajah limestone massif in Lenggong Valley, Perak (Fig. 1). This species has also been observed at other caves, namely Gua Kijang, Gua Puteri and Gua Ngaum that are also part of the Bukit Kepala Gajah limestone massif as well as its surrounding karst walls and karst forest.

Natural history. *Cnemaspis grismeri* **sp. nov.** is a lowland species found on the inner walls of limestone caves such as Gua Asar and Gua Kijang and near cave entrances and on the karst walls outside of caves as well as outcroppings in the lowland karst forest surrounding limestone massifs (Fig. 4). *Cnemaspis grismeri* **sp. nov.** is diurnal but is only observed crawling about in cracks and in the shadows of the karst boulders especially in vertical crevices. The lizards are very wary and quickly retreat deeper into their refuges when approached. Their behavior is similar to that of its upland closest relative *C. mcguirei* that behaves the same way on granite boulders at Bukit Larut, Perak (Grismer 2011). At night the color of *C. grismeri* **sp. nov.** lightens and lizards have been observed sleeping on the leaves of low vegetation near the karst walls and on vines and the aerial roots of fig trees (*Ficus* sp.) next to the limestone walls (Fig. 2 & 4). Specimens LSUHC 10942–43 are gravid females, which indicate that breeding takes place around the month of July.

FIGURE 4. Microhabitat structure of the karst formations for *Cnemaspis grismeri* **sp. nov.** from Lenggong Valley, Perak.

Etymology. This species is named in honor of Prof. Dr. L. Lee Grismer of La Sierra University, Riverside, California, USA for his tremendous contributions to the advancement of the field of herpetology in Malaysia. Coincidentally, *Cnemaspis grismeri* **sp. nov.** is the closest relative of *C. mcguirei*, a species that Dr. Grismer had named in honor of his close friend and colleague Prof. Dr. Jimmy A. McGuire of the University of California Berkeley, USA.

Comparisons. *Cnemaspis grismeri* **sp. nov.** differs from all other species of *Cnemaspis* in numerous aspects of scalation and color pattern as summarized in TABLE 1. It is most similar to its sister species *C. mcguirei* (L. Grismer *et al*. unpublished) but differs in being smaller (maximum SVL=50.6 mm in *C. grismeri* **sp. nov.** versus

SVL=65.1 mm in *C. mcguirei*) and having a significantly lower mean number of subdigital lamellae on the fourth toe (28.8 versus 32.5; *p*<0.01). Additionally, the lower, anterior shoulder spot is less prominent and the lateral baring is generally more distinct (Figs. 2 & 3). *Cnemapsis grismeri* **sp. nov.** is the sister species of *C. mcguirei* who are separated by a 7.3–11.7% sequence divergence in the mitochondrial gene ND2.

Discussion

Grismer (2011) included *Cnemaspis grismeri* **sp. nov.** as part of *C. mcguirei* but noted that the trenchant differences in body size and substrate preference (karst for *C. grismeri* **sp. nov.** and granite for *C. mcguirei*) might indicate that these are related but distinct lineages. Preliminary genetic work on the entire genus *Cnemaspis* (Grismer *et al*. unpublished) utilizing the mitochondrial ND2 gene demonstrated that they are sister species, but have a sequence divergence from one another of 7.3–11.7% which is also observed between other sister species groups. Additional differences in color pattern and scalation support the hypothesis that these populations are separate species (TABLE 1). A phylogeographic pattern of upland and lowland sister species within the Banjaran Bintang is beginning to emerge. Grismer *et al*. (2012) reported the same pattern for the upland *Cyrtodactylus bintangtinggi* (Grismer, Wood, Quah, Anuar, Muin, Sumontha, Ahmad, Bauer, Wnagkulangkul, Grismer, Pauwels) and the lowland *Cyrtodactylus bintangrendah* (Grismer, Wood, Quah, Anuar, Muin, Sumontha, Ahmad, Bauer, Wnagkulangkul, Grismer, Pauwels)—species that are syntopic with *C. mcguirei* and *C. grismeri* **sp. nov.**, respectively.

The karst regions of Peninsular Malaysia are proving to be warehouses of species diversity and endemism, especially with respect to gekkonids (Grismer 2011; Grismer & Chan 2009; Grismer *et al*. 2008a,b; 2009, 2010a,c, 2012; J. Grismer *et al*. 2010). The discovery of yet another endemic gekkonid in these poorly explored areas underscores the need for concentrated collecting efforts in these unique landscapes. Based on the latest assessment of the distribution of karst in Peninsular Malaysia (Price 2005) we estimate we have only explored 5% of what is available. Additional field work in these unexplored karst formations is needed to help better understand the herpetofaunal diversity in Peninsular Malaysia.

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APPENDIX. The following specimens were examined.

Cnemaspis affinis (Stoliczka): LSUHC 6695, 6758–59, 6773, 6788, 8975, Pulau Penang, Penang, Malaysia.

Cnemaspis aurantiacopes Grismer & Ngo: LSUHC 9528–29, 9531, 9535, 9539, Kien Giang Prov., Hon Dat Dist., Hon Dat Hill, Vietnam.

Cnemaspis baueri Das & Grismer: ZRC 2.5291 (holotype), ZRC 2.5292–99, LSUHC 3921–24, 4700–01, 4717–29, 4744, 4808, 7272–74, 7301–03, 7319, Pulau Aur, Johor, Malaysia.

Cnemaspis bayuensis Grismer, Grismer, Wood & Chan: LSUHC 9070–74, Gua Bayu, Kelantan, Malaysia.

Cnemaspis biocellata Grismer, Chan, Nurolhuda & Sumontha: ZRC 2.6693–98, Kulau Perlis, Perlis Malaysia; MS 30, Khao Tohphayawang, Muang Satun, Satun Province, Thailand.

Cnemaspis boulengeri Strauch: CAS 73745, LSUHC 9542, 9578–79, MCZ 39014-23, Pulo Condore (= Con Dao), Vietnam.

Cnemaspis caudanivea Grismer & Ngo: LSUHC 9544–48, Kien Giang Province, Kien Hai District, Hon Tre Island, Vietnam.

Cnemaspis chanthaburiensis Bauer & Das: FMNH 215979 (holotype) and FMNH 191479 (paratype), Khao Soi Daouw (Dao) Wildlife Sanctuary, Pongnomron (Pong Nam Ron) District, Chanthaburi Province, Thailand; BMNH 1917.5.14.4

(paratype), Chantaburi Province, Thailand; FMNH 215978 (paratype), Khao Khiew (Khieo) Wildlife Sanctuary, Chon Buri Province, Thailand; FMNH 215980 (paratype), Suan Kaset, Muang District, Chantaburi Province, Thailand; LSUHC 7882, Phnom Samkos, Pursat Province, Cardamom Mountains, Cambodia.

Cnemaspis dringi Das & Bauer: FMNH 148588 (holotype), Labang Camp (03º 20' N; 113º 29' E), Bintulu District, Fourth Division, Sarawak, Malaysia; FMNH 221478 (paratype), Sungai Segaham, Belaga District, Seventh Division, Sarawak, Malaysia.

Cnemaspis flavigaster Chan & Grismer: HC 0082–86, ZRC 2.6708–11, LSUHC 8835–36, Forest Research Institute Malaysia, Kepong, Selangor, Malaysia; BM 1898.9.22.216, Batu Caves, Selangor, Malaysia.

Cnemaspis flavolineata (Nicholls): LSUHC 8097, Frazer's Hill, Pahang, West Malaysia; LSUHC 9110, 9159–60, HC 303, Cameron Highlands, Pahang, West Malaysia.

Cnemaspis karsticola Grismer, Grismer, Wood, & Chan: LSUHC 9053–56, Gunung Reng, Kelantan, Malaysia.

Cnemaspis kendallii (Gray): BMNH XXII.92a (lectotype, designated by Dring, 1979), Malaysia; FMNH 223201, MCZ 157158-59, Bako National Park, Sarawak, Malaysia; FMNH 223201; MCZ 157158-59, Bidi, Sarawak, Malaysia; FMNH 184424, Bukit Lanjan, Selangor, Malaysia; BMNH 1902.12.12.12, Bidi, Sarawak, Malaysia; BMNH 1911.1.20.7–9, Bau, Sarawak, Malaysia; BPBM 7494, Alag Sungei Ayer, Pulau Tioman, Pahang, Malaysia; ZRC 2.1101, Jerantut, Pahang, Malaysia; ZRC 2.1102, Gunung Rokan, Pulau Tioman, Pahang, Malaysia; ZRC 2.1103, Sedagong, Pulau Tioman, Pahang, Malaysia; ZRC 2.3014, Bukit Timah, Singapore; ZRC 2.3015, Gunung Ladang, Melaka, Malaysia; UF 78463, ZSI 14767, 19637 Malaysia; LSUHC 3773–75, 3797, 3811, 3820, 3841, 3878–88, 4659, 4666, 6213–15, 6218, 6224, Pulau Tioman, Pahang, Malaysia; LSUHC 3894, 5056–58, Pulau Tulai, Pahang, Malaysia; LSUHC 4707, 4756–57, 4765–67 Pulau Tinggi, Johor, Malaysia; LSUHC 4954, 4958 Sungai Lembing, Pahang, Malaysia; LSUHC 5184–87, 5198, 5211 Pulau Seribuat, Johor, Malaysia; LSUHC 5244 Pulau Sembilan, Johor, Malaysia; LSUHC 5523–24, 5731–34 Pulau Babi Besar, Johor, Malaysia; LSUHC 5532 Pulau Sibu, Johor, Malaysia; LSUHC 5703, 5711 Pulau Aceh, Pahang, Malaysia; LSUHC 5749–52 Pulau Babi Hunjung, Johor, Malaysia; LSUHC 6380–83 Pulau Ibol, Johor, Malaysia; LSUHC 6562 Kepong, Selangor, West Malaysia; LSUHC 7691, 8122, 8126, 8191, 8210, Endau-Rompin, Johor, Malaysia; ZRC 2.1109–10, Pulau Siantan, Anamba, Riao Archipelago, Indonesia; ZRC 2.1112–13, Sungei Ulu, Great Natuna, Riao Archipelago, Indonesia; USNM 26573, Pulau Bunoa, Tambelan Islands, Indonesia; USNM 26555, St. Barbe Island, Indonesia; USNM 26547–49, Bunguran, Natunas, Riao Archipelago, Indonesia; USNM 28145, Pulau Lingung, Natuna, Riao Archipelago, Indonesia; USNM 28149, Sirhassen, Natuna, Riao Archipelago, Indonesia,

Cnemaspis kumpoli Taylor: LSUHC 8846–49, 8990–91, Wang Kelian, Perlis, Malaysia; MS 393–94, near the Ton Nga Chang Waterfall, Had Yai District, Songkhla Province (this is a new locality for this species).

Cnemaspis limi Das & Grismer: ZRC 2.5289 (holotype), ZRC 2.3504–06, 2.5290 (paratypes), LSUHC 3801–02, 3859, 3902, 3904, 4410, 4425, 4480–83, 4485–88, 4563–64, 4596, 4604, 4616, 4629, 4655, 5053, 5424, 5441, 5510, 5515, 5518, 5521, 6203, 6206–07, 6210, 6212, 6267 Pulau Tioman, Pahang, Malaysia.

Cnemaspis mcguirei Grismer, Grismer, Wood & Chan: LSUHC 8853–58, 8878, 8896, 8898, 9028–33, 9140, 9209, Bukit Larut, Perak, Malaysia; DWNP 1239, Gunung Bubu, Perak, Malaysia.

Cnemaspis monachorum Grismer, Norhayati, Chan, Belabut, Muin, Wood, & Grismer: LSUHC 9113–19, Wat Wanararm, Kedah, Pulau Langkawi, Malaysia.

Cnemaspis nigridius (Smith, 1925): BMNH 1946.8.22.90 (formerly BMNH 1925.9.1.8; holotype), MCZ 39024 and ZRC 2.1114-115, Mt. Gadin (= Gunung Gading), Sarawak, Malaysia; MCZ 15250, Lundu, Sarawak, Malaysia; BMNH 1925.9.1.9–10, Mt. Pueh, Sarawak, Malaysia.

Cnemaspis nuicamensis Grismer & Ngo: LSUHC 9549–50, 9552–93, 9555, An Giang Prov., Tinh Bien Dist., Nui Cam Hill, Vietnam.

Cnemaspis paripari Grismer & Chan: ZRC 2.6812, Gua Pari-pari, Bau District, Sarawak, Malaysia; LSUHC 9185, ZRC 2.6813–14, Gua Angin, Bau District, Sarawak, Malaysia.

Cnemaspis pemanggilensis Grismer & Das: ZRC 2.6043 (holotype), ZRC 2.6044–51 (paratypes), LSUHC 4457–58, 4460, 4464, 4470–76, 4495–96, 8011–16, Pulau Pemanggil, Johor, Malaysia.

Cnemaspis perhentianensis Grismer & Chan: LSUHC 8697, 8699, 9060, 9412, Pulau Perhentian Besar, Terengganu, Malaysia.

Cnemaspis pseudomcguirei Grismer, Norhayati, Chan, Belabut, Muin, Wood, & Grismer: LSUHC 9047, 9145–47, Bukit Larut, Perak, Malaysia.

Cnemaspis psychedelica Grismer, Ngo & Grismer: LSUHC 9182–85, Hon Khoai Island, Ngoc Hien District, Ca Mau Province, Vietnam.

Cnemaspis roticanai Grismer & Chan: LSUHC 9430–31, 9439, 9453, Gunung Raya, Pulau Langkawi, Kedah, Malaysia.

Cnemaspis tucdupensis Grismer & Ngo: LSUHC 8248, 9560–63, An Giang Prov., Tri Ton Dist., Tuc Dup Hill, Vietnam.

Chapter 3: Systematics and natural history of Southeast Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) with descriptions of eight new species from Malaysia, Thailand, and Indonesia

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Systematics and natural history of Southeast Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) with descriptions of eight new species from Malaysia, Thailand, and Indonesia

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Abstract

A well-supported and well-resolved phylogeny based on a concatenated data set from one mitochondrial and two nuclear genes, six morphological characters, and nine color pattern characters for 44 of the 50 species of the Southeast Asian Rock Geckos (genus *Cnemaspis* Strauch, 1887) is consistent with the previous taxonomy of *Cnemaspis* based solely on morphology and color pattern. *Cnemaspis* is partitioned into four major clades that collectively contain six species groups. The monophyly of all clades and species groups is strongly supported and they are parapatrically distributed across well-established, biogeographical regions ranging from southern Vietnam westward through southern Indochina, southward through the Thai-Malay Peninsula, then eastward to Borneo. Eight new species (*Cnemaspis omari* sp. nov. from the Thai-Malaysian border; *C. temiah* sp. nov. from Cameron Highlands, Pahang, Malaysia; *C. stongensis* sp. nov. from Gunung Stong, Kelantan, Malaysia; *C. hangus* sp. nov. from Bukit Hangus, Pahang, Malaysia; *C. sundagekko* sp. nov. from Pulau Siantan, Indonesia; *C. peninsularis* sp. nov. from southern Peninsular Malaysia and Singapore, and *C. mumpuniae* sp. nov. and *C. sundainsula* sp. nov. from Pulau Natuna Besar, Indonesia) are described based on morphology and color pattern and all but *C. sundagekko* sp. nov. are included in the phylogenetic analyses. *Cnemaspis kendallii* is polyphyletic and a composite of six species. An updated taxonomy consistent with the phylogeny is proposed for all 50 species and is based on 25 morphological and 53 color pattern characters scored across 594 specimens. Cladogenetic events and biogeographical relationships within *Cnemaspis* were likely influenced by this group's low vagility and the cyclical patterns of geographical and environmental changes in Sundaland over the last 25 million years and especially within the last 2.5 million years. The phylogeny indicates that nocturnality, diurnality, substrate preferences, and the presence of ocelli in the shoulder regions have evolved independently multiple times.

Key words: *Cnemaspis,* Gekkonidae, Southeast Asia, new species, Sunda Shelf, biogeography, phylogeography

Introduction

Southeast Asia harbors 20–25% of the planet's terrestrial biodiversity in only 4% of its landmass. This makes it one of the great megadiverse hotspots of the world (Corlett 2009) even though much of its most prominent, geographic feature, the vast Sunda Plains, lie submerged beneath the South China Sea. Given that this is the second largest subareal margin of a continental shelf in the world (Parnell 2013) means that much of Sundaland's terrestrial biodiversity is in a refugial state being restricted to small, Sundaic islands on the southern Sunda Plains and the areal, continental fringes of the Sunda Shelf (Grismer *et al.* 2011a). Furthermore, the current geographic outline of Sundaland has existed intermittently for only 2% of the last 2.4 million years (Woodruff 2010) owing to multiple, glaciostatic driven, sea-level changes that have repeatedly exposed and submerged the Sunda Plains while uniting Indochina with Borneo, Java, Sumatra, and the Thai-Malay Peninsula. Therefore, the phylogeographic relationships of Sundaic species and many species from southern Indochina cannot be accounted for by current geography and ecology alone but reconciled only in the context of cyclical changes in sea levels and concomitant climatic fluctuations (Cannon *et al.* 2009; Bell *et al.* 2010, 2011; Loredo *et al.* 2013; Woodruff 2010).

One group that may offer insight into environmentally driven, cyclical speciation events in Sundaland is the monophyletic Southeast Asian branch of the polyphyletic gekkonid genus *Cnemaspis* Strauch (Gamble *et al.* 2012). *Cnemaspis* (*sensu* Smith 1933; Gamble *et al.* 2012) contains approximately 105 Afro-Asian scansorial species whose many morphological specializations are adaptations for moving about on flat, elevated surfaces during low levels of illumination. As such, the morphology within this genus appears to have been highly conserved across the Old World. However, recent phylogenetic analyses (Gamble *et al.* 2012) have demonstrated that clades representing the major centers of radiation from Africa, South Asia, and Southeast Asia do not form a monophyletic group and are not particularly closely related to one another. Thus, their morphological similarity is due to convergence, not common ancestry. Working under this hypothesis, recent taxonomic revisions and descriptions of Southeast Asian *Cnemaspis* (Grismer *et al.* 2010a, 2013a, 2014; Wood *et al.* 2013) appropriately and expressly did not consider South Asian and African species in their analyses and only recognized Southeast Asian taxa related to the type species *C. boulengerii* Strauch, 1887 from southern Vietnam as true *Cnemaspis.*

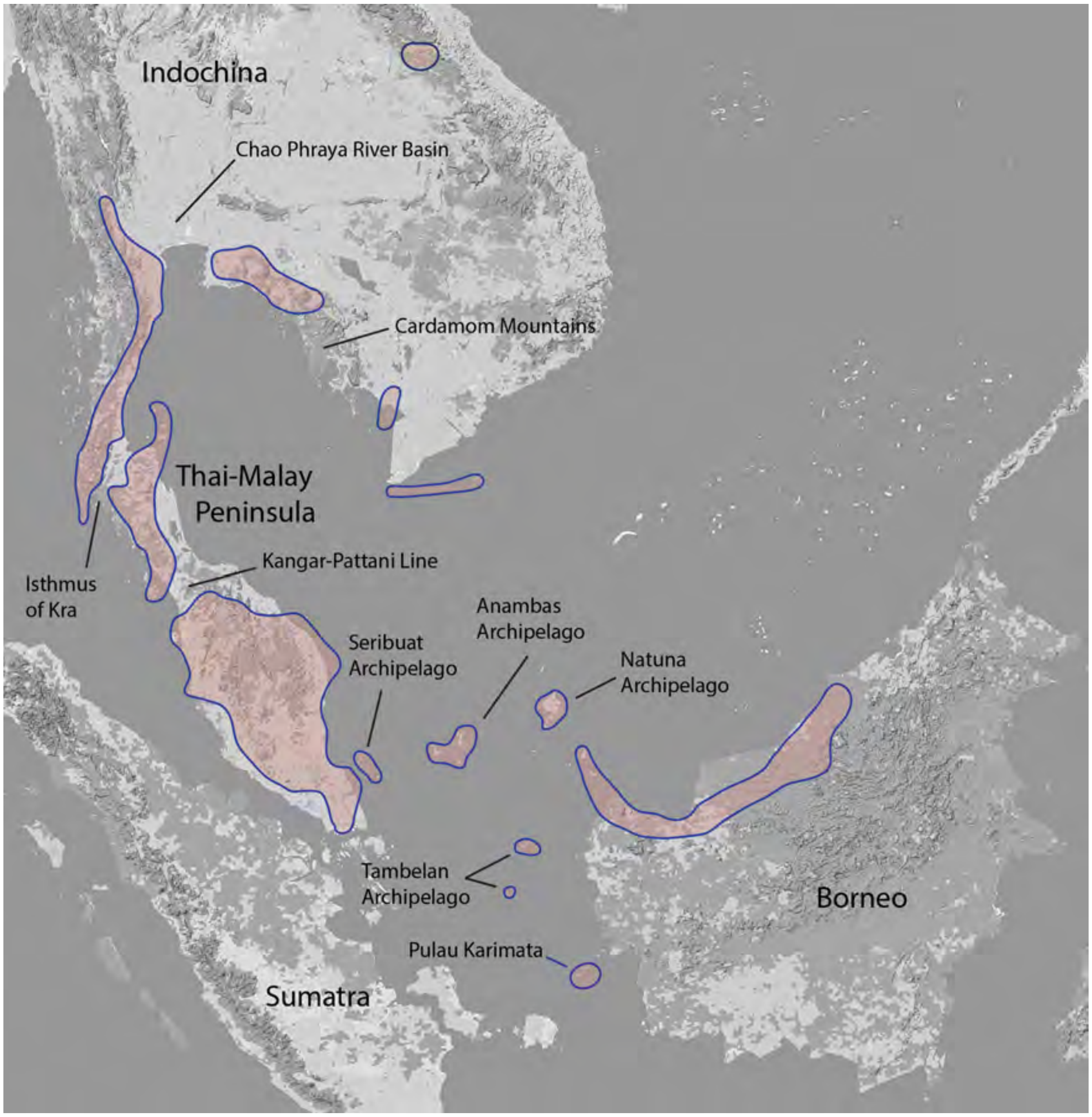

FIGURE 1. Distribution of the Sundaland Rock Gecko genus *Cnemaspis* Strauch, 1887 in Southeast Asia. The northern outlier is *C. laoensis* Grismer 2009.

A monophyletic *Cnemaspis sensu stricto* as recognized throughout this study, currently contains 50 Sundaic and Indochinese species (see below) whose collective distribution encompasses the entire areal fringe of the Sunda Shelf and several islands across the submerged Sunda Plains (Fig. 1). The genus ranges from southern Laos in the north, southward through Vietnam, Cambodia, and Thailand, and south through the Thai-Malay Peninsula and eastward to Borneo through the Seribuat, Anambas and Natuna archipelagos (Grismer & Chan 2010; Grismer *et al.* 2010a, 2013a, 2014; Wood *et al.* 2013). With some exceptions, all *Cnemaspis* are relatively small, cryptically colored species inhabiting primary and old secondary rainforests. They are secretive, microhabitat specialists that generally restrict their movements to the shaded surfaces of rocks, trees and caves during the day, or they are nocturnal. Having a body plan bearing a broad, flattened head; large, somewhat forward and upwardly directed eyes; a flattened body; and long, widely splayed limbs with long, inflected digits are adaptations for climbing on flat surfaces in all planes of orientation and show extreme interspecific conservatism despite a nearly three-fold difference in body size (maximum SVL ranging from 35.1 mm in *C. monachorum* to 88.2 mm in *C. limi* sp. nov.). This combination of cryptic behavior, microhabitat specialization, and morphological conservatism confounded species boundaries and generated considerable taxonomic confusion and instability (see Bauer & Das 1998; Chan & Grismer 2008; Das & Bauer 1998; Dring 1979; Grismer *et al*. 2008a,b, 2009). The confluence of these circumstances resulted in many species going unnoticed, unrecognized, or being buried in the synonymies of other species. However, a more informed understanding of how and where to look for *Cnemaspis* and what morphological characters are useful in establishing species boundaries has led to disentangling much of this group's taxonomic history (see Grismer *et al.* 2010a and citations therein) along with the description of 43 new species since 2003. The morphological conservatism within *Cnemaspis* and the highly restricted distributions of its species coupled with their low vagility and microhabitat specialization, makes this genus particularly well-suited for comparative, biogeographic inferences in that multiple, parallel, cladogenetic events and phylogeographic patterns will have not have been erased through episodes of dispersal.

The current taxonomy of *Cnemaspis,* however, is based solely on morphology and color pattern and in some cases, species were described using three or fewer specimens, potentially limiting the value of their diagnostic characters and the establishment of species boundaries. Furthermore, species boundaries and hypotheses of species relationships have never been tested with a molecular data set. Grismer *et al.* (2013b) demonstrated that morphology based taxonomies involving morphologically conserved taxa have great potential for underestimating species diversity, either due to cryptic speciation, character bias, or overlooked character states. They went on to provide evidence that the negative effects potentially inherent in such taxonomies can be significantly mitigated by an integrative approach (i.e., Padial *et al.* 2010). Therefore, the intent of this study is to test the morphological-based taxonomy of *Cnemaspis* using an integrative taxonomic approach to establish species level relationships in order to provide a platform for future analyses of this group's potentially adaptive radiation and evolutionary biology (Wood & Grismer in prep.). We provide an expanded morphological and color pattern data set based on 596 specimens that include eight new and 43 previously described species in order to reinforce and modify their diagnoses and in some cases, significantly expand their geographic distributions and our knowledge of their natural history. All known species were included in the morphological and color pattern analyses and 44 of the 50 known species were included in the molecular analysis. These data are presented in a monographic style in order to consolidate information published in various books and journal articles over the last 130 years.

Materials and methods

Molecular analysis

A dataset from the mitochondrial gene NADH dehydrogenase subunit 2 gene (ND2) and its flanking tRNA's (tRNAmet, tRNAtrp, tRNAala, tRNAasn, tRNAcys; 1335 bp), plus portions of two nuclear protein coding genes, Recombination Activating gene 1 (RAG-1; 1050 bp) and Matrix-Remodeling associated 5 gene (MXRA5; 839 bp) was constructed from 177 individuals of 44 of the 50 species of *Cnemaspi*s from throughout its range plus 31 outgroups (Table 1) based on Gamble *et al.* (2012). Outgroup sequences were obtained from GenBank and all new sequences were deposited with GenBank accession numbers (Table 1). Two individuals per putative species (when available) were sequenced for the two nuclear genes. Previous studies have shown that using two samples per putative species can dramatically improve accuracy and precision (Camargo *et al.* 2012).

Total genomic DNA was isolated from liver or skeletal muscle from specimens stored in 95% ethanol using the Qiagen DNeasy™ tissue kit (Valencia, CA, USA). All genes were amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions: 1.0 µl genomic DNA, 1.0 µl light strand primer 1.0 µl heavy strand primer, 1.0 µl dinucleotide pairs, 2.0 µl 5x buffer, 1.0 MgCl 10x buffer, 0.18 µl Taq polymerase, and 7.5 µl

H_2O. PCR reactions were executed on an Eppendorf Mastercycler gradient theromocycler 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 47–52°C for 35 s, followed by a cycle extension at 72°C for 35 s, for 33–35 cycles (see Table 2 for details). All PCR products were visualized on a 10 % agarose gel electrophoresis. Successful targeted PCR products were vacuum purified using MANU 30 PCR plates Millipore plates and purified products were resuspended in DNAgrade water. Purified PCR products were sequenced using the ABI Big-Dye Terminator v3.1 Cycle Sequencing Kit in an ABI GeneAmp PCR 9700 thermal cycler. Cycle sequencing reactions were purified with Sephadex G-50 Fine (GE Healthcare) and sequenced on an ABI 3730xl DNA Analyzer at the BYU DNA Sequencing Center. Primers used for amplification and sequencing are presented in Table 2. All sequences were edited in Geneious v5.5.6 (Drummond *et al.* 2011) and initially aligned by eye. MacClade v4.08 (Maddison & Maddison 2005) was used to check for premature stop codons and to ensure the correct amino acid read frame for each gene.

Phylogenetic analysis

Both partitioned Maximum Likelihood (ML) and partitioned Bayesian Inference (BI) were employed. All genes were partitioned by codon position and the tRNA's were treated as one partition for both the ML and BI analyses. The Akaike Information Criterion (AIC) as implemented in ModelTest v3.7 (Posada & Crandall 1998), was used to calculate the best-fit model of evolution for each codon position (Table 3). Partitioned Maximum Likelihood analyses were performed using RAxML HPC v7.5.4 (Stamatakis, 2006), 1000 bootstrap pseudoreplicates via the rapid 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 & Ronquist 2001; Ronquist & Huelsenbeck 2003) 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 2×10^6 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. Nodes having bootstrap support values greater than 70 and posterior probabilities above 0.95 were considered significantly supported (Huelsenbeck *et al.* 2001; Wilcox *et al.* 2002). We calculated uncorrected percent sequence divergences for ND2 in Mega v5.2.2 (Tamura *et al.* 2011).

Because it is possible for the mitochondrial and nuclear genes to have unique evolutionary histories (Hudson & Turelli 2003; Moore 1995), each gene was analyzed separately to look for discordances (Leaché & Mulcahy 2007). All analyses were performed using partitioned Maximum Likelihood implemented in RAxML HPC v7.5.4 (Stamatakis 2006) following the conditions described above and models of evolution in Table 3.

Morphological analysis

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 with Mitutoyo dial calipers to the nearest 0.1 mm under a Nikon SMZ 1500 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 90º to the inflection of the flexed wrist; tibia length (TBL), taken on the ventral surface from the posterior surface of the knee while flexed 90º 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 paravertebral row and the lateral, caudal furrow on the dorsolateral margin of the tail; lateral row—the row immediately below the lateral, caudal furrow; and ventrolateral row—the row below the lateral row on the ventrolateral margin of the tail below the lateral caudal furrow. When present, this row is usually restricted to the anterior 25% (or less) of the tail. Occasionally there may be a row of tubercles within the lateral, caudal furrow. Fifty-three color pattern characteristics were evaluated and are described in Table 7.

Much of the information on character states and their distribution throughout *Cnemaspis* was originally obtained from the literature and as such, was subject to inconsistencies between the methods of various authors in gathering and evaluating such data over the last 114 years. Grismer *et al.* (2010a), however, re-examined first-hand specimens of every species known at the time in order to standardize the character analysis. This is followed and augmented here with 25 morphological character states and 53 color pattern character states scored across all taxa (50 species totaling 596 specimens) as outlined above in the Materials and Methods. Additional material examined subsequent to the species' original description or latest review is listed at the end of each species account. The distributions of the various species groups and clades constructed herein based on the molecular analysis closely correspond to particular biogeographic regions. This underscores the low vagility and microhabitat specificity of *Cnemaspis* species and provides a hypothetical framework for placing species that were not available for the molecular analysis in particular species groups and clades. The relationships of these species are left *incertae sedis* and their accounts are presented subsequent to the following proposed phylogenetic taxonomy.

Institutional abbreviations follow Sabaj-Pérez (2010). ZRC refers to the Zoological Reference Collection at the Raffles Museum of Biodiversity, National University of Singapore, Singapore; DWNP refers to the Department of Wildlife and National Parks collection, Krau, Pahang, Peninsular Malaysia; LSUHC refers to the La Sierra University Herpetological Collection, La Sierra University, Riverside, California, USA; LSUDPC refers to the La Sierra University Digital Photo Collection; HC refers to the Herpetological Collection of the Universiti Kebangsaan Malaysia, Bangi, Selangor; USMHC refers to the Universiti Sains Malaysia Herpetological Collection at the Universiti Sains Malaysia, Penang, Malaysia; AMB refers to the collection of Aaron M. Bauer, Department of Biology, Villanova University, USA; THNHM refers to the Thailand Natural History Museum, National Science Museum, Khlong Luang, Pathum Thani, Bangkok, Thailand; CUMZ refers to the Chulalongkorn University Museum of Zoology, Bangkok, Thailand; PSUZC refers to the Prince of Songkhla University Zoological Collection, Songkhla, Thailand; UNS refers to the University of Natural Sciences in Ho Chi Minh City, Vietnam; ZMKU refers to the Zoological Museum of the Kasetsart University, Bangkok, Thailand; and KZM refers to the Nakhonratchasima Zoo Museum, ZPO, Nakhonratchasima, Thailand; CAS refers to the California Academy of Sciences, San Francisco, California, USA; FMNH refers to the Field Museum of Natural History, Chicago, Illinois, USA; MCZ refers to the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MNHN refers to the Museúm national d'Historie naturelle, Paris, France; MZB refers to the Museum Zoologicum Bogoriense, Cibinong, Indonesia; and TNHC refers to the Texas Natural heritage Collection and the University of Texas at Austin, Austin Texas, USA.

TABLE 1. Specimens used for the molecular phylogenetic analyses. Voucher number abbreviations are as follows: ABTC, Australian Biological Tissue Collection; AMS, Australian Museum, Sydney; ANWC, Australian National Wildlife Collection; CAS, California Academy of Sciences; FMNH, Field Museum of Natural History; HC, Herpetological Collection of the Universiti Kebangsaan Malaysia, Bangi, Selangor; ID, Indraneil Das field series; JB, Jon Boone captive collection; MVZ, Museum of Vertebrate Zoology (Berkeley); LSUHC, La Sierra University Herpetological Collection; LSUMZ, Louisiana State University Museum of Zoology; MZB, Museum Zoologicum Bogoriense, Cibinung, Java, Indonesia; RAH, Rod A. Hitchmough field series; TG, Tony Gamble; USMHC, Universiti Sains Malaysia Herpetological Collection at the Universiti Sains Malaysia, Penang, Malaysia; USNM, United States National Museum (Smithsonian); YPM, Yale Peabody Museum; ZRC, Zoological Reference Collection, Raffles Museum. – Indicates missing data.

			GenBank accession numbers		
Voucher number	**Species**	**Locality**	***ND2***	***MXRA5***	***RAG1***
FMNH 274474	*Agamura persica*	Pakistan: Balochistan, Makran district, Gwadar division	JX440515	JX440566	JX440675
n/a	*Anolis carolinensis*	n/a	EU747728	AAWZ02008741	AAWZ02015549
CAS 228737	*Bunopus tuberculatus*	United Arab Emirates: Sharjah	–	–	JX440676
ID 7618	*Crossobamon orientalis*	Rajasthan, India, Krom River	JX041338	–	JQ945299
LSUHC 8638	*Cyrtodactylus grismeri*	Vietnam: An Giang Province, Tuc Dup Hill	JX440538	JX440594	JX440698
JB 127	*Cyrtopodion elongatum*	captive	JX440516	JX440567	JX440677
n/a	*Dixonius melanostictus*	Thailand	HM997153	–	HM997165
LSUHC 7328	*Dixonius siamensis*	Cambodia: Pursat Provinve, Keo Seima District	EU054299	–	EU054283
TG 00723	*Gehyra fehlmanni*	Imported from Malaysia	JN393948	–	JN393986
ABTC 13940	*Gehyra insulensis*	Indonesia: Krakatau	GQ257784	–	–
LSUHC 7379	*Gehyra mutilata*	Cambodia: Pursat Province, Phnom Aural	JN393914	–	JN393959
n/a	*Gekko gecko*	unknown	EU054288	–	EF534813
MVZ 245438	*Hemidactylus angulatus*	Ghana: Volta region, Togo Hills	EU268367	–	EU268306
CAS 229633	*Hemidactylus frenatus*	Myanmar: Tanintharyi Division, Kaw Thaung District	HM559629	–	HM559695
CAS 223286	*Hemidactylus garnotii*	Myanmar: Rakhine State, Taung Gok Township	EU268363	–	EU268302
YPM 14798	*Hemidactylus mabouia*	USA: Florida	HM559639	–	HM559705
LSUMZ H-1981	*Hemidactylus turcicus*	USA: Louisiana	EU268360	–	EU268299
ANWC R6147	*Heteronotia binoei*	Australia: Northern Territory	AY369027	–	–
ZRC 24847	*Lepidodactylus lugubris*	Singapore	JN393944	–	–
n/a	*Lialis jicari*	Australia	AY369025	–	–
n/a	*Mediodactylus russowii*	captive	JX440517	–	JX440678
USNM 322160	*Nactus pelagicus*	Tonga: Eua Island	HM997161	–	–
AMS 143861	*Oedura marmorata*	Australia, Queensland	GU459951	JX440571	EF534779
n/a	*Perochirus ateles*	Federated States of Micronesia	JN393938	–	JN393984
MVZ 197233	*Pygopus nigriceps*	Australia: Northern Territory	JX440518	JX440572	EF534783
CAS 198428	*Sphaerodactylus roosevelti*	USA: Puerto Rico	JN393943	JX440573	EF534785
JB 34	*Sphaerodactylus torrei*	Cuba	JX440519	JX440574	EF534788
JB 35	*Stenodactylus petrii*	captive	–	–	JX440679
CAS 228602	*Tenuidactylus caspius*	Iran: Protected Area, Semnan Province	JX041448	–	JQ945340
JB 28	*Tropicolotes steudneri*	captive	JX440520	JX440576	JX440680
RAH292	*Woodworthia maculata*	New Zealand: Titahi Bay	GU459852	JX440577	GU459449

……*continued on the next page*

TABLE 1. (Continued)

			GenBank accession numbers		
Voucher number	**Species**	**Locality**	***ND2***	***MXRA5***	***RAG1***
LSUHC 6757	*Cnemaspis affinis*	Malaysia: Penang, Pulau Pinang	KM024684	KM024856	KM024928
LSUHC 6774	*Cnemaspis affinis*	Malaysia: Penang, Pulau Pinang	KM024681	–	–
LSUHC 6787	*Cnemaspis affinis*	Malaysia: Penang, Pulau Pinang	KM024682	–	–
LSUHC 6788	*Cnemaspis affinis*	Malaysia: Penang, Pulau Pinang	KM024683	–	–
LSUHC 6758	*Cnemaspis affinis*	Malaysia: Penang, Pulau Pinang	KM024685	KM024857	–
LSUHC 6759	*Cnemaspis affinis*	Malaysia: Penang, Pulau Pinang	KM024686	–	–
LSUHC 8304	*Cnemaspis argus*	Malaysia: Terengganu, Gunung Lawit	KM024687	KM024858	KM024930
LSUHC 10834	*Cnemaspis argus*	Malaysia: Terengganu, Gunung Tebu	KM024688	–	–
LSUHC 10835	*Cnemaspis argus*	Malaysia: Terengganu, Gunung Tebu	KM024689	–	–
LSUHC 10858	*Cnemaspis argus*	Malaysia: Terengganu, Gunung Tebu	KM024690	–	–
LSUHC 10859	*Cnemaspis argus*	Malaysia: Terengganu, Gunung Tebu	KM024691	KM024859	KM024929
LSUHC 8610	*Cnemaspis aurantiacopes*	Vietnam: Kien Giang Province, Hon Dat Hill	KM024692	KM024860	–
LSUHC 8611	*Cnemaspis aurantiacopes*	Vietnam: Kien Giang Province, Hon Dat Hill	KM024693	–	–
LSUHC 8612	*Cnemaspis aurantiacopes*	Vietnam: Kien Giang Province, Hon Dat Hill	KM024694	KM024861	KM024931
LSUHC 7301	*Cnemaspis baueri*	Malaysia: Johor, Pulau Aur	KM024695	–	–
LSUHC 7302	*Cnemaspis baueri*	Malaysia: Johor, Pulau Aur	KM024696	–	–
LSUHC 7303	*Cnemaspis baueri*	Malaysia: Johor, Pulau Aur	KM024697	KM024862	–
LSUHC 7273	*Cnemaspis baueri*	Malaysia: Johor, Pulau Aur	KM024698	–	–
LSUHC 7274	*Cnemaspis baueri*	Malaysia: Johor, Pulau Aur	KM024699	–	–
LSUHC 9070	*Cnemaspis bayuensis*	Malaysia: Kelantan, Kampung Bayu	KM024700	–	–
LSUHC 9071	*Cnemaspis bayuensis*	Malaysia: Kelantan, Kampung Bayu	KM024701	–	–
LSUHC 9072	*Cnemaspis bayuensis*	Malaysia: Kelantan, Kampung Bayu	KM024702	KM024863	KM024932
LSUHC 11444	*Cnemaspis bidongensis*	Malaysia: Terengganu, Pulau Bidong	KM024703	–	–
LSUHC 11445	*Cnemaspis bidongensis*	Malaysia: Terengganu, Pulau Bidong	KM024704	–	–
LSUHC 11446	*Cnemaspis bidongensis*	Malaysia: Terengganu, Pulau Bidong	KM024705	–	–
LSUHC 11447	*Cnemaspis bidongensis*	Malaysia: Terengganu, Pulau Bidong	KM024706	–	–
LSUHC 8789	*Cnemaspis biocellata*	Malaysia: Perlis, Gua Kelam	KM024707	KM024864	KM024933
LSUHC 8817	*Cnemaspis biolcellata*	Malaysia: Perlis, Kuala Perlis	KM024708	–	–
LSUHC 8818	*Cnemaspis biocellata*	Malaysia: Perlis, Kuala Perlis	KM024709	KM024865	KM024934
LSUHC 9278	*Cnemaspis boulengerii*	Vietnam: Ca Mau Province, Con Dao Archipelago	KM024710	KM024866	–
LSUHC 9279	*Cnemaspis boulengerii*	Vietnam: Ca Mau Province, Con Dao Archipelago	KM024711	KM024867	–
LSUHC 8577	*Cnemaspis caudanivea*	Vietnam: Kien Giang Province, Hon Tre Island	KM024712	KM024868	KM024935
LSUHC 8578	*Cnemaspis caudanivea*	Vietnam: Kien Giang Province, Hon Tre Island	KM024713	KM024869	KM024936
LSUHC 8582	*Cnemaspis caudanivea*	Vietnam: Kien Giang Province, Hon Tre Island	KM024714	–	–
LSUHC 9567	*Cnemaspis chanardi*	Thailand: Nakhon Si Thammarat Province, Thum Thong Panra	KM024715	KM024870	KM024937
LSUHC 9338	*Cnemaspis chanthaburiensis*	Cambodia: Pursat Province, Phnom Dalai	KM024716	KM024871	–

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TABLE 1. (Continued)

Voucher number	Species	Locality	GenBank accession numbers		
			ND2	***MXRA5***	***RAG1***
LSUHC 6562	*Cnemaspis flavigaster*	Malaysia: Selangor, Kepong	KM024717	–	–
LSUHC 8835	*Cnemaspis flavigaster*	Malaysia: Selangor, Kepong	KM024718	KM024873	–
LSUHC 8836	*Cnemaspis flavigaster*	Malaysia: Selangor, Kepong	KM024719	–	–
LSUHC 10380	*Cnemaspis flavigaster*	Malaysia: Selangor, Ulu Gombak	KM024720	KM024872	–
LSUHC 8079	*Cnemaspis flavolineata*	Malaysia: Pahang, Fraser's Hill, The Gap	KM024721	KM024874	KM024938
LSUHC 9969	*Cnemaspis grismeri*	Malaysia: Perak, Lenggong	KM024722	KM024875	KM024939
LSUHC 9970	*Cnemaspis grismeri*	Malaysia: Perak, Lenggong	KM024723	–	KM024940
LSUHC 9730	*Cnemaspis grismeri*	Malaysia: Perak, Lenggong	KM024724	–	–
LSUHC 9732	*Cnemaspis grismeri*	Malaysia: Perak, Lenggong	KM024725	–	–
LSUHC 9733	*Cnemaspis grismeri*	Malaysia: Perak, Lenggong	KM024726	–	–
LSUHC 9358a	*Cnemaspis hangus* sp. nov.	Malaysia: Pahang, Bukit Hangus	KM024727	–	–
LSUHC 9358b	*Cnemaspis hangus* sp. nov.	Malaysia: Pahang, Bukit Hangus	KM024728	–	–
HC 0225	*Cnemaspis hangus* sp. nov.	Malaysia: Pahang, Bukit Hangus	KM024729	KM024876	KM024941
LSUHC 9665	*Cnemaspis harimau*	Malaysia: Kedah, Gunung Jerai	KM024730	–	–
LSUHC 9667	*Cnemaspis harimau*	Malaysia: Kedah, Gunung Jerai	KM024731	KM024877	KM024942
LSUHC 9668	*Cnemaspis harimau*	Malaysia: Kedah, Gunung Jerai	KM024732	KM024878	–
LSUHC 9455	*Cnemaspis huaseesom*	Thailand: Kanchanaburi Province, Sai Yok National Park	KM024733	KM024879	KM024943
LSUHC 9457	*Cnemaspis huaseesom*	Thailand: Kanchanaburi Province, Sai Yok National Park	KM024734	–	–
LSUHC 9458	*Cnemaspis huaseesom*	Thailand: Kanchanaburi Province, Sai Yok National Park	KM024735	KM024880	KM024944
LSUHC 9054	*Cnemaspis karsticola*	Malaysia: Kelantan, Gunung Reng	KM024736	KM024881	KM024945
LSUHC 9055	*Cnemaspis karsticola*	Malaysia: Kelantan, Gunung Reng	KM024737	KM024882	KM024946
LSUHC 5317	*Cnemaspis kendallii*	Indonesia: Riau Province, Pulau Serasan	KM024738	–	–
LSUHC 9171	*Cnemaspis kendallii*	Malaysia: Sarawak, Gunung Gading	KM024739	–	–
LSUHC 9172	*Cnemaspis kendallii*	Malaysia: Sarawak, Gunung Gading	KM024740	KM024884	KM024948
LSUHC 9173	*Cnemaspis kendallii*	Malaysia: Sarawak, Gunung Gading	KM024741	–	–
LSUHC 9174	*Cnemaspis kendallii*	Malaysia: Sarawak, Gunung Gading	KM024742	–	–
LSUHC 9178	*Cnemaspis kendallii*	Malaysia: Sarawak, Santubong	KM024743	KM024883	KM024947
LSUHC 9179	*Cnemaspis kendallii*	Malaysia: Sarawak, Santubong	KM024744	–	–
LSUHC 8847	*Cnemaspis kumpoli*	Malaysia: Perlis, Perlis State Park	KM024745	KM024885	KM024950
LSUHC 8848	*Cnemaspis kumpoli*	Malaysia: Perlis, Perlis State Park	KM024746	KM024886	KM024949
LSUHC 3902	*Cnemaspis limi*	Malaysia: Pahang, Pulau Tioman	KM024747	KM024888	KM024952
LSUHC 3904	*Cnemaspis limi*	Malaysia: Pahang, Pulau Tioman	KM024748	–	–
LSUHC 3774	*Cnemaspis limi*	Malaysia: Pahang, Pulau Tioman	KM024749	–	–
LSUHC 3888	*Cnemaspis limi*	Malaysia: Pahang, Pulau Tioman	KM024750	KM024887	KM024951
LSUHC 8853	*Cnemaspis mcguirei*	Malaysia: Perak, Bukit Larut	KM024751	–	–
LSUHC 8854	*Cnemaspis mcguirei*	Malaysia: Perak, Bukit Larut	KM024752	KM024889	KM024953

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TABLE 1. (Continued)

Voucher number	Species	Locality	GenBank accession numbers *ND2*	*MXRA5*	*RAG1*
LSUHC 8855	*Cnemaspis mcguirei*	Malaysia: Perak, Bukit Larut	KM024753	KM024890	KM024954
LSUHC 9114	*Cnemaspis monachorum*	Malaysia: Kedah, Langkawi Archipelago, Pulau Langkawi	KM024754	KM024891	–
LSUHC 10807	*Cnemaspis monachorum*	Malaysia: Kedah, Langkawi Archipelago, Pulau Langgun	KM024755	–	–
LSUHC 10808	*Cnemaspis monachorum*	Malaysia: Kedah, Langkawi Archipelago, Pulau Langgun	KM024756	KM024892	KM024955
LSUHC 10809	*Cnemaspis monachorum*	Malaysia: Kedah, Langkawi Archipelago, Pulau Langgun	KM024757	–	–
LSUHC 10810	*Cnemaspis monachorum*	Malaysia: Kedah, Langkawi Archipelago, Pulau Langgun	KM024758	–	–
MZB.Lace 10155	*Cnemaspis mumpuniae* sp. nov.	Indonesia: Riau Province, Bedung fragmented forest area	KM024759	–	–
MZB.Lace 10166	*Cnemaspis mumpuniae* sp. nov.	Indonesia: Riau Province, Sekunyam Forest Reserve	KM024760	KM024893	KM024956
MZB.Lace 10167	*Cnemaspis mumpuniae* sp. nov.	Indonesia: Riau Province, Sekunyam Forest Reserve	KM024761	KM024894	KM024957
USMHC 1347	*Cnemaspis narathiwatensis*	Malaysia: Perak, Belum-Temengor, Sungai Enam	KM024762	KM024895	KM024958
USMHC 1348	*Cnemaspis narathiwatensis*	Malaysia: Perak, Belum-Temengor, Sungai Enam	KM024763	–	–
USMHC 1349	*Cnemaspis narathiwatensis*	Malaysia: Perak, Belum-Temengor, Sungai Enam	KM024764	–	–
USMHC 1350	*Cnemaspis narathiwatensis*	Malaysia: Perak, Belum-Temengor, Sungai Enam	KM024765	KM024896	KM024959
LSUHC 8478	*Cnemaspis neangthyi*	Cambodia: Pursat Province, O'Lakmeas	KM024766	–	–
LSUHC 8515	*Cnemaspis neangthyi*	Cambodia: Pursat Province, O'Lakmeas	KM024767	KM024897	KM024960
LSUHC 8516	*Cnemaspis neangthyi*	Cambodia: Pursat Province, O'Lakmeas	KM024768	–	–
LSUHC 8517	*Cnemaspis neangthyi*	Cambodia: Pursat Province, O'Lakmeas	KM024769	KM024898	KM024961
LSUHC 9168	*Cnemaspis nigridia*	Malaysia: Sarawak, Gunung Gading	KM024770	KM024899	KM024963
LSUHC 9169	*Cnemaspis nigridia*	Malaysia: Sarawak, Gunung Gading	KM024771	–	–
LSUHC 9170	*Cnemaspis nigridia*	Malaysia: Sarawak, Gunung Gading	KM024772	KM024900	KM024962
LSUHC 9568	*Cnemaspis niyomwanae*	Thailand: Trang Province, Thum Khao Ting	KM024773	KM024901	KM024964
LSUHC 9571	*Cnemaspis niyomwanae*	Thailand: Trang Province, Thum Khao Ting	KM024774	–	–
LSUHC 8646	*Cnemaspis nuicamensis*	Vietnam: An Giang Province, Nui Cam Hill	KM024775	–	–
LSUHC 8647	*Cnemaspis nuicamensis*	Vietnam: An Giang Province, Nui Cam Hill	KM024776	KM024902	–
LSUHC 8648	*Cnemaspis nuicamensis*	Vietnam: An Giang Province, Nui Cam Hill	KM024777	–	–
LSUHC 8649	*Cnemaspis nuicamensis*	Vietnam: An Giang Province, Nui Cam Hill	KM024778	KM024903	KM024965
LSUHC 9978	*Cnemaspis omari* sp. nov.	Malaysia: Perlis, Perlis State Park	KM024779	KM024904	KM024966
LSUHC 9565	*Cnemaspis omari* sp. nov.	Thailand: Satun Province, Phuphaphet Cave	KM024780	–	–
LSUHC 9184	*Cnemaspis paripari*	Malaysia: Sarawak, Gua Pari-Pari	KM024781	–	–
LSUHC 9185	*Cnemaspis paripari*	Malaysia: Sarawak, Gua Angin	KM024782	KM024905	KM024967
LSUHC 9186	*Cnemaspis paripari*	Malaysia: Sarawak, Gua Angin	KM024783	KM024906	KM024968
LSUHC 9192	*Cnemaspis paripari*	Malaysia: Sarawak, Gua Angin	KM024784	–	–
LSUHC 8011	*Cnemaspis pemanggilensis*	Malaysia: Johor, Pulau Pemanggil	KM024785	–	KM024969
LSUHC 8012	*Cnemaspis pemanggilensis*	Malaysia: Johor, Pulau Pemanggil	KM024786	–	–
LSUHC 8013	*Cnemaspis pemanggilensis*	Malaysia: Johor, Pulau Pemanggil	KM024787	–	–
LSUHC 8014	*Cnemaspis pemanggilensis*	Malaysia: Johor, Pulau Pemanggil	KM024788	–	KM024970

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TABLE 1. (Continued)

Voucher number	Species	Locality	GenBank accession numbers		
			ND2	***MXRA5***	***RAG1***
LSUHC 3773	*Cnemaspis peninsularis* sp. nov.	Malaysia: Pahang, Pulau Tioman	KM024789	–	–
LSUHC 3797	*Cnemaspis peninsularis* sp. nov.	Malaysia: Pahang, Pulau Tioman	KM024790	–	–
LSUHC 3820	*Cnemaspis peninsularis* sp. nov.	Malaysia: Pahang, Pulau Tioman	KM024791	–	–
LSUHC 4707	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Tinggi	KM024792	–	–
LSUHC 4756	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Tinggi	KM024793	–	–
LSUHC 4958	*Cnemaspis peninsularis* sp. nov.	Malaysia: Pahang, Sungai Lembing	KM024794	–	–
LSUHC 5056	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Tulai	KM024795	–	–
LSUHC 5184	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Seribuat	KM024796	–	–
LSUHC 5185	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Seribuat	KM024797	–	–
LSUHC 5307	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Aceh	KM024798	–	–
LSUHC 5703	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Aceh	KM024799	–	–
LSUHC 6380	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Ibol	KM024800	–	–
LSUHC 6381	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Ibol	KM024801	–	–
LSUHC 5523	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Babi Besar	KM024802	–	–
LSUHC 5731	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Pulau Babi Besar	KM024803	–	–
LSUHC 8122	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Endau-Rompin, Selai	KM024805	KM024907	–
LSUHC 8126	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Endau-Rompin, Selai	KM024804	–	–
LSUHC 8910	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Gunung Panti Forest Reseve	KM024806	–	–
LSUHC 8965	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Gunung Ledang	KM024807	–	–
LSUHC 8966	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Gunung Ledang	KM024808	–	–
LSUHC 8967	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Gunung Ledang	KM024809	–	–
LSUHC 9376	*Cnemaspis peninsularis* sp. nov.	Malaysia: Terengganu, Pulau Tenggol	KM024810	KM024908	KM024971
LSUHC 9377	*Cnemaspis peninsularis* sp. nov.	Malaysia: Terengganu, Pulau Tenggol	KM024811	–	–
LSUHC 9380	*Cnemaspis peninsularis* sp. nov.	Malaysia: Terengganu, Pulau Tenggol	KM024812	–	–
LSUHC 9382	*Cnemaspis peninsularis* sp. nov.	Malaysia: Terengganu, Pulau Tenggol	KM024813	–	–
LSUHC 10238	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Gunung Berlumut	KM024814	–	–
LSUHC 10239	*Cnemaspis peninsularis* sp. nov.	Malaysia: Johor, Gunung Berlumut	KM024815	–	–
LSUHC 10454	*Cnemaspis peninsularis* sp. nov.	Singapore: Nee Soon Swamp	KM024816	–	–
HC 0226	*Cnemaspis peninsularis* sp. nov.	Malaysia: Pahang, Bukit Hangus	KM024817	–	–
HC 0228A	*Cnemaspis peninsularis* sp. nov.	Malaysia: Pahang, Bukit Hangus	KM024818	–	–
HC 0228B	*Cnemaspis peninsularis* sp. nov.	Malaysia: Pahang, Bukit Hangus	KM024819	–	–
LSUHC 8699	*Cnemaspis perhentianensis*	Malaysia: Terengganu, Pulau Perhentian Besar	KM024820	–	–
LSUHC 8700	*Cnemaspis perhentianensis*	Malaysia: Terengganu, Pulau Perhentian Besar	KM024821	KM024909	KM024972
LSUHC 9060	*Cnemaspis perhentianensis*	Malaysia: Terengganu, Pulau Perhentian Besar	KM024822	–	–
LSUHC 9412	*Cnemaspis perhentianensis*	Malaysia: Terengganu, Pulau Perhentian Besar	KM024823	–	–
LSUHC 9145	*Cnemaspis pseudomcguirei*	Malaysia: Perak, Bukit Larut	KM024824	KM024910	KM024973

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TABLE 1. Continued.

Voucher number	Species	Locality	GenBank accession numbers *ND2*	*MXRA5*	*RAG1*
LSUHC 9146	*Cnemaspis pseudomcguirei*	Malaysia: Perak, Bukit Larut	KM024825	KM024911	KM024974
LSUHC 9147	*Cnemaspis pseudomcguirei*	Malaysia: Perak, Bukit Larut	KM024826	–	–
LSUHC 9243	*Cnemaspis psychedelica*	Vietnam: Can Mau Province, Hon Khoai Island	KM024827	KM024912	–
LSUHC 9244	*Cnemaspis psychedelica*	Vietnam: Can Mau Province, Hon Khoai Island	KM024828	–	–
LSUHC 9430	*Cnemaspis roticanai*	Malaysia: Kedah, Pulau Langkawi, Gunung Raya	KM024829	–	–
LSUHC 9431	*Cnemaspis roticanai*	Malaysia: Kedah, Pulau Langkawi, Gunung Raya	KM024830	KM024913	–
LSUHC 9439	*Cnemaspis roticanai*	Malaysia: Kedah, Pulau Langkawi, Gunung Raya	KM024831	KM024914	KM024975
LSUHC 11015	*Cnemaspis selamatkanmerapoh*	Malaysia: Pahang, Merapoh, Gua Gunting	KM024832	KM024915	KM024976
LSUHC 11016	*Cnemaspis selamatkanmerapoh*	Malaysia: Pahang, Merapoh, Gua Gunting	KM024833	KM024916	KM024977
LSUHC 6773	*Cnemaspis shahruli*	Malaysia: Penang, Pulau Pinang	KM024834	–	–
LSUHC 9163	*Cnemaspis shahruli*	Malaysia: Penang, Pulau Jerejak	KM024835	KM024918	–
LSUHC 9586	*Cnemaspis shahruli*	Malaysia: Kedah, Sungai Sedim	KM024836	–	–
LSUHC 9613	*Cnemaspis shahruli*	Malaysia: Penang, Pulau Jerejak	KM024837	–	KM024978
LSUHC 10375	*Cnemaspis shahruli*	Malaysia: Kedah, Pulau Pinang	–	KM024917	–
LSUHC 9474	*Cnemaspis siamensis*	Thailand: Chumpon Province, Pathio	KM024838	KM024919	KM024979
LSUHC 9485	*Cnemaspis siamensis*	Thailand: Chumpon Province, Pathio	KM024839	KM024920	–
LSUHC 11089	*Cnemaspis stongensis* sp. nov.	Malaysia: Kelantan, Gunung Stong, Kem Baha	KM024840	KM024921	KM024980
LSUHC 11090	*Cnemaspis stongensis* sp. nov.	Malaysia: Kelantan, Gunung Stong, Kem Baha	KM024841	–	–
LSUHC 11091	*Cnemaspis stongensis* sp. nov.	Malaysia: Kelantan, Gunung Stong, Kem Baha	KM024842	KM024922	KM024981
LSUHC 5314	*Cnemaspis sundainsula* sp. nov.	Indonesia: Riau Province, Pulau Natuna Besar	KM024843	–	–
MZB.Lace 9436	*Cnemaspis sundainsula* sp. nov.	Indonesia: Riau Province, Pulau Natuna Besar, Gunung Ranai	KM024844	–	–
MZB.Lace 10156	*Cnemaspis sundainsula* sp. nov.	Indonesia: Riau Province, Pulau Natuna Besar, Ceruk Forest	KM024845	KM024923	KM024982
MZB.Lace 10157	*Cnemaspis sundainsula* sp. nov.	Indonesia: Riau Province, Pulau Natuna Besar, Ceruk Forest	KM024846	KM024924	KM024983
MZB.Lace 10158	*Cnemaspis sundainsula* sp. nov.	Indonesia: Riau Province, Pulau Natuna Besar, Ceruk Forest	KM024847	–	–
MZB.Lace 10160	*Cnemaspis sundainsula* sp. nov.	Indonesia: Riau Province, Pulau Natuna Besar, Gunung Air Hiu	KM024848	–	–
LSUHC 9160	*Cnemaspis temiah* sp. nov.	Malaysia: Pahang, Cameron Highlands, Tanah Rata	KM024849	KM024925	KM024984
LSUHC 9739	*Cnemaspis temiah* sp. nov.	Malaysia: Pahang, Cameron Highlands, Tanah Rata	KM024850	–	–
LSUHC 9816	*Cnemaspis temiah* sp. nov.	Malaysia: Pahang, Cameron Highlands, Tanah Rata	KM024851	–	KM024985
LSUHC 8631	*Cnemaspis tucdupensis*	Vietnam: An Giang Province, Tuc Dup Hill	KM024852	KM024926	KM024986
LSUHC 8632	*Cnemaspis tucdupensis*	Vietnam: An Giang Province, Tuc Dup Hill	KM024853	–	–
LSUHC 8633	*Cnemaspis tucdupensis*	Vietnam: An Giang Province, Tuc Dup Hill	KM024854	–	–
LSUHC 8634	*Cnemaspis tucdupensis*	Vietnam: An Giang Province, Tuc Dup Hill	KM024855	KM024927	KM024987

TABLE 2. A list of primers used for amplification and sequencing. (int)=internal used for sequencing only; cyc/temp= number of cycles/annealing temperature.

Gene	Primer name	Primer reference	Sequence	cyc/temp
ND2	L4437b	(Macey & Schulte, 1999)	5'-AAGCAGTTGGGCCCATACC-3'	33/48
	L5002	(Macey & Schulte, 1999)	5'-AACCAAACCCAACTACGAAAAAT-3'	
	CYRTINTF1(int)	(Siler *et al.*, 2010)	5'-TAGCCYTCTCYTCYATYGCCC-3'	
	CYRTINTR1(int)	(Siler *et al.*, 2010)	5'-ATTGTKAGDGTRGCYAGGSTKGG-3'	
MXRA5	MXRA5F2	(Portik *et al.*, 2011)	5'-KGCTGAGCCTKCCTGGGTGA-3'	35/66
	MXRA5R2	(Portik *et al.*, 2011)	5'-YCTMCGGCCYTCTGCAACATTK-3'	
RAG-1	R13	(Groth & Barrowclough, 1999)	5'-TCTGAATGGAAATTCAAGCTGTT-3'	35/56
	R18	(Groth & Barrowclough, 1999)	5'-GATGCTGCCTCGGTCGGCCACCTTT-3'	

TABLE 3. Selected and applied models of molecular evolution for data partitions determined by AIC for the phylogenetic analyses.

Gene	Models selected	Models applied
ND2		
1st pos	GTR+I+Γ	GTR+I+Γ
2nd pos	GTR+I+Γ	GTR+I+Γ
3rd pos	GTR+I+Γ	GTR+I+Γ
tRNAs	TrN+I+ Γ	HKY+I+Γ
MXRA5		
1st pos	HKY+Γ	HKY+Γ
2nd pos	TIM+I	HKY+Γ
3rd pos	K81uf+ Γ	GTR+I
RAG-1		
1st pos	K81uf+ Γ	GTR+ Γ
2nd pos	K81uf+ Γ	GTR+ Γ
3rd pos	TVM+ Γ	GTR+ Γ

Species accounts

Accounts for each species are presented in phylogenetic order based on Figure 2 from most basal to most derived. Accounts of previously described species are bolstered (in most cases) with data from additional specimens and observations. All accounts include information on the holotype and type locality, a diagnosis, a color pattern description, distribution, natural history (which includes previously published data modified and supplemented by additional observations), phylogenetic relationships, remarks (if necessary), and material examined subsequent to the original description. A synonymy of all names used is presented but only major references or commonly cited references are listed. If the account is a new species description, sections on the holotype, paratypes, variation, comparisons to other species, and etymology are included as well.

Results

Data from all three loci (ND2, MXRA5, and RAG1) were analyzed separately and the resulting trees were compared. ND2 was far superior at resolving relationships in the more shallow regions of the tree whereas these relationships were largely unresolved by the nuclear genes. However, ND2 was unable to resolve some of the basal relationships in deeper regions of the tree where both nuclear genes produced the same phylogenetic sequence among basal nodes.

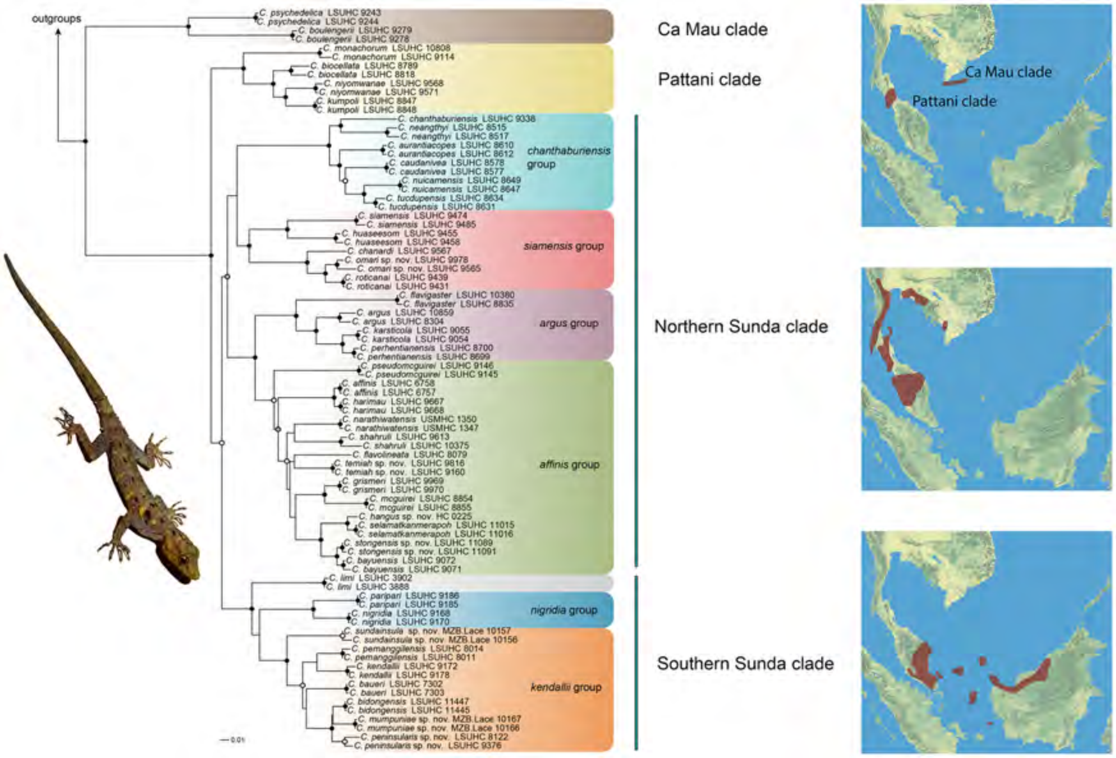

FIGURE 2. Maximum-likelihood phylogram (–In*L* 73957.608688) of the species of the genus *Cnemaspis* with Bayesian posterior probabilities (BPP) and maximum-likelihood (ML) bootstrap values, respectively based on the concatenated 3 gene dataset. Black circles are nodes supported by BBP and ML values greater than 0.95 and 70, respectively. Gray circles are nodes supported only by ML values greater than 70. White circles are nodes supported only by BPP values greater than 0.95. The distribution maps on the right delimit the ranges of the four major clades.

Only the following minor discrepancies in the shallow regions of the trees were uncovered between the three loci (see Fig. 2). Both nuclear genes supported the placement of *Cnemaspis neangthyi* Grismer, Grismer & Thou within a clade of Vietnamese species from the Mekong Delta 364 km to the east and MXRA5 further places one of the specimens within *C. siamensis* (Smith) from northern Thailand ca. 720 km to the west. However, ND2 supports the placement of *C. neangthyi* as the sister species to the nearby (25 km) *C. chanthaburiensis* Bauer & Das. Both nuclear genes also support the placement of *C. chanardi* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya from the central Thai-Malay Peninsula within this Vietnamese clade whereas ND2 strongly supports its relationship within a clade of other species from the same circumscribed region of southern Thailand. RAG1 indicates that *C. huaseesom* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya from western Thailand is paraphyletic with respect to *C. siamensis* (Smith) although MXRA5 and ND2 support its monophyly. MXRA5 places an individual of *C. peninsularis* sp. nov. from Pulau Tioman of the Seribuat Archipelago, Peninsular Malaysia as the sister species to *C. shahruli* Grismer, Chan, Quah, Muin, Savage, Grismer, Norhayati, Greer & Remegio from northwestern Peninsular Malaysia whereas RAG1 and ND2 place it with other *C. peninsularis* sp. nov. The nuclear genes were unable to resolve any relationships among the more shallow nodes within the *affinis* group although nearly all these nodes were supported by ND2 with the topology matching that of the concatenated tree (Fig. 2).

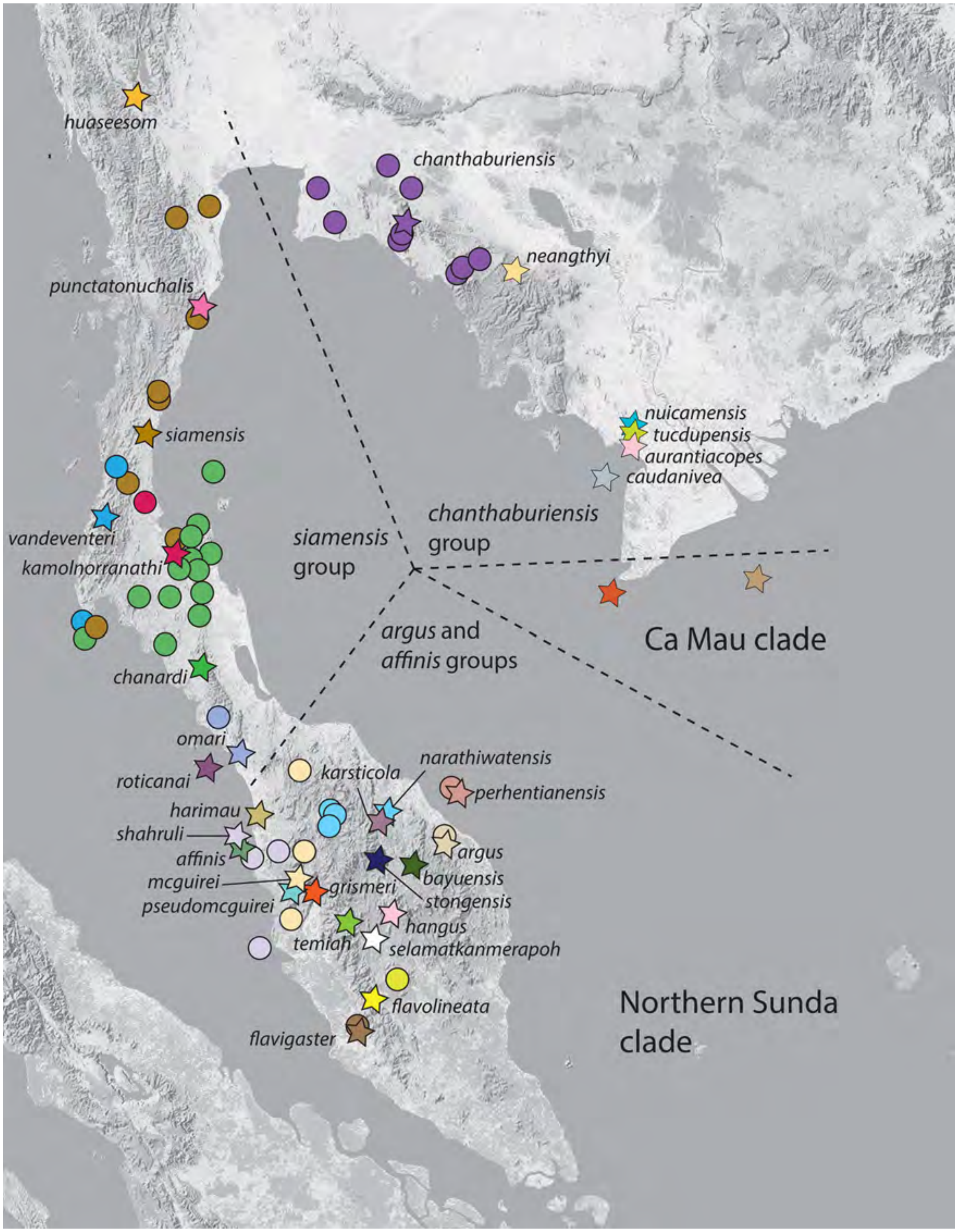

FIGURE 3. Distribution of the species and species groups in the Ca Mau and Northern Sunda clades. Stars indicate type localities.

In deeper regions of the tree, all genes supported the Ca Mau clade as basal to the remaining species of *Cnemaspis.* RAG1 supported *Cnemaspis limi* Das & Grismer as the sister species to the *nigridia* group from northwestern Borneo (Fig. 2) whereas ND2 supports it as the sister species to the *kendallii* group from southern

Peninsular Malaysia, Borneo, and Indonesia (Fig. 2). MXRA5 remained unresolved with respect to the placement of *C. limi*. All genes strongly supported the monophyly of the clades and species groups as designated herein as well as the relationships among the four species groups within the Northern Sunda clade (Fig. 2).

Because only minor discordances between the three loci were largely restricted to the placement of individual specimens in the more shallow regions of the trees, the data for all loci were concatenated to produce a single, multilocus tree (Fig 2). This tree mirrors the well-supported relationships for the basal nodes as indicated by the nuclear genes and the more shallow relationships revealed by ND2 and essentially bears the same topology as the ND2 tree. Even though the shallow relationships within the *affinis* group are not well-supported in the concatenated tree (Fig. 2), the topology is supported in the ND2 phylogeny.

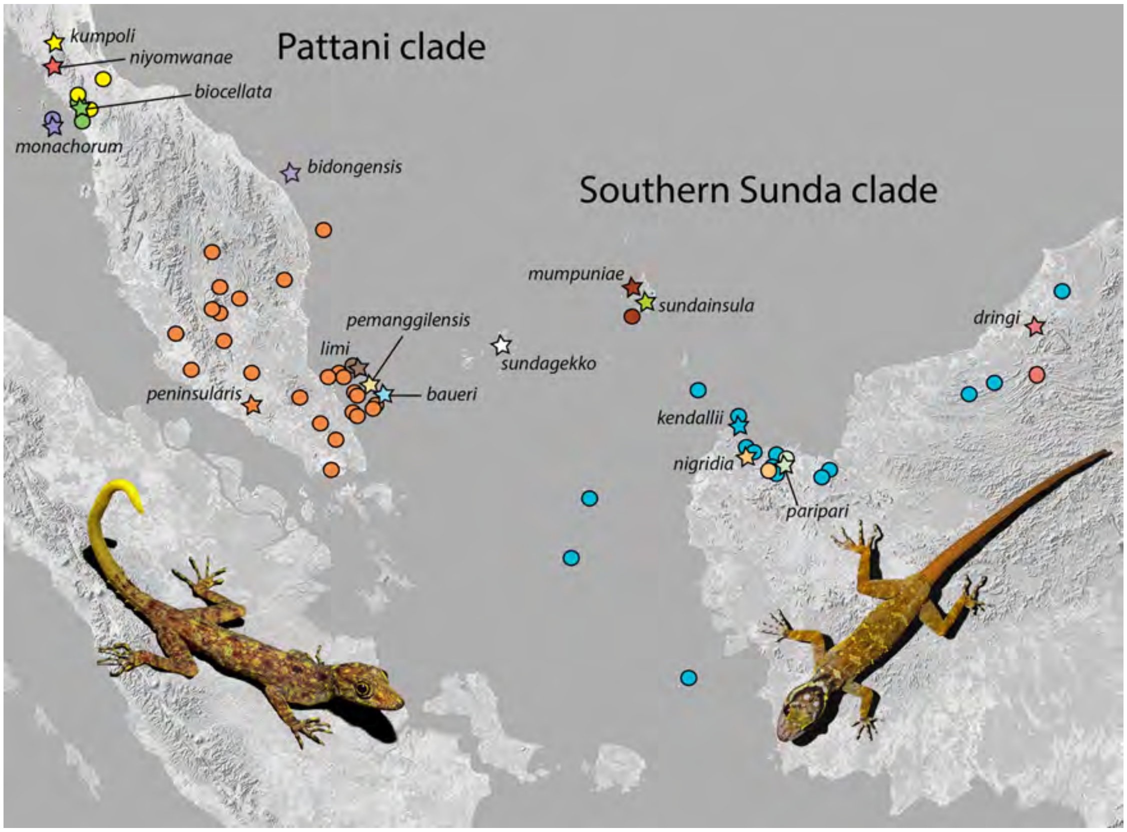

FIGURE 4. Distribution of the species in the Pattani and Southern Sunda clades. Stars indicate type localities.

The phylogenetic analyses indicate *Cnemaspis* is composed of two deeply divergent lineages: one containing the morphologically and behaviorally distinct southern Vietnamese insular endemics *C. boulengerii* Strauch and *C. psychedelica* Grismer, Ngo & Grismer referred to herein as the Ca Mau clade and the remaining species of *Cnemaspis* (Fig. 2). The remaining species form a well-supported lineage containing three major clades referred to as the Pattani, Northern Sunda, and Southern Sunda clades (Fig. 2) whose fragmented distribution along the northern, western and southern fringes of the Sunda Shelf extend from southern Vietnam, Cambodia and Thailand southward through the Thai-Malay Peninsula to Borneo (Figs. 2–4). The Pattani clade is basal to the Northern Sunda and Southern Sunda sister clades (Fig. 2) and restricted to the southernmost portion of peninsular Thailand. The Northern Sunda clade extends from Vietnam to central Peninsular Malaysia and composes a polytomy containing four well-supported, allopatric, species groups referred to as the *chanthaburiensis, siamensis, argus,* and *affinis* groups, the latter two being sister lineages (Figs. 2–4). The Southern Sunda clade is conservatively considered a polytomy composed of *C. limi* of the Seribuat Archipelago; the *nigridia* group with two species from northwestern Borneo; and the *kendallii* group containing seven species that extend from southern Peninsular Malaysia and Singapore, eastward through the Seribuat, Anambas, and Natuna Archipelagos to northern Borneo (Figs. 2,4).

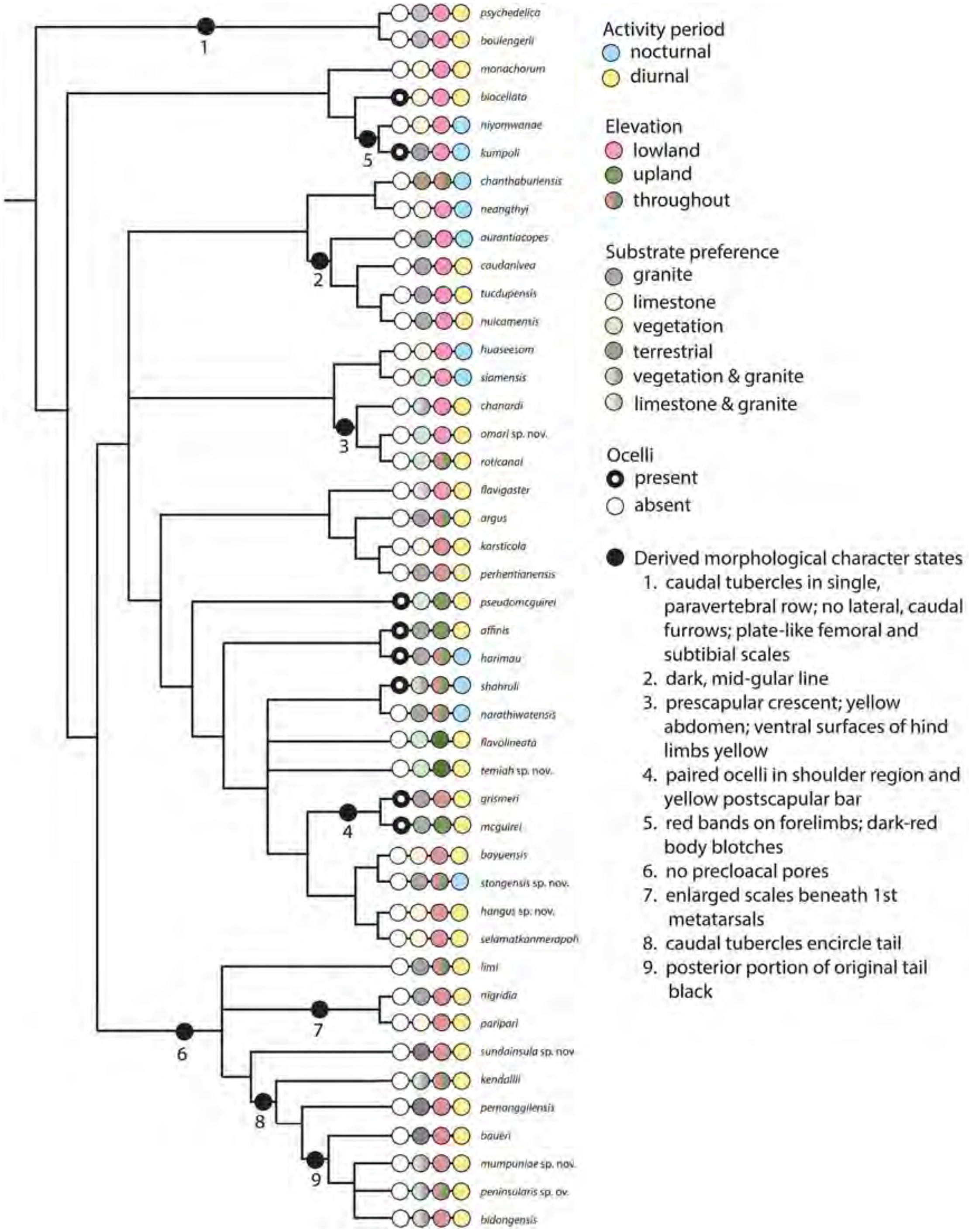

FIGURE 5. Ecological parameters of activity period, elevation (upland species are > 600 m in elevation), substrate preference (microhabitat), and the presence or absence of ocelli (eyespots) mapped onto the molecular phylogeny (Fig. 2) of the species of *Cnemaspis.* Nodes lacking significant statistical support in Figure 2 are collapsed here. Morphological and color pattern synapomorphies are indicated at the appropriate nodes and considered as additional support of the molecular phylogeny. These character states were polarized following the methodology of Maddison *et al.* (1984) and were not simply mapped onto the tree. Branch lengths do not represent genetic distance.

TABLE 4. Uncorrected *p*-distances for the genus *Cnemaspis* for the mithocondrial gene ND2 calculated in MEGAv5.2.2 (Tamura *et al*. 2011). Numbers in bold are within speceis divergence and non-bolded numbers are between species divergence.

	C. affinis	*C. argus*	*C. aurantiacopes*	*C. baueri*	*C. bayuensis*	*C. bidongensis*	*C. biocellata*	*C. boulengerii*	*C. caudanivea*	*C. chanardi*	*C. chanthaburiensis*	*C. flavigaster*	*C. flavolineata*	*C. grismeri*	*C. hangus* sp. nov.	*C. harimau*	*C. huaseesom*	*C. karsticola*	*C. kendallii*	*C. kumpoli*	*C. limi*	*C. mcguirei*
C. affinis	**0.000**																					
C. argus	0.213	**0.016**																				
C. aurantiacopes	0.265	0.268	**0.007**																			
C. baueri	0.253	0.251	0.271	**0.000**																		
C. bayuensis	0.167	0.201	0.285	0.280	**0.014**																	
C. bidongensis	0.206	0.206	0.216	0.160	0.230	**0.000**																
C. biocellata	0.211	0.237	0.223	0.280	0.231	0.204	**0.055**															
C. boulengerii	0.338	0.345	0.357	0.374	0.344	0.348	0.381	**0.005**														
C. caudanivea	0.211	0.268	0.170	0.253	0.259	0.216	0.244	0.343	**0.003**													
C. chanardi	0.216	0.205	0.201	0.222	0.216	0.191	0.220	0.348	0.249	–												
C. chanthaburiensis	0.258	0.268	0.211	0.289	0.278	0.232	0.266	0.384	0.187	0.268	–											
C. flavigaster	0.238	0.182	0.258	0.268	0.248	0.247	0.283	0.354	0.258	0.232	0.264	**0.003**										
C. flavolineata	0.258	0.205	0.284	0.284	0.194	0.263	0.296	0.376	0.314	0.222	0.294	0.228	–									
C. grismeri	0.157	0.186	0.259	0.263	0.133	0.216	0.220	0.316	0.234	0.191	0.286	0.228	0.189	**0.003**								
C. hangus sp. nov.	0.191	0.195	0.259	0.294	0.096	0.237	0.222	0.345	0.253	0.201	0.263	0.226	0.165	0.147	**0.000**							
C. harimau	0.041	0.208	0.270	0.258	0.177	0.222	0.211	0.343	0.206	0.227	0.258	0.238	0.258	0.157	0.191	**0.000**						
C. huaseesom	0.246	0.234	0.244	0.256	0.235	0.210	0.203	0.362	0.268	0.204	0.239	0.242	0.285	0.213	0.234	0.251	**0.003**					
C. karsticola	0.250	0.123	0.250	0.255	0.236	0.229	0.276	0.343	0.262	0.229	0.265	0.207	0.240	0.214	0.214	0.245	0.253	**0.005**				
C. kendallii	0.227	0.226	0.228	0.223	0.241	0.179	0.216	0.359	0.242	0.227	0.289	0.274	0.273	0.216	0.237	0.211	0.230	0.251	**0.008**			
C. kumpoli	0.242	0.214	0.244	0.247	0.215	0.186	0.158	0.374	0.265	0.232	0.247	0.254	0.278	0.214	0.222	0.232	0.179	0.255	0.206	**0.000**		
C. limi	0.228	0.228	0.258	0.236	0.238	0.195	0.230	0.338	0.254	0.226	0.264	0.224	0.246	0.220	0.218	0.218	0.226	0.259	0.218	0.223	**0.003**	
C. mcguirei	0.165	0.186	0.265	0.284	0.146	0.216	0.215	0.314	0.247	0.196	0.289	0.249	0.201	0.039	0.155	0.165	0.225	0.235	0.216	0.216	0.220	**0.000**
C. monachorum	0.221	0.241	0.271	0.248	0.239	0.246	0.180	0.352	0.264	0.218	0.277	0.281	0.285	0.215	0.228	0.221	0.238	0.256	0.257	0.212	0.255	0.231
C. mumpuniae sp. nov.	0.208	0.216	0.232	0.149	0.212	0.057	0.214	0.336	0.216	0.182	0.247	0.256	0.242	0.208	0.222	0.206	0.244	0.229	0.161	0.198	0.205	0.210
C. narathiawatensis	0.164	0.197	0.279	0.272	0.146	0.241	0.224	0.327	0.282	0.189	0.303	0.254	0.226	0.109	0.175	0.164	0.208	0.236	0.215	0.226	0.273	0.128
C. neangthyi	0.261	0.247	0.185	0.292	0.270	0.209	0.265	0.344	0.202	0.258	0.165	0.251	0.272	0.263	0.245	0.260	0.273	0.243	0.252	0.243	0.264	0.265
C. nigridia	0.225	0.186	0.227	0.271	0.218	0.216	0.196	0.329	0.249	0.216	0.259	0.259	0.261	0.201	0.194	0.225	0.220	0.226	0.220	0.198	0.165	0.206
C. niyomwanae	0.209	0.206	0.225	0.260	0.205	0.196	0.133	0.361	0.244	0.201	0.232	0.246	0.258	0.198	0.193	0.209	0.182	0.245	0.229	0.131	0.218	0.204
C. nuicamensis	0.216	0.253	0.175	0.268	0.266	0.206	0.237	0.353	0.204	0.242	0.186	0.269	0.273	0.240	0.258	0.227	0.277	0.240	0.261	0.237	0.287	0.242
C. omari sp. nov.	0.232	0.244	0.233	0.240	0.235	0.206	0.228	0.379	0.252	0.093	0.299	0.263	0.255	0.209	0.235	0.237	0.235	0.278	0.237	0.216	0.264	0.235
C. paripari	0.216	0.177	0.244	0.268	0.187	0.206	0.210	0.340	0.237	0.222	0.289	0.249	0.242	0.191	0.186	0.206	0.235	0.214	0.191	0.170	0.202	0.191
C. pemanggilensis	0.202	0.210	0.186	0.156	0.235	0.104	0.202	0.334	0.202	0.189	0.220	0.218	0.241	0.213	0.218	0.218	0.206	0.236	0.177	0.202	0.198	0.233
C. peninsularis sp. nov.	0.227	0.207	0.226	0.173	0.209	0.081	0.228	0.335	0.235	0.187	0.236	0.250	0.239	0.209	0.217	0.224	0.242	0.229	0.173	0.186	0.196	0.220
C. perhentianensis	0.214	0.116	0.263	0.276	0.231	0.235	0.265	0.335	0.270	0.235	0.284	0.189	0.235	0.219	0.209	0.219	0.253	0.052	0.246	0.250	0.241	0.235
C. pseudomcguirei	0.222	0.178	0.270	0.263	0.191	0.227	0.220	0.345	0.273	0.201	0.294	0.244	0.222	0.137	0.155	0.232	0.216	0.198	0.211	0.206	0.223	0.149
C. psychedelica	0.314	0.361	0.354	0.361	0.344	0.320	0.366	0.198	0.351	0.335	0.366	0.329	0.345	0.302	0.320	0.320	0.354	0.327	0.362	0.392	0.323	0.325
C. roticanai	0.206	0.229	0.232	0.227	0.211	0.186	0.222	0.379	0.244	0.098	0.273	0.263	0.258	0.191	0.227	0.206	0.235	0.271	0.238	0.227	0.249	0.222
C. selamatkanmerapoh	0.170	0.215	0.265	0.294	0.115	0.258	0.229	0.345	0.247	0.196	0.273	0.241	0.191	0.146	0.036	0.170	0.249	0.224	0.253	0.247	0.218	0.165
C. shahruli	0.153	0.205	0.279	0.256	0.185	0.235	0.206	0.342	0.242	0.206	0.304	0.253	0.246	0.127	0.195	0.158	0.260	0.225	0.241	0.224	0.253	0.147
C. siamensis	0.242	0.231	0.277	0.273	0.232	0.242	0.246	0.353	0.280	0.211	0.289	0.259	0.284	0.222	0.253	0.242	0.189	0.255	0.237	0.227	0.264	0.216
C. stongensis sp. nov.	0.151	0.186	0.275	0.284	0.022	0.216	0.215	0.332	0.242	0.198	0.273	0.238	0.192	0.117	0.084	0.162	0.225	0.219	0.227	0.210	0.235	0.131
C. sundainsula sp. nov.	0.263	0.223	0.285	0.216	0.273	0.186	0.256	0.340	0.258	0.232	0.253	0.238	0.263	0.253	0.242	0.247	0.254	0.214	0.232	0.253	0.213	0.268
C. temiah sp. nov.	0.170	0.133	0.265	0.263	0.146	0.211	0.211	0.345	0.263	0.186	0.278	0.218	0.180	0.124	0.139	0.170	0.241	0.193	0.227	0.201	0.228	0.139
C. tucdupensis	0.218	0.267	0.168	0.300	0.268	0.238	0.230	0.352	0.147	0.259	0.164	0.265	0.293	0.204	0.254	0.213	0.247	0.290	0.264	0.233	0.260	0.223

……*continued on the next page*

TABLE 4. (Continued)

	C. monachorum	*C. mumpuniae* sp. nov.	*C. narathiawatensis*	*C. neangthyi*	*C. nigridia*	*C. niyomwanae*	*C. nuicamensis*	*C. omari* sp. nov.	*C. paripari*	*C. pemanggilensis*	*C. peninsularis* sp. nov.	*C. perhentianensis*	*C. pseudomcguirei*	*C. psychedelica*	*C. roticanai*	*C. selamatkanmerapoh*	*C. shahruli*	*C. siamensis*	*C. stongensis* sp. nov.	*C. sundainsula* sp. nov.	*C. temiah* sp. nov.	*C. tucdupensis*
C. monachorum	**0.002**																					
C. mumpuniae sp. nov.	0.230	**0.034**																				
C. narathiawatensis	0.240	0.232	**0.003**																			
C. neangthyi	0.266	0.211	0.274	**0.095**																		
C. nigridia	0.233	0.220	0.227	0.261	**0.014**																	
C. niyomwanae	0.140	0.201	0.213	0.246	0.206	**0.010**																
C. nuicamensis	0.264	0.216	0.256	0.192	0.258	0.240	**0.000**															
C. omari sp. nov.	0.228	0.206	0.223	0.275	0.249	0.216	0.271	**0.031**														
C. paripari	0.212	0.186	0.215	0.253	0.149	0.198	0.258	0.222	**0.000**													
C. pemanggilensis	0.234	0.116	0.240	0.208	0.200	0.218	0.205	0.207	0.197	**0.006**												
C. peninsularis sp. nov.	0.230	0.075	0.236	0.206	0.215	0.198	0.219	0.206	0.194	0.120	**0.049**											
C. perhentianensis	0.261	0.236	0.231	0.248	0.221	0.245	0.237	0.278	0.209	0.236	0.233	**0.012**										
C. pseudomcguirei	0.197	0.225	0.164	0.271	0.191	0.193	0.268	0.214	0.175	0.223	0.218	0.193	**0.000**									
C. psychedelica	0.360	0.328	0.320	0.343	0.344	0.369	0.325	0.348	0.381	0.316	0.352	0.340	0.351	**0.000**								
C. roticanai	0.218	0.187	0.205	0.256	0.242	0.206	0.237	0.072	0.232	0.189	0.183	0.265	0.206	0.351	**0.000**							
C. selamatkanmerapoh	0.218	0.242	0.180	0.259	0.213	0.198	0.268	0.229	0.206	0.238	0.242	0.209	0.170	0.330	0.211	**0.000**						
C. shahruli	0.195	0.231	0.164	0.295	0.238	0.200	0.258	0.207	0.209	0.238	0.243	0.216	0.187	0.328	0.222	0.190	**0.024**					
C. siamensis	0.262	0.249	0.228	0.288	0.294	0.227	0.320	0.237	0.258	0.246	0.227	0.271	0.273	0.356	0.247	0.268	0.225	**0.000**				
C. stongensis sp. nov.	0.224	0.198	0.141	0.258	0.203	0.190	0.253	0.216	0.172	0.218	0.198	0.214	0.177	0.332	0.192	0.100	0.174	0.234	**0.003**			
C. sundainsula sp. nov.	0.236	0.180	0.262	0.235	0.220	0.255	0.289	0.260	0.206	0.174	0.199	0.229	0.211	0.335	0.247	0.253	0.258	0.278	0.263	**0.000**		
C. temiah sp. nov.	0.207	0.211	0.148	0.248	0.186	0.188	0.237	0.193	0.180	0.205	0.202	0.193	0.129	0.335	0.186	0.160	0.160	0.237	0.131	0.206	–	
C. tucdupensis	0.271	0.255	0.258	0.187	0.269	0.231	0.179	0.256	0.246	0.229	0.244	0.293	0.259	0.347	0.233	0.249	0.241	0.269	0.251	0.267	0.238	**0.003**

Taxonomy

The molecular analysis corroborates the latest morphological taxonomy proposed for *Cnemaspis* (Grismer *et al.* 2010a, 2013a; 2014; Wood *et al.* 2013) in that no paraphyletic or polyphyletic species had been described. The molecular analysis also supports the recognition of eight new species and a polyphyletic *C. kendallii*. These issues are addressed in the following species accounts. Additionally, all species groups are provided with morphological diagnoses.

Ca Mau clade

The Ca Mau clade composes the southern Vietnamese insular endemics *Cnemaspis boulengerii* and *C. psychedelica* from the Con Dao Archipelago and Hon Khoai Island, respectively, (Figs. 2, 3). Their remarkable color patterns aside, these species are unique among all other *Cnemaspis* in having caudal tubercles restricted to single paravertebral rows, no lateral caudal furrows, and plate-like femoral and subtibial scales. These character states are considered derived being that they do not occur in any other species of *Cnemaspis* nor any of the closely related outgroups. Additionally, Grismer *et al.* (2010b) reported that their behavior is quite atypical from that of other *Cnemaspis* in that they bask in sunlight and appear to be communal during evening hours. This behavior and their morphology prompted Grismer *et al.* (2010b) to consider these species closely related which is confirmed here by the molecular and morphological analyses (Figs. 2,5). The genetic divergence between the Ca Mau clade and the remaining species of *Cnemaspis* (37.6–39.2%; Table 4) is, in many cases, greater than that observed between other gekkonid genera (Gamble *et al.* 2012). However, we elect not erect a new genus for the 4821 remaining species of *Cnemaspis* (*C. boulengerii* Strauch being the type species) in order to maintain taxonomic stability as well as emphasize the monophyletic nature of these two major Southeast Asian lineages.

This clade is diagnosed as having a maximum SVL length of 69.0–75.3 mm; 7–10 supralabials; 5–8 infralabials; smooth ventral scales; no precloacal pores; 32–48 paravertebral tubercles; dorsal tubercles linearly arranged and present on flanks; caudal tubercles restricted to a single paravertebral row on each side; no lateral caudal furrows; subcaudals smooth, bearing an enlarged median row; one or two postcloacal tubercles on each side of tail base; enlarged femoral, subtibial and first metatarsal scales; subtibials smooth; 24–32 subdigital lamellae on fourth toe; and dorsal pattern on body, limbs, and tail lacking paired markings or bands.

FIGURE 6. Adult male *Cnemaspis boulengerii* (LSUDPC 8199) from Con Son Island in the Con Dao Archipelago, Ba-Ria-Vung Tau Province, Vietnam in the dark color pattern phase. Photograph by LLG.

FIGURE 7. *Cnemaspis boulengerii* from Con Son Island in the Con Dao Archipelago, Ba-Ria-Vung Tau Province, Vietnam. Upper left: adult female (LSUDPC 8219) in the dark color pattern phase. Upper right: adult female (LSUDPC 8200) in the light color pattern phase. Lower left: granite boulder microhabitat on Con Son Island. Lower right: juvenile (LSUDPC 8222) showing the more vivid, light-colored, paravertebral blotches. Photographs by LLG.

Cnemaspis boulengerii Strauch, 1887
Boulenger's Rock Gecko
Figs. 6,7

Gonatodes glaucus Smith 1920:95 (*fide* Smith 1935:76)
Cnemaspis boulengeri Smith 1935:76; Dring 1979:220; Darevsky 1990:128, 1999:34; Grismer *et al.,* 2010b:46

Holotype. Unknown. Type locality: Pulo Condore Island in the South China Sea now Con Dao Island, Ba Ria-Vung Province, Vietnam (*fide* Sang *et al.* 2009).

Diagnosis. Maximum SVL 69.0 mm; 8–10 supralabials; six or seven infralabials; smooth ventral scales; no precloacal pores; 32–38 paravertebral tubercles; tubercles linearly arranged especially on upper flanks; lateral caudal furrows absent, dorsal caudal furrow weak; caudal tubercles restricted to a single paravertebral row; subcaudals smooth, bearing a medial row of enlarged scales; one postcloacal tubercle on each side; smooth, enlarged, plate-like femoral and subtibial scales; enlarged submetatarsal scales on first toe; 25–32 subdigital fourth toe lamellae; dorsal surfaces unicolor tan; large, subcircular black spots on shoulders and nape; and thin, yellow reticulation on side of neck (Tables 6,7).

Color pattern (Figs. 6,7). Dorsal ground color brown to yellowish; dorsum unicolor except for large, black spots on nape, side of neck, and shoulders and a series of elongate, light colored, diffuse, vertebral markings extending onto caudal region and occasionally forming a weak, vertebral stripe; thin, yellowish reticulum on lateral surfaces of neck and in shoulder regions; ventral surfaces beige, immaculate. Light-colored, vertebral markings in juveniles more prominent, often bearing the typical butterfly shape seen in other species of *Cnemaspis*. At night the ground color lightens considerably and becomes a dull-yellow.

Distribution. *Cnemaspis boulengerii* is known only from Con Son and Hon Bay Canh islands, Ba Ria-Vung Tau Province, Vietnam of the Con Dao Archipelago, 185 km off the east coast of southern Vietnam (Darevsky 1990, 1999; Grismer *et al.* 2010b; Fig. 3). It is expected that *C. boulengerii* occurs on other islands of the archipelago.

Natural history. The Con Dao Archipelago contains 16 islands with Con Son Island being the largest and centrally located. Con Son is elongate, hilly, and reaches nearly 570 m in elevation. Much of the low-lying areas of the island are covered in disturbed forest but the rocky, higher elevations of the interior remain fairly intact (Fig. 7) and it is here we observed several specimens of *Cnemaspis boulengerii*. During the day, *C. boulengerii* is extremely abundant in lowland forest habitats and can be found climbing on both granite boulders and tree trunks in all planes of orientation. Many lizards were observed basking in dappled light on the tops of boulders and on tree trunks they were seen facing both head up and head down. Lizards were commonly observed in pairs or trios, only found in areas with boulders, and no lizards were observed on the ground. We believe the abundance of this species and its non-secretive nature (unlike that of nearly every other species of *Cnemaspis* we have observed) may be due to the fact that there are no other diurnal lizards with which to compete. The only other diurnal species observed in their habitat were the skinks *Eutropis multifasciata* (Kuhl) and *Scincella rufocaudata* (Darevsky & Nguyen). *Cyrtodactylus condorensis* (Smith), however, is common at night in the same microhabiats occupied by *C. boulengerii* during the day.

At night, *Cnemaspis boulengerii* was not seen on the tops of rocks or on the open faces of boulders but was observed only in rock cracks, on the undersides of rocky overhangs, and within caves. Here too, individuals are abundant and commonly found in pairs or trios. Rarely are lizards seen on trees at night and when they are, they are much more wary. Several gravid females carrying two eggs and tens of incubating eggs in communal laying sites in rock cracks and caves were found during August, indicating that this is the reproductive season. *Cnemaspis boulengerii* is very similar in all aspects of its behavior to its closest relative *C. psychedelica* (Grismer *et al.* 2010b).

Relationships. *Cnemaspis boulengerii* is the sister species of *C. psychedelica* (Fig. 2).

Material examined. Vietnam: Ria-Vung Tau Province, Con Dao Archipelago, Con Dao Island CAS 73745, LSUHC 9542, 9578–79, 11364, 11366–68, 11370, MCZ 39014-23, Pulo Condore (= Con Dao), Con Son Island, Vietnam.

Cnemaspis psychedelica **Grismer, Ngo & Grismer, 2010**

Psychedelic Rock Gecko
Fig. 8

Cnemaspis psychadelica Bauer 2013:42.

Holotype. UNS 0444. Type locality: "Hon Khoai Island, Ca Mau Province, Ngoc Hien District, Vietnam (08°26.098 N, 104°49.536 E)" at 30 m in elevation.

Diagnosis. Maximum SVL 75.3 mm; 7–10 supralabials; 5–8 infralabials; smooth ventral scales; no precloacal pores; 34–48 paravertebral tubercles; tubercles linearly arranged especially on flanks; lateral caudal furrows absent; caudal tubercles restricted to a single paravertebral row; subcaudals smooth, bearing a medial row of enlarged scales; one or two postcloacal tubercles on each side; smooth, enlarged, plate-like femoral and subtibial scales; enlarged submetatarsal scales on first toe; 24–28 subdigital fourth toe lamellae; occiput and nape bearing a dense, yellow reticulum; hands, feet, forelegs, forelimbs, lower flanks, and tail orange; transverse yellow bars on flanks; ground color of body, brachia, and thighs magenta (Tables 6,7).

Color pattern (Fig. 8). Dorsal ground color of head anterior to posterior margin of eyes greenish yellow; occipital region and nape bear a dense, bright-yellow reticulum overlaying thick, black streaks, some of which begin as thin, postorbital stripes; dorsal ground color of trunk and upper limbs immediately proximal to elbow and knee joints blue-gray to magenta; hands, feet, and distal portion of limbs bright-orange; ventral portion of flanks bright-orange bearing short, transverse, yellow bars; tail bright-orange; all ventral surfaces beige, generally immaculate except for faint stippling on throat and gular region. In alcohol, coloration is generally a uniform dark gray dorsally and beige ventrally, except for a slightly darker gular region.

FIGURE 8. *Cnemaspis psychedelica* from Hon Khoai Island, Ca Mau Province, Vietnam. Left: adult male (LSUDPC 5062) in the light color pattern phase. Upper right: adult male (LSUDPC 5070) in the dark color pattern phase. Lower right: granite boulder microhabitat on Hon Khoai Island. Photographs by LLG.

Distribution. *Cnemaspis psychedelica* is known only from Hon Khoai Island, Ngoc Hien District, Ca Mau Province, Vietnam in Rach Gia Bay 18 km off the southern tip of Point Can Mau (Grismer *et al.* 2010b; Fig. 3).

Natural history. Hon Khoai Island is a small (~8 km^2) island reaching approximately 320 m in elevation. It slopes moderately to the sea and lacks some of the precipitous, rocky bluffs characteristic of many of the nearby islands. Hon Khoai maintains a thick vegetative cover and is dominated by primary, semideciduous forest on its slopes and upper elevations with disjunct, mangrove swamps fringing its coastlines. Hon Khoai Island's granite basement gives rise to scattered, small to massive, boulder outcroppings across its lower elevations that provide the microhabitat for *Cnemaspis psychedelica* (Fig. 8). The vegetation surrounding the granite outcroppings is usually dense and composed of relatively small trees (Grismer *et al.* 2010b, 2011a).

Grismer *et al.* (2010b) noted that *Cnemaspis psychedelica* is a relatively large, robust, diurnal, lowland, saxicolous species. Lizards of both sexes and all size classes have been observed abroad on large, granite boulders in the shade of the forest canopy from 0800–1930 hrs. Some lizards were observed basking in filtered sunlight. Lizards would retreat into rock cracks, beneath ledges, or between rocks when threatened. Grismer *et al.* (2010b) noted it was common to see 2–5 lizards together on the same rock. Lizards showed no preference for any particular plane of orientation, be it vertical, horizontal, or inverted nor did they restrict their activity to only deeply shaded surfaces as do many other species of *Cnemaspis* (Chan & Grismer 2008; Das & Grismer 2003; Grismer & Chan 2008, 2009; Grismer & Das 2006; Grismer & Ngo 2007; Grismer *et al.* 2008a,b; 2009). During the evening hours from 1930 to 2400, lizards are not abundant, likely being displaced by the larger *Cyrtodactylus* sp. 1. At night, the coloration of this species is even more brilliant with the trunk becoming magenta (Fig. 8).

Relationships. *Cnemaspis psychedelica* is the sister species of *C. boulengerii* (Fig. 2).

Remarks. At the time of this writing (22 December 2013), noted Russian reptile dealers are selling illegally collected individuals of *Cnemaspis psychedelica* for 3500 euro/pair. Unfortunately, the discovery and description of this unique species on this tiny island may ultimately lead to its extinction owing to the wide-reaching criminal element in Southeast Asia. Owing to recent poaching, this species has been put on the IUCN list of threatened species, which ironically will probably increase their commercial value.

Material examined. Vietnam: Ca Mau Province, Ngoc Hien District, Hon Khoai Island LSUHC 9254–55, 9257–58, UNS 0444–49 (type series). Additional material examined subsequent to Grismer *et al.* (2010b): Vietnam: Ca Mau Province, Ngoc Hien District, Hon Khoai Island LSUHC 9524–53, 11007–12.

FIGURE 9. Adult male *Cnemaspis monachorum* (LSUDPC 6502) from Pulau Langgun of the Langkawi Archipelago, Kedah, Peninsular Malaysia in the dark color pattern phase. Photograph by LLG.

Pattani clade

The Pattani clade is a strongly supported (1.0/100), geographically circumscribed lineage composed of four species from southern Thailand and northwestern Peninsular Malaysia sandwiched between the biogeographic boundaries of the Isthmus of Kra in the north and the Kangar-Pattani Line in the south and embedded within the distribution of the Southern Indochina clade (Fig. 2). The basal species of this clade, *C. monachorum* Grismer, Norhayati, Chan, Belabut, Muin, Wood & Grismer, is an insular endemic known only from the Langkawi Archipelago of Malaysia. The sister lineage to *C. monachorum* comprises *C. biocellata* Grismer, Chan, Nurolhuda & Sumontha from the borderlands of Thailand and Malaysia and the sister species *C. niyomwanae* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya from southern Thailand and *C. kumpoli* Taylor from southern Thailand and extreme northwestern Peninsular Malaysia. The well-supported (0.99/93) sister species relationship between *C. niyomwanae* and *C. kumpoli* is further supported in that these are the only species of *Cnemaspis* to have the derived character states of red bands on their forelimbs and dark-red, dorsal blotches in males (Fig. 5). Three of the four species; *Cnemaspis monachorum, C. biocellata,* and *C. niyomwanae,* are small, diurnal, obligate karst-dwellers whereas the remaining species, *C. kumpoli,* is a much larger nocturnal species that inhabits granite boulders.

This clade is diagnosed in having a maximum SVL of 35.1–63.0; 6–11 supralabials; 5–9 infralabials; smooth ventral scales; 1–12 pore-bearing, precloacal scales with round pores; randomly arranged dorsal tubercles; 2–35 paravertebral tubercles; caudal tubercles not encircling the tail; smooth subcaudals bearing a medial row of enlarged scales; 1–3 postcloacal tubercles on either side of the tail base; no enlarged femoral, subtibial or submetatarsal scales; and 24–41 subdigital lamellae.

FIGURE 10. *Cnemaspis monachorum* (LSUDPC 6502) from the Langkawi Archipelago, Kedah, Peninsular Malaysia. Upper and middle left: ventral color pattern of male (upper; LSUDPC 8275) and female (middle; LSUDPC 8274) from Pulau Langgun. Photographs by ESHQ. Upper right: adult male (LSUDPC 4701) from Wat Wanaram, Pulau Langkawi in the dark color pattern phase. Lower left: adult female (LSUDPC 4846) from Wat Wanaram in the dark color pattern phase. Lower right: karst microhabitat on Pulau Langgun. Photographs by LLG.

Cnemaspis monachorum **Grismer, Norhayati, Chan, Belabut, Muin, Wood & Grismer, 2009**

Monks' Rock Gecko
Figs. 9,10

Holotype. ZRC 2.6774. Type locality: "Wat Wanaram, Pulau Langkawi, Kedah, Peninsular Malaysia (06° 20.275 N, 99°52.507 E)" at 35 m in elevation.

Diagnosis. Maximum SVL 35.1 mm; seven or eight supralabials; 5–7 infralabials; ventral scales smooth; three, contiguous, pore-bearing precloacal scales with round pores; 2–20 paravertebral tubercles; body tubercles randomly arranged, absent from flanks and lateral caudal furrows; no ventrolateral caudal tubercles; lateral row of caudal tubercles present anteriorly; caudal tubercles not encircling tail; subcaudals smooth bearing a medial row of enlarged scales; one or two postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials smooth; 24–30 subdigital fourth toe lamellae; gular region, throat, and abdomen in males yellow; faint, dark, lineate, mid-gular marking present (Tables 6,7).

TABLE 5. Uncorrected *p*-distances for the populations of *Cnemaspis peninsularis* sp. nov. for the mithocondrial gene ND2 calculated in MEGAv5.2.2 (Tamura *et al.* 2011). Numbers in bold are intrapopulational divergences and non-bolded numbers are interpopulational divergences.

	Bukit hangus	Gunung Berlumut	Pulau Tioman	Pulau Tinggi	Sungai Lembing	Pulau Tulai	Pualu Aceh	Pulau Seribuat	Pulau Babi Besar	Pulau Ibol	Selai	Gunung Panti	Gunung Ledang	Pulau Tenggol	Singapore
Bukit hangus	**0.003**														
Gunung Berlumut	0.057	**0.003**													
Pulau Tioman	0.050	0.045	**0.007**												
Pulau Tinggi	0.064	0.067	0.059	**0.038**											
Sungai Lembing	0.089	0.099	0.101	0.099	–										
Pulau Tulai	0.041	0.047	0.042	0.050	0.080	–									
Pualu Aceh	0.049	0.029	0.036	0.055	0.090	0.038	**0.002**								
Pulau Seribuat	0.075	0.074	0.072	0.080	0.072	0.058	0.069	**0.000**							
Pulau Babi Besar	0.045	0.043	0.026	0.052	0.095	0.037	0.033	0.067	**0.001**						
Pulau Ibol	0.052	0.054	0.046	0.025	0.090	0.039	0.042	0.070	0.036	**0.002**					
Selai	0.011	0.056	0.050	0.064	0.091	0.044	0.048	0.074	0.048	0.051	**0.002**				
Gunung Panti	0.044	0.053	0.047	0.049	0.081	0.033	0.040	0.065	0.039	0.035	0.046	–			
Gunung Ledang	0.044	0.052	0.048	0.051	0.079	0.031	0.045	0.063	0.042	0.040	0.045	0.029	**0.001**		
Pulau Tenggol	0.045	0.058	0.048	0.056	0.089	0.037	0.046	0.066	0.043	0.044	0.042	0.037	0.037	**0.009**	
Singapore	0.042	0.049	0.046	0.049	0.079	0.031	0.038	0.061	0.039	0.034	0.044	0.009	0.029	0.036	–

TABLE 6. Diagnostic morphological characters separating various species of *Cnemaspis* from one another. w =weak; ant = anterior; post = posterior; * = species that are not included in the molecular analysis; / = data unavailable.

	Ca Mau clade		**Pattani clade**				**Northern Sunda clade**														
							***chanthaburiensis* group**							***siamensis* group**							
	psychedelica	*boulengerii*	*monachorum*	*biocellata*	*niyomwanae*	*kumpoli*	*chanthaburiensis*	*neangthyi*	*laoensis**	*aurantiacopes*	*caudanivea*	*nuicamensis*	*tucdupensis*	*siamensis*	*huaseesom*	*chanardi*	*omari* sp. nov.	*roticanai*	*punctatonuchalis**	*vandeventeri**	*kamolnorranathi**
Maximum SVL	75.3	69.0	35.1	40.1	56.8	63.0	42.2	54.0	40.9	58.4	47.2	48.2	51.0	39.7	43.5	40.1	41.3	47.0	49.6	44.7	37.8
Supralabials	7–10	8–10	7,8	6–10	8–11	7–9	8–10	11–13	9	9–11	8,9	7–9	8–10	8,9	7–10	7–10	8,9	8,9	8	8,9	8,9
Infralabials	5–8	6,7	5–7	5–9	6–8	6–8	7–10	10–12	7	8–10	7,8	6–7	7–9	6–8	6–9	6–8	7,8	7,8	7,8	7–9	7,8
Ventral scales keeled (1) or smooth (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0,w
No. of precloacal pores	0	0	3	6–12	3	1–8	6–9	2	/	0	0–2	3–6	0	0	5–8	6–8	4	3–6	0	4	6,7
Precloacal pores continuous (1) or separated (0)	/	/	1	1	0,1	0	1	1	/	/	0	0	/	/	1	0	0	0	/	0	1
Precloacal pores elongate (1) or round (0)	/	/	0	0	0	0	0,1	0	/	/	0,1	0,1	/	/	0	0	0	0	/	0	1
No. of paravertebral tubercles	34–48	32-38	2–20	21–27	26–31	28–35	21–25	20–26	22	23-31	20–24	16-21	16–22	19–25	18–24	20–30	22–29	25–27	24–27	25–29	19–24
Tubercles linearly arranged (1) or more random (0)	1	1	0	0	0	0	1	1	0	1	1	1	w,1	0	w,0	0	w,0	0	w	0	w
Tubercles present (1) or absent (0) on lower flanks	1	1	0	1	0	1	1	1	1	1	0	1	1	1	1	1	w,1	1	1	0	1
Lateral caudal furrows present (1) or absent (0)	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	/	/	0	0	0	ant	1	1	1	0	0, ant	0, ant	0	0	1	0	0	1	0	0	1
Ventrolateral caudal tubercles anteriorly (1) or not (0)	0	0	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	0	1	0	0
Lateral caudal tubercle row present (1) or absent (0)	0	0	ant	ant	0	0	1	1	0	1	0, ant	0, ant	0	1	0	1	1	0	ant	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subcaudals keeled (1) or smooth (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	1	1
Single median row of keeled subcaudals (1) or smooth (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	w	w
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	1	1	1	1	1	1	0, post, w	1	w	1	0,w	1	w	1	0	1	0	w	1	1	w
No. of postcloacal tubercles in males	1,2	1	1,2	1	1,2	2,3	1–3	1	2,3	1,2	1,2	2–4	0-3	1,2	1,2	1	1	1,2	1–3	1–3	1,2
Enlarged femoral scales present (1) or absent (0)	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Subtibial scales keeled (1) or smooth (0)	0	0	0	0	0	0	0,1	1	1	1	0,w	0	0	1	0	1	1	1	0	1	0,1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	1	1	0	0	0	0	0	0	0	1	0,w	0	1	0	0	0	0	0	0	0	0
No. of 4th toe lamellae	24–28	25-32	24–30	29–37	31–34	34-41	22–29	22–25	29	27–31	23-30	27–33	26–32	24–26	21–31	25–30	25–28	26–29	29–31	24–28	24–28
Sample size	19	18	12	25.0	5	13	8	5	1	17	9	10	11	12	5	25	4	8	5	3	4

… …*continued on the next page*

TABLE 6. (Continued)

	Northern Sunda clade																
	***argus* group**				***affinis* group**												
	flavigaster	*argus*	*karsticola*	*perhentianensis*	*pseudomcguirei*	*harimau*	*affinis*	*shahruli*	*temiah* sp. nov.	*flavolineata*	*hangus* sp. nov.	*selamatkanmerapoh*	*stongensis* sp. nov.	*bayuensis*	*mcguirei*	*grismeri*	*narathiwatensis*
Maximum SVL	50.1	65.2	48.1	47.0	42.5	40.7	50.8	36.5	46.7	39.2	50.5	43.4	49.3	46.1	65.0	50.6	53.2
Supralabials	9,10	8,9	7,8	8–10	9,10	9,10	9–13	10,11	8–10	9	9	10	8–11	9,10	7–10	8	9,10
Infralabials	8–10	8,9	6,7	7–8	8–10	9,10	8–10	8–10	7–10	9	8	9,10	8–10	8,9	7–9	8	7–11
Ventral scales keeled (1) or smooth (0)	0	1	1	0,1	1	1	1	1	1	1	1	1	1	1	1	1	1
No. of precloacal pores	7,8	6–10	7,8	6–8	1–5	4	5,6	0	5–7	5,6	0	1	5–8	5–9	5–10	8–10	3–6
Precloacal pores continuous (1) or separated (0)	1	0,1	1	1	1	0	0	/	1	1	/	/	0	0	0,1	0	0
Precloacal pores elongate (1) or round (0)	0	0	0	0	0	0	0	/	0	0	/	0	0	0	0	0	0
No. of paravertebral tubercles	21–24	26–32	17–19	22–27	23–32	18–20	20–28	19–23	22–27	23	22–24	30	26–33	23–30	26–32	27–32	28–34
Tubercles linearly arranged (1) or more random (0)	0	0	0	0	0	0	0	0	0,w	1	0	w	0	0	0	0	0
Tubercles present (1) or absent (0) on lower flanks	1	1	1	1	1	1	1	1	0,1	0	w	w	1	1	1	1	0,1
Lateral caudal furrows present (1) or absent (0)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	0	0	0	0	1	1	0	1	1	1	0, ant	0	0,ant	0	1	1	1
Ventrolateral caudal tubercles anteriorly (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0	0,1	0	0	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	1	ant	1	1	1	1	ant	1	1	ant	1	1	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subcaudals keeled (1) or smooth (0)	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Single median row of keeled subcaudals (1) or smooth (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	0	1	0	0	0	ant	0	0	0	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
No. of postcloacal tubercles in males	1,2	1–4	2,3	3–4	2,3	2,3	2	1–3	2,3	2	2	3	2,3	2	2–5	2,3	1–3
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subtibial scales keeled (1) or smooth (0)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	1	0	0	0	0,1	0	0	0	0	0	0	0	0	0	0	0	0
No. of 4th toe lamellae	29–34	31–35	27–30	28–31	23–26	25–30	28,29	21–30	22–26	23	27–34	31–33	28–32	27–32	27–35	25–31	24–30
Sample size	7	5	5	9	9	10	7	11	7	2	2	2	10	4	19	10	11

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TABLE 6. (Conintued)

	Southern Sunda clade											
		nigridia **group**			***kendallii*** **group**							
	limi	*nigridia*	*paripari*	*dringi**	*kendallii*	*sundainsula* sp. nov.	*mumpuniae* sp. nov.	*pemanggilensis*	*baueri*	*bidongensis*	*peninsularis* sp. nov.	*sundagekko* sp. nov.*
Maximum SVL	88.2	75.5	50.7	46.4	58.4	84.5	60.9	76.0	67.4	58.1	60.0	68.0
Supralabials	8–12	10,11	12,13	11	10,11	8–11	9–12	10–13	11–13	9,10	10,11	11–13
Infralabials	7–10	9–11	10,11	9	8,9	7–10	8–11	8–10	8–12	7–9	7–10	8–11
Ventral scales keeled (1) or smooth (0)	w	w,1	1	1	1	1	1	1	1	1	1	1
No. of precloacal pores	0	10–16	2–6	5,6	0	0	0	0	0	0	0	0
Precloacal pores continuous (1) or separated (0)	/	0	0	0	/	/	/	/	/	/	/	/
Precloacal pores elongate (1) or round (0)	/	0	0	0	/	/	/	/	/	/	/	/
No. of paravertebral tubercles	25–35	39–43	26–31	25–27	18–26	26–37	18–25	30–37	18–27	21–26	17–25	20–25
Tubercles linearly arranged (1) or more random (0)	0	0,w	0	0	w	1	w,0	0	0	0	w,0	0,w
Tubercles present (1) or absent (0) on lower flanks	w	0	0	0	w,1	1	w,1	0,w	w,0	0	w,1	0,w
Lateral caudal furrows present (1) or absent (0)	1	1	1	1	1	1	1	1	1	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	0	1	0	0	1	1	1	1	1	1	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	1	1	1	1	1	1	1	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0	0
Subcaudals keeled (1) or smooth (0)	0	1	1	1	1	0	1	1	1	1	1	1
Single median row of keeled subcaudals (1) or smooth (0)	0	0	0	0	0	0	0	1	0	0	0	0
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	1	0	1	1	1	1	1	1
Enlarged median subcaudal scale row (1) or not (0)	w	1	1	1	0	0,w,post	1	1	1	1	0	post
No. of postcloacal tubercles in males	1,2	2–4	2	2	2	2–4	1,2	1,2	1,2	1,2	1,2	2,3
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0	0	0
Subtibial scales keeled (1) or smooth (0)	w	1	1	1	1	1	1	1	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	1	1	0	0	w,1	0	0	0	0	0	0
No. of 4th toe lamellae	29–36	26–29	26–31	32–35	25–33	25–29	29–35	27–34	26–32	26–30	27–33	33–38
Sample size	34	4	5	2	14	18	17	18	27	14	86	6

TABLE 7. Diagnostic color pattern characters separating various species of *Cnemaspis* from one another. Var = charcter variable; / = data unavailable.

	Ca Mau clade		**Pattani clade**				**Northern Sunda clade**																		
							***chanthaburiensis* group**							***siamensis* group**								***argus* group**			
	psychedelica	*boulengerii*	*monachorum*	*biocellata*	*niyomwanae*	*kumpoli*	*chanthaburiensis*	*neangthyi*	*laoensis**	*aurantiacopes*	*caudanivea*	*nuicamensis*	*tucdupensis*	*siamensis*	*huaseesom*	*chanardi*	*omari* sp. nov.	*roticanai*	*punctatonuchalis**	*vandeventeri**	*kamolnorranathi**	*flavigaster*	*argus*	*karsticola*	*perhentianensis*
Dorsal color pattern sexually dimorphic	no	no	no	yes	yes	yes	no	no	/	yes	no	no	no	no	yes	no	no	yes	yes	no	no	no	no	no	no
Ventral pattern sexually dimorphic	no	no	yes	yes	/	no	yes	no	/	yes	no	no	no	yes	yes	yes	/	yes	yes	yes	/	yes	no	no	no
Head yellow	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no
Reddish blotches on head and body	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Dense yellow reticulum on occiput and side of neck	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on occiput and nape	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on shoulder	no	no	no	yes	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Dual ocelli on shoulder	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on brachium and side of neck	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no
Thin, white, nuchal loop	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Large, black round spots on nape and anterior of body	no	yes	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Thin yellow reticulum on side of neck	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Yellowish, prescapular crescent	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	yes	yes	no	yes	var	no	no	no	no
Forelimbs yellow	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no
Hind limbs yellow	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no
Reddish blotches or bands on limbs	no	no	no	no	yes	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Forearms and forelegs orange	yes	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Dorsal ground color magenta	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Dorsal ground color reddish	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Uniform brown ground color	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Light vertebral stripe	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Yellow postscapular band	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Black, squarish, paired, paravertebral dorsal markings	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no
Small, light, round spots on flanks	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Black flanks with distinct yellowish spots	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Yellow or white bars on flanks	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Original tail yellow	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	var	no	no	no	no	no	no	no	no	no	no
Original tail orange	yes	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Regenerated tail yellow	no	no	no	no	no	no	no	no	/	no	/	no	no	no	no	no	no	yes	/	no	no	no	no	no	no
Regenerated tail orange	yes	no	no	yes	no	no	no	no	/	no	/	no	no	no	no	no	no	no	/	no	no	no	no	no	no
White, dorsal caudal tubercles	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Caudal bands present	no	no	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	yes	no	no	no	no
Wide black and yellow bands on tail	no	no	no	no	no	no	no	no	no	no	yes	no	yes	no	no	no	no	no	no	no	no	no	no	no	no
Thin, yellow caudal bands anteriorly	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Posterior portion of original tail white	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Posterior portion of original tail black	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no
Disticnt black and white caudal bands at least posteriorly	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	yes	no	yes
Gular region orange	no	no	no	no	no	no	yes	no	/	yes	no	no	yes	no	no	no	no	no	/	yes	no	no	no	no	no
Gular region yellow	no	no	yes	no	no	/	no	no	/	no	no	no	no	yes	yes	yes	yes	yes	/	no	no	no	no	no	no
Lineate gular markings	no	no	yes	no	no	no	no	no	/	yes	no	yes	no	yes	no	no	no	no	/	no	no	no	no	no	no
Throat yellow	no	no	yes	no	no	/	no	no	/	no	no	no	no	yes	yes	no	no	no	no	no	no	no	no	no	no
Throat orange	no	no	no	var	no	no	yes	no	/	yes	no	no	yes	no	no	no	no	no	yes	no	no	no	no	no	no
Pectoral region yellow	no	no	yes	no	no	/	no	no	/	no	no	no	no	yes	yes	no	no	yes	/	no	no	no	no	no	no
Pectoral region orange	no	no	no	var	no	no	no	no	/	yes	no	no	yes	no	no	no	no	no	/	var	no	yes	no	no	no
Abdomen yellow	no	no	yes	var	no	/	no	no	/	no	no	no	no	no	no	yes	yes	yes	/	no	no	no	no	no	no
Abdomen orange	no	no	no	var	no	no	yes	no	/	yes	no	no	yes	no	no	no	no	no	/	yes	no	yes	no	no	no
Ventral surfaces of forelimbs orange	no	no	no	no	no	no	no	no	/	yes	no	no	yes	no	no	no	no	no	/	yes	no	no	no	no	no
Ventral surfaces of forelimbs yellow	no	no	no	no	no	no	no	no	/	no	no	no	no	no	yes	no	no	no	/	no	no	no	no	no	no
Ventral surfaces of hind limbs orange	no	no	no	var	no	no	no	no	/	yes	no	no	yes	no	no	no	no	no	/	yes	no	yes	no	no	no
Ventral surfaces of hind limbs yellow	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	yes	yes	yes	/	no	no	no	no	no	no
Subcaudal region yellow	no	no	no	var	no	no	no	no	/	no	no	no	no	no	yes	yes	yes	yes	no	no	no	no	no	no	no
Subcaudal region orange	no	no	no	var	no	no	yes	no	/	no	no	yes	no	no	no	no	no	no	yes	yes	no	yes	no	no	no
At least posterior half of subcaudal region white	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	yes	no

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TABLE 7. (Continued)

	Northern Sunda clade													**Southern Sunda clade**											
	***affinis* group**														***nigridia* group**			***kendallii* group**							
	pseudomcguirei	*harimau*	*affinis*	*shahruli*	*temiah* sp. nov.	*flavolineata*	*hangus* sp. nov.	*selamatkanmerapoh*	*stongensis* sp. nov.	*bayuensis*	*mcguirei*	*grismeri*	*narathiwatensis*	*limi*	*nigridia*	*paripari*	*dringi**	*kendallii*	*sundainsula* sp. nov.	*mumpuniae* sp. nov.	*pemanggilensis*	*baueri*	*bidongensis*	*peninsularis* sp. nov.	*sundagekko* sp. nov.*
Dorsal color pattern sexually dimorphic	yes	yes	yes	yes	no	no	no	no	no	no	yes	yes	yes	no	no	yes	/	no	no	no	no	no	yes	yes	/
Ventral pattern sexually dimorphic	no	yes	no	yes	no	no	no	no	no	no	no	no	no	no	no	yes	/	no	yes	no	no	no	no	yes	/
Head yellow	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no
Reddish blotches on head and body	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Dense yellow reticulum on occiput and side of neck	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on occiput and nape	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on shoulder	no	yes	yes	yes	no	no	no	no	no	no	yes	yes	yes	no	no	no	no	no	no	no	no	no	no	no	no
Dual ocelli on shoulder	yes	no	no	no	no	no	no	no	no	no	yes	yes	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on brachium and side of neck	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Thin, white, nuchal loop	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no
Large, black round spots on nape and anterior of body	no	no	no	no	no	yes	no	no	no	no	no	no	no	yes	yes	no	no	no	no	no	no	yes	yes	no	yes
Thin yellow reticulum on side of neck	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no
Yellowish, prescapular crescent	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Forelimbs yellow	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no
Hind limbs yellow	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no
Reddish blotches or bands on limbs	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Forearms and forelegs orange	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Dorsal ground color magenta	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
dorsal ground color reddish	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no
Uniform brown ground color	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no
Light vertebral stripe	var	no	no	var	var	var	no	no	no	no	no	no	var	no	no	no	no	no	no	no	no	no	no	no	no
Yellow postscapular band	no	var	var	no	no	no	no	no	no	no	yes	yes	no	no	no	no	no	no	no	no	no	no	no	no	no
Black, squarish, paired, paravertebral dorsal markings	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Small, light, round spots on flanks	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	yes	yes	yes	no	no	no	no
Black flanks with distinct yellowish spots	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Yellow or white bars on flanks	yes	yes	yes	no	no	no	no	no	yes	yes	yes	yes	yes	no	yes	no	no	no	no	no	no	no	no	no	no
Original tail yellow	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Original tail orange	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Regenerated tail yellow	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	yes	no	no	no	yes	no	no	no	yes	/
Regenerated tail orange	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no
White, dorsal caudal tubercles	no	no	no	yes	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	yes	no	no	yes
Caudal bands present	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Wide black and yellow bands on tail	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no
Thin, yellow caudal bands anteriorly	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no
Posterior portion of original tail white	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no
Posterior portion of original tail black	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	yes	no	yes	no
Disticnt black and white caudal bands at least posteriorly	no	yes	no	var	no	no	no	no	yes	no	yes	yes	yes	no	no	no	/	yes	no	no	no	no	yes, f	no	yes
Gular region orange	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Gular region yellow	no	yes	yes	yes	no	no	no	no	no	no	no	no	no	no	no	no	/	no	yes	no	no	no	no	no	no
Lineate gular markings	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Throat yellow	no	yes	/	yes	no	no	no	no	no	no	no	no	no	no	no	no	/	no	yes	no	no	no	no	no	no
Throat orange	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Pectoral region yellow	no	no	/	yes	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Pectoral region orange	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Abdomen yellow	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	yes	no	no	no	no	no	no
Abdomen orange	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Ventral surfaces of forelimbs orange	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Ventral surfaces of forelimbs yellow	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Ventral surfaces of hind limbs orange	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Ventral surfaces of hind limbs yellow	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
Subcaudal region yellow	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	yes	no	no	no	no	no	no
Subcaudal region orange	no	no	/	no	no	no	no	no	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no
At least posterior half of subcaudal region white	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	yes	no	yes	yes	no	no	no	no	no	no

Color pattern in life (Figs. 9,10). Dorsal ground color brown; head, body, and limbs overlain with small, irregularly shaped, somewhat randomly arranged, black and cream colored spots varying somewhat in size; light dorsal blotches in general paravertebral arrangement; markings on top of head smaller than those on body; dark markings in caudal region tend to form bands that encircle tail; anterior gular region yellowish, most pronounced on mental scale; faint, dark, midgular stripe present; pectoral region and anterior, abdominal region orangish yellow; remainder of ventral surfaces of body and limbs beige bearing faint, dark, stippling.

Distribution. *Cnemaspis monachorum* is known only from the Langkawi Archipelago where it inhabits the islands of Langkawi (Grismer *et al.* 2009) and reported here for the first time from the smaller satellite island of Langgun (Fig. 4).

Natural history. On Pulau Langkawi, Grismer (2011a) noted that *Cnemaspis monachorum* is a lowland, saxicolous species known only from the karst outcropping of Wat Wanaram near the town of Kuah in a region dominated by a mixture of primary coastal and lowland dipterocarp forest. *Cnemaspis monachorum* is a small, swift, agile species abroad only during the day, climbing on the fragmented boulders along the periphery of karst formations as well as along the base of karst cliffsides near the edges of cracks. Lizards are wary and will rapidly retreat into a crack while curling their tail above their back and waving it from side to side. During the night, lizards are not abroad and only occasionally observed deep within limestone cracks. *Cnemaspis monachorum* is the smallest species of *Cnemaspis* and possibly associated with this small size is that gravid females carry only a single egg whereas females of all other *Cnemaspis* carry two eggs. Gravid females have been observed in October. On Pulau Langgun, *C. monachorum* is also diurnal and common throughout the island on the limestone rocky hillsides as well as the cliff faces that edge Tasik (lake) Langgun (Fig. 10). During August, no gravid females were found on Pulau Langgun suggesting that October may be the beginning of the reproductive season.

Relationships. *Cnemaspis monachorum* is the basal lineage of the Pattani clade (Fig. 2).

Material examined. Malaysia: Kedah; Pulau Langkawi LSUHC 9118, ZRC 2.6774–76 (type series). Material examined since Grismer *et al.* (2009): Malaysia: Kedah; Pulau Langkawi LSUHC 9115–17; Pulau Langgun LSUHC 10807–11.

Cnemaspis biocellata Grismer, Chan, Nurolhuda & Sumontha, 2008

Twin-spot Rock Gecko
Figs. 11,12

Holotype. ZRC 2.66693. Type locality: "Kuala Perlis, Perlis, Peninsular Malaysia (06°24.437N, 100°08.564E) at 37 m in elevation.

Diagnosis. Maximum SVL 40.1 mm; 6–10 supralabials; 5–9 infralabials; ventral scales smooth; 6–12 contiguous, pore-bearing precloacal scales with round pores; 21–27 paravertebral tubercles; body tubercles randomly arranged, present on flanks, absent from lateral caudal furrows; no ventrolateral caudal tubercles; lateral row of caudal tubercles present anteriorly; caudal tubercles not encircling tail; subcaudals smooth bearing a median row of enlarged scales; one postcloacal tubercle on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials smooth; 29–37 subdigital fourth toe lamellae; paired ocelli on occiput in males; wide, white to yellow nuchal loop in males; single ocellus in shoulder region in males; original tail yellow and regenerated tail orange in males; and throat, pectoral region, ventral surface of hind limbs, abdomen, and subcaudal region orange or yellow in males (Tables 6,7).

Color pattern in life (Figs. 11,12). Adult males: ground color of dorsal surface of head, body, limbs, and tail dull yellow; rostrum grayish with faint, light markings highlighting bright yellow, anterior, extra brillar fringe; interorbital region yellow with two, distinct, white, immaculate, well-defined occipital ocelli; ocelli accentuated by wide, black, occipital band forming anterior border of a series of closely spaced, large, white to yellow spots forming a nuchal band extending from posterior margin of one eye to posterior margin of other eye; small, black, shoulder patch enclosing a single, white to yellow ocellus; body overlain by five yellow, butterfly-shaped, vertebral blotches extending from shoulder region to base of tail; small, faint yellow blotches on flanks and limbs; blotches tend to form caudal bands; ventral surfaces yellow or orange, nearly immaculate with only a faint amount of subcaudal mottling. Adult females: ground color of dorsal surfaces light brown lacking black occipital and shoulder markings of males; occiput bears faint, straw colored, ocelli homologous to those in males; poorly defined, straw colored, butterfly-shaped, vertebral markings extend from nape to base of tail continuing posteriorly to form poorly defined, caudal bands; small, irregularly shaped, faint spots on flanks and limbs; and ventral surfaces beige, nearly immaculate with only faint, subcaudal mottling.

FIGURE 11. *Cnemaspis biocellata* from Perlis, Peninsular Malaysia. Upper left and right: adult male (LSUDCP 4231) in the dark color pattern phase and adult female (LSUDPC 4230) in the light color pattern phase, respectively, from Gua Kelam. Lower right: adult male (LSUDPC 4233) in the dark color pattern phase from Kuala Perlis. Middle left: adult female (LSUDPC 5949) in the dark color phase from Wang Kelian. Photographs by LLG. Lower left: adult male (LUSDPC 6247) from Perlis State Park in the dark color pattern phase. Photograph by ESHQ.

Distribution. *Cnemaspis biocellata* extends through the karst system of the Banjaran Nakawan from Thale Ban National Park, Satun Province, Thailand southward through Wang Kelian and Perlis State Park to Gua Kelam, Tasik Meranti, Kampung Bukit Cabang, and Kuala Perlis, Perlis in northern Peninsular Malaysia (Grismer 2011a; Fig. 4).

Natural history. Grismer (2011a) noted that *Cnemaspis biocellata* occurs in lowland areas from near sea level to approximately 200 meters in elevation and appears to be a karst-substrate specialist. Lizards have been observed on trees and cement walls (Fig. 11) but only where they were adjacent to a karst formation. *Cnemaspis biocellata* is often observed abroad during the day on the shaded, vertical surfaces of karst walls and boulders as well as within crevice microhabitats and beneath small limestone rocks piled on the ground. During the day, lizards are wary and difficult to approach and will retreat into nearby crevice microhabitats at the slightest provocation. At night, lizards move farther away from these retreats and are more approachable. At Gua Kelam, Perlis the habitat is highly disturbed and continually frequented by visitors to the neighborhood park yet *C. biocellata* are abundant and easily observed both day and night. At Tasik Meranti, Perlis, lizards occur on large karst rocks in lowland dipterocarp forest but restrict their daytime activities to shaded areas. At Wang Kelian, they are abroad only during the day, perhaps due to the presence of the much larger *Cyrtodactylus astrum* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Norhayati, Bauer, Wangkulangkul, Grismer & Pauwels and *Gekko gecko* Linnaeus at night which may even prey on them. At Kampung Bukit Cabang, lizards have been found at night within caves. At Kuala Perlis, lizards are abundant during the day and night on karst formations in the vicinity of parks, parking lots, and housing communities in areas with no immediate native vegetation. These observations suggest that the most important environmental component for this species is the karst substrate and the microhabitats it offers, regardless of the condition of the surrounding forest. This small species is amazingly quick and agile and effortlessly moves from one inclined surface to another. Upon capture, lizards release large sections of their skin in much the same manner as the Stump-tailed Gecko, *Gehyra mutilata* (Wiegmann). *Cnemaspis biocellata* is the second smallest species of *Cnemaspis* and females carrying one or two eggs have been observed only during March.

Relationships. *Cnemaspis biocellata* is a member of the Pattani clade and most closely realeted to the sister species *C. niyomwanae* and *C. kumpoli* (Fig. 2).

Material examined. Malaysia: Perlis, Kuala Perlis ZRC 2.6693–98 (type series). Specimens examined since Grismer *et al.* (2008a): Malaysia: Perlis, Gua Kelam LSUHC 8787–92, 8802, 8804–05, 9682. Kampung Bukit Chabang LSUHC 9683–84.

FIGURE 12. *Cnemaspis biocellata* from Perlis, Peninsular Malaysia. Upper right; adult female (LSUDPC 4229) from Gua Kelam in the light color pattern phase. Lower right: variation in ventral coloration in adult males from Bukit Cabang (LSUDPC 5338). Left: karst microhabitat at Wang Kelian. Photographs by LLG.

Cnemaspis niyomwanae **Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya, 2010a**

Niyomwan's Rock Gecko
Fig. 13

Holotype. THNHM 15910. Type locality: "Thum Khao Ting, Palean District, Trang Province, Thailand (07°09.943N, 99°48.142E) at 28 m in elevation."

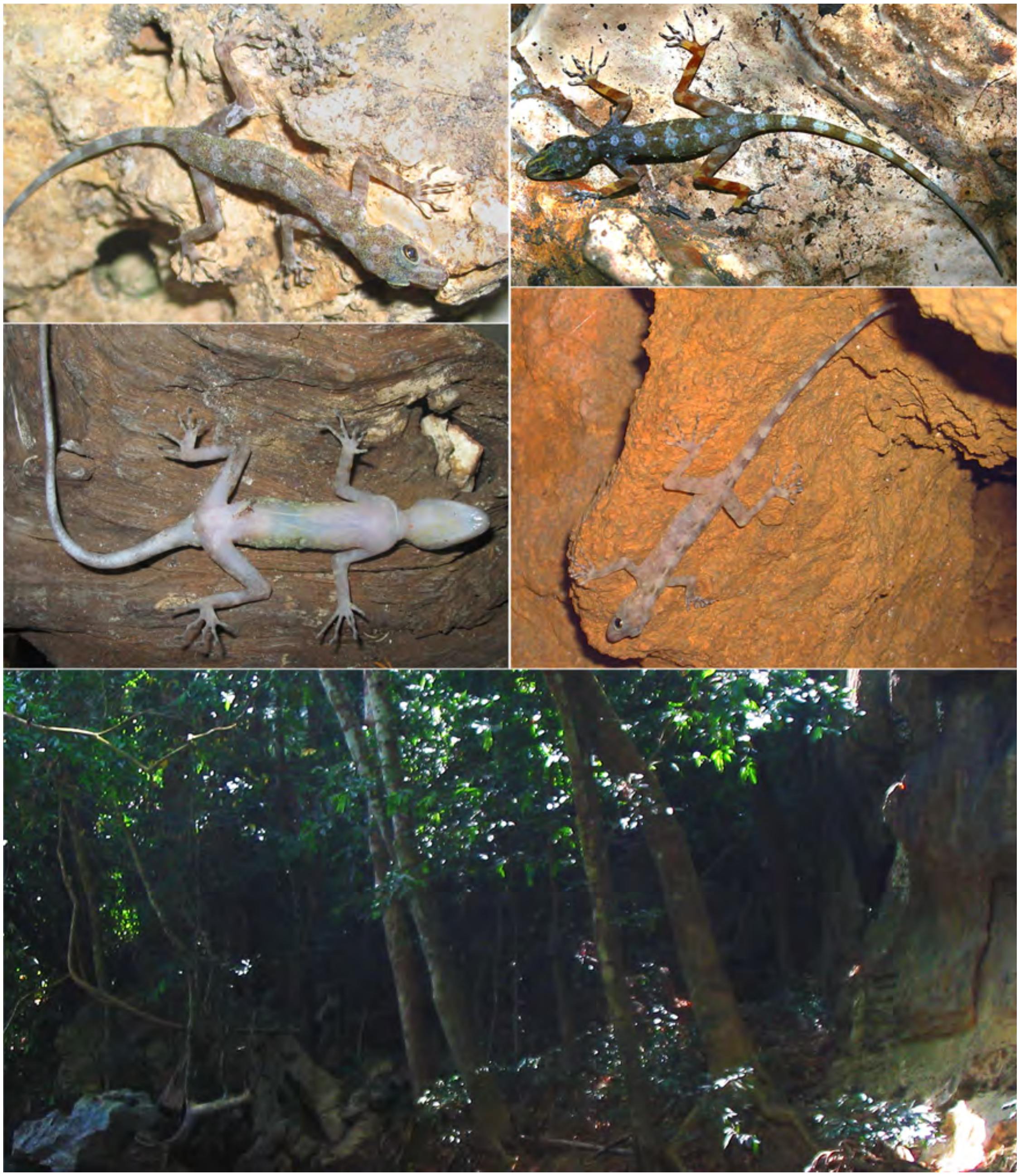

FIGURE 13. *Cnemaspis niyomwanae* from Thum Khao Ting, Palean District, Trang Province, Thailand. Upper left: adult female (LSUDPC 7035) in the light color pattern phase. Upper right: adult male (LSUDPC 7032) in the dark color pattern phase. Middle left: ventral coloration of adult female (LSUDPC 7036) which is the same as adult males. Middle right: subadult (LSUDPC 7034) in the light color pattern phase. Lower: habitat at Thum Khao Ting. Photographs by MS.

Diagnosis. Maximum SVL 56.8 mm; 8–11 supralabials; 6–8 infralabials; ventral scales smooth; three usually contiguous, pore-bearing precloacal scales with round pores; 26–31 paravertebral tubercles; body tubercles randomly arranged, absent from flanks and from lateral caudal furrows; no ventrolateral caudal tubercles; no lateral row of caudal tubercles; caudal tubercles not encircling tail; subcaudals smooth bearing a median row of enlarged scales; one or two postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials smooth; 31–34 subdigital fourth toe lamellae; and reddish bands on limbs in males (Tables 6,7).

Color pattern in life (Fig. 13). Dorsal ground color of head, body, and tail faded green; dorsal ground color of limbs faded brown; yellow stripe on each canthus rostralis; diffuse, light, paired, occipital blotches present; faint, light mottling on sides of head; whitish, medial blotch on nape followed posteriorly by five, lightly colored, paravertebral, butterfly-shaped markings between forelimb insertions and base of tail; markings continue onto tail to form lightly colored bands; enlarged, white tubercles on sides of neck, shoulders and flanks; other tubercles on body dark or lightly colored; faint, reddish dorsal blotches on body; upper regions of limbs bearing diffuse light mottling; alternating red and yellow bands on forelimbs and forelegs; digits white bearing broad, brown bands; all ventral surfaces except subcaudal region of uniform beige with fine, dark stippling in some scales; and subcaudal region grayish.

Distribution. *Cnemaspis niyomwanae* is known only from the border regions of Trang and Satun Provinces, Thailand (Fig. 4).

Natural history. Very little is known about the life history of *Cnemaspis niyomwanae.* Grismer *et al.* (2010a) reported that it occurs in lowland karst areas in the vicinity of small streams (Fig. 13) and that it is abroad at night. During the day, lizards retreat into limestone crevices and caves.

Relationships. *Cnemaspis niyomwanae* is a member of the Pattani clade and the sister species of *C. kumpoli* Taylor (Fig. 2).

Material examined. Thailand: Trang Province, Palean District, Thum Khao THNHM 15910. La-ngu District, Baan Man Pud CUMZ R-2009, 6,24-10, KZM 008, PSUZC-RT 2010.56, ZMKU Re-000315. These specimens represent the type series.

Cnemaspis kumpoli Taylor, 1963

Kumpol's Rock Gecko
Fig. 14

Holotype. FMNH 178268. Type locality: "Khao Chong, Forestry Experimental Station, Trang province, Thailand."

Diagnosis. Maximum SVL 63.0 mm; 7–9 supralabials; 6–8 infralabials; ventral scales smooth; 1–8, discontinuous, pore-bearing precloacal scales with round, poorly developed pores; 28–35 paravertebral tubercles; body tubercles randomly arranged, present on flanks; tubercles in lateral caudal furrows anteriorly; no ventrolateral caudal tubercles; no lateral caudal row of tubercles; caudal tubercles not encircling tail; subcaudals smooth bearing a median row of enlarged scales; two or three postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials smooth; 34–41 subdigital fourth toe lamellae; single ocellus in shoulder region in males; red bands on forelimbs and hind limbs in males; and reddish blotches on dorsum and tail in males (Tables 6,7).

Color pattern (Fig. 14). Adult males: dorsal ground color lime-green to yellow, overlain by red blotches on head (usually), body, limbs, and tail; round, red to brownish, paravertebral markings extend from just posterior to forelimb insertions to base of tail alternating with smaller, yellow, paravertebral blotches; smaller, more irregularly shaped, red blotches occur on flanks and limbs, those on tail tend to form bands; poorly defined, black markings occur on anterior margin of nape highlighting a white, nuchal band between it and large, black, shoulder patches; a single, whitish, longitudinal bar enclosed in each shoulder patch; shoulder patches narrowly meet on midline of body; ventral surfaces beige, immaculate; subcaudal region faintly mottled. Adult females and juveniles: ground color dull yellow; no red or brownish markings on head or limbs; no black shoulder patches enclosing ocelli; yellow markings on head anteriorly; paired, symmetrical dark and light markings on occiput; a series of white, vertebral blotches alternating with paired, dark vertebral blotches extend from nape to base of tail then transforming into indistinct, caudal bands; regularly shaped, dark and light markings on flanks and limbs; ventral surfaces beige, immaculate; faint, subcaudal mottling pattern present. The illustration of *Cnemaspis kumpoli* in Das (2010:57) is misleading and the description of this species' color pattern (Das 2010:202) does not take into account its marked sexual dimorphism.

Distribution. *Cnemaspis kumpoli* ranges from southern Thailand south of the Isthmus of Kra from the Khao Chong Forest Reserve, Trang, Satun, and Songkhla provinces, southwestern to extreme northwestern Malaysia where it is known only from Kaki Bukit, Perlis and Perlis State Park along the Thai-Malaysian border (Grismer 2011a; Grismer *et al.* 2010a; Fig. 4).

FIGURE 14. *Cnemaspis kumpoli.* Upper left and right: adult female (LSUDPC 4222) and adult male (LSUDPC 4220), respectively, from Perlis State Park, Perlis, Peninsular Malaysia in the dark color pattern phase. Lower left: granite boulder microhabitat at Perlis State Park. Photographs by LLG. Lower right: adult male (LSUDPC 8271) from Songkhla, Songkhla Province, Thailand in the light color pattern phase. Photograph by MS.

Natural history. In Peninsular Malaysia, *Cnemaspis kumpoli* occurs in rocky areas composed of granite boulders within primary, lowland dipterocarp forest and has not been observed on nearby karst formations (Grismer 2011a). Lizards are seen at night on large boulders of granite outcroppings on steep hillsides that often border streams. They are quite active, remain wary, and do not venture far from safe retreats between the rocks, within rock cracks, or from near burrows at the base of the rocks. Grismer (2011a) reported finding a pair of adults on the base of a large tree near granite boulders. No specimens have been observed abroad during the day and females carrying two eggs have been reported during June and September (Grismer 2011a).

Relationships. *Cnemaspis kumpoli* is a member of the Pattani clade and the sister species of *C. niyomwanae* (Fig. 2).

Remarks. Despite the fact that *Cnemaspis kumpoli* is a large, nocturnal, granite dwelling species embedded in a clade of small, diurnal karst-dwellers it bears none of the characteristics seen in most other large granite dwelling species (i.e., *C. argus, C. limi, C. mcguirei* and *C. perhentianensis*) such as keeled ventrals, keeled subtibials, and keeled subcaudal scales and strong dorsal tuberculation. Instead, it is weakly tubreculated and has smooth ventrals, subtibtials, and subcaudal scales bearing a median row of enlarged scales, as do many other karst-dwelling species.

Material examined. Malaysia: Perlis: Perlis State Park LSUHC 8846–49, 8990–95, 9035. Thailand: Songkhla Province, Had Yai Disrict, Nga Chang Waterfall near the Ton Nga Waterfall MS 393–94.

Northern Sunda clade

The Northern Sunda clade is a lineage containing 28 species within four species groups (the *chanthaburiensis, siamensis, argus,* and *affinis* groups) that collectively frame the northern and western borders of the South China Sea from southern Vietnam to central Peninsular Malaysia (Figs. 2,3).

***Chanthaburiensis* group**. The *chanthaburiensis* species group is composed of six species that range across southern Indochina from southern Vietnam to Thailand along the mountainous coastline bordering the northern shores of the Gulf of Thailand. The basal lineage of this group is composed of the sister species *Cnemaspis chanthaburiensis* Bauer & Das from eastern Thailand and southwestern Cambodia and *C. neangthyi* Grismer, Grismer & Chav from southwestern Cambodia (Fig. 3). The sister lineage of this group is composed of the geographically proximate, microendemic, granite-dwellers *C. aurantiacopes* Grismer & Ngo; *C. caudanivea* Grismer & Ngo; *C. nuicamensis* Grismer & Ngo; and *C. tucdupensis* Grismer & Ngo from continental and insular southern Vietnam (Fig. 3). This is a well-supported lineage that is further supported here in that they are the only species of *Cnemaspis* that have a dark, mid-gular line, which we hypothesize to be a synapomorphy based on its absence from all other *Cnemaspis* and outgroups and thus constitutes further evidence of their monophyly. Their close, circumscribed, geographic proximity across a previously connected range of mountain tops (Grismer & Ngo 2007) is consistent with this hypothesis.

This group is diagnosed by having a maximum SVL of 40.9–58.4 mm; 7–13 supralabials; 7–12 infralabials; smooth ventral scales; 0–9 pore-bearing precloacal pores; 16–31 paravertebral tubercles; smooth subcaudals bearing a slightly enlarged to enlarged median row; 0–4 postcloacal tubercles; no enlarged femoral or subtibial scales; and 22–33 subdigital lamellae on the fourth toe.

FIGURE 15. *Cnemaspis chanthaburiensis* from the Phnom Samkos Wildlife Sanctuary, Pursat Province, Cardamom Mountains, Cambodia. Upper left and right: adult males (LSUDPC 5056 and 5054, respectively) from Phnom Dalai in the dark and light color pattern phases, respectively. Lower left: subadult male (LSUDPC 2875) from the base of Phnom Samkos. Photographs by LLG. Lower right: ventral view of adult male (LSUDPC 8539) from Khao Kitchakut, Chanthaburi Province, Thailand. Photograph by PLW.

Cnemaspis chanthaburiensis Bauer & Das, 1998

Chanthaburi Rock Gecko

Fig. 15

Cnemaspis sp. A Dring 1979:220

Holotype. FMNH 215979. Type locality: "Khao Soi Daow (Dao) Wildlife Sanctuary, Pongnomron (Pong Nam Ron), Chanthaburi Province, Thailand (approximately) 13°00'N, 102°05'E)" at 100 m in elevation.

Diagnosis. Maximum SVL 42.2 mm; 8–10 supralabials; 7–10 infralabials; smooth ventral scales; 6–9 contiguous pore-bearing precloacal scales with elongate or round pores; 21–25 paravertebral tubercles; tubercles linearly arranged; caudal tubercles not restricted to a single paravertebral row nor encircling tail; tubercles in lateral caudal furrows; lateral row of tubercles present; subcaudals smooth, median row of scales ranging from not enlarged to weakly enlarged or only weakly enlarged posteriorly only; 1–3 postcloacal tubercles on each side; no enlarged femoral, subtibial or submetatarsal scales on first toe; subtibials smooth to weakly keeled; 22–29 subdigital fourth toe lamellae; in males gular region, throat, abdomen, and subcaudal region orange (Tables 6,7).

Color pattern (Fig. 15). Ground color of top of head and rostrum yellowish; ground color yellowish dorsally on body, grayish on flank transitioning to orangish on tail; dorsum bearing alternating distinct light and smaller indistinct dark vertebral and paravertebral markings; light vertebral markings sometimes fused to form an irregularly shaped stripe; light markings form yellowish caudal bands; limbs bearing cream colored bands alternating with small, irregularly shaped black markings; chin, abdomen, and subcaudal region usually orange.

Distribution. *Cnemaspis chanthaburiensis* is known from Khao Soi Dao Wildlife Sanctuary, Pong Nam Ron District, Chanthaburi Province; Khao Khieo Wildlife Sanctuary, Chon Buri Province; Khao Kitchakoot National Park, Chanthaburi Province; Khao Wong, Rayong Province; and Suan Kaset, Muang District and Namtok Pliieu, Chanthaburi Province in southeastern Thailand and from the base of Phnom Samkos, Phnom Dalai, and O'Som in the Samkos Wildlife Sanctuary of the Cardamom Mountains in southwestern Cambodia (Bauer & Das 1998; Grismer *et al.* 2008c,d; Fig. 3).

FIGURE 16. Habitat of *Cnemaspis chanthaburiensis* at Phnom Dalai, Phnom Samkos Wildlife Sanctuary, Pursat Province, Cardamom Mountains, Cambodia. Photograph by LLG.

Natural history. *Cnemaspis chanthaburiensis* is a small, secretive species restricted to hilly primary forests (Fig. 16) and ranges from near sea level to at least 968 m in elevation (Grismer *et al.* 2008d; Neang *et al.* 2010). Unlike most other species of *Cnemaspis, C. chanthaburiensis* is terrestrial and lizards are commonly found during the day inactive beneath and within logs and beneath loose bark on the forest floor (Neang *et al.* 2010). On two occasions we have even collected specimens from the fly covers of our tents (Grismer *et al.* 2008d). We have found gravid females carrying two eggs during August.

Relationships. *Cnemaspis chanthaburiensis* is the basal lineage of the *chanthaburiensis* group (Fig. 2).

Material examined. Thailand: Chanthaburi Province, Pongnomron (Pong Nam Ron) District, Khao Soi Daouw (Dao) Wildlife Sanctuary, FMNH 215979 (holotype) and FMNH 191479 (paratype); Chantaburi Province, BMNH 1917.5.14.4 (paratype); Chon Buri Province, Khao Khiew (Khieo) Wildlife Sanctuary, FMNH 215978 (paratype); Chantaburi Province, Suan Kaset, Muang District, FMNH 215980 (paratype). Material examined since Grismer *et al.* (2010): Cambodia: Phnom Samkos, Pursat Province, Cardamom Mountains LSUHC 7882, Phnom Dalai 9337–38, near O'Som LSUHC 10110–11. Thailand: Chantaburi Province, Khao Khitchakut NP LSUHC 9507–08.

Cnemaspis neangthyi Grismer, Grismer & Thou, 2010

Neang Thy's Rock Gecko
Fig. 17

Holotype. LSUHC 8485. Type locality: "…outside the village of O'lakmeas, Pursat Province, Cambodia (12°19.4339N, 103°30.6059E)" at 145 m in elevation.

Diagnosis. Maximum SVL 54.0 mm; 11–13 supralabials; 10–12 infralabials; smooth ventral scales; two round, contiguous pore-bearing, precloacal scales with round pores; 20–26 paravertebral tubercles; dorsal tubercles linearly arranged; caudal tubercles not restricted to a single paravertebral row; tubercles in lateral caudal furrows; lateral row of caudal tubercles present; ventrolateral caudal tubercles present anteriorly; caudal tubercles do not encircle tail; subcaudals smooth, bearing a median row of enlarged scales; one postcloacal tubercle on each side; no enlarged femoral, subtibial or submetatarsal scales on first toe; subtibials keeled; 22–25 subdigital fourth toe lamellae; lacks the diagnostic color pattern characteristics of the other species in the Indochina clade (Tables 6,7).

FIGURE 17. Upper left: adult male *Cnemaspis neangthyi* from near the village of O'lakmeas, Pursat Province, Cambodia. Right: siltstone microhabitat of *C. neangthyi.* Lower left: lowland, dry, deciduous dipterocarp forest habitat through which *C. neangthyi* ranges in isolated microhabitat islands. Photographs by LLG.

Color pattern (Fig. 17). Dorsal ground color of body and limbs olive-green to dull-yellow; head bearing a distinct, black parietal spot; radiating black and dull-white postorbital lines; light-green chevron marking on anterior margin of shoulder region; body overlain with light colored, paired, paravertebral blotches containing a central black dot and alternating with round, black blotches that extend onto tail to form poorly defined alternating dark and light bands; regenerated tail dull yellow, nearly unicolor; black spots on flanks invade lateral margins of abdomen; limbs stippled with light green and black; venter dull yellow with black stippling in scales.

Distribution. *Cnemaspis neangthyi* is known only from the type locality at O'Lakmeas, Pursat Province, Cambodia (Fig. 3).

Natural history. According to J. Grismer *et al.* (2010), *Cnemaspis neangthyi* is strictly nocturnal and found exclusively on boulders and cliff faces formed from sedimentary limestone-like rock. *Cnemaspis neangthyi* is most commonly found on vertical and overhanging faces, within cracks and shallow wind-eroded holes, shallow caves, and beneath exfoliations (Fig. 17). *Cnemaspis neangthyi* is adept at substrate matching and J. Grismer *et al.* (2010) found lizards only on sections of the rock wall containing light and dark green-colored lichens where their mottled color pattern enhanced their crypsis. No specimens were observed on the ground or in vegetation but when disturbed, lizards would run to the base of the rock wall to hide in cracks and holes formed by the expansive soil at the ground-rock interface.

Relationships. *Cnemaspis neangthyi* is the sister species of the Vietnamese lineage containing *C. aurantiacopes, C. caudanivea, C. tucdupensis,* and *C. nuicamensis* (Fig. 2).

Material examined. Cambodia: Pursat Province, O'Lakmeas LSUHC 8478, 8485, 8515–17 (type series).

Cnemaspis aurantiacopes Grismer & Ngo, 2007

Hon Dat Rock Gecko
Fig. 18

Holotype. UNS 49. Type locality: Hon Dat Hill, Hon Dat District, Kien Giang Province, Vietnam (10°06.7749 N, 104°53.5699 E)" at 30 m in elevation.

Diagnosis. Maximum SVL 58.4 mm; 9–11 supralabials; 8–10 infralabials; smooth ventral scales; no precloacal pores; 23–31 paravertebral tubercles; tubercles on body linearly arranged and present on flanks; caudal tubercles not restricted to a single paravertebral row; no tubercles in lateral caudal furrows; ventrolateral caudal tubercles present anteriorly; caudal tubercles do not encircle tail; lateral caudal tubercle row present; subcaudals smooth, bearing a median row of enlarged scales; one or two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; slightly enlarged submetatarsal scales on first toe; 27–31 subdigital fourth toe lamellae; faint, dark, elongate mid-gular marking; gukar region, throat, pectoral region, dorsal and ventral surfaces of forelimbs, ventral surface of hind limbs, and original tail orange in males (Tables 6,7).

Color pattern (Fig. 18). Males: dorsal ground color yellowish to saffron, overlain by rust colored, semi-transversely oriented, irregularly shaped markings extending from occiput to base of tail and enclosing a series of eight, large, yellowish-gray, oval blotches extending from nape to base of tail; top of head reddish-brown, rostrum gray; dorsal surface of limbs saffron, overlain with faint, lighter mottling on brachia and thighs and weak banding on forelimbs and forelegs; dorsal caudal region reddish-brown, no banding; three wide, faint, reddish brown, postorbital stripes, uppermost extending onto shoulder region and contacting blotch on nape; ventral surfaces of neck, body, and limbs dull orange, immaculate; gular region slightly darker; labials unicolor reddish brown. Females: overall dorsal coloration is more yellowish-gray, especially noticeable on the limbs; dark, rhomboid blotches and bands on all dorsal surfaces. Both sexes bear a faint, usually lineate, median mid-gular marking.

Distribution. *Cnemaspis auarntiacopes* is known only from the type locality at Hon Dat Hill, Hon Dat District, Kien Giang Province, Vietnam (Fig. 3).

Natural history. Hon Dat Hill composes a small cluster of mountains reaching to 100 m in elevation that supports an isolated section of secondary, highly disturbed, semi-deciduous forest in the southern reaches of the Mekong Delta flood plain (Fig. 3) and is completely surrounded by agricultural lowlands. The hill maintains abundant outcroppings of granitic rocks and caves and Grismer & Ngo (2007) noted *Cnemaspis aurantiacopes* to be common on outcrops in both highly disturbed and old secondary forest. They did not observe lizards during the day but lizards were common at night within the confines of caves. This species does not venture out onto the open surfaces of the boulders and when alarmed, may give a tail display wherein the tail is rolled slightly over the back and often moved from side to side (Grismer & Ngo 2007).

Relationships. *Cnemaspis aurantiacopes* is the basal species of the other Vietnamese species of *Cnemaspis*; *C. caudanivea* Grismer & Ngo, *C. tucdupensis* Grismer & Ngo, and *C. nuicamensis* Grismer & Ngo (Fig. 2).

Material examined. Vietnam: Kien Giang Province, Hon Dat District, Hon Dat Hill UNS 47, 49 (type series). Additional material examined since Grismer & Ngo (2007): LSUHC 8245, 9528–41.

FIGURE 18. *Cnemaspis aurantiacopes* from Hon Dat Hill, Kien Giang Province, Vietnam. Upper and lower left: adult males (LSUDPC 3131 and 3130, respectively) in the light color pattern phase. Upper right: subadult male (LSUDPC 3135) in the light color pattern phase. Lower right: adult female (LSUDPC 3133) in the dark color pattern phase. Photographs by LLG.

Cnemaspis caudanivea Grismer & Ngo, 2007

Hon Tre Island Rock Gecko
Fig. 19

Holotype. UNS 83. Type locality: "Hon Tre Island, Kien Hai District, Kien Giang Province, Vietnam (09°58.3429 N, 104°50.9559 E)" at 100 m in elevation.

Diagnosis. Maximum SVL 47.2 mm; eight or nine supralabials; seven or eight infralabials; smooth ventral scales; 0–2 round, discontinuous, pore-bearing, precloacal scales; 20–24 paravertebral tubercles; tubercles linearly arranged but absent from flanks; caudal tubercles not restricted to a single paravertebral row nor encircling tail; caudal tubercles occasionally in lateral caudal furrows anteriorly only; ventrolateral caudal tubercles variably present anteriorly; lateral caudal tubercle row occasionally present anteriorly; subcaudals smooth, sometimes bearing a median row of slightly enlarged scales; one or two postcloacal tubercles on each side; no enlarged femoral or subtibial scales; subtibials smooth to weakly keeled; weakly enlarged submetatarsal scales occasionally present on first toe; 23–30 subdigital fourth toe lamellae; large, black, round spots on nape and anterior portion of body; dark elongate mid-gular marking; wide black and yellow bands on tail; posterior portion of tail immaculate white dorsally and ventrally (Tables 6,7).

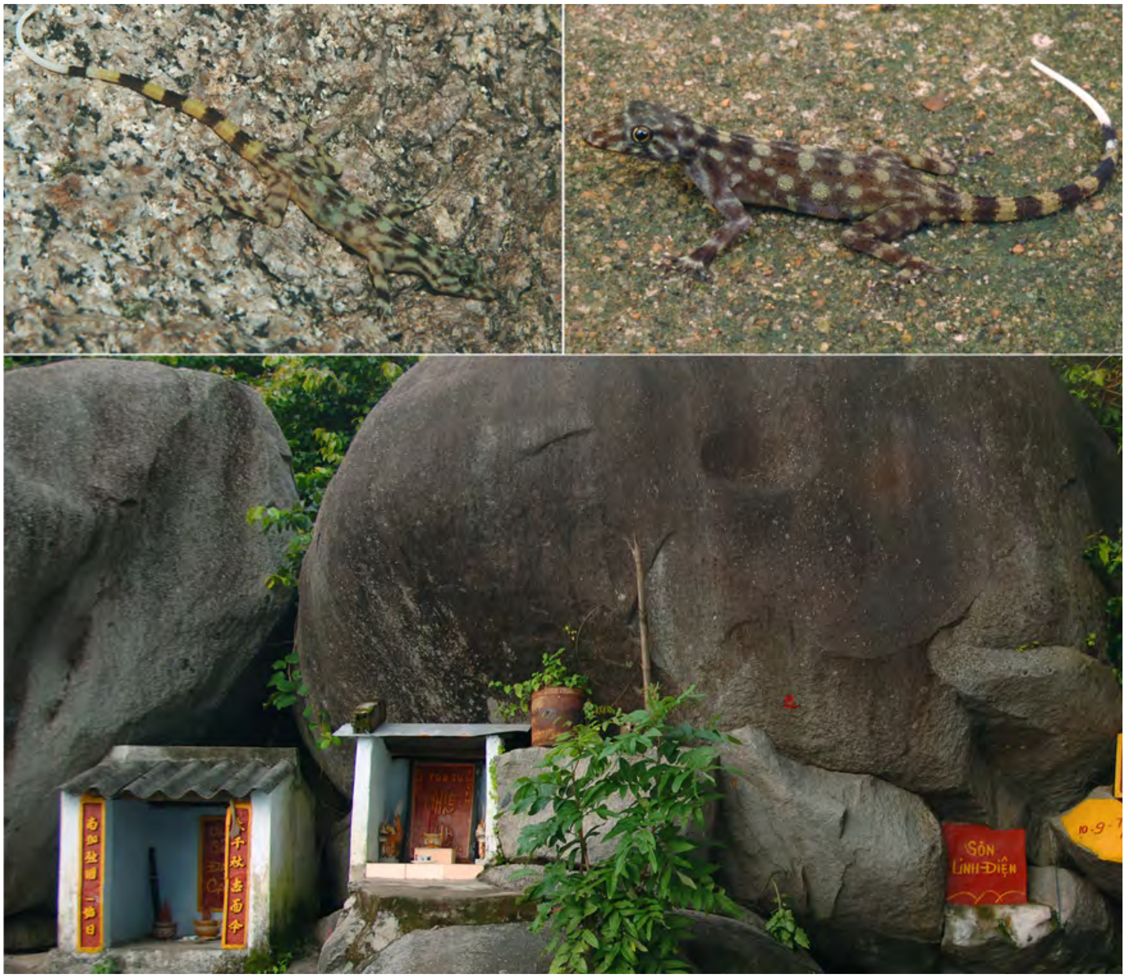

FIGURE 19. *Cnemaspis caudanivea* from Hon Tre Island, Kien Giang Province, Vietnam. Upper left: adult male (LSUDPC 3056) in the light color pattern phase. Upper right: adult female (LSUDPC 3045) in the dark color pattern phase. Lower: granite boulder microhabitat on Hon Tre Island. Photographs by LLG.

Color pattern (Fig. 19). Dorsal ground color gray, overlain by a dark pattern of reddish brown, irregularly shaped markings on top of head and snout; squarish, semi-transversely arranged, large, black blotches on neck and body separated by dull white blotches; irregularly shaped bands on limbs; wide, black and dull-yellow bands encircling tail; wide, poorly defined, dark-brown postorbital stripes edged below in white extending onto side of neck; ventral surfaces of neck, body, and limbs dull beige, immaculate; gular region smudged with darker coloration and light spots, bearing a dark mid-gular stripe; last 25% of original tail immaculate, brilliant white dorsally and ventrally.

Distribution. *Cnemaspis caudanivea* is known only from the type locality of Hon Tre Island, Kien Hai District, Kien Giang Province, Vietnam (Fig. 3).

Natural history. Hon Tre is a small (70 km^2) island lying 15 km off the southern coast of Vietnam in Rach Gia Bay, 28.3 km nearly due west of the port of Rach Gia in Kien Giang Province. The island is steep-sided, reaching 315 m in elevation and dominated by secondary and primary semi-deciduous forest covering a landscape composed of nearly continuous outcrops of large, granitic boulders (Fig. 19). Grismer & Ngo (2007) noted lizards occurred on granite boulders throughout the island, from the coastline to near the summit. During the day, lizards are only observed on shady, inclined surfaces and within rock cracks and cave-like cavities formed by boulders piled on top of one another. At night, lizards venture onto the exposed outer surfaces of the boulders but appear inactive. Lizards are exceptionally wary both day and night and typically escape capture at surprisingly high speeds, often hopping while running. Grismer & Ngo (2007) reported lizards curling and elevating their tail above their back when alarmed and moving the posterior 25% from side to side, thus displaying the strikingly white coloration. The dexterity with which the tail is waved back and forth, however, exceeds that of all other *Cnemaspis* we have observed. *Cnemaspis caudanivea* can fold the end of the tail forward 180° on itself while rolling and unrolling it slowly in a lateral plane, making it look like a small, white worm wiggling on a rock. This behavior and color pattern is maintained in regenerated tails as well, suggesting it is strongly selected for.

Relationships. *Cnemaspis caudanivea* is the sister species to a monophyletic group composed of *C. tucdupensis* and *C. nuicamensis* (Fig. 2).

Material examined. Vietnam: Kien Giang Province, Kien Hai District, Hon Tre Island UNS 83, 84 (type series). Material examined since Grismer & Ngo (2007): Vietnam; Kien Giang Province, Kien Hai District, Hon Tre Island LSUHC 8247, 9543–48.

Cnemaspis nuicamensis Grismer & Ngo, 2007

Nui Cam Hill Rock Gecko
Fig. 20

Holotype. UNS 37. Type locality: "Nui Cam Hill, Tinh Bien District, An Giang Province, Vietnam (10°29.7759 N, 105°00.4419 E)" at 100 m in elevation.

Diagnosis. Maximum SVL 48.2 mm; 7–9 supralabials; six or seven infralabials; smooth ventral scales; 3–6 pore-bearing, precloacal scales separated medially by 1–4 poreless scales; 16–21 paravertebral tubercles; tubercles linearly arranged and present on flanks; caudal tubercles not restricted to a single paravertebral row nor encircling tail; tubercles in lateral caudal furrows occasionally anteriorly; ventrolateral caudal tubercles present anteriorly; lateral caudal tubercle row absent or present only anteriorly; subcaudals smooth and bearing a median row of enlarged scales ; 2–4 postcloacal tubercles on each side; no enlarged femoral or subtibial scales; subtibials smooth; no enlarged submetatarsal scales on first toe; 27–33 subdigital fourth toe lamellae; dark, elongate mid-gular marking (Tables 6,7).

Color pattern (Fig. 20). Dorsal ground color dull-yellow, body overlain with large, reddish brown blotches and offset, black, paravertebral blotches; limbs with reddish brown and pale yellow, alternating bands; poorly defined, reddish brown, caudal bands not encircling original tail; top of head and snout with reddish brown reticulum enclosing dull white blotches; scattered, dark spots on top of head; three thin, dark, reddish brown, postorbital stripes infused with black and edged below in white, uppermost not extending onto shoulder region; all ventral surfaces gray, immaculate; gular region bearing a dark, mid-gular line.

Distribution. *Cnemaspis nuicamensis* is known only from the type locality of Nui Cam Hill 22.5 km south of Chau Doc in Tinh Bien District of An Giang Province, Vietnam near the border of Cambodia (Fig. 3).

Natural history. Nui Cam Hill is part of the Bay Nui Mountains, which are surrounded by the vast, agricultural lowlands of the Mekong Delta flood plain. Nui Cam Hill is the tallest (710 m) in this range of mountains and is dominated by old growth, secondary, semi-deciduous forest and highly disturbed forest. Lizards were all observed during the day on the surface of granite rocks or within rock cracks. Within this microhabitat, *Cnemaspis nuicamensis* is far more common on vertical surfaces in the vicinity of streams than on rocks within the forest (Fig. 20). Grismer & Ngo (2007) noted that lizards presented tail displays upon escape and no lizards were observed on rocks within disturbed forest.

Relationships. *Cnemaspis nuicamensis* is the sister species to *C. tucdupensis* (Fig. 2).

Material examined. Vietnam: An Giang Province, Tinh Bien District, Nui Cam Hill UNS 37, 38 (type series). Material examined since Grismer & Ngo (2007): Vietnam; An Giang Province, Tinh Bien District, Nui Cam Hill LSUHC 8246, 8646–52, 9549–55.

FIGURE 20. Upper; adult male *Cnemaspis nuicamensis* (LSUDPC 3136) in the light color pattern phase. Lower: Granite microhabitat of *C. nuicamensis* at Nui Cam Hill, An Giang Province, Vietnam. Photographs by LLG.

Cnemaspis tucdupensis Grismer & Ngo, 2007
Tuc Dup Hill Rock Gecko
Fig. 21

Holotype. UNS 45. Type locality: “Tuc Dup Hill, Tri Ton District, An Giang Province, Vietnam (10°22.9549 N, 104°57.3369 E) at 100 m in elevation.

Diagnosis. Maximum SVL 51.0 mm; 8–10 supralabials; 7–9 infralabials; smooth ventral scales; no precloacal pores; 16–22 paravertebral tubercles; tubercles linearly arranged or nearly so, present on flanks; caudal tubercles not restricted to a single paravertebral row nor encircling tail; tubercles not in lateral caudal furrows; ventrolateral caudal tubercles present anteriorly; no lateral caudal tubercle row; subcaudals smooth, bearing a median row of slightly enlarged scales; 0–3 postcloacal tubercles on each side; no enlarged femoral or subtibial scales; subtibials smooth; enlarged submetatarsal scales on first toe; 26–32 subdigital fourth toe lamellae; large, black, squarish, paired paravertebral markings on body; black and yellow bands on tail; posterior portion of original tail in males black; dark mid-gular marking; gular region, throat, pectoral region, abdomen, ventral surfaces of limbs and subcaudal region in males orangish (Tables 6,7).

FIGURE 21. *Cnemaspis tucdupensis* from Tuc Dup Hill, An Giang Province, Vietnam. Upper left: adult female (LSUDPC 3140) in the light color pattern phase. Upper right: adult male (LSUDCP 3141) in the dark color pattern phase. Lower: granite boulder microhabitat at Tuc Dup Hill. Photographs by LLG.

Color pattern (Fig. 21). Dorsal ground color gray, body overlain with large, black and pale yellow spots; limbs bearing reddish brown and pale yellow alternating bands; poorly defined, black and yellow caudal bands encircling tail; posterior portion of original tail black; regenerated tail beige, immaculate; top of head and snout with faint, dark reticulum enclosing dull whitish blotches; thin, dark, postorbital stripes edged below in white, uppermost extending onto nape; dark mid-gular marking; gular region, throat, pectoral region, abdomen, ventral surfaces of limbs and subcaudal region in males orangish.

Distribution. *Cnemaspis tucdupensis* is known only from the type locality of Tuc Dup Hill located 36.3 km south of Chau Doc in Tinh Bien District of An Giang Province, Vietnam near the border of Cambodia (Fig. 3).

Natural history. Tuc Dup Hill is a prominence of Co To Mountain that lies at the southern end of the Bay Nui Mountains in Tri Ton District of An Giang Province in southern Vietnam. Co To Mountain reaches 584 m in elevation and is covered with primary semi-deciduous forest where numerous granitic outcroppings and caves are common (Fig. 21). At Tuc Dup, the boulders are particularly large (up to 5 m in diameter) and enclose a myriad of spaces and chambers where they lie on top of one another. The type locality served as a Viet Cong headquarters during the Vietnam War and currently serves as a museum celebrating Tuc Dup Hill as a strategic military hideout. *Cnemaspis tucdupensis* is most prevalent in caverns near areas wherein sunlight can filter down during the day supporting plant growth and mosses on the boulders and serving as areas where lizards can forage (Grismer & Ngo 2007). Lizards avoid direct sunlight and remain on the shaded vertical and inverted rocky surfaces nearby. At night, lizards venture out into open areas within the cavern as well as onto boulder surfaces exposed to the outside and appear inactive. Lizards present weak tail displays immediately before and after escaping.

Relationships. *Cnemaspis tucdupensis* is the sister species of *C. nuicamensis* (Fig. 2).

Material examined. Vietnam: An Giang Province, Tri Ton District, Tuc Dup Hill UNS 42–43, 45 (type series). Material examined since Grismer & Ngo (2007): Vietnam; An Giang Province, Tri Ton District, Tuc Dup Hill LSUHC 8245, 8609–22, 9527–41. Grismer & Ngo (2007) mistakenly listed the holotype as UNS 49 when it should have been UNS 45.

***Siamensis* group.** The *siamensis* group is a well-supported lineage that contains parapatric sister lineages on opposite sides of the Isthmus of Kra in the central portion of the Thai-Malay Peninsula (Figs. 2,3). This group may be the sister lineage to the *chanthaburiensis* group although this relationship lacks strong statistical support (Fig. 2). The northern lineage contains *C. siamensis* (Smith) that extends throughout northern Peninsular Thailand (and probably Myanmar) and its sister species *C. huaseesom* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya known only from western Thailand just north of the Thai-Malay Peninsula (Grismer *et al.* 2010a). The southern lineage contains *C. chanardi* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya in the north and the sister species *C. omari* sp. nov. from southern Thailand and northern Peninsular Malaysia and *C. roticanai* Grismer & Chan from Langkawi Island in extreme northwestern Malaysia (Fig. 3). These three species form a well-supported monophyletic group in the molecular analysis that is further supported here by them having the derived character states of a light-colored prescapular crescent, a yellow belly, and yellow ventral surfaces of the hind limbs. Some individuals of *C. biocellata* from the Pattani clade have a yellow belly, which we consider convergent.

The *siamensis* group is diagnosed by having a maximum SVL of 37.8–47.0 mm; 7–10 supralabials; 6–9 infralabials; 0–8 pore-bearing, precloacal scales; linearly arranged dorsal tubercles; 18–30 paravertebral tubercles; caudal tubercles not restricted to a single paravertebral row and encircling tail; no ventrolateral caudal tubercles anteriorly; one or two postcloacal tubercles on each side; no enlarged femoral, subtibial or scales beneath first metatarsal; 21–31 lamellae beneath the fourth toe.

***Cnemaspis siamensis* (Smith, 1925)**

Siam Rock Gecko
Fig. 22

Gonatodes siamensis Smith, M. A., 1925:21.
Gonatodes kendallii Smith, M. A. 1916:151. *non* Boulenger *fide* Taylor, 1963:740.
Gonatodes siamensis Smith, 1930:16.

Holotype. BMNH 1946.8.19.83. Type locality: “Maprit, near Patiyu (=Pathio, Chumpon Province), Peninsular Siam [Thailand]” at 10 m in elevation.

Diagnosis. Maximum SVL 39.7 mm; eight or nine supralabials; 6–8 infralabials; keeled ventral scales; no precloacal pores; 19–25 paravertebral tubercles; dorsal tubercles on body randomly arranged; tubercles on flanks;

caudal tubercles not restricted to a single paravertebral row nor encircling tail; no tubercles in lateral caudal furrows; no ventrolateral caudal tubercles; lateral caudal tubercle row present; subcaudals keeled; median row of enlarged subcaudal scales present; one or two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales on first toe; 24–26 subdigital fourth toe lamellae; gular region, throat, and pectoral region yellow in males; dark, longitudinally arranged spots in gular region (Tables 6,7).

Color pattern (Fig. 22). Dorsal ground color gray to light brown overlain with short, dark, zig-zag, transverse bands on body countershaded with white markings; top of head and flanks mottled with light and dark irregularly shaped markings; limbs and tail bearing poorly defined dark bands; gular region, chest and posterior portion of original tail in males yellow; dark longitudinally arranged spots on a yellow gular region; belly and anterior portion of tail cream colored, immaculate; ventral surfaces of limbs gray.

FIGURE 22. *Cnemaspis siamensis* from Pathio, Chumpon Province, Thailand. Upper right: adult male (LSUDPC 5241) in the dark color pattern phase. Middle right: adult female (LSUDPC 5228) in the light color pattern phase. Lower right: ventral coloration of adult male (LSUDPC 5242). Left: microhabitat structure. Photographs by LLG.

Distribution. *Cnemaspis siamensis* ranges throughout the lowland, hilly regions east of the Tenasserim and Phuket Mountains from Kaeng Krachan National Park, Phetchaburi Province in the north, southward to Khao Mod, Surat Thani Province on the east coast and to Phuket Island, Phuket Province in the west (Grismer *et al.* 2010a; Fig. 3).

Natural history. Grismer *et al.* (2010a) stated that *Cnemaspis siamensis* is not a saxicolous, microhabitat specialist but a nocturnal, lowland, scansorial, forest-dwelling gecko that opportunistically utilizes rocky microhabitats when available. We have observed lizards at the type locality on both vegetation (Fig. 22) and rocks.

Relationships. *Cnemaspis siamensis* is the sister species of *C. huaseesom* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya (Fig. 2).

Material examined. Thailand: Chumphon Province, Krom Luang District THNHM 0372; Pha To District, Ngao National Park THNHM 1086; Pathio LSUHC 9474, 9485, MCZ 39025; Kapoh Water Fall FMNH 215977. Phetchaburi Province, Muang District THNHM 1441–42, 1448–49. Prachuap Khiri Khan Province, Pa-La-U, Kaeng Krachan National Park, Hua Hin District, Prachuap Khiri Khan THNHM 1336–37; Thap Sakae District THNHM 2000. Surat Thani Province, Kanchanadit District MS16, Kaeng Krung National Park THNHM 1084.

FIGURE 23. *Cnemaspis huaseesom* from Sai Yok National Park, Kanchanaburi Province, Thailand. Upper left; ventral views showing color pattern variation in adult males (LSUDPC 5225). Upper right; adult male (LSUDPC 5213) in the dark color pattern phase. Lower right: adult female (LSUDPC 5214) in the light color pattern phase. Photographs by LLG. Lower left: adult male (LSUDPC 8276) showing variation in color pattern in that it lacks a yellow tail. Photograph by MS.

Cnemaspis huaseesom Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya, 2010
Yellow-headed Rock Gecko
Figs. 23,24

Holotype. THNHM 15909. Type locality: "Sai Yok National Park, Kanchanaburi Province, Thailand (14°20.09N, 98°51.35E)" at 125 m in elevation.

Diagnosis. Maximum SVL 43.5 mm; 7–10 supralabials; 6–9 infralabials; smooth ventral scales; 5–8 contiguous, pore-bearing, precloacal scales with round pores; 18–24 paravertebral tubercles; tubercles on flanks; tubercles in lateral caudal furrows; no ventrolateral caudal tubercles; lateral caudal tubercle row absent; subcaudals smooth, with no enlarged or weakly keeled median scale row; one or two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials smooth; no enlarged submetatarsal scales on first toe; 21–31 subdigital fourth toe lamellae; head, forelimbs, tail, gular region, throat, pectoral region, underside of forelimbs, and subcaudal region yellow in males (Tables 6,7).

Color pattern (Figs. 23,24). Males: *Cnemaspis huaseesom* are capable of considerable change in coloration from a light to darker phase. The description that follows is of the darker phase: dorsal ground color of head, forelimbs and tail yellow, with faint banding on tail; dorsal ground color of trunk and hind limbs dark-gray and bearing large, light-gray, paravertebral spots extending from occiput to base of tail; dorsal surface of hind limbs bearing large, light-gray spots; dorsal surface of forelimbs bearing small, yellow markings; top of head mottled; dark postorbital stripes faint; large, round, whitish markings on nape; trunk uniformly gray; tubercles on body lightly colored; belly pale gray; ventral surface of hind limbs gray; fine, dark stippling on all ventral surfaces, most dense on belly. Some adult males may have a gray, as opposed to yellow tail. Females: lack yellow head, forelimbs, and tail, have same general trunk color as males in dark phase; overall ground color of head, body, limbs, and tail light brown; large, lighter, paravertebral markings extend from nape to base of tail where they continue posteriorly to form lightly colored, caudal bands; flanks densely stippled with cream-colored markings and bear faint, gray bars; limbs mottled; all ventral surfaces beige with faint stippling that is most dense on belly and tail.

Distribution. *Cnemaspis huaseesom* is known only from the type locality of Sai Yok National Park, Kanchanaburi Province, Thailand (Fig. 3).

Natural history. Grismer *et al.* (2010a) stated that *Cnemaspis huaseesom* is most commonly found on hillsides in lowland areas with karst boulders in semideciduous, dipterocarp forest amongst thick vegetation including bamboo. Lizards are generally active at night on karst boulders but may be found on vine-like vegetation near the boulders (Fig. 24). This species is fast, wary, and flees into deep cracks and crevices at the slightest provocation. More than one lizard is usually found on a given outcropping. Lizards are only rarely observed during the day.

Relationships. *Cnemaspis huaseesom* is the sister species of *C. siamensis* (Fig. 2).

Material examined. Thailand: Kanchanaburi Province, Sai Yok National Park THNHM 15909, PSUZC-RT 2010.55, CUMZ-R 2009, 6, 24–4 (type series). Material examined since Grismer *et al.* (2010a): Thailand: Kanchanaburi Province, Sai Yok National Park LSUHC 9455–58.

FIGURE 24. Left: karst microhabitat of *Cnemaspis huaseesom* at Sai Yok National Park, Kanchanaburi Province, Thailand. Photograph by LLG. Right: adult female (LSUDPC 8278) from Sai Yok National Park in the light color pattern phase. Photograph by MS.

Cnemaspis chanardi Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya, 2010

Chan-ard's Rock gecko
Fig. 25

Gonatodes siamensis Smith, 1930:16 (in part)
Cnemaspis siamensis Smith, 1935:71; Taylor, 1963:740 (in part)

Holotype. THNHM 6983. Type locality: "Ban Chong, Chong, Nayong District, Trang Province, Thailand…between 400 and 600 m a.s.l."

Diagnosis. Maximum SVL 40.1 mm; 7–10 supralabials; 6–8 infralabials; keeled ventral scales; 6–8 discontinuous pore-bearing precloacal scales with round pores; 20–30 paravertebral tubercles; tubercles on flanks; no tubercles in lateral caudal furrows; ventrolateral caudal tubercles absent anteriorly; caudal tubercles not encircling tail; lateral caudal tubercle row present; subcaudals keeled; median row of enlarged subcaudal scales present; one postcloacal tubercle on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales on first toe; 25–30 subdigital fourth toe lamellae; yellowish, prescapular crescent; gular region, belly, underside of hind limbs, and subcaudal region yellow in males (Tables 6,7).

Color pattern (Fig. 25). Dorsal ground color of head, body, limbs and tail gray; top of head bearing small, diffuse, faint, darker colored markings giving it a somewhat mottled appearance; dark postorbital stripes faint; large, round, whitish markings on nape; trunk uniformly gray except for lightly colored tubercles on body; forelimbs mottled bearing a slight banding pattern; ventral surface of gular region, abdomen, hind limbs and tail yellow; abdomen and hind limbs sometimes pale gray; fine, dark stippling on all ventral surfaces, most dense on belly.

FIGURE 25. Left: tree hole microhabitat of *Cnemaspis chanardi* at the Phuphaphet Cave area, Satun Province, Thailand. Upper right: adult male *C. chanardi* (LSUDPC 8304) from Dad Fa Waterfall, Surat Thani Province, Thailand in the dark color pattern phase. Middle right: adult female (LSUDPC 8288) from Khao Luang National Park, Nakhon Si Thammarat Province, Thailand in the dark color pattern phase. Lower right: ventral view of adult male (LSUDPC 8301) from Dad Fa Waterfall, Surat Thani Province, Thailand. Photographs by MS.

Distribution. *Cnemaspis chanardi* occurs in the foothills of the Nakhon Si Thammarat and Sankalakhiri Mountains and lowland regions from the southern terminus of the Isthmus of Kra in Donsak District, Surat Thani Province, southward to Khao Chong and Nayong district, Trang Province. From the foothills of these mountains, *C. chanardi* extends westward through the lowlands to at least Khlong Thom District, Krabi Province (Fig. 3). *Cnemaspis chanardi* is not known to occur in the foothills or lowlands east of the crests of the Nakhon Si Thammarat and Sankalakhiri mountains (Fig. 3). Grismer *et al.* (2010a) considered the presence of *C. chanardi* (as opposed to the geographically more proximate *C. siamensis*) on Ko Tao Island approximately 85 km off the coast from Muang District, Chumpon Province, (Fig. 3), consistent with the geological history of this part of Peninsular Thailand. The island chain consisting of Ko Tao and the intervening islands Ko Samui and Ko Phangan, are offshore extensions of the Nakhon Si Thammarat Mountains to which they were connected during the last glacial maximum (Sathiamurthy & Voris 2006) and lie to the east of the Isthmus of Kra (Fig. 3). It is likely that *C. chanardi* also occurs on Ko Samui and Ko Phangan.

Natural history. Grismer *et al.* (2010a) and Taylor (1963) noted that *Cnemaspis chanardi* is a diurnal, scansorial species that utilizes large, open, above-ground substrates (i.e. tree trunks and boulders; Fig. 25) and does not occupy habitats that do not contain both trees and rocks. Lizards are occasionally found beneath small rocks. *Cnemaspis chanardi* ranges from near sea level at Khlong Thom to just under 600 m at Khao Chong. Smith (1930) reported specimens from Khao Whip (=Khao Wang Hip), Nakhon Si Thammarat Province but gave no elevation.

Remarks. Based on the geographically outlying southernmost paratype LSUHC 9564 from the Phuphaphet Cave, Satun Province, Thailand, Grismer *et al.* (2010a) considered this locality to be southern extent of the known range of *Cnemaspis chanardi* but posited that its range probably continued approximately 45 km further south to the Banjaran Nakawan mountains on the Thai-Malaysian border. However, genetic data from LSUHC 9565 from the same cave and from LSUHC 9978–79 from the Banjaran Nakawan mountains in Perlis, Malaysia (considered to be *C. roticanai* by Grismer [2011a]) indicate these populations are conspecific, fall outside of *C. chanardi* and *C. roticanai,* and are most closely related to the latter. Therefore, we consider the Phuphaphet Cave and Perlis populations to be the new species *C. omari* sp. nov. described below. We remove LSUHC 9564 from the type series of *C. chanardi* and consider *C. roticanai* to be endemic to Langkawi Island as was originally considered (Grismer & Chan 2010; Fig. 3).

Relationshsips. *Cnemaspis chanardi* is the sister species of the lineage containing *C. omari* sp. nov. and *C. roticanai* Grismer & Chan (Fig. 2).

Material examined. Thailand: Trang Province, Nayong District, Ban Chong, Chong, FMNH 176863, THNHM 6983 (holotype); Surat Thani Province, Ban Nasan District, Dad Fa Waterfall in Tai Rom Yen National Park CUMZ-R-2009, 6, 24-6, Donsak District, near Donsak Pier MS 395; Kanchanadit District, Petphanomwung Cave ZMKU Rep-000313, KZM 009; Ko Tao Island USNM 76143–44; Krabi Province, Khlong Thom District, Khao Nor Chuchi, Khlong Thom THNHM 12434, 12439–40; Nakhon Si Thammarat Province, Lan Saka District, Khao Luang National Park THNHM 1334-35, 14111, Nopphitam District, Krung Nang Waterfall in Khao Nan National Park, THNHM 10705, Khao Nan National Park, THNHM 10115, Tha Sala District, Khao Nan National Park THNHM 10135, Nopphitham District, Ban Yod Leong, THNHM 10383, Thum Panra District; Thum Thong Panra, PSUZC-RT 2010.53–54.

Cnemaspis omari sp. nov.

Omar's Rock Gecko
Fig. 26

Cnemaspis chanardi Grismer *et al.* 2010a:24 (in part)
Cnemaspis roticanai Grismer 2011a:367 (in part)

Holotype. Adult male (LSUHC 9978) collected by Evan S. H. Quah and M. A. Muin on 11 March 2011 at Wang Kelian, Perlis, Peninsular Malaysia (06°41.805 N, 100°10.751 E) at 150 meters above sea level.

Paratypes. Adult female (LSUHC 9979) bears the same data as the holotype. Adult females (LSUHC 9564–65) collected by Kirati Kunya from the Phuphaphet Cave, Muang District, Satun Province, Thailand on 6 October 2009. LSUHC 9564 was previously considered a paratype of *C. chanardi* (Grismer *et al.* 2010a:17).

Diagnosis. Maximum SVL 41.3 mm; eight or nine supralabials; seven or eight infralabials; keeled ventral scales; four contiguous pore-bearing precloacal scales with round pores; body tuberculation strong; 22–29 paravertebral tubercles; dorsal tubercles bear weak linear arrangement; tubercles present on flanks; no tubercles in lateral caudal furrows; ventrolateral caudal tubercles absent; caudal tubercles encircling tail; lateral caudal tubercle row present; subcaudals keeled, no enlarged median row; one postcloacal tubercle on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales on first toe; and 25–28 subdigital fourth toe lamellae; light colored prescapular crescent; gular region, belly, underside of hind limbs, and subcaudal region yellow in males (Tables 6,7).

FIGURE 26. *Cnemaspis omari* sp. nov. Upper left: adult male holotype (LSUHC 9978) from Perlis State Park, Perlis, Peninsular Malaysia in the light color pattern phase. Middle left: adult female paratype (LSUHC 9979) from Perlis State Park, Perlis, Peninsular Malaysia in the light color pattern phase. Photographs by ESHQ. Upper and middle right: adult female paratype (LSUHC 9564) and subadult (LSUDPC 8299), respectively, from Phuphapet Cave, Satun Province, Thailand in dark color pattern phase. Photographs by MS. Lower: type series of *C. omari* sp. nov. Photograph by LLG.

Description of holotype. Adult male; SVL 41.3 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.27), somewhat narrow (HW/SVL 0.17), flat (HD/HL 0.41), distinct from neck; snout short (ES/HL 0.50), concave in lateral profile; postnasal region constricted medially, raised; scales of rostrum weakly keeled, larger than similarly shaped scales on occiput; moderate, supraorbital ridges; shallow frontonasal sulcus; canthus rostralis smoothly rounded; eye large (ED/HL 0.23); extra-brillar fringe scales small in general but largest anteriorly; pupil round; ear opening oval, taller than wide; rostral concave dorsally, dorsal 75% divided by longitudinal groove; rostral bordered posteriorly by two supranasals and one smaller azygous scale, laterally by first supralabials and nostrils; 8R,L raised supralabials of similar size; 7R,L infralabials, decreasing gradually in size posteriorly; nostrils small, oblong, oriented dorsoposteriorly, bordered posteriorly by small, granular, postnasal scales; mental large, triangular, medially concave, extending to level of second infralabial, bordered posteriorly by three postmentals, lateral postmentals largest; gular and throat scales raised, smooth, somewhat pointed; throat scales larger.

Body slender, elongate (AG/SVL 0.50); small, weakly keeled, dorsal scales equal in size throughout body, intermixed with numerous, large, multi-keeled, semi-longitudinally arranged tubercles; tubercles extend from occiput to base of tail and are smallest anteriorly; 29 paravertebral tubercles; pectoral and abdominal scales flat, keeled, subimbricate, equal in size, much larger than dorsals; four pore-bearing, precloacal scales arranged in a 2(R)–2(L) chevron, separated medially by two non-pore-bearing scales; forelimbs moderately long (FL/SVL 0.17), slender, dorsal scales keeled; ventral scales of forearm smooth, juxtaposed to subimbricate; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; claws recurved; subdigital lamellae unnotched; subdigital lamellae wide throughout proximal portion of digits to inflection, more granular after inflection, bearing a larger scale at the digital inflections; interdigital webbing absent; fingers increase in length from first to fourth with fifth slightly shorter than fourth; hind limbs longer and thicker than forelimbs (TBL/SVL 0.21); dorsal scales keeled, raised, juxtaposed; ventral scales of thigh, raised, keeled; subtibials keeled, larger than dorsal tibials; plantar scales smooth, slightly raised, juxtaposed; no enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae wide throughout length of digits except at base where scales are more granular; enlarged, scale at the digital inflections; interdigital webbing absent; toes increase in length from first to fourth with fourth being longest; 27R,26L subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; caudal scales raised, keeled, juxtaposed anteriorly; moderate, middorsal furrow; deep, single, lateral furrow; subcaudals keeled, no enlarged median row of scales; opposing paravertebral, dorsolateral, and lateral rows of large, keeled, equally sized, caudal tubercles; no ventrolateral caudal tubercles; caudal tubercles encircle tail, absent from lateral furrow; 1R,L postcloacal tubercle on lateral surface of hemipenal swellings at base of tail; anterior 11.9 mm original, reamainder 17.0 mm regenerated.

Coloration in life (Fig. 26). Dorsal ground color of head, body, limbs and tail pale-yellow; rostrum bearing diffuse, faint brown spots; single, diffuse, black, postorbital stripe extending to occiput; diffuse, light yellow, oblong, vertebral marking on nape; paired, brown nape spots followed by pair of brown, paravertebral spots on neck followed by five small, irregularly shaped, brown, spots terminating at base of tail; original portion of tail faintly banded; regenerated portion of tail uniform pale gray; butterfly-shaped, pale-yellow, vertebral markings between paired, brown spots; yellow prescapular crescent followed by faint, semi-transversely arranged, yellow bars on flanks; forelimbs bearing yellowish blotches and scattered faint, dark markings; hind limbs bearing yellowish blotches and dark markings resembling a reticulate pattern; digits bearing dark bands; gular region yellowish orange; throat beige; abdomen, ventral surface of hind limbs, and subcaudal region yellow; ventral surface of forelimbs beige; all ventral scales bearing small, black stippling.

Variation. The paratypes resemble the holotype in coloration (Fig. 26). The difference is that the Thai specimens are generally darker and more boldly patterned. The light nape marking on LSUHC 9979 is particularly apparent. Meristic and mensural differences are presented in Table 8.

TABLE 8. Meristic and mensural character states of the type series of *Cnemaspis omari* sp. nov. w = weak; f = female; and m = male. Meristic abbreviations are listed in the Materials and Methods. For TL, the measurement for the original portion of the tail is on the left and the measurement for the regenerated portion is on the right.

	LSUHC 9564 paratype	LSUHC 9565 paratype	LSUHC 9978 holotype	LSUHC 9979 paratype
SVL (mm)	40.5	39.7	41.3	39.9
Supralabials	9	9	8	9
Infralabials	8	8	7	8
Ventral scales keeled (1) or not (0)	1	1	1	1
No. of precloacal pores	/	/	4	/
Precloacal pores continuous (1) or separated (0)	/	/	0	/
Precloacal pores elongate (1) or round (0)	/	/	0	/
No. of paravertebral tubercles	22	26	29	24

......*continued on the next page*

TABLE 8. (Continued)

	LSUHC 9564 paratype	LSUHC 9565 paratype	LSUHC 9978 holotype	LSUHC 9979 paratype
Tubercles linearly arranged (1) or more random (0)	0	0	w	w
Tubercles present (1) or absent (0) on flanks	1	w	1	1
Caudal tubercles in lateral furrow (1) or not (0)	0	/	0	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	0	/	0	0
Lateral caudal tubercle row present (1) or absent (0)	1	/	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	/	0	0
Subcaudals keeled (1) or not (0)	0	/	1	1
Single median row of keeled subcaudals (1) or not (0)	0	/	0	0
Caudal tubercles encircle tail (1) or not (0)	1	/	1	1
Enlarged median subcaudal scale row (1) or not (0)	0	/	0	0
Postcloacal spurs	/	/	1	/
Enlarged femoral scales present (1) or absent (0)	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0	0
No. of 4th toe lamellae	25	25	26	28
Sex	f	f	m	f
TL	53.6	23.5	11.9/17.0	15.8/23.2
TW	4.1	4.1	4	5.1
FL	6.8	6.8	7.2	6.6
TBL	7.9	8.3	8.5	8.1
AG	18	18.7	20.2	18.3
HL	10.7	10.5	11	10.3
HW	6.2	6.2	7.1	6.4
HD	4	4.1	4.5	4.4
ED	2.2	2.5	2.4	2.3
EE	2.9	2.7	2.9	2.8
ES	5	4.8	5.5	5.1
EN	3.8	3.6	3.9	3.5
IO	2.2	2.6	2.9	2.4
EL	1	1	1.3	1.1
IN	0.8	1.1	1.2	1

Comparisons. *Cnemaspis omari* sp. nov. is one of five confirmed species in the *siamensis* group (Fig. 2). Within this group, it forms a monophyletic lineage with *C. chanardi* and its sister species *C. roticanai.* This lineage is diagnosed by the presence of a light colored prescapular crescent. *Cnemaspis omari* sp. nov. most closely resembles *C. roticanai* but differs from it in being smaller (max SVL 41.3 vs 47.0); having a lateral row of caudal tubercles; caudal tubercles that encircle the tail; and having a sequence divergence of 7.2% from *C. roticanai* (Table 4). It differs from *C. chanardi* in having four as opposed to 6–8 pore-bearing precloacal scales; and lacking a median row of enlarged subcaudal scales. From *C. siamensis, C. omari* is separated by having as opposed to lacking precloacal pores; having caudal tubercles that encircle the tail; lacking a row of enlarged median subcaudal scales; having a light colored pre-scapular crescent; and lacking dark, gular blotches. Form *C. huaseesom, C. omari* sp. nov. differs in having keeled as opposed to smooth ventral scales; having four pore-bearing scales with round pores as opposed to 5–8 pore-bearing scales with elongate pores; having keeled as opposed to smooth subcaudal and subtibial scales; having caudal tubercles that encircle the tail; having a light-colored pre-scapular crescent; and lacking a yellow head, forelimbs, and tail in adult males.

Etymology. We name this species in honor of the current Vice-Chancellor of Universiti Sains Malaysia, Penang, Professor Dato' Omar Osman. This is a sign of appreciation for all the support and funding from the university and for accelerating the research of biodiversity and wildlife studies in Peninsular Malaysia for many years.

Natural history. At the Phuphaphet Cave area in Satun, Thailand at 220 m in elevation, Grismer *et al.* (2010a) reported lizards being collected and observed during the day on the buttresses of trees and within tree holes between 1.5–2 m above the ground along a footpath in old, secondary forest. All the trees upon which the lizards were observed had holes into which the lizards would retreat upon provocation. Several rock outcrops were nearby but no lizards were observed on them. We have made similar observations on lizards from Perlis, Malaysia (Fig. 27), observing them at night on the trunks of large trees. LSUHC 9564 from the Phuphaphet Cave area was carrying two eggs indicating that the reproductive season extends through October.

FIGURE 27. Lowland dipterocarp forest of *Cnemaspis omari* sp. nov. at Perlis State Park, Perlis, Peninsular Malaysia. Photograph by LLG.

Cnemaspis roticanai Grismer & Chan, 2010
Roti Canai Rock Gecko
Fig. 28

Holotype. ZRC 2.6860. Type locality: "743 m a.s.l. on Gunung Raya, Pulau Langkawi, Kedah, Peninsular Malaysia (06°22.114N, 99°49.270 E)" at 790 m in elevation.

Diagnosis. Maximum SVL 47.0 mm; eight or nine supralabials; seven or eight infralabials; keeled ventral scales; 3–6 discontinuous, pore-bearing precloacal scales with round pores; 25–27 paravertebral tubercles; tubercles on flanks; tubercles in lateral caudal furrows; no ventrolateral caudal tubercles; caudal tubercles do not encircle tail; lateral caudal tubercle row absent; subcaudals keeled; median row of weakly enlarged subcaudal scales present; one or two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales on first toe; 26–29 subdigital fourth toe lamellae; light colored prescapular crescent; gular and pectoral regions, abdomen, underside of hind limbs, and subcaudal region yellow in males (Tables 6,7).

FIGURE 28. *Cnemaspis roticanai* from Gunung Raya, Pulau Langkawi, Kedah, Peninsular Malaysia. Upper left: ventral coloration of adult male (lower) and adult female (upper) showing sexual dimorphism (LSUDPC 5192). Upper right: adult male (LSUDPC 5184) in light color pattern phase. Lower right: adult female (LSUDPC 5189) in dark color pattern phase. Lower left: microhabitat on Gunung Raya. Photographs by LLG.

Color pattern (Fig. 28). Males: dorsal ground color of head, body, limbs and tail pale-yellow; faint, brownish markings on top of head; single, diffuse, black, postorbital stripe extending to occiput and terminating at oblong, longitudinally oriented, yellow spot on nape followed by a pair of black, paravertebral spots on neck; rhomboidially shaped, brown, transverse markings between limb insertions extending onto tail as zig-zag-shaped, caudal bands; butterfly-shaped, pale-yellow interspaces between rhomboid markings; yellow, prescapular crescent followed by semi-transversely arranged, yellow bars on flanks separated by dark makings; forelimbs bearing yellowish blotches and scattered dark markings; hind limbs bearing yellowish blotches and dark markings resembling banding pattern; gular region yellowish orange; throat beige; abdomen, ventral surface of hind limbs, and subcaudal region yellow; ventral surface of forelimbs beige; all ventral scales bearing small, black stippling. Sexual dimorphism is marked in this species. Females: darker in overall coloration with much less yellow and a more contrasted dorsal pattern; dark markings on trunk appear as paravertebral blotches and in strong contrast to the pale-yellow interspaces; tail strongly banded; ventral surfaces yellowish throughout.

Distribution. *Cnemaspis roticanai* is known only from Gunung Raya on Pulau Langkawi, Kedah, Peninsular Malaysia (Fig. 3). This species is expected to range more widely throughout the island.

Natural history. *Cnemaspis roticanai* is a scansorial species occurring in open habitats with small, widely scattered rocks in hill dipterocarp forest above 400 m in elevation (Fig. 28). Grismer & Chan (2010) observed specimens on the underside of leaves, on tree trunks, and within cement drains. We hypothesize here that *C. roticanai* is a diurnal species being that the specimens we have observed at night were inactive and sleeping on tree trunks and the undersides of leaves. Others were found between rocks.

Relationships. *Cnemaspis roticanai* is the sister species of *C. omari* sp. nov. (Fig. 2).

Material examined. Malaysia: Kedah, Pulau Langkawi, Gunung Raya LSUHC 9453, ZRC 2.6860–62 (type series). Material examined since Grismer & Chan (2010): Kedah, Pulau Langkawi, Gunung Raya LSUHC 9430–31, 9439, 10802.

***Argus* group.** The *argus* group contains four species with a somewhat anomalous distribution pattern (Fig. 3). The basal species, *Cnemaspis flavigaster* Chan & Grismer occurs in central Peninsular Malaysia west of the Banjaran Titiwangsa mountains on the outskirts of Kuala Lumpur in Kepong, Ulu Gombak, and Batu Caves, Selangor (Chan & Grismer 2008) whereas the remaining three species, *C. argus* Dring and the sister species *C. karsticola* Grismer, Grismer, Wood & Chan and *C. perhentianensis* Grismer & Chan have restricted distributions in northeastern Peninsular Malaysia. *Cnemaspis argus* is known only from the mountainous region of Gunung Lawit (Dring 1979) and Gunung Tebu, Terengganu (Grismer *et al.* 2013c), *C. karsticola* is known from a single tower karst formation at Gunung Reng (Grismer *et al.* 2008b), and *C. perhentianensis* is endemic to two islands in the Perhentian Archipelago, Kelantan (Grismer & Chan 2008).

The *argus* group is the sister lineage to the *affinis* group of central Peninsular Malaysia (Fig. 2) and is diagnosed by having a maximum SVL of 47.0–65.2 mm; 7–10 supralabials; 6–10 infralabials; 6–10 contiguous, pore-bearing, precloacal scales with round pores; randomly arranged dorsal tubercles extending onto the lower flanks; 17–32 paravertebral tubercles; no caudal tubercles in lateral furrows; a lateral row of caudal tubercles; no tubercles encircling the tail; no ventrolateral caudal tubercles; no median row of enlarged or keeled subcaudal scales; 1–4 postcloacal tubercles on each side of the base of the tail; no enlarged femoral or subtibial scales; subtibials keeled; and 27–35 lamellae beneath the fourth toe.

Cnemaspis flavigaster Chan & Grismer, 2008

Orange-bellied Rock Gecko
Fig. 29

Cnemaspis affinis Boulenger 1912:39
Cnemaspis kumpoli Dring 1979:223

Holotype. HC 00282. Type locality: "the canopy walk trail at Forest Research Institute Malaysia (FRIM), state of Selangor, Peninsular Malaysia (3°14'23.04"N, 101°37'59.80" E)" at 120 m in elevation.

Diagnosis. Maximum SVL 50.1 mm; nine or ten supralabials; 8–10 infralabials; smooth ventral scales; seven or eight contiguous pore-bearing precloacal scales with round pores; 21–24 paravertebral tubercles; tubercles on flanks; tubercles absent from lateral caudal furrows; no ventrolateral caudal tubercles; lateral caudal row of tubercles present; caudal tubercles do not encircle tail; subcaudals smooth with no enlarged, median scale row; one or two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; enlarged submetatarsal scales on first toe; 29–34 subdigital fourth toe lamellae; wide, black, oblique stripe in shoulder region; distinct black and white bands on tail; pectoral region, abdomen, ventral surface of hind limbs, and subcaudal region orange in males (Tables 6,7).

Color pattern (Fig. 29). Dorsal ground color brown to dark grey; sides of the head bearing yellow markings; three faint, postorbital stripes radiate from eye; three dark spots across the occiput anteriorly with another elliptical, medial spot posteriorly; paired, paravertebral spots on nape; dark, dorsolateral line extending from nape to forelimb insertion and onto brachium; paired, paravertebral, dorsal spots on body alternating with large, whitish blotches extending from shoulder to base of tail; another series of spots on flanks; flanks bear irregularly shaped, yellow blotches; dorsal surface of limbs bear irregularly shaped, dark and light markings; black and dull white bands nearly encircle tail; undersides of head and limbs mottled with fine, dark stippling; throat whitish; and chest, abdomen and underside of tail orange in males and beige in females. Coloration lightens considerably at night, highlighting the blotched dorsal pattern.

Distribution. *Cnemaspis flavigaster* is known only from the Forest Research Institute of Malaysia, Batu Caves, Selangor (Chan & Grismer 2008), and is newly reported here from Ulu Gombak, Selangor (Fig. 3).

Natural history. *Cnemaspis flavigaster* is a scansorial species restricted to granite rocks or karst (Flower 1899; Grismer & Chan 2008; Fig. 29) in lowland, old secondary forest and is only occasionally seen on tree trunks or fallen logs but never on leafy vegetation (Grismer 2011a). Grismer (2011a) noted that *C. flavigaster* is quite wary while abroad during the day on the shaded sides of rocks and deep within small alcoves. At night however, lizards venture farther out into open areas on the rocks and are more stationary. Grismer *et al.* (2010c) outlined a number of examples where sympatric species of *Cnemaspis* seem to be partitioning their habitat by having different activity periods, body sizes, substrate preferences or varying combinations of each. Inconsistent with these observations was finding *C. flavigaster* at Ulu Gombak in syntopy on granite boulders with *C. peninsularis* sp. nov., *Cnemaspis peninsularis* sp. nov., however, is a habitat generalist and its presence on other substrates at Ulu Gombak may be enough to not preclude strong competition for resources. At Batu Caves, *C. flavigaster* has been observed at the entrance to Dark Cave.

Relationships. *Cnemaspis flavigaster* is the basal species of the *argus* group (Fig. 2).

Material examined. Malaysia: Selangor, Kepong, Forest Research Institute of Malaysia HC 00282, 00286; ZRC 2.6708–11 (type series). Material examined since Chan & Grismer (2008): Malaysia: Selangor, Kepong, Forest Research Institute of Malaysia LSUHC 6562, 8835–36; Ulu Gombak LSUHC 10380.

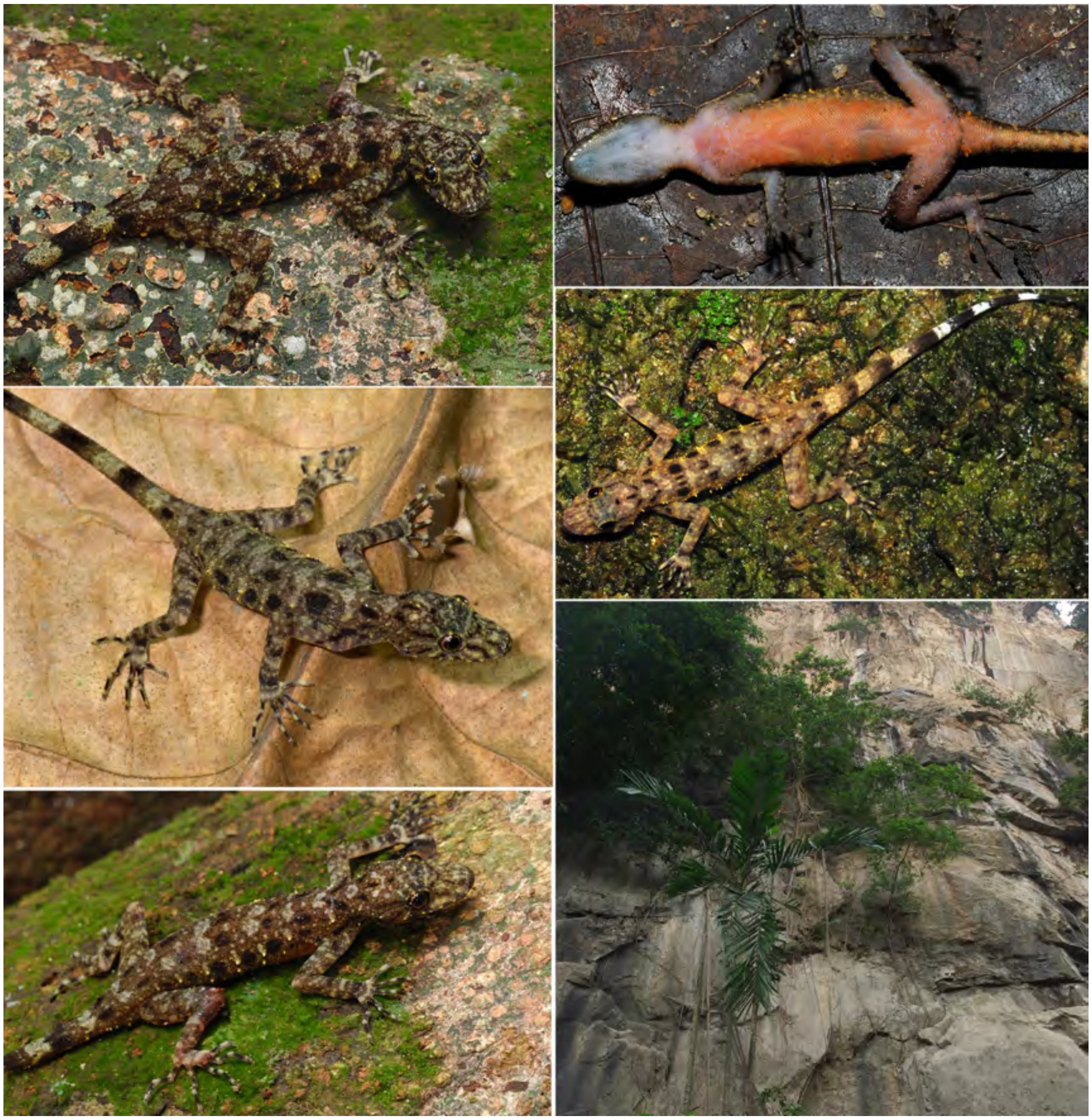

FIGURE 29. *Cnemaspis flavigaster* from FRIM, Kepong, Selangor, Peninsular Malaysia. Upper left: adult male (LSUDPC 4173) in the dark color pattern phase. Upper right: ventral view of adult male (LSUDPC 4181). Photographs by LLG. Middle left: adult female (LSUDPC 4601) in the dark color pattern phase. Photograph by CKO. Middle right: adult male (LSUDPC 4671) in the light color pattern phase. Lower left: subadult (LSUDPC 4178) in dark color pattern phase. Lower right; karst microhabitat at the Batu Caves, Selangor, Peninsular Malaysia. Photographs by LLG.

Cnemaspis argus Dring, 1979
Argus Rock Gecko
Fig. 30

Holotype. BM 1974.4911. Type locality: "790 m on the east ridge of Gunung Lawit", Terengganu, Peninsular Malaysia.

Diagnosis. Maximum SVL 65.2 mm; eight or nine supralabials; eight or nine infralabials; keeled ventral scales; 6–10 pore-bearing precloacal scales; 26–32 paravertebral tubercles; tubercles not linearly arranged, present on flanks; tubercles absent from lateral caudal furrows; no ventrolateral caudal tubercles, lateral row of caudal tubercles present; caudal tubercles not encircling tail; subcaudals keeled, no enlarged median scale row; 1–4 postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales on first toe; 31–35 subdigital fourth toe lamellae; distinct black and white bands on tail (Tables 6,7).

Color pattern (Fig. 30). Dorsal ground color greyish yellow; interorbital region green; yellow markings on head; paired, black, paravertebral, subelliptically shaped blotches extending from nape to tail and transforming into black bands; large patches of yellow tubercles and short transverse bars on flanks; limbs bearing faded, alternating, dark and light bands; non-regenerated tail bearing black and white bands; all ventral surfaces dull-white.

FIGURE 30. Left: microhabitat of *Cnemaspis argus* on Gunung Lawit, Terengganu, Peninsular Malaysia. Upper right: adult male (LSUDPC 6564) from Gunung Tebu, Terengganu, Peninsular Malaysia in the light color pattern phase. Photographs by LLG. Lower right: adult female (LSUDPC 6390) from Gunung Tebu in the dark color pattern phase. Photograph by ESHQ.

Distribution. *Cnemaspis argus* is known from Gunung Lawit (Dring 1979) and newly reported here from Gunung Tebu, Terengganu 10 km to the north along the same mountain range (Fig. 3).

Natural history. Dring (1979) reported *Cnemaspis argus* to occur at 790 m in elevation in primary forest from Gunung Lawit and Grismer (2011a) considered it an upland endemic that would probably never be seen again because the trail up to Gunung Lawit had become overgrown and lost. However, we did find additional populations from the base of Gunung Lawit at 230 m in elevation and on Gunung Tebu from 40 m in elevation at Hutan Lipur Lata Belatan up to 750 m near the peak. All lizards were seen on large granite rocks within the forest (Fig. 30). These data indicate that *C. argus* is not an upland endemic but a microhabitat specialist restricted to granite rocks wherever they may occur within its range. During the day, lizards remain wary and occur on the shady, vertical or inverted surfaces. They are in dark in overall coloration and difficult to approach. During the evening hours, lizards are much lighter in color and far less wary, tending to venture farther out onto the open areas of the boulders where they appear generally inactive.

Relationships. *Cnemaspis argus* is most closely related to the sister species *C. karsticola* and *C. perhentianensis* (Fig. 2).

Material examined. Malaysia: Terengganu, Gunung Lawit BM 1974.4910–11 (type series; photographs LSUDPC 2276–78), LSUHC 8304; Gunung Tebu LSUHC 10834–35, 10858–59.

FIGURE 31. *Cnemaspis karsticola* from Gunung Reng, Kelantan, Peninsular Malaysia. Upper left: adult female (LSUDPC 4424) in the dark color pattern phase. Upper right: adult male (LSUDPC 4421) in the dark color pattern phase. Lower; karst microhabitat at Gunung Reng. Photographs by LLG.

Cnemaspis karsticola Grismer, Grismer, Wood & Chan, 2008b

Karst Rock Gecko

Fig. 31

Holotype. ZRC 2.6765. Type locality: "Gunung Reng, Kelantan, Peninsular Malaysia (05°42.905 N, 101°44.726 E)" at 113 m in elevation.

Diagnosis. Maximum SVL 48.1 mm; seven or eight supralabials; six or seven infralabials; ventral scales keeled; seven or eight contiguous, pore-bearing precloacal scales with round pores; 17–19 paravertebral tubercles; body tubercles not linearly arranged, present on flanks; tubercles absent from lateral caudal furrows; no ventrolateral caudal tubercles; lateral row of caudal tubercles present; caudal tubercles not encircling tail; all subcaudals keeled, no enlarged median scale row; two or three postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no submetatarsal scales on first toe; 27–30 subdigital fourth toe lamellae; subcaudal region white (Tables 6,7).

Color pattern (Fig. 31). Dorsal ground color yellowish brown; head and body overlain with faded, irregularly shaped, white markings; no dark, postorbital striping; three, dark, radiating, anteriorly projecting lines occur on occiput; paired, dark, paravertebral markings extend from nape to base of tail, similar markings on flanks; no transversely elongate, white markings on flanks; irregularly shaped, dark and light markings on limbs; diffuse, alternating, light markings on dorsal surface of tail; subcaudal region white, immaculate; regenerated portion of tail beige, immaculate.

Distribution. *Cnemaspis karsticola* is known from only from Gunung Reng, Kelantan, Peninsular Malaysia (Grismer *et al.* 2008b).

Natural history. Grismer *et al.* (2008b) noted that *Cnemaspis karsticola* is a lowland saxicolous species known only from the karst outcropping of Gunung Reng, a large isolated tower karst formation reaching 200 m in height situated along the east bank of the Pergau River at its junction with Batu Melintang, Kelantan. The base of the tower is undercut and numerous cracks and indentations accentuate and define its periphery (Fig. 31). Lizards were found during the day along the periphery of the karst formation and within cracks on the shaded surfaces of large, disconnected, karst boulders that have fragmented and fallen off the core. Lizards were not found deep within the larger cave system. Specimens were seen in cracks, on shaded overhangs, and on the cave walls no more than 2 m above the ground. No lizards were seen at night indicating this is a diurnal species. The color variation in the type series indicates this species is adept at substrate matching (Grismer *et al.* 2008b).

Relationships. *Cnemaspis karsticola* is the sister species of *C. perhentianensis* Grismer & Chan (Fig. 2).

Material examined. Malaysia: Kelantan, Gunung Reng ZRC 2.6763–65, LSUHC 9054. Additional material examined since Grismer *et al.* (2008b): Malaysia: Kelantan, Gunung Reng LSUHC 9053, 9055–56.

Cnemaspis perhentianensis Grismer & Chan, 2008

Perhentian Island Rock Gecko
Fig. 32

Holotype. ZRC 2.6675. Type locality: "Pulau Perhentian Besar, Terengganu, West Malaysia (05°54.054 N, 102°44.726343 E)" at 40 m in elevation.

Diagnosis. Maximum SVL 47.0 mm; 8–10 supralabials; seven or eight infralabials; ventral scales smooth to keeled; 6–8 contiguous, pore-bearing precloacal scales with round pores; 22–27 paravertebral tubercles; tubercles not linearly arranged, present on flanks; tubercles absent from lateral caudal furrows; no ventrolateral caudal tubercles; lateral row of caudal tubercles present; caudal tubercles not encircling tail; all subcaudals keeled, no median row of enlarged subcaudals; three or four postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no submetatarsal scales on first toe; 28–31 subdigital fourth toe lamellae; distinct black and white bands on tail (Tables 6,7).

Color pattern (Fig. 32). Dorsal ground color grey to brown, overlain by irregularly shaped, white markings on top of head and snout; paired, white markings on occiput; no postorbital stripes; squarish, medial, white marking on neck; distinct, irregularly shaped, paravertebral, white markings on dorsum extending from shoulder region to base of tail and alternating with transversely elongate, distinct, white markings on flanks; three small, elongate, dark blotches at base of occiput; paired, dark, poorly defined, paravertebral blotches extend from nape to anterior portion of tail alternating with light, paravertebral markings; dark blotches on flanks alternating with white, transverse markings; black and dull white bands nearly encircle tail; irregularly shaped, dark and light markings on limbs; ventral surfaces of neck, body, and limbs beige, immaculate; gular region smudged with dark stippling.

FIGURE 32. Upper: adult male *Cnemaspis perhentianensis* (LSUDPC 5159) from Pulau Perhentian Besar, Terengganu, Peninsular Malaysia in the dark color pattern phase. Photographs by LLG. Lower: granite boulder microhabitat on Pulau Perhentian Besar. Photograph by Peter Carin.

Distribution. *Cnemaspis perhentianensis* is known from only from Perhentian Besar and Perhentian Kecil islands (Grismer & Chan 2008; Grismer *et al.* 2011a) of the Perhentian Archipelago, Terengganu off the northeast coast of Peninsular Malaysia (Fig. 3).

Natural history. The Perhentian Archipelago is composed of 11 relatively small islands lying 21 km off the east coast of the state of Terengganu (Fig. 3). The largest of these islands, Pulau Perhentian Besar (ca. 857 hectares) is a rugged, hilly island reaching 249 m in elevation. The majority of the island is covered in primary, lowland dipterocarp forest and its granite bedrock is the source of extensive boulder outcroppings that add a significant degree of habitat and microhabitat complexity to the island's ecosystem, which in turn, supports various saxicolous species (Grismer *et al.* 2011a). Grismer & Chan (2008) noted that *Cnemaspis perhentianensis* is restricted solely to the granite outcroppings (Fig. 32). Specimens collected or observed during the day were found on the shaded surfaces of both large and small rocks and would retreat into cracks at the slightest provocation. Upon retreat, lizards would roll their tail over their back and wag the tip from side to side. At night, lizards could be found on all surfaces of the rocks at greater distances from their crevice microhabitats and appreaed inactive. No lizards were seen on tree trunks or other types of vegetation. Grismer & Chan (2008) reported that the activity of *C. perhentianensis* may be closely tied to precipitation, noting that on multiple trips, specimens were only observed following periods of rain.

Relationships. *Cnemaspis perhentianensis* is the sister species of *C. karsticola* (Fig. 2).

Material examined. Malaysia: Terengganu, Pulau Perhentian Besar ZRC 2.6675–79 (type series). Additional material examined since Grismer & Chan (2008): Malaysia: Terengganu, Pulau Perhentian Besar LSUHC 8673, 8675–76, 8697–700, 9060, 9412.

***Affinis* group.** The *affinis* group contains 13 species that collectively range throughout central Peninsular Malaysia and is comprised of three basal lineages: *Cnemaspis pseudomcguirei* from northwestern Peninsular Malaysia; the sister species *C. affinis* and *C. harimau* from northwestern Peninsular Malaysia and their sister lineage that contains the remaining 10 species (Figs. 2,3). The latter lineage, for the most part, is a polytomy. However, the sister species relationship between *C. mcguirei* and *C. grismeri* associated with the Banjaran Bintang Mountains and the relationships between the diminutive, lowland karst-dwellers *C. hangus* sp. nov., *C. selamatkanmerapoh,* and *C. bayuensis* east of the Banjaran Titiwangsa Mountains and the small, upland granite-dweller *C. stongensis* sp. nov. in the northern Banjaran Titiwangsa Mountains are strongly supported (Fig. 2). The sister species relationship between *C. mcguirei* and *C. grismeri* is strongly supported in the molecular analysis and further supported in the morphological analysis by them having a pair of ocelli in the shoulder region which we consider to be a derived condition in that it occurs in no other species of *Cnemaspis.*

The molecular analysis indicates that *Cnemaspis flavolineata* from the type locality at the Gap below Fraser's Hill, Pahang is not conspecific with *C. flavolineata* from Cameron Highlands (18.0% sequence divergence; Table 4), 76 km to the north and the two species may not even be closely related (Fig. 2). We also found significant differences in tuberculation separating these two populations. Smith (1922) was the first to report this species from Fraser's Hill which he considered conspecific with *C. kendallii* (Gray) but later (Smith 1930) and without comment, referred to it as *C. affinis.* Although Nicholls (1949) was the first to recognize this population as a distinct species, his brief description did not provide a single diagnostic character separating it from either *C. affinis* or *C. kendallii* (quite frankly, he got lucky). As such we provide a redescription of this species below based on the holotype and a second specimen recently collected from the type locality and describe the Cameron Highlands population as a new species (*C. temiah* sp. nov.).

The *affinis* group is diagnosed as having a maximum SVL of 36.5–65.0 mm; 7–13 supralabials; 7–11 infralabials; keeled ventral scales; 0–10 pore-bearing precloacal scales with round pores; 18–34 paravertebral tubercles; tubercles on flanks; lateral row of caudal tubercles present; subcaudals keeled; no median row of enlarged subcaudal scales; 1–5 postcloacal tubercles on each side of base of tail; no enlarged femoral or subtibial scales; subtibials keeled; no submetatarsal scales on first toe; and 21–35 lamellae beneath the fourth toe.

***Cnemaspis affinis* (Stoliczka, 1870)**

Penang Island Rock Gecko
Fig. 33

Gymnodactylus affinis Boulenger 1885:42
Gonatodes penangensis Flower 1896:863

FIGURE 33. *Cnemaspis affinis* from Penang Hill, Pulau Pinang, Penang, Peninsular Malaysia. Upper left: adult male (LSUDPC 9078) in the dark color pattern phase. Lower left: adult female (LSUDPC 9079) in the light color pattern phase. Upper right: microhabitat of *C. affinis* on Penang Hill. Lower right: ventral coloration of male (left) and female (right) *C. affinis.* Photographs by LLG.

Holotype. ZSI 5964. Type locality: "Penang Hills", Penang Island, Penang, Peninsular Malaysia at approximately 800 m in elevation.

Diagnosis. Maximum SVL 50.8 mm; 9–13 supralabials; 8–10 infralabials; ventral scales keeled; five or six discontinuous, pore-bearing precloacal scales with round pores; 20–28 paravertebral tubercles; dorsal tubercles not linearly arranged, present on flanks; tubercles absent from lateral caudal furrows; ventrolateral caudal tubercles absent; lateral caudal row present; caudal tubercles not encircling tail; all subcaudals keeled, no enlarged median scale row; two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no submetatarsal scales on first toe; 28 or 29 subdigital fourth toe lamellae; gular region yellow in males; single ocellus in shoulder region in males, yellow post-scapular band in males; and transverse yellow bars on flanks (Tables 6,7).

Color pattern in life (Fig. 33). Adult males: dorsal ground color grey to brown; paired white markings on occiput; dark pre- and postorbital stripes are present with latter extending onto nape; medial, white marking on nape followed by distinct, large, black shoulder patches in males usually enclosing a white to yellow ocellus anteriorly and edged posteriorly by yellow spot; irregularly shaped, paravertebral, white markings on dorsum extending to base of tail and confluent with transversely elongate, distinct, yellow markings on flank. Adult females: slightly less boldly marked; tend to lack postscapular band, more yellowish overall.

Distribution. *Cnemaspis affinis* is endemic to Penang Island, Penang, Peninsular Malaysia (Grismer *et al.* 2008b; Fig. 3).

Natural history. Grismer *et al.* (2008b) indicated that *Cnemaspis affinis* is found only in the upland regions of Penang Island in the vicinity of 720 m where it occurs on large granite boulders in disturbed forest (Fig. 33). During the day, lizards are active on the shaded surfaces of the boulders and quite wary but at night, venture farther out onto the boulder's surface (Flower 1896). Flower (1896) reported finding a specimen beneath the bark of a large tree. We suspect, however, this was not *C. affinis* but the similarly appearing *C. shahruli,* which is a habitat generalist and known to occur on vegetation (Grismer *et al.* 2010c; Grismer 2011a). Gravid females carrying two eggs have been observed during July.

Relationships. *Cnemaspis affinis* is the sister species of *C. harimau* (Fig. 2).

Material examined. Malaysia: Penang, Penang Island LSUHC 6758–59, 6773–74, 6787–88, ZRC 2.1098, 2.5203, 2.4858, 2.6017–18, ZSI 5964 (holotype). Additional material examined since Grismer & Chan (2008): Malaysia: Penang, Penang Island LSUHC 10347.

Cnemaspis harimau Chan, Grismer, Shahrul, Quah, Muin, Savage, Grismer, Norhayati, Remegio & Greer, 2010b

Tiger Rock Gecko
Fig. 34

Holotype. ZRC 2.6894. Type locality: "Sungai Badak (=Badak river), Gunung Jerai, Kedah, Peninsular Malaysia (N 05°48.59', E 100°23.53')" at 600 m in elevation.

FIGURE 34. *Cnemaspis harimau* from Sungai Badak, Gunung Jerai, Kedah, Peninsular Malaysia. Upper left: adult male (LSUDPC 6381) in the dark color pattern phase. Upper right: adult female (LSUDPC 5334) in the light color pattern phase. Lower left: adult female (LSUDPC 6382) in the light color pattern phase. Photographs by LLG. Middle right: juvenile male (LSUDPC 6520) in light color pattern phase. Photograph by ESHQ. Lower right: ventral view of adult male (LSUDPC 5337). Photograph by LLG.

FIGURE 35. Microhabitat of *Cnemaspis harimau* at Sungai Badak, Gunung Jerai, Kedah, Peninsular Malaysia. Photograph by LLG.

Diagnosis. Maximum SVL 40.7 mm; nine or 10 supralabials; nine or 10 infralabials; ventral scales keeled; four discontinuous, pore-bearing precloacal scales with round pores; 18–20 paravertebral tubercles; tubercles not linearly arranged, present on flanks; tubercles in lateral caudal furrows; ventrolateral caudal tubercles absent anteriorly; lateral row of caudal tubercles present; caudal tubercles encircling tail; all subcaudals keeled, no enlarged median scale row; two or three postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales on first toe; 25–30 subdigital fourth toe lamellae; gular region and throat yellow in males; single ocellus in shoulder region in males; yellow postscapular band variable; transverse yellow bars on flanks (Tables 6,7).

Color pattern in life (Fig. 34). Ground color of dorsum grayish-brown; top of head yellowish with an indistinct, gray speckling pattern on occiput; faint, preorbital stripe; three black lines radiate from anterior region of nape onto base of occiput; light, gray, irregularly shaped, paravertebral blotches extend from nape to base of tail; broken, dark, paravertebral, longitudinal streaks begin with paired streaks in prescapular region and alternate with paravertebral blotches posteriorly, terminating at base of tail; black shoulder patch bordered anteriorly by short, yellow band enclosing a whitish ocellus and bordered posteriorly by a longer, yellow band; shoulder patch absent in females; a series of yellow bands on flanks decreasing in length posteriorly with last band terminating just anterior to hind limb insertion; dorsal surfaces of limbs speckled with dark and yellowish markings; tail distinctly marked with diffuse, dark-gray and whitish bands; gular region and throat yellow-orange in males; ventral surfaces of limbs, remainder of body, and base of tail light gray; and subcaudal region darkly stippled.

Distribution. *Cnemaspis harimau* is endemic to Gunung Jerai, Kedah in northwestern Peninsular Malaysia (Chan *et al.* 2010b; Fig. 3).

Natural history. Gunung Jerai is an isolated mountain reaching 1217 m in elevation on the northwest shore of Peninsular Malaysia. Chan *et al.* (2010b) reported finding lizards on granite rocks and at the base of trees at 600 m in elevation during the day and night in hill forest vegetation (Fig. 35). Lizards appear to be far more active during the day and are much more sedentary at night. When frightened, lizards will seek refuge in the porus matrices formed by the dry expansive soil at the base of the rocks (Grismer 2011a). We have observed lizards on isolated rocks along the edge of the main road leading to the summit of Gunung Jerai beginning at approximately 400 m in elevation.

Relationships. *Cnemaspis harimau* is the sister species of *C. affinis* (Fig. 2).

Material examined. Malaysia: Kedah, Gunung Jeari LSUHC 9665, 9667, 9669, ZRC 2.6894–97 (type series). Additional material examined since Chan *et al.* (2010): Malaysia: Kedah, Gunung Jerai LSUHC 8229, 8232–33, 9666, 9668.

Cnemaspis pseudomcguirei Grismer, Norhayati, Chan, Belabut, Muin, Wood & Grismer, 2009

False-McGuire Rock Gecko
Fig. 36

Holotype. ZRC 2.6777. Type locality: "Bukit Larut, Perak, Peninsular Malaysia along the road from the Gunung Hijau Rest House to the Telekom Tower (04°51.715 N, 100°47.993 E)" at 1351 m in elevation.

Diagnosis. Maximum SVL 42.5 mm; nine or 10 supralabials; 8–10 infralabials; ventral scales keeled; 1–5 continuous, pore-bearing precloacal scales with round pores; 23–32 paravertebral tubercles; body tubercles randomly arranged, present on flanks; tubercles present in lateral caudal furrows; no ventrolateral caudal tubercles; lateral row of caudal tubercles present anteriorly; caudal tubercles not encircling tail; all subcaudals keeled, no enlarged median scale row; two or three postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; usually no enlarged submetatarsal scales on first toe; 23–26 subdigital fourth toe lamellae; and two ocelli in the shoulder region in males; vertebral stripe variable (Tables 6,7).

Color pattern in life (Fig. 36). Dorsal ground color of head, body, limbs and tail golden brown; top of head bearing small, black and yellow markings; thin, black, postorbital stripe; thin, yellow, postorbital stripes unite on nape and may continue posteriorly to form a wide, vertebral stripe that fades in pelvic region; vertebral stripe variably present, often replaced by white, paravertebral markings edged anteriorly in black; dark markings on nape anterior to yellow stripe; black shoulder patch encloses a larger, upper, posterior white ocellus and smaller, lower, anterior ocellus; single, light, postscapular spot posterior to black shoulder patches; faint, yellow, transverse markings on flanks; faint, dark and dull-yellow reticulum on limbs; tail faintly marked with light-brown and dull-yellow bands; all ventral surfaces beige with weak stippling. The color pattern lightens considerably at night and many lizards appear nearly unicolor light-yellow to white.

FIGURE 36. *Cnemaspis pseudomcguirei* from Bukit Larut, Perak, Peninsular Malaysia. Upper left: adult male (LSUDPC 4723) in the dark color pattern phase. Upper right: adult female (LSUDPC 4756) in light color pattern phase sleeping on a leaf at night. Lower left: gravid female (LSUDPC 4731) in the dark color pattern phase. Lower right: hatchling (LSUDPC 6397). Photographs by LLG.

Distribution. *Cnemaspis pseudomcguirei* is known from Bukit Larut and Gunung Inas in the Banjaran Bintang Mountains, Perak, in northwestern Peninsular Malaysia (Grismer *et al.* 2009; Laidlaw 1901; Fig. 3).

Natural history. Grismer (2011a) noted that *Cnemaspis pseudomcguirei* is an upland species found in hill dipterocarp forests from at least 1,000–1,300 meters in elevation (Fig. 37). During the day, lizards are found beneath small stones and logs on the forest floor or within rotten logs. Unlike the sympatric species *C. mcguirei, C. pseudomcguirei* does not occur on large granite boulders and lizards are commonly found great distances (>1 km) from boulder outcroppings. At Gunung Inas, Laidlaw (1901) reported lizards being numerous "amongst boulders on the course of a small stream" which we believe he confused with the sympatric and similarly appearing *C. mcguirei.* During the night, *C. pseudomcguirei* can be found exposed sleeping on the surfaces of leaves 0.5–1.5 m above the ground. Females carrying two eggs have been found during March and October suggesting this species breeds through the rainy season.

Relationships. *Cnemaspis pseudomcguirei* is part of the basal tritomy of the *affinis* group (Fig. 2).

Material examined. Malaysia: Perak; Bukit Larut ZRC 2.6777–82 (type series). Material examined since Grismer *et al.* (2009): Malaysia: Perak, Bukit Larut LSUHC 9074, 10640, 10645.

FIGURE 37. Microhabitat of *Cnemaspis pseudomcguirei* at Bukit Larut, Perak, Peninsular Malaysia. Photograph by LLG.

Cnemaspis shahruli Grismer, Chan, Quah, Mohd, Savage, Grismer,Norhayati, Greer & Remegio, 2010c

Shahrul's Rock Gecko
Fig. 38

Holotype. ZRC 2.6898. Type locality: "Telok Bahang Recreational Forest Reserve, Penang (05°27.233'N, 100°12.324'E)" at 67 m in elevation.

Diagnosis. Maximum SVL 36.5 mm; 10 or 11 supralabials; 8–10 infralabials; ventral scales keeled; no precloacal pores; 19–23 paravertebral tubercles; body tubercles randomly arranged, present on flanks; tubercles within lateral caudal furrows; ventrolateral caudal tubercles absent anteriorly; lateral row of caudal tubercles present anteriorly; caudal tubercles not encircling tail; all subcaudals keeled, no enlarged median row; 1–3 postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; usually no enlarged submetatarsal scales on first toe; 21–30 subdigital fourth toe lamellae; light-colored vertebral stripe variably present; gular region, throat and pectoral region yellow in males; dark, central, elongate marking occurs in mental region; a single ocellus in the shoulder region in males; white, dorsal, caudal tubercles; distinct black and white caudal bands variably present (Tables 6,7).

Color pattern in life (Fig. 38). Dorsal ground color of head, body, limbs and tail pale brown; top of head with dark and light diffuse markings; dark, postorbital blotches; when present, a wide, light colored, vertebral stripe extends from occiput to base of tail; offset, opposing, paravertebral, dark markings extend from nape to base of tail; large, black, square, shoulder patches enclose a whitish to yellow ocellus in adult males, absent in females and juveniles; dark shoulder patches become greatly reduced in the nighttime color phase; large, light-colored markings occur on flanks and tend to form transverse bands; forelimbs and hind limbs mottled; gular region, throat, and anterior pectoral region yellow; gular region often faintly mottled; a dark, central, elongate marking occurs in mental region; ventral surfaces of limbs and body beige with small, black stipples in each scale; subcaudal region darker; tail faintly banded; regenerated tail mottled.

FIGURE 38. *Cnemaspis shahruli* from Peninsular Malaysia. Upper left: microhabitat of *C. shahruli* on Pulau Pangkor, Perak. Upper right: adult male (LSUDPC 5320) from Pulau Pinang, Penang in the dark color pattern phase. Photographs by LLG. Middle right: adult female (LSUDPC 6304) from Pulau Pangkor in the dark color pattern phase. Photograph by J. van Rooijen. Lower right: juvenile (LSUDPC 5880) from Bukit Mertajam, Penang in the light color pattern phase. Photograph by ESHQ. Lower left: ventral coloration of adult male (LSUDPC 5317) from Pulau Pinang.

Distribution. In northwestern Peninsular Malaysia, *Cnemaspis shahruli* is known from Penang Island and the adjacent island of Jerejak, Penang and the mainland localities of Sungai Sedim, Kedah and Bukit Mertajam, Penang. One hundred thirteen km farther south, *C. shahruli* is known from Pulau Pangkor, Perak, (Grismer 2011a; Grismer *et al.* 2010c; Fig. 3) and it is expected to occur in the intervening mainland areas between Pulau Pangkor and Bukit Mertajam.

Natural history. *Cnemaspis shahruli* is generally a nocturnal species that is only occasionally seen during the day. It is also a habitat generalist that occurs in both riparian and non-riparian microhabitats from near sea level to approximately 500 m in elevation and can be found on both rocks and vegetation (Grismer *et al.* 2010c; Fig. 38). In lowland areas on Penang Island, *C. shahruli* occurs in riparian areas where it is usually found on granite rocks and boulders that may or may not be covered in lichen or vegetation. Lizards are occasionally found on adjacent tree trunks provided they are near large rocks. On Pulau Jerejak, *C. shahruli* has been found in disturbed areas on rocks and tree trunks (Grismer *et al.* 2010c). Lizards are occasionally found beneath logs and at the base of trees. The only specimen known from Pulau Pangkor, Perak was collected during the day along a forest trail while it was clinging upside down to the underside of a leaf approximately 0.5 m above the ground.

Relationships. *Cnemaspis shahruli* may be the sister species to *C. narathiwatensis* (Fig. 2) although this relation is not statistically supported.

Material examined. Malaysia: Penang; Pulau Pinang ZRC 2.6898–902; Pulau Jerejak ZRC 2.6903; Sungai Sedim ZRC 2.6904. Perak: Pulau Pangkor ZRC 2.6905 (type series). Additional specimens examined since Grismer *et al.* (2010c): Malaysia: Penang; Pulau Pinang LSUHC 8875, 8879, 9572, 9575, 9595, 9862; Bukit Mertajam LSUHC 10375.

FIGURE 39. Adult male *Cnemaspis mcguirei* (LSUDPC 5173) from Bukit Larut, Perak, Peninsular Malaysia in the light color pattern phase. Photograph by LLG.

Cnemaspis mcguirei Grismer, Grismer, Wood & Chan, 2008b

McGuire's Rock Gecko

Figs. 39, 40

Gonatodes affinis Laidlaw 1901:304; Boulenger 1903:148, 1912:38; Smith 1930:16
Gonatodes kendalli Boulenger 1912:38
Cnemaspis kendallii Das & Bauer 1998:13 (in part)

Holotype. ZRC 2.6765. Type locality: "Bukit Larut, Perak, Peninsular Malaysia (04°51.715 N, 100°47.993)" at 1351 m in elevation.

Diagnosis. Maximum SVL 65.0 mm; 7–10 supralabials; 7–9 infralabials; ventral scales keeled; 5–10 usually discontinuous, pore-bearing precloacal scales with round pores; 26–32 paravertebral tubercles; body tubercles not linearly arranged, present on flanks; tubercles present in lateral caudal furrows; no ventrolateral caudal tubercles; lateral row of caudal tubercles present; caudal tubercles not encircling tail; all subcaudals keeled, no enlarged median subcaudal scale row; 2–5 postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales on first toe; 27–35 subdigital fourth toe lamellae; two ocelli in the shoulder region in males; wide, white to yellow postscapular band; yellow bars on flanks; distinct black and white caudal bands posteriorly (Tables 6,7).

FIGURE 40. *Cnemaspis mcguirei* (LSUDPC 5173) from Bukit Larut, Perak, Peninsular Malaysia. Upper left: adult male (LSUDPC 6303) in the dark color pattern phase. Photograph by CKO. Upper right: adult male (LSUDPC 5175) in the dark color pattern phase illustrating the dorsal ocelli. Lower right: adult female (LSUDPC 6409) in the dark color pattern phase in the typical diurnal position of clinging upside down to the underside of an overhang on a granite rock. Lower left: granite boulder microhabitat at Bukit Larut. Photographs by LLG.

Color pattern (Figs. 39, 40). Dorsal ground color grey to brown; head and body overlain with irregularly shaped, dark blotches; light markings on top of head; dark, postorbital stripe extends onto nape and contacts dark, anteriorly projecting, median stripe; medial, white marking occurs on nape followed by distinct, large, black, shoulder patches in males enclosing one or two (usually two) yellow ocelli; shoulder patches edged posteriorly by wide, postscapular band that is yellow laterally and white dorsally; irregularly shaped, paravertebral, white markings occur on body and extend to base of tail; transversely elongate, distinct, yellow markings occur on flanks; diffuse, brown and dull white bands encircle tail; irregularly shaped, dark and light markings occur on limbs; ventral surfaces of head, body, and limbs dull beige, immaculate and darkened laterally; females less boldly marked than males. Coloration lightens considerably at night.

Distribution. Grismer *et al.* (2008b) noted that *Cnemaspis mcguirei* ranges through Banjaran Bintang Mountains (Fig. 3) beginning at an isolated population from Gunung Bubu, Perak in the south, northward through the continuous central section of the Banjaran Bintang Mountains from Bukit Larut to Gunung Inas (Laidlaw 1901; Boulenger 1912) in the north (Fig. 3). From here the Banjaran Bintang Mountains continue northward and merge with the more extensive Banjaran Titiwangsa Mountains and these continue farther north as a series of smaller, parallel, north to south tending, somewhat isolated ranges, terminating just south of Pattani, Pattani Province, Thailand. At Namtok Sai Khao on the northeast perimeter of this range, Boulenger (1903) provided descriptions of four specimens that match the description of *C. mcguirei* and Grismer *et al.* (2008b), based on the examination of photographs (LSUDPC 4581–82) of these specimens (BM 1903.4.15.11–14), considered them to represent the northern extent of *C. mcguirei.* We follow that taxonomy here but note that this presents a 200 km hiatus from its northernmost distribution at Gunung Inas and that a firsthand examination of these specimens and a molecular analysis of this population may indicate they are different species.

FIGURE 41. *Cnemaspis grismeri* from Gua Asar, Bukit Kepala Gajah, Lenggong, Perak, Malaysia. Upper: adult female (LSUDPC 6693) in the dark color pattern phase. Lower: adult male (LSUDPC 6696) in the dark color pattern phase. Photographs by ESHQ.

FIGURE 42. Upper: juvenile *Cnemaspis grismeri* (LSUDPC 6695) from Gua Asar, Bukit Kepala Gajah limestone massif, Lenggong, Perak, Malaysia in light color pattern phase. Lower: karst microhabitat of at Gua Asar. Photographs by ESHQ.

Natural history. Grismer (2011a) noted that *Cnemaspis mcguirei* occurs in rocky, hilly terrain from approximately 900–1,300 m in elevation in lowland and hill dipterocarp and lower montane forests and occurs almost exclusively on granite rocks (Fig. 40) devoid of moss or on the areas of rock where moss is not growing. Only occasionally are lizards found on logs or the mossy parts of rocks. Lizards are commonly seen during the day in heavily shaded areas at the edges of their retreats or clinging upside down to the undersides of large boulders (Fig. 40). In such microhabitats, lizards are cryptic and often noticed only by the yellow ocelli that appear as eye-spots. Lizards are wary and quickly move to deeper cover at the slightest provocation, often waving their tails from side to side over their backs as they retreat. At night, *C. mcguirei* takes on a much lighter coloration and ventures further out onto the surface of the rocks (Fig. 39) and is easily approached. Lizards have been observed abroad at night during heavy rains resting in dry, open patches on rocks sheltered from water. Several termites were found in the gut of one lizard and females carrying two eggs were observed during March and October suggesting *C. mcguirei* breeds throughout the year.

Relationships. *Cnemaspis mcguirei* is the sister species of *Cnemaspis grismeri* (Fig. 2).

Material examined. Malaysia: Perak, Bukit Larut ZRC 2.6765–69 (type series). Material examined since Grismer *et al.* (2008b): Malaysia: Perak, Bukit Larut ZRC 2.5663–64, LSUHC 8855, 8858, 9140, 9028–33, 9209, 9845; Gunung Bubu LSUHC 11013.

Cnemaspis grismeri Wood, Quah, Anuar & Muin, 2013

Grismer's Rock Gecko
Figs. 41,42

Cnemaspis mcguirei Grismer 2011a:349.

Holotype. LSUHC 10996. Type locality: "Gua Asar, Bukit Kepala Gajah limestone massif, Lenggong, Perak, Malaysia (5°07.53'N, 100°58.82'E)" at 78 m in elevation.

Diagnosis. Maximum SVL 50.6 mm; eight supralabials and infralabials; ventral scales keeled; 8–10 discontinuous, pore-bearing precloacal scales with round pores; 27–32 paravertebral tubercles; body tubercles not linearly arranged, present on flanks; tubercles present in lateral caudal furrows; ventrolateral caudal tubercles present anteriorly; lateral row of caudal tubercles present; caudal tubercles not encircling tail; all subcaudals keeled, no enlarged median scale row; two or three postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no submetatarsal scales on first toe; 25–31 subdigital fourth toe lamellae; two ocelli in the shoulder region in males; wide, white to yellow postscapular band; yellow bars on flanks; nearly immaculate white bands on tail (Tables 6,7).

Color pattern (Figs. 41,42). Dorsal ground color grey to brown; head and body overlain with irregularly shaped, small, dark and yellowish flecks giving an overall mossy appearance; cream to yellowish markings on top of head; thin, dark, postorbital stripe extending onto nape; paired, elongate, medial, yellowish markings on nape followed by small, indistinct, black shoulder patches enclosing two yellow ocelli, ocellus dorsal to forelimb insertion distinct and another anterior to forelimb insertion weak; shoulder patch edged posteriorly by wide, offset, postscapular band that is yellow laterally and white medially; irregularly shaped, offset, paravertebral, yellowish markings on dorsum extend to base of tail; distinct, transversely elongate, yellow bars on flanks; diffuse, brown and white bands encircle tail posteriorly, bands yellowish anteriorly; posterior portion of tail regenerated and uniform dark brown; irregularly shaped yellowish to dull white markings on limbs; dark and light diffuse bands encircling digits; ventral surfaces of head, body, and limbs dull beige, immaculate, darkening laterally; subcaudal region suffused with pigment, not immaculate.

Distribution. *Cnemaspis grismeri* is known only from the type locality at Gua Asar, Bukit Kepala Gajah limestone massif, Lenggong, Perak, Malaysia (Wood *et al.* 2013; Fig. 3).

Natural history. *Cnemaspis grismeri* is a lowland species found on the inner walls of limestone caves, cave entrances, karst walls outside of caves, and outcroppings in the lowland karst forest surrounding limestone massifs at Gua Asar and Gua Kijang (Fig. 42). Wood *et al.* (2013) reported that *C. grismeri* is diurnal but only observed lizards moving about in cracks and on shadowed surfaces of karst boulders. Lizards are wary and quickly enter into retreats when approached. Their behavior is similar to that of its upland closest relative *C. mcguirei* that resides on granite boulders at Bukit Larut, Perak (Grismer 2011a). At night, the color of *C. grismeri* lightens considerably and

FIGURE 43. Upper: adult male *Cnemaspis flavolineata* (LSUHC 8079) from the Gap at Fraser's Hill, Pahang, Peninsular Malaysia. Lower: microhabitat at Fraser's Hill. Photographs by LLG.

lizards have been observed sleeping on leaves in low vegetation near the karst walls and on vines and the aerial roots of fig trees next to the limestone walls (Wood *et al.* 2013). Gravid females bearing two eggs have been found during July.

Relationships. *Cnemaspis grismeri* is the sister species of *C. mcguirei* (Fig. 2) and both are closely associated with the Banjaran Bintang Mountains (Fig. 1), *C. grismeri* being the lowland form and *C. mcguirei* the upland species. A parallel phylogeographic pattern occurs in the upland *Cyrtodactylus bintangtinggi* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Norhayati, Bauer, Wangkulangkul, Grismer & Pauwels and *C. bintangrendah* Grismer, Wood, Quah, Anuar, Muin, Sumontha, Norhayati, Bauer, Wangkulangkul, Grismer & Pauwels (Grismer *et al.* 2012, 2014) from the same localities.

Material examined. Malaysia: Perak, Lenggong LSUHC 9969–73, 10941–44, 10996 (type series).

Cnemaspis flavolineata (Nicholls, 1949)

Fraser's Hill Rock Gecko
Fig. 43

Gonatodes kendallii Smith 1922:268
Gonatodes affinis Smith 1925:23; 1930:16
Gonatodes flavolineatus Nicholls 1949:47
Cnemaspis flavolineatus Manthey & Grossmann 1997:211; Leong & Lim, 2003:9

Holotype. ZRC 2.6777. Type locality: "the Gap below Fraser's Hill, on the Pahang-Selangor boundary", Peninsular Malaysia at approximately 800 m in elevation.

Diagnosis. Maximum SVL 39.2 mm; nine supralabials; nine infralabials; ventral scales keeled; five or six contiguous, pore-bearing precloacal scales with round pores; 23 paravertebral tubercles; body tubercles linearly arranged, absent on flanks; tubercles present in lateral caudal furrows; no ventrolateral caudal tubercles; lateral caudal row present anteriorly; caudal tubercles encircle tail anteriorly; subcaudals keeled, no enlarged median scale row; two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales; and 23 subdigital fourth toe lamellae; large, black, round spots on nape and anterior portion of body; light vertebral stripe variably present (Tables 6,7).

Redescription of species. The redescription of this species is based on a specimen (LSUHC 8079) collected from the Gap below Fraser's Hill, Pahang and the holotype (ZRC 2.6777). Maximum SVL 38.6–39.2 mm; head oblong in dorsal profile, moderate in size, somewhat narrow, flattened, distinct from neck; snout short, flat in lateral profile; postnasal region constricted medially, flat; scales of rostrum keeled, raised, larger than similarly shaped scales on occiput; weak, supraorbital ridges and frontorostral sulcus; canthus rostralis smoothly rounded; eye large; extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral slightly concave, divided dorsally by longitudinal groove; rostral bordered posteriorly by supranasals and two smaller scales and laterally by first supralabials; 9R,L raised supralabials of similar size; 9R,L infralabials, decreasing in size slightly posteriorly; nostrils elliptical, oriented posterolaterally, bordered posteriorly by small, granular, postnasal scales; mental large, triangular, bordered posteriorly by three postmentals, outer two largest; gular scales raised, keeled; throat scales larger, raised, keeled.

Body slender; small, keeled, dorsal scales equal in size throughout body, intermixed with much larger, multicarinate tubercles more or less linearly arranged; tubercles extend from occiput to base of tail; no tubercles on flanks; 23 paravertebral tubercles; pectoral scales raised, keeled, not elongate; abdominal scales slightly larger than dorsals, flat, keeled; five or six precloacal pores; forelimbs moderately long, slender; dorsal scales of brachium raised, keeled; dorsal scales of forearm keeled, raised; ventral scales of brachium keeled, raised, juxtaposed; ventral scales of forearm smooth, raised, juxtaposed; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges wide; 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 nearly equal in length; hind limbs slightly longer and thicker than forelimbs; dorsal scales of thigh keeled, raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh keeled; subtibial scales keeled, flat, imbricate, with no enlarged anterior row; plantar scales smooth, juxtaposed, raised; no enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges wide; 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 being slightly longer than fifth; 23 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; dorsal caudal scales raised anteriorly, weakly keeled, juxtaposed; middorsal and lateral caudal furrows; no row of enlarged, median subcaudal scales; subcaudal scales keeled; caudal tubercles encircle tail anteriorly; caudal tubercles present in lateral furrow; two enlarged postcloacal tubercles on lateral surface of hemipenal swellings at base of tail.

Color pattern in life based on LSUHC 8079 (Fig. 43). Dorsal ground color brown to olive-brown; small, dark and light markings on top of head; faint, dark lines radiate out from eyes; elongate, paired, dark, paravertebral markings edging a wide, cream-colored vertebral stripe extending from nape to base of tail; flanks slightly lighter in color; large, white, dorsal tubercles in vertebral region extending from nape onto the tail; limbs mottled with dark and light, irregularly shaped blotches; no black shoulder patches or postscapular band; faint, dark and light brownish bands encircle tail; ventral surfaces of head, body, and limbs dull beige, immaculate; subcaudal region darker.

Distribution. *Cnemaspis flavolineata* is known only from the type of the Gap below Fraser's Hill, Pahang (Nicholls 1949; Fig. 3).

Natural history. This species is known from only two specimens. No collection data were provided with the holotype but LSUHC 8079 was taken on 26 August 2006 at night while sleeping on the underside of a horizontal branch at the edge of a slow moving, marshy stream edged by large granite boulders in hill dipterocarp forest at 900 m in elevation (Fig. 43).

Remarks. Although *Cnemaspis flavolineata* and *C. temiah* sp. nov. are very similar in morphology and color pattern, the molecular analysis indicates that they are not the same species or each others closest relatives (Fig. 2). *Cnemaspis flavolineata* can be separated from *C. temiah* sp. nov. by having a distinct series of large, white, transversely arranged, vertebral tubercles extending from the nape onto the tail which do not occur in *C. temiah* sp. nov. Additionally, the anteriormost caudal tubercles in *C. flavolineata* encircle the tail whereas no caudal tubercles encircle the tail in *C. temiah* sp. nov.

Material examined. Malaysia: Pahang; the Gap below Fraser's Hill ZRC 2.6777 (holotype) and LSUHC 8079.

***Cnemaspis temiah* sp. nov**

Temiah Rock Gecko
Fig. 44

Cnemaspis affinis Grandison 1972:80; Dring 1979:221
Cnemaspis flavolineata Manthey & Grossmann 1997:211 (in part); Chan-ard et al 1999:104, Grismer 2008:30; Grismer *et al.* 2008c:9 (in part); Grismer 2011a:317
Cnemaspis flavolineatus Lim *et al.* 2002:51

Holotype. Adult female LSUHC 9110 collected on 11 November 2008 by L. Lee Grismer, Norhayati Ahmad, and Chan K. Onn on trail 11, Tanah Rata, Cameron Highlands, Pahang, Peninsular Malaysia (03°09.01 N, 106°14.03 E) at approximately 1600 m in elevation.

Paratypes. All paratypes are from the same locality as the holotype. LSUHC 9159–60 have the same collectors and collection dates. LSUHC 9739 was collected by Chan K. Onn on 22 March 2010; LSUHC 9816–18 were collected by L. Lee Grismer, Chan K. Onn, and R. Gregory on 27 August 2010.

Diagnosis. Maximum SVL 46.7 mm; eight or nine supralabials; 7–9 infralabials; ventral scales keeled; 5–7 continuous, pore-bearing precloacal scales with round pores; 22–27 paravertebral tubercles; body tubercles semi-linearly arranged, weakly present on flanks; tubercles present in lateral caudal furrows; no ventrolateral row of caudal tubercles; lateral row of caudal tubercles present; caudal tubercles not encircling tail; all subcaudals keeled, no enlarged median scale row; three postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no enlarged submetatarsal scales on first toe; 22–26 subdigital fourth toe lamellae; light-colored, vertebral stripe variably present (Tables 6,7).

FIGURE 44. *Cnemaspis temiah* sp. nov. from Tanah Rata, Cameron Highlands, Pahang, Peninsular Malaysia. Upper left: adult female (LSUDPC 5677) in the dark color pattern phase. Upper right: hatchling (LSUDPC 5382). Middle right: adult male (LSUDPC 5668) in the light color pattern phase. Middle left: microhabitat at trail 10, Tana Rata, Cameron Highlands. Lower: type series of *C. temiah* sp. nov., adult male holotype (LSUHC 9110) on far left. Photographs by LLG.

Description of holotype. Adult female; SVL 38.6 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.27), somewhat narrow (HW/SVL 0.18), flattened (HD/HL 0.39), distinct from neck; snout short (ES/HL 0.46), flat in lateral profile; postnasal region constricted medially, flat; scales of rostrum keeled, slightly raised, larger than similarly shaped scales on occiput; low, supraorbital ridges; weak frontorostral sulcus; canthus rostralis smoothly rounded; eye large (ED/HL 0.21); extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral slightly concave, dorsal 75% divided by longitudinal groove; rostral bordered posteriorly by supranasals and two smaller scales and laterally by first supralabials; 9R,8L raised supralabials of similar size; 9R,L infralabials, decreasing in size slightly posteriorly; nostrils elliptical, oriented dorsoposteriorly;

bordered posteriorly by small, granular, postnasal scales; mental large, triangular, bordered posteriorly by four postmentals, outer two largest; gular scales raised, keeled; throat scales larger, raised, keeled.

Body slender, not particularly long (AG/SVL 0.43); small, keeled, dorsal scales equal in size throughout body, intermixed with much larger, multicarinate tubercles more or less randomly arranged; tubercles extend from occiput to base of tail; tubercles on flanks prominent; 26 paravertebral tubercles; pectoral scales raised, keeled, not elongate; abdominal scales slightly larger than dorsals, flat, keeled; no precloacal pores; forelimbs moderately long (FL/SVL 0.15), slender; dorsal scales of brachium raised, keeled; dorsal scales of forearm keeled, raised; ventral scales of brachium keeled, raised, juxtaposed; ventral scales of forearm smooth, raised, juxtaposed; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges wide; 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 nearly equal in length; hind limbs slightly longer and thicker than forelimbs (TBL/SVL 0.20); dorsal scales of thigh keeled, raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh keeled; subtibial scales keeled, 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 wide; 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 being slightly longer than fifth; 25 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; dorsal caudal scales raised anteriorly, weakly keeled, juxtaposed; middorsal and lateral caudal furrows present; no row of enlarged, median subcaudal scales; subcaudal scales keeled; caudal tubercles do not encircle tail; caudal tubercles present in lateral caudal furrow; no enlarged postcloacal tubercles on lateral surface of hemipenal swellings at base of tail.

Color pattern in life (Fig. 44). Dorsal ground color light brown to yellowish; head, body (including flanks), and limbs overlain with irregularly shaped, blotched, dark markings, those in the paravertebral region somewhat paired and alternating with somewhat larger, yellowish marking; tail generally immaculate; ground color of all ventral surfaces beige, weak dark stippling on throat, pectoral region, limbs and tail. There is no sexual dimorphism in color pattern and the pattern lights considerably at night.

Variation. Paratypes LSUHC 9160 and 9816 resemble the holotype in all aspects of coloration and pattern (Fig. 44). The other paratypes show differing degrees of vertebral stipping. LSUHC 9159 and 9739 have a wide, yellow vertebral stipe extending from occiput to onto the tail. LSUHC 9817 also bears a vertebral stripe but it is interrupted just posterior to the shoulder region. LSUHC 9818 has a vertebral stripe that extends only to a point midway down the body between the limb insertions. LSUHC 9159–60,9739, 9816 have broken tails. LSUHC 9816 is a male with a series of seven, contiguous, pore-bearing precloacal scales with round pores. Morphometric variation and variation in scalation are presented in Table 9.

TABLE 9. Meristic and mensural character states of the type series of *Cnemaspis temiah* sp. nov. w = weak; f = female; m = male; ant = anterior; and b = broke. Meristic abbreviations are listed in the Materials and Methods.

	LSUHC 9110 holotype	LSUHC 9159 paratype	LSUHC 9160 paratype	LSUHC 9739 paratype	LSUHC 9816 paratype	LSUHC 9817 paratype	LSUHC 9818 paratype
Supralabials	9	8	9	8	9	9	8
Infralabials	9	7	9	8	7	8	8
Ventral scales keeled (1) or not (0)	1	1	1	1	1	1	1
No. of precloacal pores	/	/	/	/	7	/	/
Precloacal pores continuous (1) or separated (0)	/	/	/	/	1	/	/
Precloacal pores elongate (1) or round (0)	/	/	/	/	0	/	/
No. of paravertebral tubercles	26	23	27	22	26	22	22
Tubercles linearly arranged (1) or more random (0)	w	0	1	1	w	0	0

......*continued on the next page*

TABLE 9. (Continued)

	LSUHC 9110 holotype	LSUHC 9159 paratype	LSUHC 9160 paratype	LSUHC 9739 paratype	LSUHC 9816 paratype	LSUHC 9817 paratype	LSUHC 9818 paratype
Tubercles present (1) or absent (0) on flanks	1	w	w	w	w	0	w
Caudal tubercles in lateral furrow (1) or not (0)	1	1	1	1	1	1	1
Ventrolateral caudal tubercles anteriorly (1) or not (0)	0	0	0	0	0	0	0
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	1	1	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	0	0
Subcaudals keeled (1) or not (0)	1	1	1	1	1	1	1
Single median row of keeled subcaudals (1) or not (0)	0	0	0	0	0	0	0
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	0	0	0	0	0	0
Postcloacal spurs	/	/	/	/	3	/	/
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0	0	0	0	0
No. of 4th toe lamellae	25	22	22	26	24	26	22
sex	f	f	f	f	m	f	f
SVL	38.6	38.4	34.1	34	31.1	35.3	33.3
TL	48.7	19.3	16.5b	10.2b	19.4	42.3	42.4
TW	2.5	2.7	2.5	2.7	2.5	2.4	2.6
FL	5.9	6.5	5.3	5.9	5.2	5.7	5.3
TBL	7.6	7.9	6.2	7.1	6.1	7.3	6.8
AG	16.8	16.2	15.7	14.8	13.8	14.3	14.3
HL	10.5	10.6	4	9.7	8.2	9.3	9.2
HW	7	6.8	3	5.9	5.7	6.2	6
HD	4.1	4.4	5.8	4.1	3.5	4	3.8
ED	2.3	2.2	1.9	2.1	2	2.1	2
EE	2.9	3.2	2.8	2.8	2.3	2.7	2.9
ES	4.9	5.1	4.3	4.8	3.9	4.4	5
EN	3.7	4	3.3	3.5	3.2	3.1	3.5
IO	2.4	2.4	2	2.2	2	2.4	2.6
EL	0.9	0.9	0.5	0.8	0.5	0.9	0.4
IN	1.2	0.8	0.8	0.9	0.8	0.9	1.1

Distribution. *Cnemaspis temiah* sp. nov. is known only from the Cameron Highlands plateau, Pahang, Peninsular Malaysia (Fig. 3).

Natural History. Grismer (2011a) reported *Cnemaspis temiah* sp. nov. to be an inhabitant of hill dipterocarp forests occurring in the vicinity of 1,150 meters in elevation (Fig. 44). Unlike most Sundaic species of *Cnemaspis* that have a high affinity for rocky microhabitats, *C. temiah* sp. nov. occurs exclusively on vegetation. It is assumed this species is secretive and diurnal although it has never been observed during the day. Grismer (2011a) noted that all the lizards observed at night were sleeping on the trunks of trees or on the surfaces of leaves. *Cnemaspis temiah* sp. nov. appears to be very localized in distribution as well. At Cameron Highlands, lizards are found regularly but only along one 200 m stretch of a certain trail. They are very rare elsewhere. Gravid females carrying two eggs have been found during March, April and October (Grismer 2011a), suggesting *C. temiah* sp. nov. may breed year-round.

Etymology. The specific epithet *temiah* is an invariable noun in apposition in reference to the Temiah Tribe of Orang Asli people that are also endemic to the Cameron Highland region.

Comparisons. *Cnemaspis temiah* sp. nov. is a member of the *affinis* group and was previously considered conspecific with *C. flavolineata* (see Grismer 2011a and references therein). The molecular analysis indicates that not only is *C. temiah* sp. nov. separate from *C. flavolineata* but may not even its closest relative (Fig. 2). *Cnemaspis temiah* sp. is separated from *C. flavolineata* by not having caudal tubercles that encircle the tail as opposed to having caudal tubercles encircling the tail anteriorly. It is further separated by lacking as opposed to having large, white, dorsal tubercles on the body and tail and having an uncorrected *p*-distance of 18.0% (Table 4). *Cnemaspis temiah* sp. nov. differs from species of the *affinis* group as follows. From all species of the *affinis* group except *C. bayuensis, C. flavolineata, C. hangus* sp. nov., *C. selamatkanmerapoh,* and *C. stongensis* sp. nov. *C. temiah* sp. nov. differs by lacking an ocellus in the shoulder region. From all species of the *affinis* group except *C. harimau* it differs by having as opposed to lacking caudal tubercles that encircle the tail at least anteriorly. *Cnemaspis temiah* sp. nov. differs from *C. affinis, C. bayuensis, C. hangus* sp. nov., *C. selamatkanmerapoh,* and *C. stongensis* sp. nov. and *C. mcguirei* by having fewer subdigital lamellae on the fourth toe (22–26 versus 27–35 collectively). From *C. affinis, C. bayuensis, C. grismeri, C. harimau,* and *C. narathiwatensis* it differs by having as opposed to lacking precloacal pores. *Cnemaspis temiah* sp. nov. differs further from *C. harimau* and *C. selamatkanmerapoh* in having 22–27 as opposed to 18–20 and 30 paravertebral tubercles, respectively. From *C. affinis* and *C. bayuensis* it differs in having as opposed to lacking tubercles in the lateral caudal furrows. It differs from *C. shahruli* by not having a yellow gular region and from *C. grismeri* and *C. mcguirei* by not having nearly immaculate white caudal bands and a wide, yellow, postscapular band.

Relationships. The sister species relationship between *Cnemapspis temiah* sp. nov. and *C. flavolineata* is not supported and the two are separated by an uncorrected *p*-distance of 18.0% (Fig. 2; Table 4).

***Cnemaspis narathiwatensis* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya, 2010**

Narathiwat Rock Gecko
Fig. 45

Holotype. THNHM 1436. Type locality "Waeng District, Narathiwat Province, Thailand. Exact locality, collector, and date of collection unknown".

Diagnosis. Maximum SVL 53.2 mm; nine or 10 supralabials; 7–11 infralabials; keeled ventral scales; 3–6 discontinuous, pore-bearing precloacal scales with round pores; 28–34 paravertebral tubercles; body tubercles randomly arranged, present or absent on flanks; tubercles in lateral caudal furrows; ventrolateral row of caudal tubercles present; lateral row of caudal tubercles present; caudal tubercles do not encircle tail; subcaudals keeled; no enlarged, median row of subcaudals; 1–3 postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; submetatarsal scales of first toe not enlarged; subtibials keeled; 24–30 subdigital fourth toe lamellae; white ocellus in shoulder region of males; light-colored vertebral stripe variably present; whitish to yellow bars on flanks; black and white caudal bands posteriorly (Tables 6,7).

Color pattern (Fig. 45). Dorsal ground color of head, body, limbs and tail gray to brown; top of head mottled with yellow, bearing two dark, diffuse, postorbital stripes; lower postorbital stripe extending onto upper portion of forelimb; upper postorbital stripe wider, incomplete, extending onto occiput and nearly meeting opposing stripe; shoulder region dark and in males encloses a whitish ocellus composed of large tubercles; a series of light-colored bars on flanks which tend to fade posteriorly; small, dark, paired, paravertebral markings on trunk between forelimb insertion and base of tail alternating with large, round, light-colored paravertebral markings; ventrolateral tubercles on base of tail light-colored; limbs generally uniform light-brown to yellowish bearing small, randomly arranged, diffuse markings; ventral surfaces uniform beige with fine, dark stippling in each scale; throat darker; infralabials and mental light-yellow; subcaudal region bearing whitish rings.

Distribution. *Cnemaspis narathiwatensis* is known only from the Thai-Malaysian border region from Hala-

Bala of the district of Waeng in Narathiwat Province and from Bang Lang National Park and Bannang Sata District, Yala Province, Thailand and the Belum-Temengor region of Perak in northern Peninsular Malaysia (Fig. 3).

Natural history. Grismer *et al* (2010a) noted that lizards from Thailand were observed at night sheltering in rocky crevices between 200–500 m in elevation and suggested this may indicate this species is a diurnal, rocky, microhabitat specialist (Fig. 45). This was confirmed with findings of *C. narathiwatensis* in Belum-Temengor region of Peninsular Malaysia where lizards were found on granite boulders near a stream during the day but were not seen at night.

Relationships. *Cnemaspis narathiwatensis* may be the sister species of *C. shahruli* (Fig. 2) also this relation is not statistically supported.

Material examined. Thailand: Narathiwat Province, Waeng District THNHM 1338, 1436; Yala Province, Bannang Sata District, Bang Lang National Park THNHM 12435. These specimens represent the type series. Material examined since Grismer *et al.* (2010a): Malaysia: Perak, Belum-Temengor region LSUHC 11271–74.

FIGURE 45. *Cnemaspis narathiwatensis* from Sungai Enam, Belum, Perak, Peninsular Malaysia. Upper left: ventral view of an adult male and female (LSUDPC 7940). Upper right: adult female (LSUDPC 7009) in the dark color pattern phase. Lower right: adult male (LSUDPC 7011) in the dark color pattern phase. Lower left: granite boulder microhabitat at Sungai Enam. Photographs by ESHQ.

Cnemaspis hangus sp. nov.

Bukit Hangus Rock Gecko
Fig. 46

Holotype. Adult male (HC 00227) collected on 24 June 2008 by Chan Kin Onn at 1030 hrs from Bukit Hangus, Pahang, Peninsular Malaysia (04°16.142'N, 102°13.370'E) at 10 m in elevation.

Paratypes. Adult female (HC 00225) has the same collection data as the holotype.

Diagnosis. *Cnemaspis hangus* sp. nov. differs from all other Southeast Asia species of *Cnemaspis* in having the unique combination of adult males reaching 50.5 mm SVL, adult females reaching 47.0 mm SVL; nine supralabials; eight infralabials; ventrals keeled; no precloacal pores; moderately prominent dorsal tubercles; 22–24 paravertebral tubercles; dorsal body tubercles semi-randomly arranged; tuberculation weak on flanks; caudal tubercles not encircling tail; tubercles may be within lateral caudal furrows anteriorly only; lateral row of caudal tubercles present; ventrolateral caudal tubercles absent; subcaudals keeled; no enlarged, median subcaudal scale row; two postcloacal tubercles; no enlarged femoral, subtibial, or submetatarsal scales; subtibials keeled; and 27–34 subdigital lamellae on fourth toe (Tables 6,7). *Cnemaspis hangus* sp. nov. lacks the diagnostic color pattern characteristics of other species in the Peninsular clade.

Description of holotype. Adult male; SVL 50.5 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.25), somewhat narrow (HW/SVL 0.17), flattened (HD/HL 0.42), distinct from neck; snout short (ES/HL 0.48), slightly concave in lateral profile; postnasal region constricted medially, flat; scales of rostrum weakly keeled, slightly raised, same size as similarly shaped scales on occiput; low, supraorbital ridges; moderate frontorostral sulcus; canthus rostralis smoothly rounded; eye large (ED/HL 0.22); extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral slightly concave, dorsal 75% divided by longitudinal groove; rostral bordered posteriorly by supranasals and one small, azygous scale and laterally by first supralabials; 9R,L raised supralabials of similar size; 8R,L infralabials, decreasing in size slightly posteriorly; nostrils elliptical, oriented dorsoposteriorly; bordered posteriorly by small, granular, postnasal scales; mental large, triangular, bordered posteriorly by six small postmentals of similar size; gular scales raised, weakly keeled; throat scales larger, raised, keeled.

FIGURE 46. *Cnemaspis hangus* sp. nov. from Bukit Hangus, Pahang, Peninsular Malaysia. Upper left: adult male holotype (HC 0227) in the light color pattern phase. Lower left: ventral view of adult female (HC 0225) showing same coloration as adult males. Right: karst microhabitat at Bukit Hangus. Photographs by CKO.

Body slender, elongate; small, keeled, dorsal scales equal in size throughout body, intermixed with larger, multicarinate tubercles more or less randomly arranged; tubercles extend from occiput to base of tail; tubercles on flanks sparse, moderate in size; 22 paravertebral tubercles; pectoral and abdominal scales raised, keeled, not elongate, same size throughout; abdominal scales slightly larger than dorsals; no precloacal pores; forelimbs moderately long, slender; dorsal scales of brachium raised, keeled; dorsal scales of forearm keeled, raised; ventral scales of brachium smooth, raised, juxtaposed; ventral scales of forearm weakly raised, juxtaposed; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; 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 present; fingers increase in length from first to fourth with fourth and fifth nearly equal in length; hind limbs slightly longer and thicker than forelimbs; dorsal scales of thigh keeled, raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh weakly keeled; subtibial scales keeled, flat, imbricate, with no enlarged anterior row; plantar scales smooth, juxtaposed, raised; no enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges granular proximally but wider distally; lamellae beneath phalanx immediately following inflection granular, lamellae of distal phalanges wide; interdigital webbing present; toes increase in length from first to fourth with fourth being slightly longer than fifth; 34 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; caudal scales flat anteriorly, weakly keeled, juxtaposed; deep middorsal and lateral furrows; no enlarged, median subcaudal scales; subcaudal scales keeled; no median row of enlarged keeled subcaudal scales; caudal tubercles do not encircle tail; caudal tubercles may or may not be present in lateral furrow anteriorly; one enlarged postcloacal tubercle on lateral surface of hemipenal swellings at base of tail.

Color pattern in life (Fig. 46). Dorsal ground color dark, ashy grey; head and body overlain with irregularly shaped, indistinct darker blotchs; light yellowish, medial blotch on occiput following three smaller dark spots; rostrum bearing yellowish spots; single, faded, dark, postorbital stripe extending to base of occiput; paravertebral, faded yellowish markings on extending to base of tail alternating with faded irregularly shapred, smaller, dark markings; transversely elongate, yellowish markings on flanks alternating with darker spots; tail regenerated, unicolor gray; irregularly shaped, small, dark and light markings on limbs; dark and light diffuse bands encircling digits; ventral surfaces dark grey. There is no sexual dimorphism in color pattern and the pattern lightens considerably at night.

Variation. The paratype (HC 0225) approaches the holotype in coloration and pattern except that its dorsal pattern is bolder, its ventral surfaces are slightly lighter, and most of its tail is original and bears a faded banding pattern. Morphometric variation and variation in scalation are presented in Table 10.

TABLE 10. Meristic and mensural character states of the type series of *Cnemaspis hangus* sp. nov. w = weak; f = female; and m = male. Meristic abbreviations are listed in the Materials and Methods. For TL, the measurement for the original portion of the tail is on the left and the measurement for the regenerated portion is on the right.

	HC 227 holotype	HC 225 paratype
SVL (mm)	50.5	47
Supralabials	9	9
Infralabials	8	8
Ventral scales keeled (1) or not (0)	1	1
No. of precloacal pores	0	/
Precloacal pores continuous (1) or separated (0)	/	/
Precloacal pores elongate (1) or round (0)	/	/
No. of paravertebral tubercles	22	24
Tubercles linearly arranged (1) or more random (0)	0	0
Tubercles present (1) or absent (0) on flanks	w	w
Caudal tubercles in lateral furrow (1) or not (0)	ant	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	0	0
Lateral caudal tubercle row present (1) or absent (0)	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0
Subcaudals keeled (1) or not (0)	1	1

......continued on the next page

TABLE 10. (Continued)

	HC 227 holotype	HC 225 paratype
Single median row of keeled subcaudals (1) or not (0)	0	0
Caudal tubercles encircle tail (1) or not (0)	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	0
Postcloacal spurs	2	/
Enlarged femoral scales present (1) or absent (0)	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0
Subtibial scales keeled (1) or not (0)	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0
No. of 4th toe lamellae	34	27
Sex	m	f
TL	16.1/44.4	28.3/21.3
TW	5.3	4.5
FL	8.8	8.4
TBL	10.3	9.8
AG	21.7	20.4
HL	12.7	13.1
HW	8.7	8.6
HD	5.3	5.5
ED	2.8	3.2
EE	3.7	3.9
ES	6.1	5.5
EN	4.6	4.2
IO	2.7	2.3
EL	1.5	1.2
IN	1	/

Distribution. *Cnemaspis hangus* sp. nov. is known only from Bukit Hangus, Pahang, Peninsular Malaysia (Fig. 3).

Natural History. Lizards were seen abroad during the day on karst boulders and walls within a lowland dipterocarp forest and on boulders near the entrances of cave openings (Fig. 46). All were wary and quick to take cover in crevices and on the backsides of boulders at the slightest provocation. Multiple lizards were observed to occupy the same boulder and no lizards were seen at night indicating that *C. hangus* sp. nov. is diurnal. HC 0225 was a gravid female carrying two eggs indicating that reproduction takes place in June.

Etymology. The specific epithet *hangus* is an invariable noun in apposition in reference to the Malay word "*hangus*" which means to burn or scorch and refers to this species' overall burnt appearance in the dark color pattern phase.

Comparisons. *Cnemaspis hangus* sp. nov. is a member of the *affinis* group within which it is the sister species to *C. selamatkanmerapoh. Cnemaspis hangus* sp. nov. differs from *C. selamatkanmerapoh* in having a larger maximum larger SVL (50.5 mm versus 43.4 mm); lacking precloacal pores as opposed to having pores; having fewer paravertebral tubercles (22–24 versus 30); and semi-randomly arranged versus linearly arranged, dorsal tubercles. *Cnemaspis hangus* sp. nov. and *C. selamatkanmerapoh* bear a 3.6% sequence divergence from one another as well (Table 4). It differs from *C. pseudomcguirei, C. harimau,* and *C. shahruli* by having a greater maximum SVL (50.5 mm versus 36.5–43.2) and being considerably smaller than *C. mcguirei* (maximum SVL 65.0 mm). It differs from all species of the *affinis* group except *C. shahruli* in lacking as opposed to having precloacal pores. From *C. mcguirei, C. grismeri* and *C. narathiwatensis* in having fewer paravertebral tubercles (22–24 versus 23–34) and from *C. harimau* and *C. shahruli* in have more precloacal pores (11–23). It can be further separated from all species of the *affinis* group except *C. affinis, C. bayuensis* and *C. selamatkanmerapoh* by lacking tubercles in the lateral caudal furrows. From *C. grismeri* and *C. narathiwatensis* it differs in lacking as opposed to having a row of ventrolateral caudal tubercles. Having 27–34 subdigital lamellae on the fourth toe separates if from *C. pseudomcguirei, C. flavolineata* and *C. temiah* sp. nov. (23–26).

Relationships. *Cnemaspis hangus* sp. nov. is the sister species of *C. selamatkanmerapoh* (Fig. 2).

Cnemaspis selamatkanmerapoh Grismer, Wood, Mohamed, Chan, Heinz, Sumarli, Chan & Loredo, 2013a

Merapoh Rock Gecko
Fig. 47

Holotype. Adult male (LSUHC 11016) "collected on 23 June 2013 by L. Lee Grismer at 2200 hrs at 23 m from Gua Gunting, Merapoh, Pahang, Peninsular Malaysia (4°42.069 N, 101°58.512 E)".

Diagnosis. Maximum SVL 43.4 mm SVL; 10 supralabials; nine or 10 infralabials; keeled ventrals; at least one, round precloacal pore in males; 30 paravertebral tubercles; dorsal body tubercles semi-randomly arranged; tuberculation weak on flanks; caudal tubercles not encircling tail; lateral caudal tubercles not within lateral caudal furrows; ventrolateral caudal tubercles absent; subcaudals keeled; no enlarged, median subcaudal scale row; three postcloacal tubercles; no enlarged femoral, subtibial, or submetatarsal scales; subtibials keeled; and 31–33 subdigital lamellae on fourth toe (Tables 6,7). *Cnemaspis selamatkanmerapoh* sp. nov. lack diagnostic color pattern characteristics.

Color pattern in life (Fig. 47). Dorsal ground color grey; top of head bearing small dark spots; thin, dark postorbital stripes meeting medially on occiput and turning anteriorly; rostrum and supralabial region greenish; paired, light colored, paravertebral, blotches extend from nape to base of tail where they transform into light colored caudal bands, blotches united on nape and shoulder region into a single blotch; flanks bearing dark mottling and yellowish spots; limbs darkly mottled with a faint banding pattern; overall color of venter unicolor beige with all scales bearing black stippling. There is no sexual dimorphism in color pattern and coloration lightens considerably at night.

Distribution. *Cnemaspis selamatkanmerapoh* is known only from the type locality of Gua Gunting, Merapoh, Pahang, Peninsular Malaysia (Fig. 2). Grismer *et al.* (2013a) reported finding eggs on the connected karst outcrop Gua Goyang.

Natural History. Grismer *et al.* (2013a) noted that *Cnemaspis selamatkanmerapoh* is a lowland, diurnal species found only on karst substrate. Specimens were observed approximately 1 m above the ground along the perimeter of an extensive karst system surrounded by a limestone forest (Fig. 47) and lizards often position themselves adjacent to cracks into which they can escape if threatened. A gravid female carrying two eggs was collected during June.

Relationships. *Cnemaspis selamatkanmerapoh* is the sister species of *C. hangus* sp. nov. (Fig. 2).

Material examined. Malaysia: Pahang; Mearpoh, Gua Gunting LSUHC 11015–16 (type series).

Cnemaspis bayuensis Grismer, Grismer, Wood & Chan, 2008

Kampung Bayu Rock Gecko
Fig. 48

Holotype. ZRC 2.6759. Type locality: "Gua Bayu, Kelantan, Peninsular Malaysia (05°05.650 N, 102°13.265 E)" at 120 m in elevation.

Diagnosis. Maximum SVL 46.1 mm; nine or 10 supralabials; eight or nine infralabials; ventral scales keeled; 5–9 discontinuous, pore-bearing precloacal scales with round pores; 23–30 paravertebral tubercles; tubercles not linearly arranged, present on flanks; tubercles absent from lateral caudal furrows; no ventrolateral caudal tubercles; lateral caudal row present; caudal tubercles not restricted to a single paravertebral row nor encircling tail; all subcaudals keeled, no enlarged median scacle row; two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; subtibials keeled; no submetatarsal scales on first toe; 27–32 subdigital fourth toe lamellae; whitish bars on flanks (Tables 6,7).

FIGURE 47. Upper: adult male holotype (LSUHC 11016) *Cnemaspis selamatkanmerapoh* in the dark color pattern phase. Lower: microhabitat at Gua Goyang, Merapoh, Pahang, Peninsular Malaysia. Photographs by LLG.

FIGURE 48. *Cnemaspis bayuensis* from Gua Bayu, Kelantan, Peninsular Malaysia. Left: karst microhabitat of *C. bayuensis* near Kampung Bayu. Upper right: adult male (LSUDPC 4417) in the dark color pattern phase. Lower right: adult female (LSUDPC 4420) in the light color pattern phase. Photographs by LLG.

Color pattern in life (Fig. 48). Ground color of dorsal surfaces of head, body, limbs, and tail brown; head and body overlain with irregularly shaped, dark spots; light markings on occiput; a single, thin, dark, postorbital stripe extends onto nape does not contact medially with an opposing postorbital stripe; dark, anteriorly projecting, triangular marking between opposing postorbital stripes; white, paravertebral markings on nape followed by distinct, white, alternating, paravertebral blotches extending to base of tail; transversely elongate, distinct, white bars on flanks; dark blotches often on body; diffuse brown and mottled white bands encircle tail; dark caudal banding sometimes present; irregularly shaped, dark and light markings on limbs; dark and light, diffuse bands encircle digits; gular region bears a faint, brown, reticulate pattern; ventral surfaces of body and limbs dull beige, immaculate and darkened laterally; subcaudal region suffused with dark pigment.

Distribution. *Cnemaspis bayuensis* is known only from the type locality of Gua Bayu, Kelantan, Peninsular Malaysia (Grismer *et al.* 2008b: Fig. 3) but is likely to be found throughout the nearby karst region.

Natural history. Grismer *et al.* (2008b) noted that *Cnemaspis bayuensis* is a saxicolous species restricted to the lowland karst outcroppings (Fig. 48) of the Gua Bayu region surrounding the village of Bayu. Lizards are diurnal and occur along the periphery of the karst formations in cracks as well as on cave walls and ceilings as high as 5 m above the ground. Lizards have not been found deep within the cave systems. This species is adept at matching the color of its substrate be it the light colored cave walls or the dark, lichen-colored isolated karst boulders scattered along the periphery of the karst towers. Females carrying two eggs have been observed during mid-June.

Relationships. *Cnemaspis bayuensis* is the sister species of *C. stongensis* sp. nov. (Fig. 2).

Material examined. Malaysia: Kelantan, Gua Bayu ZRC 2.6759–61, LSUHC 9073 (type series).

Cnemaspis stongensis sp. nov.

Gunung Stong Rock Gecko

Fig. 49

Holotype. Adult male LSUHC 11089 collected on 26 June 2013 by Chan Kin Onn, L. Lee Grismer and Jacob A. Chan at 1030 hrs at 10 m from Kem Baha, Gunung Stong, Kelantan, Peninsular Malaysia (5°20.465 N, 101°58.001 E) at 461 m elevation.

Paratypes. Adult males LSUHC 11091, 11093–94, 11100, 11139 and adult female LSUHC 11092 has the same collection data as the holotype.

Diagnosis. *Cnemaspis stongensis* sp. nov. differs from all other Southeast Asia species of *Cnemaspis* in having the unique combination of adult males reaching 49.3 mm SVL, adult females reaching 48.4 mm SVL; 8–11 supralabials; 8–10 infralabials; ventrals keeled; 5–8, continguous, pore-bearing precloacal scales with round pores; moderately prominent dorsal tubercles; 26–33 paravertebral tubercles; dorsal body tubercles generally randomly arranged; tubercles present on flanks; caudal tubercles not encircling tail; lateral caudal tubercles usually within lateral caudal furrows anteriorly only; ventrolateral caudal tubercles may or may not be present anteriorly only; lateral row of caudal tubercles present anteriorly only; subcaudals keeled; no enlarged, median subcaudal scale row; two or three postcloacal tubercles; no enlarged femoral, subtibial, or submetatarsal scales; subtibials keeled; and 28–32 subdigital lamellae on fourth toe. These differences are summarized across all Southeast Asian species in Table 6. *Cnemaspis stongensis* sp. nov. lacks diagnostic color pattern characteristics.

Description of holotype. Adult male; SVL 49.3 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.25), somewhat narrow (HW/SVL 0.17), flattened (HD/HL 0.43), distinct from neck; snout short (ES/HL 0.49), slightly concave in lateral profile; postnasal region constricted medially, flat; scales of rostrum keeled, raised, slightly larger than similarly shaped scales on occiput; low, supraorbital ridges; moderate frontorostral sulcus; canthus rostralis smoothly rounded; eye large (ED/HL 0.23); extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral concave, dorsal 90% divided by longitudinal groove; rostral bordered posteriorly by two small supranasals and two large scales between the supranasals and laterally by first supralabials; 9R,L raised supralabials of similar size; 8R, 9L infralabials, decreasing in size slightly posteriorly; nostrils elliptical, oriented dorsoposteriorly; bordered posteriorly by small, granular, postnasal scales; mental large, triangular, bordered posteriorly by four small postmentals of similar size; gular scales raised, keeled; throat scales same size, raised, keeled.

Body slender, elongate (AG/SVL 0.43); small, keeled, dorsal scales equal in size throughout body, with intermixed larger, multicarinate tubercles more or less randomly arranged; tubercles extend from occiput to base of tail; tubercles on flanks sparse, moderate in size; 32 paravertebral tubercles; pectoral and abdominal scales raised, keeled, not elongate, same size throughout; abdominal scales slightly larger than dorsals; eight pore-bearing precloacal scales with round pores in a chevron pattern separated on the left side of the chevron by a single non-pore-bearing scale; forelimbs moderately long, slender (FL/SVL 0.18); dorsal scales of brachium raised, keeled; dorsal scales of forearm keeled, raised; ventral scales of brachium smooth, raised, juxtaposed; ventral scales of forearm raised, juxtaposed; palmar scales raised, smooth, juxtaposed; digits long with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges granular proximally, widened distally; lamellae beneath phalanx immediately following inflection granular, lamellae of distal phalanges wider; interdigital webbing absent; fingers increase in length from first to fourth with fourth and fifth nearly equal in length; hind limbs slightly longer and thicker than forelimbs (TBL/SVL 0.21); dorsal scales of thigh keeled, raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh keeled; subtibial scales keeled, flat, imbricate, with no enlarged anterior row; plantar scales raised, smooth, juxtaposed; no enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges granular proximally but wider distally; lamellae beneath phalanx immediately following inflection granular, lamellae of distal phalanges wider; interdigital webbing absent; toes increase in length from first to fourth with fourth being slightly longer than fifth; 32 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; caudal scales flat anteriorly, weakly keeled, juxtaposed; middorsal and lateral furrows; no enlarged, median subcaudal scales; subcaudal scales keeled; caudal tubercles present in lateral furrow anteriorly; two enlarged postcloacal tubercles on lateral surface of hemipenal swellings at base of tail.

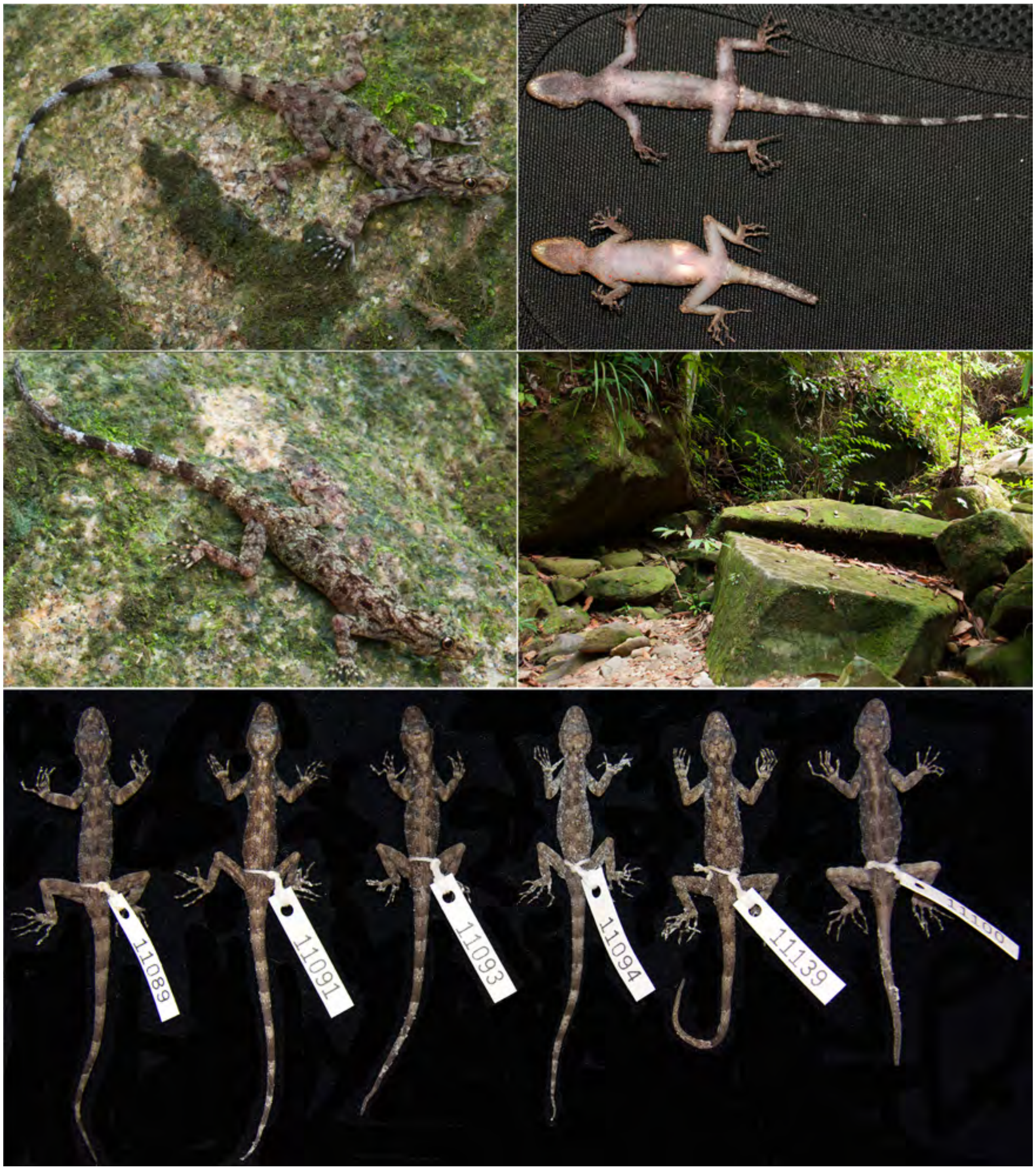

FIGURE 49. *Cnemaspis stongensis* sp. nov. from Kem Baha, Gunung Stong, Peninsular Malaysia. Upper left: adult male holotype (LSUHC 11091) in dark color pattern phase. Upper right: ventral view of the holotype and a gravid female paratype (LSUHC 11091 upper and 11100 lower, respectively). Middle left: adult female paratype (LSUHC 11100) in dark color pattern phase. Middle right: granite boulder microhabitat at Kem Baha, Gunung Stong, Peninsular Malaysia. Lower: type series of *C. stongensis* sp. nov. Photographs by LLG.

Color pattern in life (Fig. 49). Dorsal ground color of head, limbs, and body grey; black, irregular striping on snout; black, transverse, azygous marking on top of head; black, postorbital stripe extending onto nape; black, medial, teardrop-shaped marking on nape; a series of seven, black, paravertebral markings extending from shoulder region to base of tail; similar black markings on flanks; dull-white, butterfly-shaped, paravertebral markings alternating with black, paravertebral markings and becoming completely separated posteriorly; dull-white, transverse bars on flanks; light-colored, caudal bands, anterior two yellowish and posterior seven white; light caudal bands alternate with black caudal bands; limbs bearing irregularly shaped, whitish bands; ventral surfaces of head, throat, pectoral, and abdominal regions, and limbs grey, gular region and abdomen slightly darker; caudal bands encircle tail but are less vivid in subcaudal region.

Variation. The paratypes closely resemble the holotype in coloration and pattern (Fig. 49). The dorsal pattern of LSUHC 11094 and 11139 appears slightly more speckled overall and LSUHC 11100 has a faint, wide, light-colored, vertebral stripe. Morphometric variation and variation in scalation are presented in Table 11.

Distribution. *Cnemaspis stongensis* sp. nov. is known only from the type locality and surrounding areas on Gunung Stong, Kelantan, Peninsular Malaysia (Fig. 3).

Natural History. Lizards were observed to be active only at night on large granite boulders (Fig. 49) ranging in elevation from 50 m at the base of Gunung Stong at Hutan Lipur Jelawang in lowland dipterocarp forest up to the type locality of Kem Baha at 461 m in hill dipterocarp forest. The majority of specimens were found in the vicinity of water but were not necessarily restricted to these areas. Within their microhabitat, lizards were most commonly seen on the undersides or on the lower sections of boulders (Fig. 49) making escape much easier. We expect this species extends to higher elevations on Gunung Stong above Kem Baha.

TABLE 11. Meristic and mensural character states of the type series of *Cnemaspis stongensis* sp. nov. w = weak; f = female; m = male; ant = anterior; and r = regenerated. Meristic abbreviations are listed in the Materials and Methods. For TL, the measurement for the original portion of the tail is on the left and the measurement for the regenerated portion is on the right.

	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC
	11089	11091	11092	11093	11094	11100	11139
	holotype	paratype	paratype	paratype	paratype	paratype	paratype
Supralabials	9	8	10	8	9	10	11
Infralabials	8	8	9	8	10	7	9
Ventral scales keeled (1) or not (0)	1	1	1	1	1	1	1
No. of precloacal pores	8	6	/	7	5	5	5
Precloacal pores continuous (1) or separated (0)	1	1	/	1	1	1	1
Precloacal pores elongate (1) or round (0)	0	0	/	0	0	0	0
No. of paravertebral tubercles	32	29	30	33	29	28	26
Tubercles linearly arranged (1) or more random (0)	0	0	0	0	0	0	0
Tubercles present (1) or absent (0) on flanks	1	1	1	1	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	ant	ant	ant	0	ant	/	ant
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	1	0	1	1	/	1
Lateral caudal tubercle row present (1) or absent (0)	ant	ant	ant	ant	ant	/	ant
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	/	0
Subcaudals keeled (1) or not (0)	1	1	1	1	1	/	1
Single median row of keeled subcaudals (1) or not (0)	0	0	0	0	0	/	0
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	0	/	0
Enlarged median subcaudal scale row (1) or not (0)	0	0	0	0	0	/	0
Postcloacal spurs	2	2	/	2	2	3	2
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	1	1	1

......*continued on the next page*

TABLE 11. (Continued)

	LSUHC 11089 holotype	LSUHC 11091 paratype	LSUHC 11092 paratype	LSUHC 11093 paratype	LSUHC 11094 paratype	LSUHC 11100 paratype	LSUHC 11139 paratype
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0	0	0	0	0
No. of 4th toe lamellae	32	28	28	29	31	31	31
Sex	m	m	f	m	m	m	m
SVL	49.3	48.4	46.2	44.3	43.9	48.5	47.2
TL	68.9	67.6	62.1	49.5/11.1	61.5	42.3r	38.1/,19.1
TW	4.8	5.3	5.1	4.4	5.4	4.7	4.6
FL	8.8	8.3	7.9	8.4	8.2	8.3	9.1
TBL	10.3	10.1	9.4	9.9	9.9	10.9	10.4
AG	21.2	20.1	21.1	18.4	19.7	20.9	21.1
HL	12.1	13.1	12.2	12.5	11.9	12.9	13.1
HW	8.4	8.3	7.9	7.5	7.7	8.3	7.9
HD	5.2	5.5	4.5	4.8	4.7	5.3	5.3
ED	2.8	2.7	2.3	2.4	2.3	2.6	2.5
EE	4.1	4.1	4.1	3.5	3.3	3.9	3.7
ES	5.9	6.3	5.9	5.5	5.6	5.9	6.1
EN	4.6	4.7	4.4	4.4	4.2	4.5	4.6
IO	2.7	2.9	2.6	2.7	2.7	2.9	2.8
EL	0.9	1.2	0.9	1.1	0.9	0.7	0.9
IN	1.3	1.1	1.1	1.2	1.2	1.3	1.2

Etymology. The specific epithet *stongensis* is an adjective in reference to Gunung (mountain) Stong on which the type locality of Kem Baha is located.

Comparisons. *Cnemaspis stongensis* sp. nov. is a member of the *affinis* group within which it is the sister species of *C. bayuensis. Cnemaspis stongensis* sp. nov. differs from *C. bayuensis* in having caudal tubercles anteriorly in the lateral caudal furrow as opposed to lacking them; having a lateral row of caudal tubercles present anteriorly as opposed to throughout the length of the tail; and lacking distinct black and white caudal bands as opposed to having them. However, these two species bear only a 2.2% sequence divergence from one another (Table 4). *Cnemaspis stongensis* sp. nov. differs from *C. pseudomcguirei, C. harimau,* and *C. shahruli* by having a greater maximum SVL (49.3 mm versus 36.5–43.2) and being considerably smaller than *C. mcguirei* (maximum SVL 65.0 mm). It differs from *C. shahruli* and *C. hangus* sp. nov. in having as opposed to lacking pre-cloacal pores. From *C. harimau, C. shahruli, C. flavolineata, C. temiah* sp. nov. and *C. hangus* sp. nov. it differs in having more paravertebral tubercles (26–33 versus 18–27). *Cnemaspis stongensis* sp. nov. can be further separated from all species of the *affinis* group except *C. affinis, C. hangus* sp. nov.*, C. selamatkanmerapoh,* and *C. bayuensis* by generally lacking tubercles in the lateral caudal furrows. It is seaparated from *C. harimau* and *C. temiah* sp. nov. by not having caudal tubercles that encircle the tail. Having 28–32 subdigital lamellae on the fourth toe separates it from *C. pseudomcguirei, C. flavolineata,* and *C. temiah* sp. nov.

Comments. The relatively close morphological and genetic similarity between *Cnemaspis stongensis* sp. nov. and *C. bayuensis* is surprising in that these sister species are separated by at least 85 km of uninhabital terrane and the former is a granite boulder specialist and the latter is a karst specialist.

Relationships. *Cnemaspis stongensis* sp. nov. is the sister species of *C. bayuensis* (Fig. 2).

Additional material examined. Malaysia: Kelantan; Gunung Stong, Kem Baha LSUHC 11090, 11095, 11138.

Southern Sunda clade

The Southern Sunda clade is a strongly supported lineage that contains the 12 southernmost species of *Cnemaspis* (Fig. 2) 10 from which we had molecular data. This clade ranges from southern Peninsular Malaysia and Singapore eastward through the Seribuat, Anambas, and Natuna archipelagos, to at least west-central and northern Borneo (Figs. 1,3). It forms a polytomy comprised of three well-supported lineages: the insular endemic *C. limi* Das & Grismer from Tioman and Tulai islands in the Seribuat Archipelago; the sister species *C. nigridia* (Smith) and *C. paripari* Grismer & Chan from northwestern Borneo referred to here as the *nigridia* group; and the *kendallii* group containing the remaining seven species, *C. kendallii sensu stricto* (Gray) from East Malaysia and Indonesia, *C. sundainsula* sp. nov. from Natuna Besar Island of the Natuna Archipelago, Indonesia and a lineage containing the Peninsular Malaysian *C. pemanggilensis* Grismer, Grismer & Das from Pulau Pemanggil, *C. baueri* Das & Grismer from Aur and Dayang islands, *C. mumpuniae* sp. nov. from Natuna Besar, Indonesia, *C. bidongensis* Grismer, Wood, Amirrudin, Sumarli, Vazquez, Ismail, Lukman, Nance, Muhammad, Mohaamad, Syed, Kuss, Murdoch & Cobos from Pulau Bidong and *C. peninsularis* sp. nov. from Peninsular Malaysia, Singapore, and the Seribuat Archipelago (Figs. 2,4). The relationship of these species is further supported in that they are the only *Cnemaspis* in the Southern Sunda clade that lack precloacal pores (Fig. 5) which is considered derived in that precloacal pores are widespread throughout the Gekkonidae (Kluge 1987). In the molecular analysis, there is an unresolved polytomy among these species (Fig. 2), however, the morphological analysis supports the monophyly of *C. kendallii*, *C. pemanggillensis, C. baueri, C. mumpuniae* sp. nov., *C. bidongensis* and *C. peninsularis* sp. nov. to the exclusion of *C. sundainsula* in that they are the only species of *Cnemaspis* in the Southern Sunda clade that have caudal tubercles encircling the tail (Fig. 5). Furthermore, the monphyly of *C. baueri, C. mumpuniae* sp. nov., *C. bidongensis* and *C. peninsularis* sp. nov., is supported in that they are the only species (with the exception of some individuals of *C. tucdupensis* from the *chnathaburiensis* group) wherein the posterior portion of the original tail is black (Fig. 5).

Cnemaspis limi Das & Grismer, 2003

Lim's Rock Gecko
Fig. 50

Cnemaspis sp. Hendrickson 1966:56
Cnemaspis nigridius Manthey & Grossmann 1997:214; Lim & Lim 1999:142
Cnemaspis cf. *nigridia* Chan-ard *et al.* 1999:104

Holotype. ZRC 2.5289. Type locality: "Gua Tengkuk Air, Gunung Kajang, adult male …collected from Pulau Tioman [Pahang] (02°50' N, 104°09' E), West Malaysia" at 980 m in elevation.

Diagnosis. Maximum SVL 88.2 mm; 8–12 supralabials; 7–10 infralabials; ventral scales weakly keeled; no precloacal pores; 25–35 paravertebral tubercles; body tubercles randomly arranged, weakly present on flanks, absent from lateral caudal furrows; no ventrolateral caudal tubercles; lateral row of caudal tubercles present; caudal tubercles not encircling tail; subcaudals smooth bearing a median, weakly enlarged, scale row; one or two postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials weakly keeled; 29–36 subdigital fourth toe lamellae; large, black, round spots on nape and anterior portion of body; dorsal caudal tubercles white; at least posterior one-half of subcaudal region white (Tables 6,7).

Color pattern in life (Fig. 50). Dorsal ground color of head, body, limbs, and tail dark brown; thin yellow reticulum on top of head and body; a dark, upper, postorbital stripe extends onto nape; a dark, lower, postorbital stripe extends onto shoulder region; a medial, dark marking on nape; 5–7 dark, paravertebral spots occur on back and flanked by diffuse, dark blotches on sides; faint, dark mottling on hind limbs and more on forelimbs; diffuse, dark bands on tail; anterior two-thirds of tail encircled by large, white to cream-colored tubercles; ventral surfaces of head, lateral sections of belly, limbs, and anterior one-third of tail dull-brown, immaculate; ventral surfaces of belly beige. At night the brown ground color of the dorsum fades to white, accenting the black body spots and the yellow reticulum.

Distribution. *Cnemaspis limi* is known only from Pulau Tioman, Pahang and the adjacent island of Tulai, Johor in the Seribuat Archipelago of Peninsular Malaysia (Grismer 2011a,b; Fig. 4).

Natural History. According to Grismer (2011a), *Cnemaspis limi* is a saxicolous gecko inhabiting primary and secondary coastal vegetation in lowland and hill dipterocarp forests (Fig. 50) from sea level to the summit of Gunung Kajang at 1,026 m in elevation. Lizards are found almost exclusively on large granite boulders where, during the day, they are active on vertical, shaded surfaces, within crevices, and within the cave-like situations formed by the aggregations of boulders piled on top of one another. In the latter microhabitat, densities can be surprisingly high. Lizards usually sit facing head-down or upside down and run to the base of the rock to escape. At night, however, *C. limi* is less active and almost exclusively restricted to cave-like situations. This is especially true for lizards near the summit of Gunung Kajang. Bullock (1966) found the larvae of butterflies, grasshoppers, beetles, and pieces of ants in the stomachs of lizards he examined, indicating *C. limi* does not feed on the ground like *C. peninsularis* sp. nov. with which it is sympatric. Grismer (2011a) reported females carrying one or two eggs having been observed during July and September and eggs stuck to the undersides of rocks during April indicating *C. limi* breeds throughout the year.

Relationships. *Cnemaspis limi* is a basal lineage in a tritomy composing the Southern Sunda clade (Fig. 2).

FIGURE 50. *Cnemaspis limi* from Pulau Tioman, Pahang, Peninsular Malaysia. Upper left: adult male (LSUDPC 6185) in the light color pattern phase. Upper right: adult female (LSUDPC 5623) in the dark color pattern phase. Lower: granite boulder microhabitat on the Tekek-Juara Trail, Pulau Tioman. Photographs by LLG.

Material examined. Peninsular Malaysia: Pahang, Pulau Tioman ZRC 2.5289–90, 2.3504–06 (type series). Material examined since Das and Grismer (2003): Peninsular Malaysia: Johor: Pulau Tulai LSUHC 5053; Pahang, Pulau Tioman LSUHC 3801–02, 3859, 3888, 3902, 3904, 4410, 4425, 4480–82, 4485–88, 4563–64, 4596, 5424, 5441, 5510, 5515, 5518, 5521, 6203, 6206–07, 6210, 6212, 6267, 8035.

***Nigridia* group.** The *nigridia* group contains two very dissimilar species from extreme northwestern Borneo; the large, nocturnal, granite boulder-dwelling *Cnemaspis nigridia* and the much smaller, diurnal, karst-dwelling species *C. paripari* (Fig. 2). The monophyly of this group is further supported in that these are the only species in the Southern Sunda clade to have enlarged scales beneath the first metatarsals. This character state occurs in the two species of the Ca Mau clade, four of 22 species of the Northern Sunda clade and does not occur in the Pattani clade (Table 6). Therefore, we consider this character state to be derived.

The *nigridia* group is diagnosed as having a maximum SVL of 50.7–75.5 mm; 10–13 supralabials; 9–11 infralabials; weakly to strongly keeled ventral scales; 2–16 contiguous, pore-bearing precloacal scales with round pores; 26–43 paravertebral tubercles; randomly to occasionally weakly aligned dorsal tubercles on the body; no tubercles on flanks or in the lateral caudal furrows; caudal tubercles do not encircle tail; lateral row of caudal tubercles present; subcaudals keeled and bearing a median row of enlarged, keeled scales; 2–4 postcloacal tubercles on either side of the base of the tail; no enlarged femoral or subtibial scales; subtibials keeled; submetatarsal scales of first toe enlarged; and 26–31 lamellae beneath the fourth toe.

FIGURE 51. *Cnemaspis nigridia* from Gunung Gading, Sarawak, East Malaysia. Upper left: adult female (LSUDPC 4882) in dark color pattern phase. Upper right: adult male (LSUDPC 4344) in light color pattern phase. Lower: granite boulder microhabitat at Gunung Gading. Photographs by LLG.

Cnemaspis nigridia (Smith, 1925)

Black Rock Gecko

Fig. 51

Heteronota Kendallii Gray, 1845:174 (in part)
Gonatodes affinis Shelford, 1901:49
Gonatodes nigridius Smith, 1925:22
Cnemaspis nigridius Brongersma, 1934:165; Manthey & Grossmann, 1997:214; Cox, van Dijk, Nabhitabhata & Thirakhupt, 1998:90; Auliya 2006:180
Cnemaspis cf. *nigridia* Chan-ard, Grossmann, Gumprecht & Schulz, 1999:104

Holotype. BM 1946.8.22.90. Type locality: "Mt. Gadin" = Gunung Gading, Sarawak, East Malaysia (01°41.16 N, 109°50.35 E) at approximately 100 m in elevation.

Diagnosis. Maximum SVL 75.5 mm; 10 or 11 supralabials; 9–11 infralabials; ventral scales weakly to moderately keeled; 10–16 contiguous, pore-bearing, precloacal scales with round pores; 39–43 paravertebral tubercles; tubercles semi-linear to randomly arranged, absent from flanks and lateral caudal furrows; ventrolateral caudal tubercles present; lateral row of caudal tubercles present; caudal tubercles not encircling tail; subcaudals keeled but bearing an enlarged median row of smooth scales; 2–4 postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; submetatarsal scales of first toe enlarged; subtibials keeled; 26–29 subdigital fourth toe lamellae; a pair of large, round, black spots in shoulder region; yellow to white bars on flanks; wide, black and dull-yellow caudal bands (Tables 6,7).

Color pattern in life (Fig. 51). Dorsal coloration of head, body and tail dark brown overlain with large, oval, black spots on anterior portion of body and nape; cream- colored, vertebral markings on nape and dorsum; thin, semi-transversely oriented, yellow bands on body and flanks; limbs bearing wide, dark and yellowish alternating faint bands; yellow caudal bands containing dark pigmentation; all ventral surfaces dark-gray.

Distribution. *Cnemaspis nigridia* is known from the type locality of Gunung Gading as well as Gunung Pueh, Gunung Beremput, and the Bau Limestone Area (Smith 1925; Naming & Das 2004; Das 2006), Sarawak, East Malaysia (Fig. 4).

Natural History. We have observed *Cnemaspis nigridia* only at night on the surfaces of large granite boulders in the vicinity of streams within old lowland secondary forest in forest (Fig. 51). Surveys during the day resulted in finding only *C. kendallii* in these areas. In all the locations from which this species has been reported except the Bau Limestone Area (which may be erroneous, see below) it is restricted to granite boulders.

Remarks. Naming & Das (2004) report *Cnemaspis nigridia* as occurring on karst formations in the Bau Limestone Area. However, it is not clear if specimens were actually examined as there is no character support for their identification or voucher specimens listed. Only the habitat generalists *C. kendallii* and *C. peninsularis* sp. nov. and *C. flavigaster* occur on both karst and granite and we suspect the Bau population may not be *C. nigridia* but the karst-adapted *C. paripari* which occurs in that region (Grismer & Chan 2009).

Relationships. *Cnemaspis nigridia* is the sister species of *C. paripari* from northwestern Borneo (Fig. 2).

Material examined. East Malaysia: Sarawak, Gunung Gading LSUHC 9167–70.

Cnemaspis paripari Grismer & Chan, 2009

Fairy Rock Gecko

Figs. 52, 53

Holotype. ZRC 2.6812. Type locality: "Gua Pari-pari, Bau District, Sarawak, [East] Malaysia (01°22.867 N, 110°07.164 E)" at approximately 30 m inelevation.

Diagnosis. Maximum SVL 50.7 mm; 12 or 13 supralabials; 10 or 11 infralabials; ventral scales keeled; 2–6, discontinuous, pore-bearing, precloacal scales with round pores; 26–31 paravertebral tubercles; body tubercles randomly arranged, absent on flanks and from lateral caudal furrows; ventrolateral caudal tubercles absent; lateral row of caudal tubercles present; caudal tubercles not encircling tail; subcaudals keeled but bearing an enlarged median row of smooth scales; two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; submetatarsal scales of first toe enlarged; subtibials keeled; 26–31 subdigital fourth toe lamellae; head, limbs, and regenerated tail yellow in males; posterior one-half of original tail white in males (Tables 6,7).

FIGURE 52. Adult male *Cnemaspis paripari* (LSUDPC 4920) from Gua Pari-pari, Sarawak, East Malaysia in the dark color pattern phase. Photograph by LLG.

Color pattern in life (Figs. 52, 53). Males: dorsal ground color of body yellowish brown; limbs yellow; head (especially snout) bright yellow bearing small, irregularly shaped, brownish, occipital flecks and a faint, brownish, postorbital stripe; ground color of nape and shoulder region gray bearing paravertebral, irregularly shaped, black blotches; incomplete, transverse, yellow bands between forelimb and hind limb insertions; smaller, scattered, dark spots between bands; limbs generally immaculate; anterior one-half of tail gray bearing faint, dark bands; posterior one-half of tail immaculate, white; all ventral surfaces gray except for posterior half of tail which is white and beige; regenerated tail bright yellow. Females: adult females have an overall brown ground color, lack a yellow head and a yellow or white tail; yellow banding on body faint; dark blotching pattern on nape; tail brown at base, gradually turning to gray posteriorly; weakly banded.

Distribution. *Cnemaspis paripari* is known only from the karst formations that extend approximately 4.2 km from Gua Angin to Gua Pari-pari within the Bau Limestone Area, Sarawak, Malaysia (Fig. 4).

Natural History. According to Grismer and Chan (2009), *Cnemaspis paripari* is a diurnal, lowland, saxicolous species that appears to be restricted to the karst outcroppings extending from Gua Angin to Gua Pari-pari that are surrounded by lowland dipterocarp forest (Fig. 53). They reported seeing several specimens around and slightly within the openings of caves where light could still penetrate as well as on rocks along the periphery of the outcroppings. No specimens were observed deep within the caves. Most lizards were observed on vertical surfaces in shaded areas and would retreat into nearby cracks at the slightest provocation. Males would often curl their tail up over their back and wave the bright yellow (regenerated) or white (original) posterior section from side to side.

Relationships. *Cnemaspis paripari* and its sister species of *C. nigridia* from the *nigridia* species group (Fig. 2).

Material examined. East Malaysia: Sarawak, Gua Pari-pari ZRC 2.6812; Gua Angin LSUHC 9185, ZRC 2.6813–14 (type series).

FIGURE 53. *Cnemaspis paripari* from Gua Angin, Sarawak, East Malaysia. Upper left: adult male (LSUDPC 4924) in the dark color pattern phase. Upper right: gravid female (LSUDPC 4923) in the dark color pattern phase. Lower: karst microhabitat at Gua Angin. Photographs by LLG.

***Kendallii* group.** The *kendallii* group is a well-supported lineage containing a morphologically diverse group of endemic, insular species from the Seribuat (*Cnemaspis baueri* and *C. pemanggilensis*) and Natuna (*C. mumpuniae* sp. nov. and *C. sundainsula* sp. nov.) archipelagos along with *C. bidongensis* from Pulau Bidong from Peninsular Malaysia; *C. peninsularis* sp. nov. from Peninsular Malaysia and Singapore, and *C. kendallii* from East Malaysia and Indonesia (Figs. 2, 4). As noted above, the monophyly of this group is further supported in that these seven species lack precloacal pores (Fig. 5). The relationships within the *kendallii* group clearly indicates that *C. kendallii* is polyphyletic, being that it has at least six separate, independent origins (Fig. 2 and see below): *C. kendallii* from Borneo; *C. kendallii* from Peninsular Malaysia (= *C. peninsularis* sp. nov.), and *C. kendallii* from the Natuna Archipelago, Indonesia (*Gonatodes kendallii fide* De Rooij [1915] = *C. mumpuniae* sp. nov. and *Gonatodes kendallii fide* Günther [1895] = *C. sundainsula* sp. nov.). The precise phylogenetic placement of *C. kendallii* (*Gonatodes kendallii fide* Smedley [1928] = *C. sundagekko* sp. nov.) from Pulau Siantan of the Anambas Archipelago, Indonesia is not yet known but will likely add an additional independent origin (see below). The polyphyletic nature of *C. kendallii* was first noted by Grismer *et al.* (2008b) and Grismer (2011a:334). Leong *et al.* (2003) indicated that populations on a number of Indonesian Islands were also likely to be different species. In their revision of *C. kendallii,* Das & Bauer (1998) considered the population from the upland region of Bukit Larut in Peninsular Malaysia, all Peninsular Malaysian and Seribuat Archipelago populations, and the Natuna Besar and Anambas Island populations to compose *C. kendallii* which in fact is a composite of six species (Grismer *et al.* 2008b and herein), some of which occur in different clades. The phylogeny also indicates that the Peninsular

Malaysian and Seribuat Archipelago populations (i.e. *C. peninsularis* sp. nov.) and the Natuna Besar Island populations are not closely related to Bornean *C. kendallii*, which which is the provenance of the holotype (Gray 1845). Additionally, examination of the population from Pulau Siantan from the Anambas Archipelago reveals that it too is not conspecific with Bornean *C. kendallii* but likely related to a clade containing *C. baueri, C. pemanggilensis, C. mumpuniae* sp. nov., *C. bidongensis,* and *C. peninsularis* sp. nov. being that it has the derived character state of caudal tubercles encircling the tail. Therefore, *C. kendallii sensu lato* is reclassified and the new species are described below.

In the molecular analysis, *Cnemaspis sundainsula* sp. nov. is the basal species in a well-supported monophyletic group comprised of it and *C. pemanggilensis, C. kendallii sensu stricto, C. baueri, C. mumpuniae* sp. nov., *C. bidongensis,* and *C. peninsularis* sp. nov. The monophyly of these latter species is supported in that they are the only species of *Cnemaspis* that have caudal tubercles encircling the tail and the monophyly of *C. baueri, C. mumpuniae* sp. nov., *C. bidongensis,* and *C. peninsularis* sp. nov. is supported in that they are the only *Cnemaspis* in which the posterior portion of the original tail is black.

The *kendallii* group is diagnosed by having a maximum SVL 58.1–84.5 mm; 9–13 supralabials; 7–12 infralabials; keeled ventral scales; 0–6, contiguous, round, pore-bearing, no precloacal pores; body tuberculation moderate; 17–37 paravertebral tubercles; caudal tubercles not restricted to a single paravertebral row; lateral row of caudal tubercles present; 1–4 postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; and 25–38 subdigital fourth toe lamellae.

Cnemaspis sundainsula sp. nov.

Sunda Island Rock Gecko

Fig. 54

Gonatodes kendallii Günther 1895:500; De Rooij 1915:26 (in part)
Cnemaspis cf. *nigridia* Leong, Grismer & Mumpuni 2003:170
Cnemaspis kendallii Das & Bauer 1998:13

Holotype. Adult male MZB. Lace.9438 collected by Awal Riyanto on 24 October 2011 from Mount Ranai, Bunguran Timur district , Natuna Regency , Kepulauan Riau Province, Bunguran (Great Natuna) Island, Indonesia (03°57'24.5"N, 108°21'08.3"E) at 345 m above sea level .

Paratypes. Adult male paratypes MZB.Lace 9436–37 and adult female paratypes MZB.Lace 9439–40 have the same data as the holotype except that MZB.Lace 9440 was collected on 25 October 2011; adult maleTNHC 64276, adult female TNHC 62277 and adult male MZB.Lace.4621 were collected on 3 April 2003 by B. J. Evans, Mohd. Iqbal Setiadi and Gandhi Probowo from Mount Ranai, Bunguran Timur District, Natuna Regency , Kepulauan Riau Province, Bunguran Island, Indonesia (03°57.381' N, 108°21.319' E); adult female USNM28139 was collected on 2 July1900 by W. L. Abbott from Bunguran (=Pulau Natuna Besar), Kepulauan Riau Province, Indonesia (03°57.381' N, 108°21.319' E); adult males MZB.Lace 10156 and 10159 were collected on 26 August 2013 and 27 August 2013, respectively by Awal Riyanto and Zamri at Ceruk Forest Conserve, Selemam Village, Bungaran Timur Laut District, Natuna Regency, Kepulauan Riau Province, Bunguran Island, Indonesia(03°58'31.6" N, 108°17'52.2" E) at 51 m above sea level; and adult males MZB.Lace 10160–61 were collected on 28 August 2013 by Awal Riyanto and Zamri at Gunung Air Hiu Recreation Area, Ceruk Village, Bungaran Timur Laut District, Natuna Regency, Kepulauan Riau Province, Bunguran Island , Indonesia (03°59'03.7" N, 108°19'06.0"E) at 117 m above sea level.

Additional specimens examined. Adult males MZB.Lace 10157–58 collected on 26 August 2013 and 27 August 2013, respectively by Awal Riyanto and Zamri at Ceruk Forest Conserve, Selemam Village, Bungaran Timur Laut District, Natuna Regency, Kepulauan Riau Province, Bunguran Island, Indonesia; subadult males MZB.Lace 9439–40 and MZB.Lace 10162 were collected on 28 August 2013 by Awal Riyanto and Zamri at Gunung Air Hiu Recreation Area, Ceruk Village, Bungaran Timur Laut District, Natuna Regency, Kepulauan Riau Province, Bunguran Island, Indonesia.

Diagnosis. Maximum SVL 84.5 mm; 8–11 supralabials; 7–10 infralabials; ventral scales keeled; no precloacal pores; 26–37 paravertebral tubercles; tubercles linearly arranged, preent on flanks but absent in lateral caudal furrows; ventrolateral caudal tubercles present; lateral row of caudal tubercles present; caudal tubercles not encircling tail; subcaudals smooth but bearing an enlarged median row of smooth scales occasionally posteriorly; 2–4 postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; submetatarsal scales of first toe weakly enlarged to enlarged; subtibials keeled; 25–29 subdigital fourth toe lamellae; small, light-colored round sponts on flanks; gukar region, throat, and lateral sections of abdomen orange; anterior subcaudal region yellow, posterior region white (Tables 6,7).

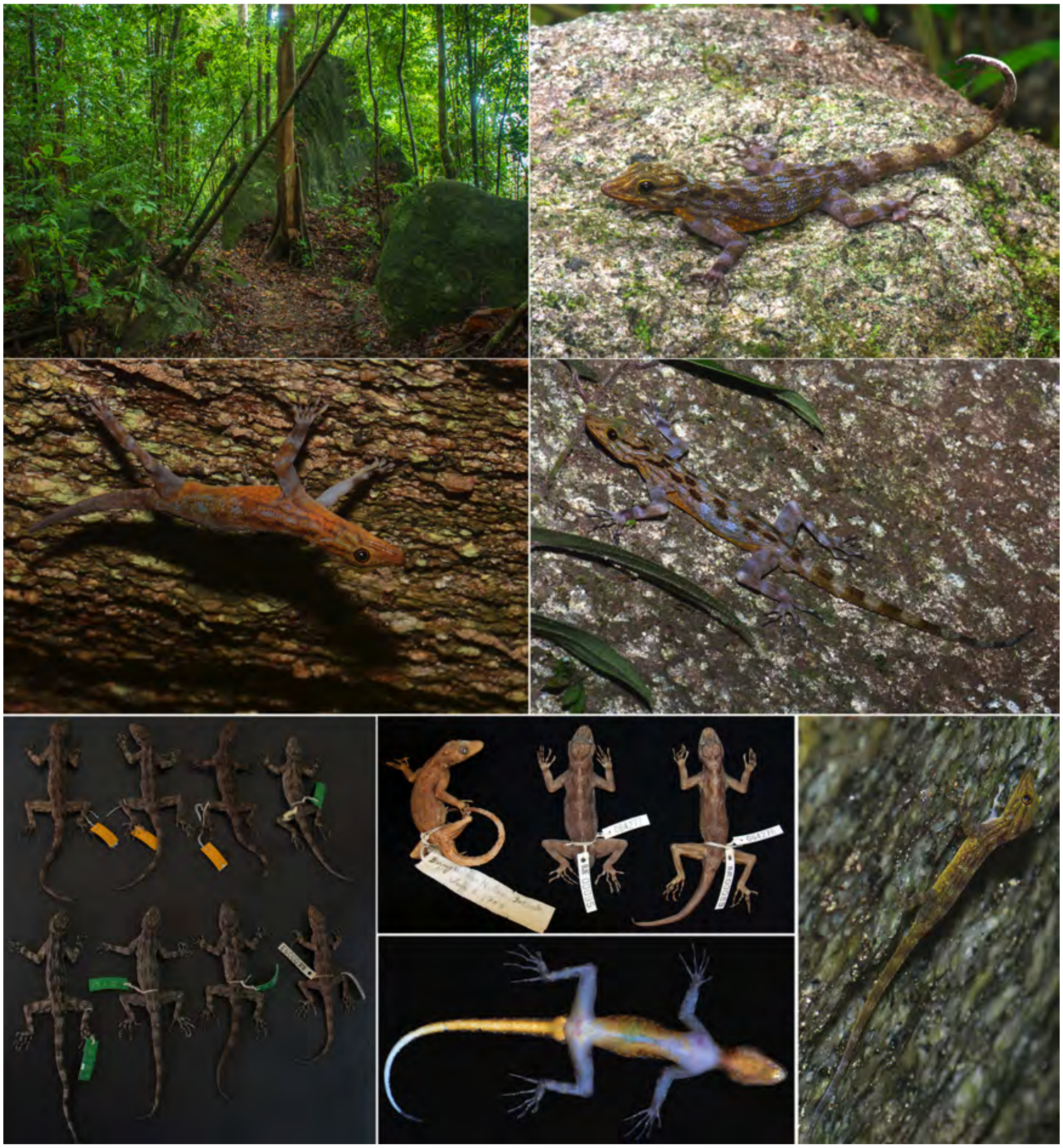

FIGURE 54. *Cnemaspis sundainsula* sp. nov. from Mount Ranai, Kecamatan Bunguran Timur, Kabupaten Natuna, Propinsi Kepulauan Riau, Bunguran (Great Natuna) Island, Indonesia. Upper left: granite bolder habitat in primary forest at the type locality at the base of Mount Ranai. Upper right: adult male (LSUDPC 8790) in dark color phase. Middle left: adult female (LSUDPC 8796) *in situ* displaying orange flanks and undersides. Middle right: adult male (LSUDPC 8813) *in situ* at night in light color phase. Lower left: holotype MZB.Lace.9438 (upper left) and paratypes MZB.Lace 9436, 9437 and 10161 (upper row from left to right) and paratypes MZB.Lace 10156, 10160, 10159, and 4621 (lower row from left to right). Lower middle, upper: paratypes holotype USNM 28136 (left) and paratypes THNC 64276–77 (middle and right, respectively). Lower middle, lower: underside of adult male (uncataloged). Lower right: hatchling (LSUDCP 8829) *in situ.* Photographs by LLG.

Description of holotype. Adult male, SVL 84.1 mm; head robust, oblong in dorsal profile, moderate in size (HL/SVL 0.23), not narrow (HW/SVL 0.15), flattened (HD/HL 0.41), distinct from neck; snout moderate (ES/HL 0.42), slightly concave in lateral profile; postnasal region constricted medially; scales of rostrum keeled, raised, larger than scales on occiput; distinct, supraorbital ridges; no frontorostral sulcus; canthus rostralis rounded; eye large (ED/HL 0.22); extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral concave dorsally, posterior 90% divided by longitudinal groove; rostral bordered posteriorly by two large supranasals and external nares, laterally by first supralabials; 9R,L raised supralabials decreasing in size posteriorly; 8R,L infralabials, decreasing in size posteriorly; nostrils round, oriented dorsoposteriorly; mental large, triangular, flat, bordered posteriorly by six postmentals, first two on either side largest; gular and throat scales granular, keeled, raised; pectoral scales slightly larger.

Body robust (AG/SVL 0.43); small, granular, rugose, dorsal scales generally equal in size throughout body, intermixed with larger, multicarinate tubercles more or less linearly arranged; tubercles extend from occiput to base of tail; tubercles on flanks; 32 paravertebral tubercles; pectoral and abdominal scales small, granular, keeled, same size throughout; abdominal scales slightly larger than dorsals; no precloacal pores; forelimbs moderately long, robust (FL/SVL 0.19); dorsal scales of brachium raised, keeled; dorsal scales of forearm raised, keeled; ventral scales of brachium keeled, raised, juxtaposed; ventral scales of forearm keeled, raised, juxtaposed; palmar scales, juxtaposed, raised, broadly keeled; digits long with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae wide throughout digit; interdigital webbing absent; fingers increase in length from first to fourth with fourth longer than fifth; hind limbs robust, slightly longer and thicker than forelimbs (TBL/SVL 0.24); dorsal scales of thigh keeled, raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh keeled; subtibial scales raised, keeled, juxtaposed, with no enlarged anterior row; plantar scales smooth, juxtaposed, raised; weakly enlarged to enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected joint; claws recurved; subdigital lamellae unnotched, wide throughout digit; interdigital webbing weak to absent; toes increase in length from first to fourth with fourth being slightly longer than fifth; 28 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; dorsal caudal scales raised, keeled, juxtaposed; deep middorsal and lateral caudal furrows; subcaudal scales smooth; median row of enlarged subcaudal scales posteriorly; caudal tubercles do not encircle tail; tubercles absent from lateral furrows; three enlarged postcloacal tubercles on lateral surface of hemipenal swellings at base of tail.

Coloration in life (Fig. 54). Dorsal ground color of head, body and limbs yellowish brown; paired, yellowish, lineate markings on rostrum; irregularly shaped yellowish markings on top of head; thin, black, upper postorbital stripe extending to occiput; thin, black, lower postorbital stripe extending onto flank; thin, yellowish, postorbital stripe highlighting row of tubercles on latter surface of occiput; transverse, beige marking on nape followed by one square and two rectangular medial beige markings on body alternating with small, elongate, thin, black vertebral markings; light rectangular markings on body grade into diffuse, light caudal bands alternating with darker brown bands; caudal bands do not encircle tail; diffuse light blotches on flanks; tubercles on flanks white; dark, diffuse, rectangular markings on back and flanks alternate with light markings; gular region and throat yellow-orange; lateral margins of abbomen and lower flanks yellow-orange; anterior one-half of subcaudal region yellow, posterior one-half white; ventral surfaces of pectoral region and limbs beige.

Variation (Fig. 54). All paratypes closely resemble the holotype in coloration and pattern although TNHC 64276–77 and MZB.Lace 4621 are not nearly as boldly marked. The color pattern of MZB.Lace 10156 is much bolder than that of the holotype in that the dark and light dorsal markings stand in distinct contrast to one another. The dark dorsal markings of MZB.Lace 10161 are elongate as opposed to being more square to roundish as in the other specimens. TNHC 64277 lacks a tail and the tail of TNHC 64276 is regenerated and composed of small, dark, roundish, juxtaposed scales that are weakly keeled on the dorsal surface whereas the subcaudals are smooth beige, and slightly larger. USNM 28139 is badly faded and only a general color pattern that matches that of the holotype is visible. Hatchlings tend to have yellow undersides. Meristic differences are listed in Table 12.

Comparisons. Within the Southern Sunda clade, *Cnemaspis sundainsula* sp. nov. is differentiated from the species of the *nigridia* group (*C. nigridia* and *C. paripari*) by having a greater maximum SVL (84.5 mm versus 50.7–75.5 mm); lacking as opposed to having precloacal pores; having tubercles on the flanks as opposed to lacking them; having smooth as opposed to keeled subcaudals; generally lacking as opposed to having a median row of enlarged, subcaudal scales; and lacking as opposed to having weakly enlarged, metatarsal scales beneath the first toe. From the species of the *kendallii* group (*C. baueri, C. pemanggilensis, C. mumpuniae* sp. nov., *C.*

bidongensis, and *C. peninsularis* sp. nov.) of which it is a member, it can be differentiated by having a much greater maximum SVL (84.5 mm versus 58.1–76.0 mm), having smooth as opposed to keeled subcaudal scales, and not having caudal tubercles that encircle the tail. From *C. limi, C. sundainsula* sp. nov. is separated by having linearly as opposed to randomly arranged dorsal tubercles, and having a ventrolateral row of caudal tubercles. *Cnemaspis sundainsula* sp. nov. can be differentiated from *C. sundagekko* sp. nov, by having a much larger maximum SVL (84.5 mm versus 68.0 mm), a greater number of paravertebral tubercles (26–37 versus 20–25), smooth as opposed to keeled subcaudals, caudal tubercles that do not encircle the tail, and fewer subdigital lamellae on the fourth toe (26–31 versus 33–38).

TABLE 12. Meristic and mensural character states of the type series of *Cnemaspis sundainsula* sp. nov. w = weak; f = female; m = male; post = posterior; / = data unavailable; and r = regenerated. Meristic abbreviations are listed in the Materials and Methods. For TL, the measurement for the original portion of the tail is on the left and the measurement for the regenerated portion is on the right.

	USNM	TNHC	TNHC	MZB.Lace	MZB.Lace	MZB.Lace	MZB.Lace	MZB.Lace	MZB.Lace	MZB.Lace	MZB.Lace
	28139	64276	64277	9438	9436	9437	10161	10156	10160	10159	4621
	paratype	paratype	paratype	holotype	paratype	paratype	paratype	paratype	paratype	paratype	paratype
Supralabials	10	9	10	9	9	9	11	8	10	9	10
Infralabials	8	7	9	8	10	8	9	9	8	8	9
Ventral scales keeled (1) or not (0)	1	1	1	1	1	1	1	1	1	1	1
No. of precloacal pores	0	0	0	0	/	0	/	0	0	0	/
Precloacal pores continuous (1) or separated (0)	/	/	/	/	/	/	/	/	/	/	/
Precloacal pores elongate (1) or round (0)	/	/	/	/	/	/	/	/	/	/	/
No. of paravertebral tubercles	35	31	37	32	31	34	26	33	31	29	31
Tubercles linearly arranged (1) or more random (0)	1	1	1	1	1	1	1	1	1	1	1
Tubercles present (1) or absent (0) on flanks	1	1	1	1	1	1	1	1	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	0	/	/	0	0	0	0	0	0	0	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	/	/	1	1	1	1	1	1	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	/	/	1	1	1	1	1	1	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	/	/	0	0	0	0	0	0	0	0
Subcaudals keeled (1) or not (0)	0	/	/	0	0	0	0	0	0	0	0
Single median row of keeled subcaudals (1) or not (0)	0	/	/	0	0	0	0	0	0	0	0
Caudal tubercles encircle tail (1) or not (0)	0	/	/	0	0	0	0	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	/	/	w,post	w,post	w,post	/	w,post	post	/	w,post
Postcloacal spurs	4	4	2	3	/	/	3	3	2	2	/
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	1	1	1	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	w	w	w	1	1	1	1	1	1	1	1
No. of 4th toe lamellae	28	28	29	25	26	27	28	26	27	26	29
Sex	f	m	f	m	f	f	f	m	m	m	f
SVL	80	81	79.7	84.5	77.5	82.3	75.2	75.2	77.7	75.2	68.9
TL	97.6	65.9	/	82.4/12.8	75.6/14.8	69.3/19.3	34.6/35.1	93.8	90.4	38.9/42.3	83.5
TW	8.9	9.6	10.6	8.9	9.8	8.5	7.9	7.8	8.4	7.5	6.9
FL	15.4	16.8	15.7	15.7	16.9	15.1	14.7	13.8	14.6	14.8	13.9
TBL	19.1	19.2	19.1	20.7	20.9	19.6	17.5	18.5	18.8	18.2	16.6
AG	34.5	34.2	30.8	35.9	33.4	33.1	32.1	32.7	31.9	31.7	27.9
HL	18.4	20	20.3	20.6	20.4	20.6	19.2	20.1	19.8	20.3	17.4
HW	13.6	13.4	14.6	13.9	12.9	12.6	12.7	12.8	12.8	12.9	12.1
HD	8.9	8.9	9.2	9.1	8.5	7.8	8.1	8.2	8.1	7.1	7.5
ED	4.2	3.9	4.2	4.5	4.3	4.3	3.9	3.6	3.9	3.7	3.5
EE	6.1	2.5	2.3	6.3	4.9	6.1	5.7	5.9	5.6	5.9	5.3
ES	10	9.7	9.6	10.1	9.6	10.1	9.3	9.5	9.1	8.2	8.4
EN	7.7	7.5	7.4	7.6	7.2	7.9	6.9	7.4	6.9	6.3	6.6
IO	1.9	4	4.5	4.9	4.5	4.8	4.5	4.7	4.5	4.7	4.5
EL	1.7	2.4	2.2	2.2	2.1	2.4	1.9	1.7	2.1	1.2	2.1
IN	1.8	1.7	1.8	2.1	1.7	1.9	1.7	1.8	1.9	1.8	1.9

Distribution.*Cnemaspis sundainsula* sp. nov. is known only from Bunguran Island (= Pulau Natuna Besar/ Great Natuna) of the Natuna Archipelago, Kepulauan Riau Province, Indonesia (Fig. 4) but is likely to occur on nearby islands in the archipelago.

Natural History. *Cnemaspis sundainsula* sp. nov. inhabits primary and secondary forests along the base of

Mount Ranai from at least 51–345 m above sea level (De Rooij 1915; Günther 1895). It is not certain if this species extends up to the summit but if granite boulders are present we suspect it does. Lizards occur almost exclusively on large granite boulders (Fig. 54) and are only rarely found on tree trunks. This species is abundant and active during the day while in its dark color phase (Fig. 54) and often in male-female pairs. While active during the day, lizards remain wary and will not venture too far out onto the exposed boulder surfaces but rather remain near cracks or narrow spaces between adjacent boulders were escape is possible. Lizards are commonly seen upside down suspended from the undersides of boulders with their limbs outstretched displaying their birght-orange lower flanks, throat, and abdomens (Fig. 54). Before escaping into cover lizards, roll their tails up over their backs and display the immaculate, white posterior subcaudal region (Fig. 54). In dark crevices and boulder spaces, often the subcaudal region is all that can be seen. At night, lizards venture farther out onto the exposed boulder surface and sequester themselves in a shallow depression or crease or along the edge of a small ridge where they are generally inactive. During this period, lizards are in their light color phase (Fig. 54) and are much more approachable. We have observed gravid females carrying two eggs, hatchings, and juvenlies during April.

Cnemaspis sundainsula sp. nov. occurs syntopically with *C. mumpuniae* sp. nov. and *Cyrtodactylus hikidai* Riyanto when the latter two species occur on granite boulders. The ecological pattern of temporal partitioning on islands seen between *C. sundainsula* sp. nov. and *Cyrtodactylus hikidai* is similar to that between *C. psychedelica* on Hon Khoai Island, Vietnam which is diurnal and found syntopically with the nocturnal *Cyrtodactylus* sp. nov. 1 (Grismer *et al.* 2010b); *C. boulengerii* on Con Son Island in the Con Dao Archipelago, Vietnam which is diurnal and syntopic with the larger *Cyrtodactylus condorensis* (Smith); and the large, diurnal, granite boulder-dwelling *C. limi* from Pulau Tioman, Peninsular Malaysia which is syntopic with the larger nocturnal *Cyrtodactylus tiomanensis* Das & Lim. Additionally, *C. sundainsula* sp. nov. and *C. mumpuniae* sp. nov. partition their habitat by SVL, elevation, and general microhabitat preference where *C. sundainsula* sp. nov. is a large, rock-dweller and *C. mumpuniae* is the smaller, habitat generalist. A parallel system exists on Pulau Tioman, Malaysia with the smaller, habitat generalist *C. peninsularis* sp. nov. and the larger, rock-dwelling *C. limi* (Grismer 2011a).

Etymology. The specific epithet *sundainsula* is derived from the word Sunda which originally referred to a Hindu Kingdom in western Java existing from 669–1579. Sunda is now commonly used as an adjective associated with particular geographic features in the western regions of Southeast Asia associated with the South China Sea and its fringing continental areas. The Latin *insula* (singular) means island and *sundainsula* is an invariable noun in apposition in reference to this species being endemic to an island on the submerged Sunda Plains.

Relationships. *Cnemaspis sundainsula* sp. nov. is part of the *kendallii* group within the Southern Sunda clade and is basal to a group containing *C. pemanggilensis, C. kendallii sensu stricto, C. baueri, C. mumpuniae* sp. nov., *C. bidongensis,* and *C. peninsularis* sp. nov. (Fig. 2).

***Cnemaspis kendallii* (Gray, 1845)**

Kendall's Rock Gecko
Figs. 55, 56

Heteronota kendallii Gray, 1845:174 (in part)
Gonatodes kendalli (in part) Boulenger, 1885:63; Shelford, 1901:48
Gonatodes affinis Shelford, 1901:49
Gonatodes kendallii de Rooij, 1915:25 (in part)

Lectotype. BM XXII.92 (designated by Dring 1979:223). Type locality: "Borneo" (02°34.44 N, 104°19.53 E) at 100 m in elevation.

Diagnosis. Maximum SVL 58.4 mm; 10 or 11 supralabials; eight or nine infralabials; keeled ventral scales; no precloacal pores; 18–26 paravertebral tubercles; body tubercles semi-linearly arranged, weak to present on flanks, tubercles absent from lateral caudal furrows; ventrolateral and lateral row of caudal tubercles present; caudal tubercles encircle tail; subcaudals keeled with no enlarged median row; two postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials keeled; 25–33 subdigital fourth toe lamellae; distinct black and white caudal bands on posterior portion of tail; subcaudal region immaculate white (Tables 6,7).

FIGURE 55. *Cnemaspis kendallii.* Left: adult female (LSUDPC 4903) from Santubong, Sarawak, East Malaysia in the light color pattern phase. Upper right: adult male (LSUDPC 4875) from Gunung Gading, Sarawak, East Malaysia in the dark color pattern phase. Photographs by LLG. Lower right: adult male (LSUDPC 6804) from Pulau Karimata, Kalimantan, Indonesia. Photograph by Umilaela Arafin.

Color pattern in life (Figs. 55, 56). Coloration differs greatly depending on the time of the day. Diurnal coloration: dorsal ground color of the head, body, and limbs grey to dark brown; dark and yellow markings on top of head; thin, dark, diffuse, postorbital stripe extends onto nape; medial, black marking on nape followed by black, vertebral spots extending from shoulder region to base of tail and flanked laterally by additional row of spots on each side on anterior portion of body; dorsum and upper portions of limbs bearing whitish to yellowish spots, those in vertebral region largest; black and white caudal bands in males and females, bands encircling tail in females; subcaudal region nearly immaculate white in males in both original and regenerated tails; dorsal pattern of regenerated tail beige with dark flecking; ventral surfaces of head and neck dull-beige; pectoral region, abdomen and ventral surfaces of limbs beige, usually immaculate. Nocturnal coloration: ground color of dorsal surface of head and body nearly white to light yellow, highlighting dark markings on head and spotting on dorsum; ground color of limbs and tail yellowish.

Distribution. *Cnemaspis kendallii* ranges throughout northwestern Borneo in Sarawak, East Malaysia (Das & Bauer 1998) and western Kalimantan, Indonesia. It ranges northward to Pulau Serasan of the Southern Natuna Islands and onto Pulau Buona of the Tambelan Islands, Pulau Pedjantan [sic.] (=Pejantan), and Pulau Karimata (Umilaela *et al.* 2009) to the south (Fig. 4). Das and Bauer (1998) erroneously reported this species from "Pulo [sic] Lingga" based on specimen USNM 28145. However, Pulau Lingga is an island south of Pulau Bintan, Indonesia that lies just south of Singapore on the western edge of the South China Sea. The original hand written collection label on USNM 28145 reads "Pulau Lingung [=Pulau Lagong] near Natuna Besar" which is a small island off the southern tip of Pulau Natuna Besar (Fig. 4). USNM 28145 is recognized here as *C. mumpuniae* sp. nov.

FIGURE 56. Upper: adult male *Cnemaspis kendallii* (LSUDPC 4901) at Santubong, Sarawak, East Malaysia in the dark color pattern phase displaying the white underside of the original tail. Lower: habitat of *Cnemaspis kendallii* at Matang, Sarawak, East Malaysia. Photographs by LLG.

FIGURE 57. Upper: adult male *Cnemaspis pemanggilensis* (LSUDPC 2578) from Pulau Pemanggil, Johor, Peninsular Malaysia in the dark color pattern phase. Lower: habitat on Pulau Pemanggil. Photographs by LLG.

Natural history. *Cnemaspis kendallii* is a habitat generalist that ranges throughout primary, secondary, and old secondary forests. Lizards are generally diurnal and can be found on the shaded surfaces of large granite boulders, limestone formations, tree roots, and tree trunks (Fig. 56). Upon retreat, males often roll their tail over their back displaying its white, immaculate underside (Fig. 56) while waving the tip back and forth. At Gunung Gading, we observed lizards during the day on the same granite boulders wherein we observed the much larger *C. nigridia* at night, indicating these species may be partitioning their microhabitat by means of body size and activity period as has been suggested for other sympatric pairs of *Cnemaspis* (Grismer *et al.* 2010b). At night, *C. kendallii* is often found abroad sleeping on tree trunks and other vegetation and in open areas on the faces of granite boulders.

Relationships. *Cnemaspis kendallii* is the sister species of *C. pemanggilensis* (Fig. 2).

Remarks. We examined two specimens from the Tambelan Archipelago, Indonesia collected in 1899: one from Pulau Benua (=Buona) and another from Pulau Pejantan (USNM 26573 and 26555, respectively). Both were very faded and in poor shape overall. More importantly, both lacked tails meaning that eight of some of the most important diagnostic character states used to delimit species boundaries between *Cnemaspis* were unavailable for examination. The combination of the remaining character states such as no precloacal pores, keeled ventrals and subtibials, SVLs of 51.5 and 55.7 mm coupled with their locality off the west coast of Borneo would place them in *C. kendallii* as was reported by Das and Bauer (1998). However, being that this archipelago has been separated from Borneo for nearly as long as the Anambas and Natuna archipelagos (which collectively harbor at least three species of endemic *Cnemaspis*) and their specific identity is not possible, we recognize these populations as *C.* cf. *kendallii.* Plans are in preparation to collect additional specimens.

Material examined. East Malaysia: Sarawak, Gunung Gading LSUHC 9171–73, 9176, USNM 76633; Santubong LSUHC 9178–81. Indonesia: Riau Province, Natuna Archipelago, Pulau Serasan TNHC 64278; Tambelan Archipelago, Pulau Buona USNM 26573; Pulau Pejantan USNM 26555.

Cnemaspis pemanggilensis Grismer & Das, 2006

Pemanggil Island Rock Gecko

Fig. 57

Holotype. ZRC 2.6043. Type locality: "Batu Buau, a small rocky hill behind Kampung Buau on the west side of Pulau Pemanggil, Johor, West Malaysia" (02°34.44 N, 104°19.53 E) at 100 m in elevation.

Diagnosis. Maximum SVL 76.0 mm; 10–13 supralabials; 8–10 infralabials; keeled ventral scales; no precloacal pores; 30–37 paravertebral tubercles; body tubercles randomly arranged, weak to absent on flanks, absent from lateral caudal furrows; ventrolateral row of caudal tubercles present anteriorly; lateral row of caudal tubercles present; caudal tubercles encircle tail; subcaudals keeled, bearing an enlarged median row of keeled scales; one or two postcloacal tubercles on each side of tail base; no enlarged femoral or subtibial scales; distal submetatarsal scales of fourth toe enlarged; subtibials keeled; 27–34 subdigital fourth toe lamellae; small, yellow spots on flanks (Tables 6,7).

Color pattern in life (Fig. 57). Ground color of head, body, limbs, and tail grey; dark, bifurcating, medial stripe on snout; single, dark, preorbital stripe; three dark, postorbital stripes with dorsalmost extending onto nape and forming a tripartite band; middle stripe extends onto nape forming a second tripartite band posterior to and larger than the first; ventralmost stripe extends onto upper portions of forelimb insertions; dark, transversely arranged spots extend from nape to base of tail; distinctive, yellowish spots occur on flanks invading lateral portions of abdominal region; weak, banding pattern on limbs; dark, diffuse banding on anterior portion of tail; ventral surfaces beige bearing dark and light spots. During the day, the dorsal ground color is nearly solid black with virtually no discernable pattern. At night, the dorsal ground color changes to light grey which greatly accentuates a prominent series of dark, transverse, body bands and head stripes.

Distribution. *Cnemaspis pemanggilensis* is known only from the island of Pemanggil (Grismer & Das 2006; Grismer *et al.* 2006; Grismer 2011b; Fig. 4).

Natural history. The habitat on Pulau Pemanggil is severely degraded and has no discernable primary forest (Youmans *et al.* 2002). Nonetheless, the cave-like systems formed by the piling up of large, granite boulders (Fig. 57) on top of one another maintain the microhabitats and refugia necessary to support a dense population of *Cnemaspis pemanggilensis* (Grismer & Das 2006). According to Grismer (2011a), lizards are found in nearly every cave system at all elevations from sea level to 250 meters. During the day, lizards remain inside the caves on all vertical and inverted surfaces where they are extremely wary and rapidly move into deep crevices and cracks at the slightest provocation. At night, however, lizards will venture out along the cave openings and on large boulders immediately outside the caves and become much more approachable.

Relationships. *Cnemaspis pemanggilensis* is the sister species to *C. kendallii* (Figs. 2,5).

Material examined. West Malaysia: Johor, Pulau Pemanggil ZRC 2.6043–51 (type series). Material examined since Grismer & Das (2006): West Malaysia: Johor, Pulau Pemanggil LSUHC 4458, 4460, 4464, 4476, 4495, 8011–16.

FIGURE 58. *Cnemaspis baueri* from Pulau Aur, Johor, Peninsular Malaysia. Upper left: granite boulder microhabitat on Pulau Aur. Upper right: adult female (LSUDPC 958) in the dark color pattern phase. Middle right: juvenile male (LSUDPC 959) in the dark color pattern phase. Lower right: adult male (LSUDPC 961) in the dark color pattern phase. Lower left: adult male (LSUDPC 957) in the dark color pattern phase. Photographs by LLG.

Cnemaspis baueri Das & Grismer, 2003
Bauer's Rock Gecko
Fig. 58

Holotype. ZRC 2.5291. Type locality: "Kampung Berhala (2°27.507 N, 104°30.163 E), Pulau Aur, Johor, West Malaysia" at 50 m in elevation.

Diagnosis. Maximum SVL 67.4 mm; 11–13 supralabials; 8–12 infralabials; keeled ventral scales; no precloacal pores; 18–27 paravertebral tubercles; body tubercles randomly arranged, absent to weakly present on flanks; tubercles absent from lateral caudal furrows; ventrolateral and lateral caudal rows of tubercles present; caudal tubercles encircle tail; subcaudals keeled; a median row of enlarged, keeled subcaudals present; one or two postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials keeled; 26–32 subdigital fourth toe lamellae; uniform brown dorsal ground color; thin, yellow reticulum on occiput and nape; large, black, round spots on nape and anterior portion of body; thin, yellow, caudal bands anteriorly; posterior portion of original tail black in males; anterior caudal tubercles white (Tables 6,7).

Color pattern in life (Fig. 58). Ground color of dorsal surface of head, body, and limbs dark-brown to olive; thin, yellow reticulum on the top of head; dark, postorbital stripe extends onto nape; medial, dark marking on nape; black, shoulder patches absent; 5–7 dark, vertebral blotches flanked in shoulder region by elongate, dark blotches followed by dark spots extending onto midsection of body; limbs and body faintly mottled with slightly lighter coloration; posterior two-thirds of tail black; anterior one-third encircled by large, cream-colored tubercles; regenerated tail unicolor brown; ventral surfaces of head, body, limbs, and anterior one-third of tail dull beige, immaculate; sexual dimorphism absent.

Distribution. *Cnemaspis baueri* is known only from Pulau Aur, Johor and the nearby rocky island of Dayang (Grismer 2011a; Fig. 4). Das (2010) erroneously reports this species as being endemic to Pulau Tulai, Johor.

Natural History. Grismer (2011a) reported that *Cnemaspis baueri* is a saxicolous gecko common on rocky outcroppings in primary and secondary, lowland, coastal forests where it is found almost exclusively on the vertical surfaces of large granite boulders, within deep crevices, and within cave-like microhabitats formed by the aggregation of large boulders (Fig. 58). During the day, the activity of *C. baueri* is restricted to the shaded surfaces of large boulders under the forest canopy or within the cave-like environments wherein lizards can be found in surprisingly high densities. At night, lizards venture farther out into the open onto all surfaces of the rocks but are far less active. Das & Grismer (2003) estimated finding 200–250 egg scars on the underside of a large boulder in a communal laying site. Females carrying two eggs have been observed during July (Grismer 2011a).

Relationships. *Cnemaspis baueri* is the sister species of a monophyletic group containing *C. mumpuniae* sp. nov., *C. bidongensis,* and *C. peninsularis* sp. nov. (Figs. 2, 5).

Material examined. West Malaysia: Johor, Pulau Aur ZRC 2.5291–99 (type series). Material examined since Das and Grismer (2003): West Malaysia: Johor, Pulau Aur LSUHC 3921–24, 4700–01, 4717–23, 4725, 4727, 4729, 4744, 4808, 7272–74, 7301–03, 7319, ZRC 2.5093, 2.5095–96.

Cnemaspis mumpuniae sp. nov.
Mumpuni Rock Gecko
Fig. 59

Cnemaspis kendallii Das & Bauer 1998:12 (in part)
Cnemaspis cf. *kendalli* Leong, Grismer & Mumpuni 2003:170

Holotype. Adult male MZB.Lace 10167 collected by Awal Riyanto and Zamri on 31 August 2013 from Sekunyam Forest Reserve, Mekarjaya Village, Bunguran Barat district, Natuna Regency, Kepulauan Riau Province, Bunguran Island, Indonesia (03°40'30.8"N; 108°09'18.2"E) at 80 m above sea level.

Paratypes. Adult male MZB.Lace 10166 bears the same data as the holotype. Adult male MZB.Lace 10163 collected by Awal Riyanto and Zamri on 3 September 2013 respectively from Harapan Jaya Village, Bunguran Tengah District, Natuna Regency, Kepulauan Riau Province, Bunguran Island, Indonesia (03°51'29.8"N; 108°17'59.3"E) at 46 m above sea level, adult maleMZB.Lace.9441collected by some collectors of holotype 24 October 2011, from Mount Ranai, Bunguran Timur District, Natuna Regency, Kepulauan Riau Province, Bunguran Island, Indonesia (03°57'24.5"N, 108°21'08.3"E) at 345 m above sea level. Adult male MZB.Lace 10169 and adult female MZB.Lace 10168 collected by Awal Riyanto and Zamri on 1 September 2013 from Teluk Lampa Forest, Pulau Tiga District, Natuna Regency, Kepulauan Riau Province, Bunguran Island, Indonesia (03°40'04.9" N; 108°08'20.2" E) at 10 m above sea level.

FIGURE 59. *Cnemaspis mumpuniae* sp. nov. from Pulau Natuna Besar. Upper left: Adult male (LSUDPC 8784) from Gunung Ranai. Upper middle: *in situ* adult female (LSUDPC 8815) from Gunung Ranai. Upper right: adult male (LSUDPC 8784) from Selamam. Middle left: hatchling (LSUDPC 8823) from Gunung Ranai. Lower left: *in situ* adult male (LSUDPC 8784) from Gunung Ranai. Lower right: type series from Sekunyam Forest Reserve, Desa Mekarjaya, Kecamatan Bunguran Barat, Kabupaten Natuna, Kepulauan Riau Province, Indonesia, MZB.Lace 10167 (holotype) far left and paratypes 10166, 9941, 10169, 10168, and 10163 from left to right. Photographs by LLG.

Additional specimens examined. Adult female MZB.Lace 10155 collected by Awal Riyanto and Zamri on 25August 2013 from a fragmented forest area at Bedung Village, Bunguran Tengah District, Natuna Regency, Kepulauan Riau Province, Bunguran Island, Indonesia (03°56'36.8" N; 108°13'19.9" E) at 41 m above sea level. Adult females MZB.Lace 10164–65 have the same data as the holotype.

Diagnosis. *Cnemaspis mumpuniae* sp. nov. differs from all other species of *Cnemaspis* in having a maximum SVL reaching 56.6 mm SVL; 10 or 11 supralabials; 8–11 infralabials; keeled ventrals; no precloacal pores; moderate dorsal tuberculation; 18–24 paravertebral tubercles; dorsal body tubercles semi-linearly arranged; weak tuberculation on flanks; caudal tubercles encircling tail; tubercles absent from lateral caudal furrows; ventrolateral and lateral row of caudal tubercles present; subcaudals keeled; single, median row of enlarged subcaudals; one or two postcloacal tubercles on either side of base of tail; no enlarged femoral, subtibial or submetatarsal scales; subtibials usually keeled; 29–35 subdigital lamellae on fourth toe; thin, white, nuchal loop; dorsal ground color brick-red; small, light, round spots on flanks; regenerated tail yellow; posterior portion of original tail black in males (Tables 6,7).

Description of holotype. Adult male SVL 51.6 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.26), somewhat narrow (HW/SVL 0.17), flattened (HD/HL 0.41), distinct from neck; snout short (ES/HL 0.50), concave in lateral profile; postnasal region weakly constricted medially, flat; scales of rostrum weaklykeeled, slightly raised, slightly larger than similarly shaped scales on occiput; low, supraorbital ridges; weak frontorostral sulcus; canthus rostralis not very discernable; eye large (ED/HL 0.23); extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral concave dorsally, dorsal 90% divided by longitudinal groove; rostral bordered posteriorly by two large supranasals, an equally sized azygous scale, and external nares; boredered laterally by first supralabials; 10R,L raised supralabials decreasing in size posteriorly; 8R,L infralabials, decreasing in size slightly posteriorly; nostrils elliptical, oriented dorsoposteriorly; bordered posteriorly by small, granular, postnasal scales; mental large, triangular, concave medially, bordered posteriorly by two large, rectangular, lateral postmentals of similar size and one smaller azygous scale; gular scales raised, smooth; throat scales larger, raised, weakly keeled. Body slender, elongate (AG/SVL 0.43); small, keeled, dorsal scales generally equal in size throughout body, intermixed with larger, multicarinate tubercles in semi-linearly arranged; tubercles extend from occiput to base of tail; tubercles moderate in size; tuberculation weak on lower flanks, 18 paravertebral tubercles; pectoral and abdominal scales raised, keeled, not elongate, same size throughout; abdominal scales slightly larger than dorsals; no precloacal pores; forelimbs moderately long, slender (FL/SVL 0.21); dorsal scales of brachium raised, keeled; dorsal scales of forearm raised, keeled; ventral scales of brachium smooth, raised, juxtaposed; ventral scales of forearm weakly keeled, raised, juxtaposed; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae wide throughout digit; interdigital webbing present; fingers increase in length from first to fourth with fourth longer than fifth; hind limbs slightly longer and thicker than forelimbs (TBL/SVL 0.23); dorsal scales of thigh keeled, raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh keeled; subtibial scales raised, keeled, juxtaposed, with no enlarged anterior row; plantar scales smooth, juxtaposed, raised; no enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges granular proximally but wider distally throughout digit; interdigital webbing present; toes increase in length from first to fourth with fourth being slightly longer than fifth; 32 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; dorsal caudal scales flat anteriorly, keeled, juxtaposed; weak middorsal and deep lateral caudal furrows; subcaudal scales keeled; median row of enlarged, keeled subcaudal scales; caudal tubercles encircle tail; tubercles absent from lateral furrows; two enlarged postcloacal tubercles on lateral surface of hemipenal swellings at base of tail.

Color pattern (Fig. 59). Dorsal ground color brick-red; medial, whitish spot on rostrum, canthus rostralis bearing whitish line; thin, white nuchal loop extending from posterior margin of one orbit to the other; thin, white postorbital line below nuchal loop extending obliquely to corner of mouth; paired whitish markings on occiput; small, white, linearly arranged spots on side of neck and nape; large, faint, dark, linearly arranged blotches on anterior portion of body and nape; flanks bearing small, round, white spots thatextend onto lateral margins of abdomen; five whitish bands consisting of a row of three, transversely aligned blotches occur between limb insertions and extend onto anterior one-half of tail transforming into light, caudal bands that alternate with dark bands, posterior one-half of tail black; dorsal surfaces of limbs mottled with white; ventral surface of gular, pectoral, abdominal, and anterior subcaudal region beige; throat and limbs darker; posterior one-half of subcaudal region black; all other ventral surfaces suffused with black stippling in scales.

Variation (Fig. 59). The type series shows a modest array of color pattern variation. MZB.Lace 10168 closely resembles the holotype in overall coloration whereas the dorsal ground color in MZB.Lace 10166 and 10168 is lighter and the overall blotching lighter, giving them a less contrasted and spotted appearance. MZB.Lace 10168 is a female and lacks the black posterior caudal region. The posterior one-half of the tail in MZB.Lace 10169 is regenerated and unicolor tan. MZB.Lace 10163 is very faded overall but most likely matches MZB.Lace 9441 and MZB.Lace 10168 in general coloration. The flanks of all specimens of the type series are not as boldly marked as in the holotype. Meristic and mensural variation is listed in Table 13.

Comparisons. *Cnemaspis mumpuniae* sp. nov. is a member of the Southern Sunda clade which includes *C. limi, C. nigridia, C. paripari, C. kendallii, C. sundainsula* sp. nov.*, C. pemanggilensis, C. baueri, C. bidongensis,* and *C. peninsularis* sp. nov. Within this clade, it is part of an unresolved polytomy that includes *C. kendallii, C. sundainsula* sp. nov.*, C. pemanggilensis, C. baueri, C. bidongensis,* and *C. peninsularis* sp. nov. of the *kendallii* group (Fig. 2). *Cnemaspis mumpuniae* sp. nov. is easily separated from *C. limi* by being much smaller (maximum SVL 56.6 mm versus 88.2 mm); having fewer paravertebral tubercles (18–24 versus 25–35); having keeled versus smooth subcaudal scales; the presence versus the absence of a ventrolateral row of caudal tubercles; having caudal tubercles that encircle the tail versus not having tubercles encircling the tail; and lacking versus having white caudal tubercles. From *C. paripari, C. mumpuniae* sp. nov. lacks precloacal pores as opposed to having them; has fewer paravertebral tubercles (18–24 versus 26–31); has as opposed to lacks tubercles on the flanks; has as opposedto lacks a ventrolateral row of caudal tubercles; has caudal tubercles that encircle the tail versus not having tubercles encircling the tail; lacks as opposed to having an enlarged, median subcaudal scale row; and males lack as opposed to having a yellow head, limbs, and back and the posterior one-half of the original tail being white. Within the *kendallii* group, *C. mumpuniae* sp. nov. is distinguished from *C. sundainsula* sp. nov., *C. pemanggilensis,* and *C. baueri* by being much smaller (maximum SVL 56.6 mm versus 67.4–84.5 mm) and from *C. sundainsula* sp. nov. it is further separated by having caudal tubercles that encircle the tail rather than not having such tubercles. *Cnemaspis mumpuniae* sp. nov. is further separated from *C. pemanggilensis* by having fewer paravertebral tubercles (18–24 versus 30–37) and lacking as opposed to having an enlarged, median row of keeled subcaudal scales. From *C. baueri, C. mumpuniae* sp. nov is further differentiated by lacking an enlarged, median row of keeled subcaudal scales and not having a uniform brown dorsal color pattern bearing large, elongate black blotches on the nape and shoulder region. *Cnemaspis mumpuniae* sp. nov. is differentiated from *C. kendallii sensu stricto* in that the posterior two-thirds of the original tail in adult male *C. mumpuniae* sp. nov. is black dorsally and ventrally and in adult male *C. kendallii* the tail is banded dorsally throughout its length and the subcaudal region is essentially immaculate white. The regenerated tail in adult male *C. mumpuniae* sp. nov. is yellow and immaculate dorsally and ventrally whereas that of *C. kendallii sensu stricto* is straw-colored with small black flecks dorsally and the subcaudal region is immaculate white. Additionally, *C. kendallii sensu stricto* has a row of nearly contiguous tubercles on the lateral margins of the occipital region bordering the nape which are nearly always absent in *C. mumpuniae* sp. nov. Within the *kendallii* group, *C. mumpuniae* sp. nov. is most closely related to the sister species *C. bidongensis* and *C. peninsularis* sp. nov. (Fig. 2). It differs from them in having a brick-red ground color and a thin, white, nuchal loop. It is differentiated further from *C. peninsularis* sp. nov. having as opposed to lacking an enlarged, median, subcaudal scale row.

TABLE 13. Meristic and mensural character states of the type series of *Cnemaspis mumpuniae* sp. nov. w = weak; f = female; m = male. Meristic abbreviations are listed in the Materials and Methods. For TL, the measurement for the original portion of the tail is on the left and the measurement for the regenerated portion is on the right.

	MZB.Lace	MZB.Lace	MZB.Lace	MZB.Lace	MZB.Lace	MZB.Lace
	10167	9944	10169	10168	10166	9941
	holotype	paratype	paratype	paratype	paratype	paratype
Supralabials	10	10	10	11	11	11
Infralabials	8	10	8	9	10	11
Ventral scales keeled (1) or not (0)	1	1	1	1	1	1
No. of precloacal pores	0	0	0	0	0	0
Precloacal pores continuous (1) or separated (0)	/	/	/	/	/	0
Precloacal pores elongate (1) or round (0)	/	/	/	/	/	0
No. of paravertebral tubercles	18	19	21	19	19	24
Tubercles linearly arranged (1) or more random (0)	0	w	w	w	w	w
Tubercles present (1) or absent (0) on flanks	w	w	w	w	w	/
Caudal tubercles in lateral furrow (1) or not (0)	0	0	0	0	0	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	1	1	1	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	1	1	0
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	0
Subcaudals keeled (1) or not (0)	1	1	1	1	1	1
Single median row of keeled subcaudals (1) or not (0)	0	0	0	0	0	1
Caudal tubercles encircle tail (1) or not (0)	1	1	1	1	1	1
Enlarged median subcaudal scale row (1) or not (0)	1	1	1	1	1	1

......continued on the next page

TABLE 13. (Continued)

	MZB.Lace 10167 holotype	MZB.Lace 9944 paratype	MZB.Lace 10169 paratype	MZB.Lace 10168 paratype	MZB.Lace 10166 paratype	MZB.Lace 9941 paratype
Postcloacal spurs	2	2	2	/	1	0
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	2
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	1	0
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0	0	0	1
No. of 4th toe lamellae	32	29	30	29	35	30
sex	m	m	m	f	m	m
SVL	51.6	56.6	52.5	55	53.6	53.3
TL	58.3	42.1/12.8	14.1/28.8	33.3/22.2	67.5	59.1
TW	6.2	5.6	5.2	5.2	4.9	4.4
FL	10.8	9.9	10.7	10.4	10.3	10.1
TBL	12.1	13.2	13.1	12.2	12.2	13.7
AG	22.1	2.6	23.3	25.4	22.9	24.8
HL	13.7	15.6	13.9	14.2	14.4	16.4
HW	8.7	8.9	8.8	8.9	8.4	9.4
HD	5.6	5.9	6.1	5.7	5.4	6.1
ED	3.2	3.2	3.1	2.8	2.8	2.6
EE	3.7	4.1	4.5	4.2	3.9	3.6
ES	6.8	7.9	6.7	6.6	6.7	6.9
EN	6.1	6.2	5.4	5.4	5.1	5.1
IO	2.9	2.7	3.4	3.2	3.2	4
EL	1	1.1	1.2	1	1.3	0.8
IN	1.4	1.7	1.7	1.5	1.4	1.5

Distribution. *Cnemaspis mumpuniae* sp. nov. is endemic to the northern group of islands of the Natuna Archipelago, Riau Province, Indonesia. It is known to occur on the islands of Natuan Besar and Lagong but is likely present on many of the other islands as well (Fig. 4).

Natural History. *Cnemapsis mumpuniae* sp. nov. is a diurnal, habitat generalist found in disturbed and undisturbed forests and is widespread throughout Pulau Natuna Besar from sea level to 345 m along the base of Mount Ranai. Lizards occur on both granite boulders and vegetation and are quite adept at substrate matching (Fig. 59). During the day on granite boulders, their ground color is dark-red. On lighter substrates, such as tree trunks in rubber plantations, the ground color can be grayish. At night, when inactive, lizards are nearly white. This species is quite agile and wary during the day, jumping from rock to rock or from trees to rocks to seek shelter in dark crevices and rock spaces. While fleeing, lizards usually elevate the black posterior portion of their tail up over their back and wave it from side to side. At night lizards are quite approachable and can be seen sleeping on the open surfaces of boulders and tree trunks. We observed one lizard sleeping on a leaf at least 5 m above the forest floor. Hatchlings were observed during April.

Etymology. The specific epithet recognizes Mrs. Mumpuni, one of the senior herpetologist at the MZB and honors her many contributions over the years to Indonesian herpetology.

Relationships. Within the *kendallii* group, *C. mumpuniae* sp. nov. is most closely related to the sister species *C. bidongensis* and *C. peninsularis* sp. nov. (Fig. 2).

***Cnemaspis peninsularis* sp. nov.**

Peninsular Rock Gecko

Figs. 60, 61

Gonatodes kendalli Flower 1896:833 (in part), 1899:627 (in part); Ridley, 1899:193; Boulenger 1912:38 (in part); Sworder 1925:63; Smith 1930:16 (in part); Nicholls 1949:48

Gonatodes kendallii Smith 1925:23 (in part)

Cnemaspis kendalli Henrickson, 1966:55; Bullock 1966:94; Dring, 1979:220; Denzer & Manthey, 1991:313; Lim & Lim, 1992:122

Cnemaspis kendallii Manthey & Grossmann 1997:212 (in part); Das & Bauer 1998:12 (in part); Grandison, 1972:80; Werner & Chou, 2002:185; Das & Grismer, 2003:549; Grismer & Das 2006:5 (in part); Grismer, Youmans, Wood & Grismer, 2006:112; Grismer & Ngo 2007:486 (in part); Baker & Lim, 2008:78; Chan & Grismer 2008:55 (in part); Grismer 2008:30; Grismer & Chan 2008:5 (in part); Grismer, Chan, Nurolhuda & Sumontha 2008a:57 (in part); Grismer, Grismer, Wood & Chan 2008b:24 (in part); Grismer & Chan 2009:30 (in part); Grismer, Norhayati, Chan, Belabut, Muin, Wood, & Grismer 2009:59 (in part); J. Grismer, Grismer & Thou 2010:30 (in part); Grismer, 2010:59 (in part); Grismer & Chan 2010:61 (in part); Grismer, Chan, Quah, Muin, Savage, Grismer, Norhayati, Greer, Remegio 2010c:64 (in part); Grismer, Ngo & Grismer 2010b:57 (in part); Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya 2010a:12 (in part); Grismer 2011a:330 (in part), 2011b:112 (in part); Wood, Quah, Shahrul, & Muin 2013:546 (in part); Grismer, Wood, Amirrundin, Sumarli, Vazquez, Chan, Ismail, Nance, Muhammad, Mohamad, Syed, Kuss, Murdoch & Cobos 2014:449.

FIGURE 60. *Cnemaspis peninsularis* sp. nov. from Gunung Ledang, Johor, Peninsular Malaysia. Upper right: adult male (LSUDPC 6704) in the dark color pattern phase. Photograph by ESHQ. Lower right: adult male (LSUDPC 4428) in the light color pattern phase. Photograph by LLG. Left: karst microhabitat at Gua Senyum, Pahang, Peninsular Malaysia. Photograph by LLG.

Holotype. Adult female LSUHC 8965 collected on 7 June 2008 by L. L. Grismer, P. L. Wood, Jr., J. L. Grismer and Chan K. O. at 1030 hrs from the base of Gunung Ledang Johor, Peninsular Malaysia (02°20.25’ N, 102°37.11’ E) at 100 m in elevation.

Paratypes. Adult male LSUHC 8966 has the same data as the holotype. Adult male LSUHC 4756 collected on 23 July 2002 by J. L. Grismer at the waterfall on Pulau Tinggi, Johor, Peninsular Malaysia (02°18.013' N, 104°06.261 E) at 210 m in elevation. Adult male LSUHC 5731 collected on 30 August 2003 by T. A. Youmans on Pulau Babi Besar, Johor, Peninsular Malaysia (02°26.166 N, 103°58.466 E) at 55 m in elevation. Adult male LSUHC 6213 collected on 30 June 2004 by L. Lee Grismer on the Tekek-Juara Trail, Pulau Tioman, Pahang, Peninsular Malaysia (02°48.433 N, 104°9.525 E) at 260 m in elevation. Adult female LSUHC 8210 and adult male LSUHC 8126 collected on 4 September 2006 by L. L. Grismer at Selai, Lubuk Tapah, Endau-Rompin, Johor, Peninsular Malaysia (02°25.129' N, 103°15.409' E) at 102 m in elevation. Adult male LSUHC 9376 collected on 8 September 2009 by Chan, K. O. and L. Lee Grismer on Pulau Tenggol, Terengganu, Peninsular Malaysia (04°48.111 N, 103°40.478' E) at 83 m in elevation. Adult males (LSUHC 10710–11) collected on 24 June 2008 by Chan Kin Onn at 1030 hrs from Bukit Hangus, Pahang, Peninsular Malaysia (04°16.142' N, 102°13.370' E) at 10 m in elevation. Adult male LSUHC 10454 collected on 2 June 2011 by Evan S. H. Quah from the Nee Soon Swamp, Singapore (01°48.40 N, 103°49.41 E) at 20 m in elevation.

Diagnosis. Maximum SVL 60.0 mm; 10 or 11 supralabials; 7–10 infralabials; keeled ventrals; no precloacal pores; moderately prominent dorsal tubercles; 17–25 paravertebral tubercles; dorsal body tubercles generally randomly arranged; tubercles absent to weak on flanks; caudal tubercles encircling tail; no tubercles in lateral caudal furrows; ventrolateral and lateral rows of caudal tubercles present; subcaudals keeled; no single, median row of enlarged, subcaudal scales; one or two postcloacal tubercles on either side of base of tail; no enlarged femoral, subtibial, or submetatarsal scales; subtibials keeled; 27–33 subdigital lamellae on fourth toe; regenerated tail yellow in males; posterior portion of original tail in males black (Tables 6,7).

FIGURE 61. *Cnemaspis peninsularis* sp. nov. Upper left: adult male (LSUDPC 962) from Pulau Tioman, Pahang, Peninsular Malaysia in the light color pattern phase sleeping on the underside of a leaf. Photograph by LLG. Upper right: adult male (LSUDPC 6703) from Gunung Ledang, Johor, Peninsular Malaysia with a regenerated tail exhibiting a caudal display. Photo by ESHQ. Lower right: juvenile (LSUDPC 964) from Pulau Tioman in the light color pattern phase sleeping on the top side of a leaf. Lower left: forest habitat of *C. peninsularis* sp. nov. on Pulau Tioman. Photographs by LLG.

Description of holotype. Gravid female; SVL 55.2 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.27), somewhat narrow (HW/SVL 0.16), flattened (HD/HL 0.37), distinct from neck; snout short (ES/HL 0.47), slightly concave in lateral profile; postnasal region constricted medially, flat; scales of rostrum weakly keeled, slightly raised, same size as similarly shaped scales on occiput; low, supraorbital ridges; very weak frontorostral sulcus; canthus rostralis not very discernable; eye large (ED/HL 0.19); extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral concave dorsally, dorsal 75% divided by longitudinal groove; rostral bordered posteriorly by two large supranasals and external nares, and laterally by first supralabials; 10R,L raised supralabials decreasing in size posteriorly; 8R,9L infralabials, decreasing in size slightly posteriorly; nostrils elliptical, oriented dorsoposteriorly; bordered posteriorly by small, granular, postnasal scales; mental large, triangular, concave medially, bordered posteriorly by two large, rectangular, lateral postmentals of similar size and one smaller azygous scale; gular scales raised, smooth; throat scales larger, raised, weakly keeled.

Body slender, elongate (AG/SVL 0.48); small, keeled, dorsal scales generally equal in size throughout body, intermixed with larger, multicarinate tubercles more or less randomly arranged; tubercles extend from occiput to base of tail; tubercles absent from lower flanks, moderate in size; 22 paravertebral tubercles; pectoral and abdominal scales raised, keeled, not elongate, same size throughout; abdominal scales slightly larger than dorsals; no precloacal pores; forelimbs moderately long, slender (FL/SVL 0.19); dorsal scales of brachium raised, keeled; dorsal scales of forearm raised, keeled; ventral scales of brachium smooth, raised, juxtaposed; ventral scales of forearm weakly keeled, raised, juxtaposed; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae wide throughout digit; interdigital webbing absent; fingers increase in length from first to fourth with fourth longer than fifth; hind limbs slightly longer and thicker than forelimbs (TBL/SVL 0.22); dorsal scales of thigh keeled, raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh keeled; subtibial scales raised, keeled, juxtaposed, with no enlarged anterior row; plantar scales smooth, juxtaposed, raised; no enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae beneath first phalanges granular proximally but wider distally throughout digit; interdigital webbing absent to weak; toes increase in length from first to fourth with fourth being slightly longer than fifth; 31 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; dorsal caudal scales flat anteriorly, keeled, juxtaposed; deep middorsal and lateral caudal furrows; subcaudal scales keeled; no median row of enlarged keeled subcaudal scales; caudal tubercles encircle tail; tubercles absent from lateral furrows.

Color pattern in life. Dorsal ground color yellowish; head and body overlain with irregularly shaped pattern of interconnected brownish markings highlighting white to yellowish irregularly shaped blotches; small, black, elongate medial marking on nape followed by similarly colored, paired, elongate, paravertebral markings extending to midway down body; similar vertebral markings extend from midbody to base of tail transforming into poorly defined, diffuse, dark caudal bands; limbs bearing a faint, brownish banding pattern becoming more evident distally; digits banded; ventral ground color beige; faint, darker reticulum on belly; posterior subcaudal region dark.

Variation. The type series shows a modest array of color pattern variation that is not necessarily related to substrate matching although this species does tend to show differences in overall hue with respect to substrate (see Geographic variation below). LSUHC 5731 and 6253 match the holotype in general coloration and pattern although both lack the larger dark markings and appear less mottled overall. Both differ from the holotype in having a dark belly with distinct white spots as do LSUHC 10454 and 10710–11. The other specimens show a modest degree of belly mottling. LSUHC 10710–11 have a much darker color pattern that highlights the overlying lighter markings as well as a distinct, thin, whitish, nuchal loop. A distinct nuchal loop also occurs in LSUHC 4756, 8210, 8966, and 10454. LSUHC 9376 has a faded nearly unicolor dorsal pattern bearing only faint dark and light spots and LSUHC 8126 has a unicolor regenerated tail. Sexual dimorphism in caudal coloration is discussed below (see Comparisons). Meristic and mensural variation is listed in Table 14 and various color patterns can be seen in Figures 60 and 61 and in Grismer (2011a).

Distribution. *Cnemaspis peninsularis* sp. nov. ranges as far north as Bukit Hangus, Pahang on the peninsula and to Pulau Tenggol off the east coast, and southward to Singapore (Grismer 2011a: Fig. 4). In the Seribuat Archipelago, Grismer *et al.* (2006) reported *C. peninsularis* sp. nov. from the islands of Aceh, Babi Besar, Babi Hujung, Ibol, Sembilang, Seribuat, Sibu, Sibu Tenggah, Tinggi, Tioman, and Tulai (Fig. 4).

Natural History. According to Grismer (2011a) and references therein, *Cnemaspis peninsularis* sp. nov. is a scansorial, diurnal gecko found on logs, tree trunks, low vegetation, and rocks (Figs. 60, 61). It is a common inhabitant of both primary and secondary, lowland and hill, dipterocarp forests and to a lesser extent peatswamps and ranges up to approximately 500 m in elevation. During the day, *C. peninsularis* sp. nov. is active on trees and rocks beneath closed canopy forests and does not restrict its movements to dark, shaded surfaces as is commonly seen in many other species of *Cnemaspis.* On Pulau Tioman, Pahang, Grismer (2011a) noted that lizards may bask in sun spots on the trunks of trees. Werner and Chou (2002) indicated *C. peninsularis* sp. nov. is a sit and wait predator that usually perches head down on tree trunks waiting to ambush prey. When threatened, males often curl their tail over their back to display the yellow underside (Fig. 61). This display is usually exaggerated by slowly moving the tail from side to side and performed just prior to fleeing to take refuge within a rock crack or beneath exfoliating bark. At night, the ground color of *C. peninsularis* sp. nov. becomes nearly white and somewhat transparent, highlighting the dark dorsal spots on the body and the black tail in the males (Figs. 60, 61). During this time, lizards are commonly seen sleeping on tree trunks, leaves, rocks, and clinging to the underside of leaves as high as 10 m above the ground. Grismer (2011a) reported gravid females on several islands in the Seribuat Archipelago from March through August; during June at Gunung Ledang, Johor; and at Endau-Rompin, Johor during September. In Singapore, gravid females have been observed during August and pairs of eggs stuck to rocks and cement structures have been found during November and December (Werner & Chou 2002). Hatchlings and gravid females in Singapore have been observed during December (Werner & Chou 2002). These data suggest *C. peninsularis* sp. nov. breeds year round. Bullock (1966) reported finding ants, beetles, earthworms, millipedes, and soil in the stomachs of lizards from Pulau Tioman indicating that foraging takes place on the ground.

TABLE 14. Meristic and mensural character states of the type series of *Cnemaspis peninsularis* sp. nov. w = weak; f = female; m = male; and / = data unavailable. Meristic abbreviations are listed in the Materials and Methods. For TL, the measurement for the original portion of the tail is on the left and the measurement for the regenerated portion is on the right. G. = Gunung; E. = Endau; B. = Bukit; P. = Pulau.

	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC	LSUHC
	8965	8966	8126	8210	10710	10711	10454	9376	6213	4756	5731
	holotype G. Ledang	paratype G. Ledang	paratype E. Rompin	paratype E. Rompin	paratype B. Hangus	paratype B. Hangus	paratype Singapore	paratype P. Tenggol	paratype P. Tioman	paratype P. Tinggi	paratype P. Besar
Supralabials	10	11	10	10	11	10	10	10	10	11	10
Infralabials	8	9	10	7	9	8	9	9	9	10	8
Ventral scales keeled (1) or not (0)	1	1	1	1	1	1	1	1	1	1	1
No. of precloacal pores	/	/	/	/	/	/	/	/	/	/	/
Precloacal pores continuous (1) or separated (0)	/	/	/	/	/	/	/	/	/	/	/
Precloacal pores elongate (1) or round (0)	/	/	/	/	/	/	/	/	/	/	/
No. of paravertebral tubercles	22	22	21	17	19	22	25	19	24	21	23
Tubercles linearly arranged (1) or more random (0)	0	0	/	0	w	0	0	0	w	0	w
Tubercles present (1) or absent (0) on flanks	w	1	/	0	w	w	0	0	0	w	0
Caudal tubercles in lateral furrow (1) or not (0)	0	0	/	0	/	0	0	0	0	0	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	1	/	1	/	1	1	1	1	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	1	/	1	/	1	1	1	1	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	/	0	/	0	0	0	0	0	0
Subcaudals keeled (1) or not (0)	1	1	/	1	/	1	1	1	1	1	1
Single median row of keeled subcaudals (1) or not (0)	0	0	/	0	/	0	0	0	0	0	0
Caudal tubercles encircle tail (1) or not (0)	1	1	/	1	/	1	1	1	1	1	1
Enlarged median subcaudal scale row (1) or not (0)	0	0	/	0	/	0	0	0	0	0	0
Postcloacal spurs	/	1	2	1	/	1	1	2	1	1	1
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	1	1	1	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0	0	0	0	0	0	0	0	0
No. of 4th toe lamellae	31	29	30	28	29	29	31	29	33	27	31
Sex	f	m	m	f	m	m	m	m	m	m	m
SVL	55.2	54.7	43.4	54.6	52.6	54.6	47.3	53.0	51.3	51.1	52.1
TL	64.1	51.2	36.1	47.8	49.0	53.5	14.7	71.7	56.4	47.5	67.8
TW	5.5	5.3	3.7	5.4	4.8	5.7	4.5	5.4	5.0	5.0	5.6
FL	10.3	9.4	7.2	10.3	10.5	10.9	9.1	9.9	9.4	9.4	9.0
TBL	12.2	11.6	9.5	12.9	12.4	13.6	10.9	11.8	12.2	11.6	11.6
AG	26.3	25.2	19.1	24	22.7	25.5	20.7	22.9	22.4	22.3	21.3
HL	14.9	14	12.2	13.7	14.3	14.5	13.0	13.9	13.0	13.1	13.8
HW	8.7	8.7	7.1	8.5	8.5	8.6	7.2	8.2	8.5	7.5	8.2
HD	5.5	5.8	4.4	5.7	5.4	5.8	4.9	5.4	6.1	5.4	5.2
ED	2.9	2.9	2.4	3.0	3.0	2.9	2.7	2.9	2.9	2.9	2.6
EE	3.2	3.9	3.0	3.5	3.7	4.0	2.9	3.7	3.7	3.5	3.3
ES	7.0	6.6	5.8	6.7	6.7	7.1	5.9	6.9	6.6	6.5	6.9
EN	5.2	4.8	4.3	5.3	5.2	5.6	4.4	5.5	5.3	5.1	5.3
IO	3.2	1.3	2.6	1.3	2.8	1.3	2.6	1.4	3.0	2.9	3.0
EL	1.7	1.4	1.2	1.5	1.7	1.8	1.2	1.3	1.5	1.4	1.5
IN	1.3	1.3	1.1	1.3	1.4	1.4	1.3	1.4	1.3	1.3	1.2

Etymology. The specific epithet *peninsularis* is an adjective in reference to the distribution of this species being restricted to Peninsular Malaysia and Singapore and their adjacent islands.

Geographic variation. Geographic variation in *Cnemaspis peninsularis* sp. nov. does not show geographically related trends as seen in some other species of lizards from Peninsular Malaysia (Grismer 2011a) but there is some noteworthy localized variation in some populations. Lizards from Pulau Tioman, Pahang generally have a more boldly marked abdomen than lizards from populations of Peninsular Malaysia. This is especially true in adult males. In extreme cases, the bellies of some males may be dark brown with white spots and that pattern may extend onto the undersides of the hind limbs. The dorsal pattern of lizards from Pulau Ibol, Johor is nearly unicolor brown. A similar pattern occurs in lizards from Sungai Lembing, Pahang except that lizards from here maintain the large, black, elongate dorsal blotches and appear superficially similar to *C. baueri* of Pulau Aur, Johor.

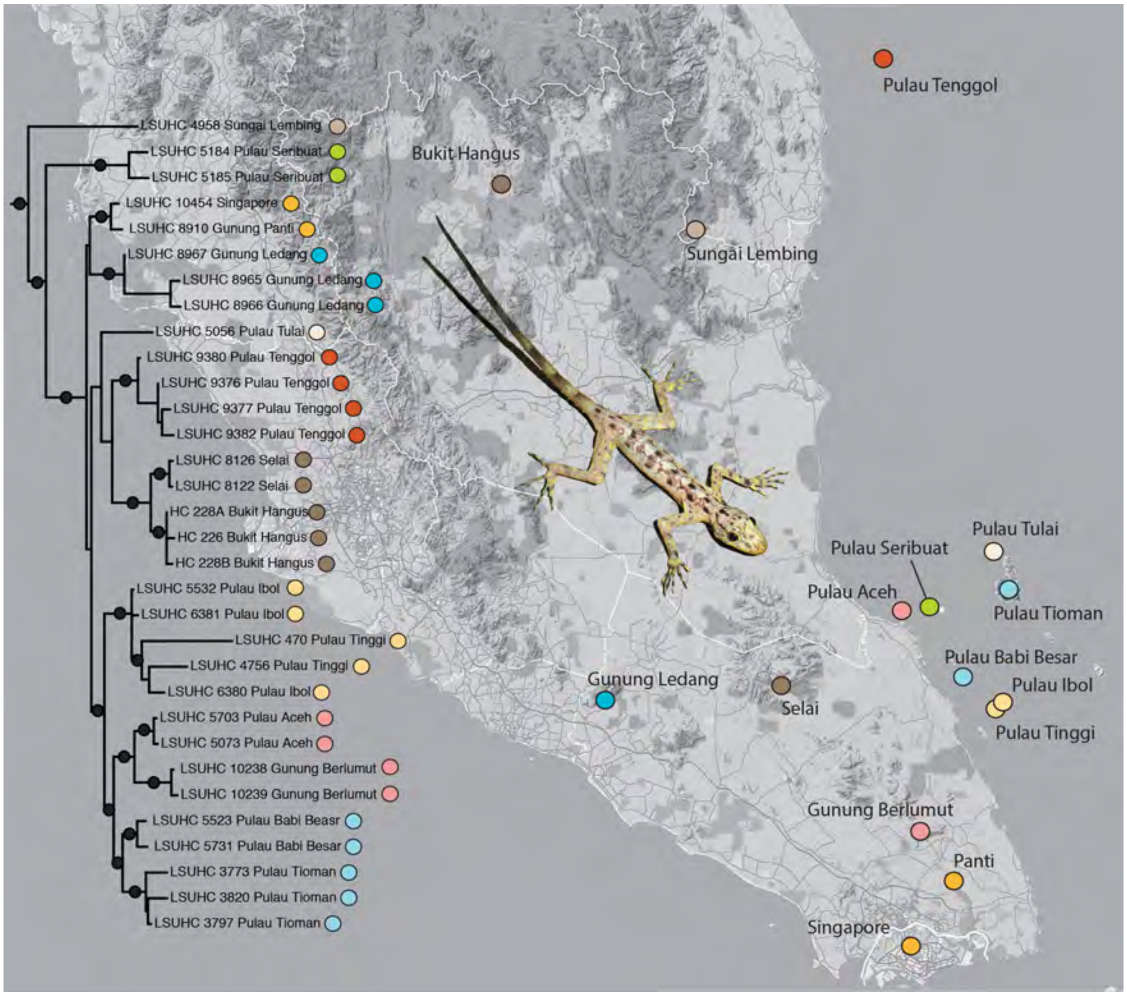

FIGURE 62. Maximum likelihood phylogram (–In*L* 73957.608688) of *Cnemaspis peninsularis* sp. nov. based on the mitochondrial gene ND2 and the geographic distribution of the specimens sampled. Closed black circles are nodes with BBP values and ML bootstrap values > 0.95 and 70, respectively.

Comparisons. *Cnemaspis peninsularis* sp. nov. is a member of the Southern Sunda clade which includes *C. limi, C. nigridia, C. paripari, C. kendallii, C. sundainsula* sp. nov.*, C. pemanggilensis, C. baueri, C. mumpuniae* sp. nov. and *C. bidongensis.* Within this clade, it is part of an unresolved polytomy that composes *C. kendallii, C. sundainsula* sp. nov.*, C. pemanggilensis, C. mumpuniae* sp. nov., *C. bidongensis, C. peninsularis* sp. nov., and *C. baueri* of the *kendallii* group (Fig. 2). *Cnemaspis peninsularis* sp. nov. is easily separated from *C. limi* by being much smaller (maximum SVL 55.2 mm versus 88.2 mm); having fewer paravertebral tubercles (17–25 versus 25–35); having keeled versus smooth subcaudal scales; the presence versus the absence of a ventrolateral row of caudal tubercles; having caudal tubercles that encircle the tail versus not having tubercles that encircle the tail; and lacking versus having white caudal tubercles. From *C. paripari, C. peninsularis* sp. nov. lacks precloacal pores as opposed to having them; has fewer paravertebral tubercles (17–25 versus 26–31); has as opposed to lacks tubercles on the flanks; has versus lacks a ventrolateral row of caudal tubercles; has caudal tubercles that encircle the tail versus not having tubercles encircling the tail; lacks versus has an enlarged, median subcaudal scale row; and males lack as opposed to having a yellow head, limbs, and back and the posterior one-half of the original tail being white. Within the *kendallii* group, *C. peninsularis* sp. nov. is easily distinguished from *C. sundainsula* sp. nov., *C. pemanggilensis,* and *C. baueri* by being much smaller (maximum SVL 55.2 mm versus 67.4–84.5 mm) and from *C. sundainsula* sp. nov. it is further separated by having keeled versus smooth ventral scales, and caudal tubercles that encircle the tail rather than not having such tubercles. *Cnemaspis peninsularis* sp. nov. is further separated from *C. pemanggilensis* by having fewer paravertebral tubercles (17–25 versus 30–37) and lacking as opposed to having an enlarged, median row of keeled subcaudal scales. From *C. baueri, C. peninsularis* sp. nov is further differentiated by lacking an enlarged, median row of keeled subcaudal scales and not having a uniform brown dorsal color pattern bearing large, elongate black blotches on the nape and in the shoulder region. *Cnemaspis peninsularis* sp. nov. can not be differentiated from *C. kendallii* (with which it was previously considered conspecific) on the basis of scale counts. However, these species do differ notably in that the abdomen of *C. peninsularis* sp. nov. is mottled with a diffuse, dark reticulum enclosing lighter spots whereas in *C. kendallii* the abdomen is beige and generally immaculate; the posterior two-thirds of the original tail in adult male *C. peninsularis* sp. nov. is black dorsally and ventrally and in adult male *C. kendallii* the tail is banded dorsally throughout its length and the subcaudal region is essentially immaculate white. The regenerated tail in adult male *C. peninsularis* sp. nov. is yellow and immaculate dorsally and ventrally whereas that of *C. kendallii* is straw colored with small black flecks dorsally and the subcaudal region is white and immaculate. Additionally, *C. kendallii* has a row of nearly contiguous tubercles on the lateral margings of the occipital region bordering the nape which are nearly always absent in *C. peninsularis* sp. nov. Another row of tubercles generally absent in *C. peninsularis* sp. nov. occurs immediately anterior to the shoulder region in *C. kendallii.* All these tubercles are usually accentuated by being white. Within the *kendalli* group, *C. peninsularis* sp. nov. is most closely related to *C. bidongensis* and *C. mumpuniae* sp. nov. (Fig. 2). It differs from *C. mumpuniae* in lacking a brick-red ground color and a thin, white, nuchal loop. It is differentiated further from *C. bidongensis* sp. nov. by lacking as opposed to having an enlarged, median, subcaudal scale row.

Relationships. *Cnemaspis peninsularis* sp. nov. forms a polytomy with *C. bidongensis* from Pulau Bidong, Peninsular Malaysia and *C. mumpuniae* sp. nov. from Pulau Natuna Besar, Indonesia (Fig. 2).

Remarks. *Cnemaspis peninsularis* sp. nov. is the most widely distributed species withn a genus that is composed primarily of microhabitat specialist with highly circumscribed distributions (Figs. 3, 4). One of the reasons for its relatively wide distribution is that it is a habitat generalist active both day and night on all rocky and vegetative substrates. To encompass the phylogeographic structure within *C. peninsularis* sp. nov., we sampled 32 specimens from throughout the extent of its distribution from Singapore in the south to Bukit Hangus, Pahang, and Pulau Tenggol, Terengganu in the north (Fig. 62) as well as from seven of the 11 islands on which it is known to occur in the Seribuat Archipelago (Fig. 62). An ND2 phylogeny shows that *C. peninsularis* sp. nov. is composed of three well-supported, major lineages (Fig. 62). The basal lineage is represented by a northern population from Sungai Lembing, Pahang and its sister lineage is composed of a southern population from Pulau Seribuat, Johor of the Seribuat Archipelago and its sister lineage containing the remaining populations that generally encompasses the entire range of *C. peninsularis* sp. nov. (Fig. 62). The overall phylogeographic structure within the latter widespread population is polytomous with little concordance between geographic distribution and phylogenetic substructuring (Fig. 62). We consider this lack of geographic clustering to be evidence of gene flow within this widely distributed, habitat generalist (see Grismer *et al.* [2012] and Johnson *et al.* [2012] for other gekkonid examples with similar phylogeographic structure from Peninsular Malaysia). Additionally, the phylogeny indicates that the presence of *C. peninsularis* sp. nov. in the Seribuat Archipelago may be due to sequential vicariant events associated with episodic changes is sea levels or independent dispersal events. The first event established the Pulau Seribuat population followed by the establishment of a population on Pulau Tulai. The widespread clade of insular populations in the Seribuat Archipelago may have resulted from the most recent vicariant event and being that the peninsular, Gunung Berlumut population is deeply embedded within this island clade, suggests an upstream recolonization of Peninsular Malaysia may have occurred (Fig. 62). These hypotheses and others are currently being tested with fine-scaled geographic sampling and re-analysis (Wood & Grismer in prep.).

The uncorrected pairwise genetic distances among the three major lineages of *Cnemaspis peninsularis* sp. nov. ranges from 1.1%–9.9% whereas that within the most widespread lineage (i.e. the lineage that does not include Sungai Lembing and Pulau Seribuat; Fig. 62) ranges from 1.1%–6.7% (Table 5). The distances between the Sungai Lembing and Pulau Seribuat populations to each other and all other *C. peninsularis* sp. nov. are commensurate with that between other species of gekkonids (see Grismer *et al.* 2013b) and their specific status will also be evaluated (Wood & Grismer in prep.).

Additional material examined. Peninsular Malaysia: Johor: Bunker Trail ZRC 2.5602; Endau-Rompin LSUHC 7691, 8122, 8126, 8191, 8210; Gunung Ledang ZRC 2.5437–38, LSUHC 8965–67; Pulau Babi Besar LSUHC 5731–34; Pulau Babi Hujung LSUHC 5749–52; Pulau Ibol LSUHC 6380–83; Pulau Sembilang LSUHC 5244; Pulau Seribuat LSUHC 5184–87, 5198, 5211; Pulau Tinggi LSUHC 4707, 4756–57, 4765–67; Pulau Tulai LSUHC 3894, 5056–58. Pahang: Bukit Ringgit DWNP 2231; Gemas ZRC 2.1105–06; Jerantut ZRC 2.1101; Kuala Gandah DWNP 475–76; Lakum Forest Reserve DWNP 2278–79; Pulau Tioman DWNP 1833, LSUHC 3773–75, 3797, 3811, 3820, 3841, 3878–88, 4566, 4570, 4615, 4658–59, 4666; 5436, 5445–46, 5454, 5462, 5477, 5482, 6213–18, 6224, 8036; Sungai Lembing LSUHC 4954, 4958. Negeri Sembilan: Gallah Forest Reserve DWNP 2281. Selangor: Sungai Lalang DWNP 169; Ulu Gombak DWNP 1828. Singapore: ZRC 2.107–08, 2.3014, 2.3520, 2.3544, 2.4992, 2.5644, 2.5891.

Cnemaspis bidongensis **Grismer, Wood, Amirrudin, Sumarli, Vazquez, Ismail, Nance, Muhammad, Mohamad, Syed, Kuss, Murdoch & Cobos, 2014**

Pulau Bidong Rock Gecko

Fig. 63

Holotype. Adult female (LSUHC 11455) collected on 26 August 2013 by Jacob A. Chan at 2200 hrs at 34 m from Pulau Bidong, Terengganu, Peninsular Malaysia (5°37.201 N 103°03.244 E) at 49 m in elevation.

Paratype. Adult males (LSUHC 11447, 11452–54) and adult female LSUHC 11451 bear the same data as the holotype except they were collected between 1800 and 2400 hrs.

Diagnosis. Maximum SVL 58.1 mm; nine or 10 supralabials; 7–9 infralabials; keeled ventral scales; no precloacal pores; 21–26 paravertebral tubercles; no tubercles on flanks; caudal tubercles encircling tail; no tubercles in lateral caudal furrows; ventrolateral caudal tubercles present anteriorly; subcaudals keeled; a median row of enlarged, keeled subcaudals; one or two postcloacal tubercles on each side; no enlarged femoral, subtibial, or submetatarsal scales; subtibials keeled; 26–30 subdigital lamellae on fourth toe; large, round, black blotches on nape and anterior portion of body; distinct black and white caudal bands in females (Tables 6,7).

Color pattern in life (Fig. 63). Females: dorsal ground color of head, body, limbs and tail brown; a series of diffuse, yellowish lines on rostrum extend posteriorly onto frontal region; dorsal pattern on occiput consisting of a series of dull white spots surrounding a dark brown, tear-drop shaped, vertebral marking; three diffuse, dark brown, postorbital stripes radiate from eyes; dorsal pattern of neck and body consists of a vertebral series of six dull-white blotches extending to base of tail paralleled by similar blotches on flanks; a series of seven diffuse dark brown blotches extend from side of neck along flanks to base of tail on each side of body; intervening area between all body blotches consists of a network of dark and light mottling that extends onto the limbs; nine white caudal bands infused with faint black speckling encircle tail; interband areas bear black mottling; ventral surfaces of head body and limbs beige to dull yellow with weak black stippling in each scale; anterior gular region yellow; subcaudal region bearing white, irregularly shaped bands; small, dark, elongate blotch on mental and medial postmental. Males: overall yellowish to dull-orange dorsal pattern on the head, body and tail and lack the dull-white blotching seen in females yet retain the darker blotching pattern. The caudal pattern is banded but the light bands are not white as in the females and the dark bands are dark brown as opposed to black. The ventral pattern of males is similar to that of females except that the lateral margins of the abdomen tend to near dark network enclosing small, lighter spots. Also, subcaudal banding is faint.

Distribution. *Cnemaspis bidongensis* is presumed to be endemic to Pulau Bidong, Terengganu, Peninsular

Malaysia (Grismer *et al.* 2014; Fig. 4) being that it has not been found in any other archipelago or any other island in the Bidong Archipleago (Vazquez *et al.* 2014.).

Natural History. Grismer *et al.* (2014) noted that *Cnemaspis bidongensis* occurs in secondary, coastal forest and is widespread throughout the island. During the Vietnamese refugee period from May 1975 to October 1991, the island's primary forest was severely degraded by cutting. During this time, as many as 250,000 people fleeing the communist take over of southern Vietnam spent time on Pulau Bidong and in June 1979 it was considered the most heavily populated place on earth (http://en.wikipedia.org/wiki/Bidong_Island). Although this had a catastrophic effect on the native forest, *C. bidongensis* was able to survive because it is not a microhabitat specialist as are many other species of *Cnemaspis* (Grismer & Ngo 2007; Grismer & Chan 2009; Grismer *et al.* 2010a,b; 2013a; Grismer 2011a; Wood *et al.* 2013). During the course of our fieldwork, lizards were observed day and night on both granite rocks and vegetation (Fig. 63). Lizards were wary, swift, agile and would seek shelter at the slightest provocation. During the day, lizards would often jump from rocks to nearby trees and escape by ascending 3–5 meters up the trunk—a behavior not observed in any other species of *Cnemaspis.* Lizards would also avoid capture by retreating into rock cracks. During the evening, lizards were commonly seen on rocks, branches, and leaves where they appeared to be sleeping. When aroused, many would drop to the forest floor from as high as 1.5 meters and escape into the leaf litter—a behavior also uncharacteristic of *Cnemaspis*. Hatchlings and juveniles were not observed and the presence of gravid females carrying two eggs suggests that July is the beginning of the reproductive season.

Relationships. *Cnemaspis bidongensis* froms a polytomy with *C. peninsularis* sp. nov. from Peninsular Malaysia and *C. mumpuniae* sp. nov. from Pulau Natuna Besar, Indonesia (Fig. 2).

FIGURE 63. *Cnemaspis bidongensis* from Pulau Bidong, Terengganu, Peninsular Malaysia. Upper left: adult female (LSUDPC 8090) in the dark color pattern phase. Upper right: adult male (LSUDPC 8096) in the dark color pattern phase. Lower left: ventral view of adult male (upper) and (lower) female (LSUDPC 8108). Lower right: granite boulder and forest microhabitat on Pulau Bidong. Photographs by LLG.

Species *Incertae Sedis*

We were unable to acquire tissue for five previously described and one newly described species herein: *Cnemaspis laoensis* Grismer; *C. punctatonuchalis* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya; *C. vandeventeri* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya; *C. kamolnorranathi* Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya; *C. dringi* Das & Bauer, and *C. sundagekko* sp. nov. Thus, their phylogenetic relationships remain unknown. However, based on morphology and the fact that the smaller clades (*i.e*., Ca Mau and Pattani) and species groups are restricted to well-circumscribed regions with virtually no overlap in distribution (except for the Pattani and Northern Sunda clades) we can use these data to hypothesize to which clade and/or group each species may belong.

Cnemaspis laoensis Grismer, 2010
Lao Rock Gecko
Fig. 64

Holotype. THNHM 12433. Type locality: "Dong Phu Vieng National Protected Area, Savannakhet, Laos".

Diagnosis. Maximum SVL 40.9 mm; nine supralabials; seven infralabials; smooth ventral scales; no precloacal pores; 22 paravertebral tubercles; body tubercles randomly arranged, present on flanks; tubercles present in lateral caudal furrows; no ventrolateral or lateral caudal row of tubercles; caudal tubercles do not encircle tail; subcaudals smooth, bearing a slightly enlarged median row; two or three postcloacal tubercles; no enlarged femoral, subtibial or submetatarsal scales; subtibials keeled; and 29 subdigital fourth toe lamellae (Table 6). *Cnemaspis laoensis* lacks the diagnostic color characteristics of other Southern Indochina clade species.

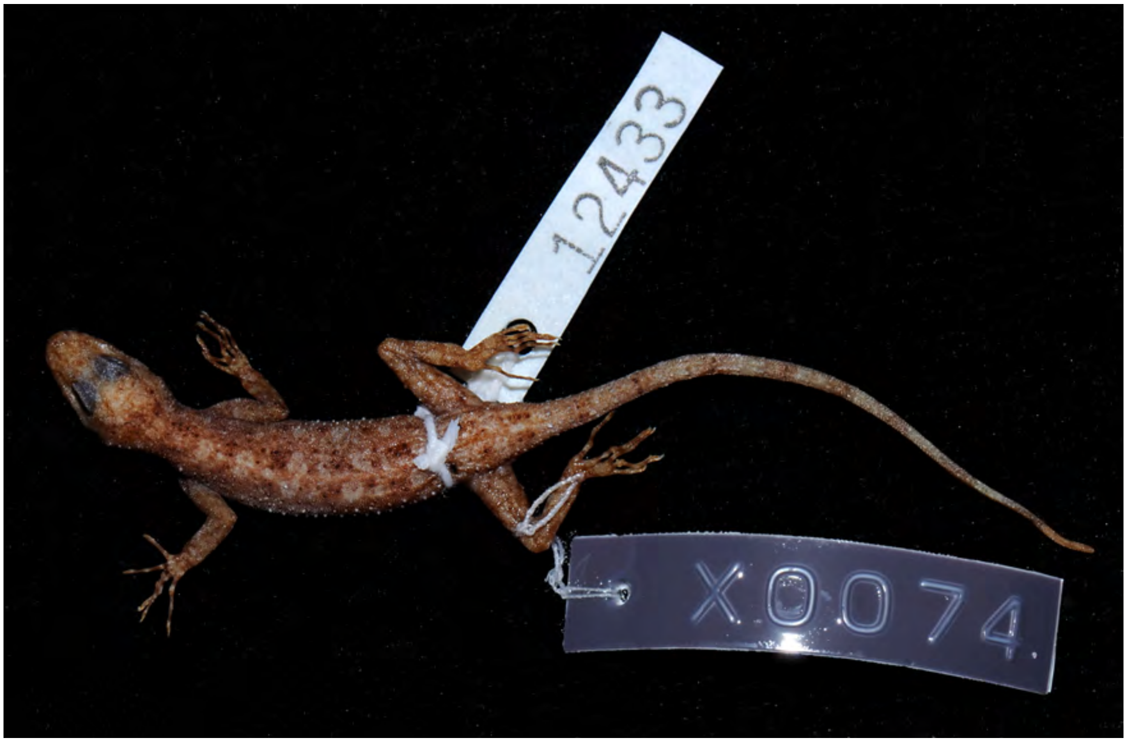

FIGURE 64. Adult female holotype of *Cnemaspis laoensis* (THNHM 12433) from Dong Phu Vieng National Protected Area, Savannakhet, Laos. Photograph by LLG.

Color pattern (Fig 64). Dorsal ground color of head, body, limbs and tail pale brown; rostrum and top of head bearing diffuse, faint, brown markings; postorbital stripes absent; light-colored, subelliptical, paired, paravertebral markings extending from nape to base of tail, continuing onto tail as wide, diffuse, light-colored, caudal bands separated by thinner, dark-brown bands; dark-brown markings within interspaces between light markings; large, light-colored markings on flanks; forelimbs and hind limbs mottled; all ventral surfaces beige bearing small, black stipples in each scale.

Distribution. *Cnemaspis laoensis* is known only from the type locality at Dong Phu Vieng, Savannakhet, along the Laotian portion of the Ho Chi Minh Trail (Fig. 1).

Natural History. Nothing is known of the natural history of *Cnemaspis laoensis.* However, Grismer (2010) hypothesized that on the basis of having smooth ventral and subcaudal caudal scales, this species is a likely karst-dweller. All other karst dwelling, microhabitat specialists share this combination of characters although its prominent dorsal tuberculation would suggest otherwise. Additionally, there are numerous outcroppings of karst tower formations in the general area of the type locality.

Relationships. The distribution or *Cnemaspis laoensis* in southern Laos (Fig. 1) would suggest that it could potentially belong in the Ca Mau clade, the *caudanivea* group of the Southern Indochina clade of southern Vietnam or the *chanthaburiensis* group of southern Thailand and southwestern Cambodia of the Southern Indochina clade. The fact that this species has a small SVL (40.9 mm); dense, prominent, dorsal tuberculation; lacks enlarged femoral, subtibial and submetatarsal scales; has a dorsolateral row of caudal tubercles; and tubercles in the lateral caudal furrow would likely preclude it from being a member of the Ca Mau clade (Table 6). Its dense arrangement of prominent dorsal tubercles; lack of a ventrolateral row of caudal tubercles; and lack of a dark, mid-gular stripe would likely preclude it from being a member of the *caudanivea* group (Table 6). It differs from members of the *chanthaburiensis* group only in lacking a lateral row of caudal tubercles and thus its inclusion in this group would be the most likely (Table 6). However, given that *C.laoensis* is separated from the nearest member of the *chanthaburiensis* group in Khao Ang Ru Ni, Chachoengsao Province in southeastern Thailand by approximately 600 km, two mountain ranges, and the Tonle Sap Basin would indicate that it will likely prove to be in its own species group within the Southern Indochina clade. For now, we tentatively place it in the *chanthaburiensis* group.

Material examined. Laos: Savannakhet, Dong Phu Vieng National Protected Area THNHM 12433 (holotype).

Cnemaspis punctatonuchalis **Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya, 2010**
Spotted-neck Rock Gecko
Fig. 65

Holotype. THNHM 2001. Type locality: "Thap Sakae District, Prachuap Khirikhan Province, Thailand" at approximately 70 m in elevation.

Diagnosis. Maximum SVL 49.6 mm; eight supralabials; seven or eight infralabials; smooth ventral scales; no precloacal pores; 24–27 paravertebral tubercles; body tubercles semi-linearly arranged, present on flanks; tubercles absent from lateral caudal furrows; ventrolateral caudal row of tubercles present anteriorly; lateral caudal row of tubercles present; caudal tubercles do not encircle tail; subcaudals smooth, bearing an enlarged median scale row; 1–3 postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials smooth; 29–31 subdigital fourth toe lamellae; white ocelli on brachia and side of neck in males; throat and subcaudal region orange in males (Tables 6,7).

Color pattern in life (Fig. 65). Dorsal ground color of head, body, limbs and tail light brown; top of head bearing large, diffuse, light and dark-colored markings giving it a mottled appearance; postorbital stripes absent; large, whitish markings on side of head forming a reticulum that extends ventrally onto throat; three, radiating, elongate blotches on occiput bordering the anterior margin of a large, white spot; lower sides of neck black, enclosing a large, white ocellus; black neck patch edged posteriorly by white antebrachial and brachial markings; lightly colored, paravertebral, butterfly-shaped markings between forelimb insertions and base of tail; markings continue onto tail to form light-colored bands; patches of enlarged tubercles on flanks white; other tubercles on body dark or light-colored; limbs generally uniform brown bearing elbow and knee patches; all ventral surfaces uniform beige with fine, dark stippling in some scales. Sexual dimorphism is distinct. Adult males have a brownish-green head with a yellow neck that accentuates the black, neck patch bearing the whitish ocelli. The body and limbs are grayish green and the body bears a series of alternating dark and light, paravertebral blotches. The ground color of the tail is deep-yellow and overlain with lighter, yellow bands. Adult females have a greyish dorsal ground color overall that is overlain by a prominent series of light and dark blotches on the head and a large, light-colored, central nape blotch. Alternating dark and light, paravertebral blotches occur on the body and transform into a lighter banding pattern on the tail. The limbs are somewhat banded distally and spotted proximally. The tubercular patches on the flanks are smaller in females than in males.

FIGURE 65. *Cnemaspis punctatonuchalis* from Thap Sakae District, Prachuap Khirikhan Province, Thailand. Upper left: adult male (LSUDPC 8087) in the dark color pattern phase. Upper right: adult female (LSUDPC 8088) in the dark color pattern phase. Lower: granite boulder microhabitat at Thap Sakae. Photographs by MS.

Distribution. *Cnemaspis punctatonuchalis* is known only from the type locality of the district of Thap Sakae, Prachuap Khiri Khan Province, Thailand (Grismer *et al.* 2010a; Fig. 3).

Natural history. Specimens have only been observed at night on granite boulders in lowland forest (Grismer *et al.* 2010a; Fig. 65).

Relationships. The distribution of *Cnemaspis punctatonuchalis* in Peninsular Thailand would align it with members of the *siamensis* group (Fig. 3). Like the northern sister species of this group *C. huaseesom* and *C. siamensis, C. punctatonuchalis* occurs north of the Isthmus of Kra and lacks the light colored, prescapular crescent that diagnoses the monophyletic group composed of *C. chanardi, C. omari* sp. nov., and *C. roticanai* that occurs south of the Isthmus of Kra, suggesting it may be more closely related to the northern species (Table 6).

Material examined. Thailand: Prachuap Khirikhan Province, Thap Sakae District THNHM 1899, 2001; Thap Sakae District, Hauy Yang ZMKU Rep-000314 (type series).

Cnemaspis vandeventeri Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya, 2010

Vandeventer's Rock Gecko

Fig. 66

Gonatodes siamensis Smith, 1925:22?
Cnemaspis siamensis Smith, 1935:72; Taylor, 1963:743
Cnemaspis siamensis (?) Pauwels *et al.,* 2000:129

Holotype. THNHM 8261. Type locality "Khlong Naka Wildlife Sanctuary (9°26.0N, 98° 35.0E), Kapur District, Ranong Province; Thailand" at approximately 11 m in elevation.

Diagnosis. Maximum SVL 44.7 mm; eight or nine supralabials; 7–9 infralabials; keeled ventral scales; four pore-bearing precloacal scales with round pores; 25–29 paravertebral tubercles; body tubercles randomly arranged, absent from flanks; tubercles absent from lateral caudal furrows; no ventrolateral row of caudal tubercles; lateral row of caudal tubercles present; caudal tubercles do not encircle tail; subcaudals keeled, bearing a weakly keeled, enlarged median scale row; 1–3 postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials keeled; 24–28 subdigital fourth toe lamellae; yellowish, prescapular crescent; gular region, throat, pectoral region, underside of limbs, belly, and subcaudal region orange (Tables 6,7).

FIGURE 66. *Cnemaspis vandeventeri* from Phuket Island, Phuket Province, Thailand. Upper right: adult male (LSUDPC 4362) in the dark color pattern phase. Photograph by H. Bringsoe. Lower right: juvenile (LSUDPC 8541) from Ranong Province in the light color pattern phase. Left: vegetative microhabitat on Phuket Island with a potential predator *Dryocalamus subannulatus* Duméril, Bibron & Duméril, 1854 (striped pattern phase). Photographs by MS.

Color pattern (Fig. 66). Dorsal ground color of head, body, limbs and tail brown; top of head bearing small, faint, brown markings and postorbital stripes; series of small, light-colored, vertebral blotches extend from nape to level of hind limb insertions; yellowish, prescapular crescent followed by a series of irregularly shaped, light-colored blotches on flanks; limbs faintly mottled with diffuse, dark markings; all ventral surfaces cream-colored, immaculate except for small, individual stipples in each scale.

Distribution. *Cnemaspis vandeventeri* is restricted to the west side of the Tenasserim Mountains and the contiguous Phuket Mountains along the west coast of southern Peninsular Thailand (Grismer *et al.* 2010a; Fig. 3). It ranges from the Khlong Naka Wildlife Sanctuary in the north, southward approximately 58 km to Khlong Had Sompen, Ranong and onto Phuket Island. Pauwels *et al.* (2000) collected two specimens (MNHN 1999.7707–08) from Phang-Nga Wildlife Breeding Station, Phang-Nga located west of the Phuket Mountains that they referred to as *C. siamensis* which could have also been *C. vandeventeri.* Unfortunately, the specimens could not be located (P. David, *in lit.* 2009). *Cnemaspis vandeventeri* may extend farther north along the western flanks of the Tenasserim Mountains into Myanmar.

Natural history. *Cnemaspis vandeventeri* has been observed on or within vegetation at night in lowland vegetation as well as on granite rocks suggesting it is a habitat generalist (Fig. 66).

Relationships. The distribution of *Cnemaspis vandeventeri* in Peninsular Thailand would align it with members of the *siamensis* group (Fig. 3). Unlike the northern sister species of this group *C. huaseesom* and *C. siamensis, C. vandeventeri* is restricted to the northwestern edge of the Isthmus of Kra and has the yelowish, prescapular crescent that diagnoses the monophyletic lineage composed of *C. chanardi, C. omari* sp. nov., and *C. roticanai* that occurs south of the Isthmus Kra, suggesting it may be more closely related to these species (Table 6).

Material examined. Thailand: Ranong Province, Kapur District, Khlong Naka Wildlife Sanctuary THNHM 8260–1; Muang District, Ranong Province, Khlong Had Sompen, CUMZ-R- 2009,6,24–11. These represent the type series.

FIGURE 67. *Cnemaspis kamolnorranathi* from the Petchphanomwat Waterfall, in Tai Rom Yen National Park, Surat Thani Province, Thailand. Upper right; adult male (LSUDPC 8530) in the light color pattern phase. Lower right: juvenile (LSUDPC 8533) in the dark color pattern phase. Right: habitat at Petchphanomwat Waterfall. Photographs by MS.

Cnemaspis kamolnorranathi Grismer, Sumontha, Cota, Grismer, Wood, Pauwels & Kunya, 2010

Kamolnorranath's Rock Gecko
Fig. 67

Cnemaspis siamensis Grismer, Chan, Nurolhuda, & Sumontha, 2008a:54

Holotype. THNHM 15908. Type locality "Petchphanomwat Waterfall, in Tai Rom Yen National Park, Ban Nasan District, Surat Thani Province (8°56.88'N 99°31.82'E)", Thailand at 5 m in elevation.

Diagnosis. Maximum SVL 37.8 mm; eight or nine supralabials; seven or eight infralabials; smooth to weakly keeled ventral scales; six or seven contiguous, pore-bearing, precloacal scales with elongate pores; 19–24 paravertebral tubercles; body tubercles semi-linearly arranged, present on flanks; tubercles present in lateral caudal furrows; ventrolateral row of caudal tubercles absent; lateral row of caudal tubercles; caudal tubercles do not encircle tail; subcaudals keeled, bearing a median row of weakly enlarged scales; one or two postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials may or may not be keeled; 24–28 subdigital fourth toe lamellae; light-colored prescapular crescent variably present (Tables 6,7).

Color pattern in life (Fig. 67). Dorsal ground color of head, body, limbs and tail brown to pale-yellow; rostrum bearing dark and light irregular markings; occiput darker than top of head; postorbital stripping faint to prominent; light vertebral blotch on nape followed by 4–6, lightly colored, butterfly-shaped, vertebral blotches on body which may fade immediately anterior to level of groin; white markings weakly edged in darker coloration; no light-colored bars on flanks; light-colored prescapular crescent variably present; limbs bearing dark and light-colored mottling faintly resembling a banding pattern; ventral surfaces uniformly beige with faint, black stippling in all scales; distinct dark and light color phases.

Distribution. *Cnemaspis kamolnorranathi* is known only from the type locality at Petchphanomwat Waterfall, in Tai Rom Yen National Park, Kanchanadid District, Surat Thani Province and Tham Khao Sonk hill, Thachana District, Surat Thani Province, Thailand (9°34'N 99°10'E), approximately 110 km to the north (Grismer *et al.* 2010a; Fig. 3).

Natural history. Grismer *et al.* (2010a) noted that *Cnemaspis kamolnorranathi* expresses a wide range of substrate utilization. Lizards have been found on karst, beneath rocks, and on vegetation and buildings during evening hours in lowland forests (Fig. 67).

Remarks. Grismer *et al.* (2010a) noted that the relatively wide separation (~110 km) between the Petchphanomwat Waterfall and Tham Khao Sonk suggests there are probably undiscovered, geographically intervening populations of *Cnemaspis kamolnorranathi* in the appropriate habitat separating these two localities. Unlike other species of *Cnemaspis, C. kamolnorranathi* shows intrapopulational variation in the degree of keeling of the ventral and subtibial scales suggesting *C. kamolnorranathi* may be composed of more than one species.

Relationships. The distribution of *Cnemaspis kamolnorranathi* in Peninsular Thailand would align it with members of the *siamensis* group (Fig. 3). Unlike the northern sister species of this group *C. huaseesom* and *C. siamensis, C. kamolnorranathi* is restricted to the Isthmus of Kra but has a variably present light-colored, prescapular crescent that diagnoses a monophyletic group composed of *C. chanardi, C. omari* sp. nov., and *C. roticanai* that occurs south of the Isthmus Kra (Table 6). This would suggest *C. kamolnorranathi* may be more closely related to southern species.

Material examined. Thailand: Surat Thani Province, Ban Nasan District, Tai Rom Yen National Park, Petchphanomwat Waterfall THNHM 15908, PSUZC-RT 2010.52, KZM 006; Thachana District, Tham Khao Sonk hill CUMZ-R 2009,6,24-3. These specimens represent the type series.

Cnemaspis dringi Das & Bauer, 1998
Dring's Rock Gecko
Fig. 68

Holotype. FMNH 148588. Type locality "Labang Camp (03° 20'N; 113°29'E), Bintulu District, Fourth Division, Sarawak, East Malaysia, Borneo" at approximately 30 m in elevation.

Diagnosis. Maximum SVL 46.4 mm; 11 supralabials; nine infralabials; keeled ventral scales; five or six discontinuous, pore-bearing, precloacal scales with round pores; 25–27 paravertebral tubercles; body tubercles randomly arranged, absent from flanks; tubercles absent from lateral caudal furrows; no ventrolateral row of caudal tubercles; lateral row of caudal tubercles present; caudal tubercles do not encircle tail; subcaudals keeled; enlarged median row of subcaudals present; two postcloacal tubercles on each side of tail base; no enlarged femoral, subtibial or submetatarsal scales; subtibials keeled; 32–35 subdigital fourth toe lamellae; distinct, whitish spots on a dark flank (Tables 6,7).

Color pattern (Fig. 68). Dorsal ground color pale brown overlain with a vertebral series of irregularly shaped, light-colored markings flanked by a linear, dark, paravertebral series of markings extending from nape to beyond base of tail; two dark-brown, postorbital stripes extending to ear opening; upper surface of limbs bearing dark bands; ventral surfaces pale-brown with scattered clusters of off-white scales, manifesting a very weakly mottled appearance; flanks dark-brown bearing distinct, whitish spots of varying size.

FIGURE 68. Type series of *Cnemaspis dringi* from Sarawak, East Malaysia. Upper: adult male (FMNH 148588; upper) from Fourth Division, Bintulu District, Labang Camp and adult male (FMNH 221478: lower) from seventh Division, Belaga District. Lower: FMNH 221448 showing diagnostic spotting on flank.

Distribution. *Cnemaspis dringi* is known only from Labang Camp, Bintulu District, Fourth Division and Sungai Segaham, Belaga District, Seventh Division, Sarawak, East Malaysia (Das & Bauer 1998; Fig. 4).

Natural history. According to Das and Bauer (1998), the only known aspect of this species' natural history is that the paratype from Sungai Segaham was taken from a log.

Relationships. The distribution of *Cnemaspis dringi* in East Malaysia would suggest it belongs within the Southern Sunda clade (Fig. 4). Having precloacal pores like all species of the *nigridia* group of East Malaysia differentiates *C. dringi* from all species in the *kendallii* group as well as *C. limi.* Like all species of the *nigridia* group, *C. dringi* lacks tubercles encircling the tail, which further separates it from the *kendallii* group. These data (Tables 6,7) would suggest that *C. dringi* is most closely related to the East Malaysian *nigridia* group.

Material examined. Malaysia: Sarawak, Fourth Division, Bintulu District, Labang Camp FMNH 148588; seventh Division, Belaga District FMNH 221478. These specimens represent the type series.

FIGURE 69. Type series of *Cnemaspis sundagekko* sp. nov. from Pulau Siantan, Anambas Archipelago, Riau Province, Indonesia. Upper: adult male holotype USNM 26549 (far left) and adult male paratypes USNM 26547–48 middle and right, respectively. Lower: paratypes ZRC. 2.1109–11 from left to right, respectively.

Cnemaspis sundagekko sp. nov.

Anambas Rock gecko
Fig. 69

Gonatodes kendalli Smedley 1928:76
Cnemaspis cf. *kendallii* Leong, Grismer & Mumpuni 2003:168

Holotype. Adult male USNM 26549 collected during September of 1899 by W. Abbott on Pulau Siantan, Anambas Archipelago, Riau Province, Indonesia (03°09.01 N, 106°14.03 E). Elevation unkown but less than 400 m, the maximum height of the island.

Paratypes. All paratypes are from Pulau Siantan. Adult males USNM 26547–48 bear the same data as the holotype. Adult males ZRC 2.1109–10 and adult female ZRC 2.1111 were collected on 5 September 1925 by F. N. Chasen.

Diagnosis. *Cnemaspis sundagekko* sp. nov. differs from all other Southeast Asia species of *Cnemaspis* in having the unique combination of adult males reaching 65.6 mm SVL, adult females reaching 68.0 mm SVL; 11–13 supralabials; 8–11 infralabials; keeled ventrals; no precloacal pores; moderate to prominent dorsal tubercles; 20–25 paravertebral tubercles; dorsal body tubercles generally randomly arranged; tubercles absent to weak on flanks; caudal tubercles encircle tail; no tubercles in lateral caudal furrows; ventrolateral and lateral rows of caudal tubercles present; subcaudals keeled; a sinlge, median row of enlarged, keeled subcaudals posteriorly; two or three postcloacal tubercles on either side of base of tail; no enlarged femoral, subtibial, or submetatarsal scales; subtibials keeled; 31–38 subdigital lamellae on fourth toe; large, dark, round spots on nape and anterior portion of body; dorsal caudal tubercles white. These characters are scored across all species in Tables 6 and 7.

Description of holotype. Male; SVL 55.2 mm; head oblong in dorsal profile, moderate in size (HL/SVL 0.27), somewhat narrow (HW/SVL 0.17), flattened (HD/HL 0.37), distinct from neck; snout short (ES/HL 0.50), slightly concave in lateral profile; postnasal region constricted medially, flat; scales of rostrum smooth, raised, larger than scales on occiput; low, supraorbital ridges; no frontorostral sulcus; canthus rostralis not very discernable; eye large (ED/HL 0.19); extra-brillar fringe scales largest anteriorly; pupil round; ear opening oval, taller than wide; rostral concave dorsally, nearly completely divided by longitudinal groove; rostral bordered posteriorly by two large supranasals and external nares, and laterally by first supralabials; 13R,11L raised supralabials decreasing in size posteriorly; 10R,9L infralabials, decreasing in size slightly posteriorly; nostrils elliptical, oriented dorsoposteriorly; bordered posteriorly by small, granular, postnasal scales; mental large, triangular, flat, bordered posteriorly by two large, rectangular, lateral postmentals of similar size and one smaller azygous scale; gular scales raised, weakly keeled; throat scales larger, raised, keeled.

Body moderate in stature (AG/SVL 0.41); small, keeled, dorsal scales generally equal in size throughout body, intermixed with larger, multicarinate tubercles more or less randomly arranged; tubercles extend from occiput to base of tail, moderate in size; tubercles absent from lower flanks; 25 paravertebral tubercles; pectoral and abdominal scales raised, keeled, not elongate, same size throughout; abdominal scales same size as dorsals; no precloacal pores; forelimbs moderately long, slender (FL/SVL 0.20); dorsal scales of brachium raised, keeled; dorsal scales of forearm raised, keeled; ventral scales of brachium keeled, raised, juxtaposed; ventral scales of forearm weakly keeled, raised, juxtaposed; palmar scales smooth, juxtaposed, raised; digits long with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae wide throughout digit; interdigital webbing absent; fingers increase in length from first to fourth with fourth longer than fifth; hind limbs slightly longer and thicker than forelimbs (TBL/SVL 0.22); dorsal scales of thigh keeled, slightly raised, juxtaposed; scales of anterior margin of thigh keeled; ventral scales of thigh keeled; subtibial scales raised, keeled, juxtaposed, with no enlarged anterior row; plantar scales smooth, juxtaposed, raised; no enlarged submetatarsal scales beneath first metatarsal; digits elongate with an inflected joint; claws recurved; subdigital lamellae unnotched; lamellae wide throughout digit; interdigital webbing absent to weak; toes increase in length from first to fourth with fourth being slightly longer than fifth; 31 subdigital lamellae on fourth toe; caudal scales arranged in segmented whorls; dorsal caudal scales flat anteriorly, keeled, juxtaposed; deep middorsal and lateral caudal furrows; subcaudal scales keeled; median row of enlarged, keeled, subcaudal scales posteriorly; caudal tubercles encircle tail; tubercles absent from lateral furrows; two enlarged, postcloacal tubercles on lateral surface of hemipenal swellings at base of tail.

Color pattern (Fig. 69). The type material was collected between 1899 and 1925 and is currently devoid of pattern save for some very faint markings. Smedley (1928) provides a brief color description taken from notes made in the field by Mr. F. N. Chasen in 1925 as follows: "Greyish-green above, blotched with brown; brighter green before eyes. Light rings on tail greyish-white; dark rings greenish brown. Below whitish. Distinct large brown spots on head and shoulders. Chiefly dark brown above; large oval spots on neck, nape and shoulders and no green anywhere." From these descriptions and what can be discerned from the type material, *Cnemaspis sundagekko* sp. nov. has a series of medium-sized dark dorsal blotches alternating with similarly sized lighter blotches. The large, keeled, spinose caudal tubercles are accentuated by being white.

Variation. No useful color pattern variation can be gleamed from the faded condition of the type material. Meristic and mensural variation is listed in Table 15.

TABLE 15. Meristic and mensural character states of the type series of *Cnemaspis sundagekko* sp. nov. w = weak; f = female; m = male; post = posterior; and / = data unavaiable. Meristic abbreviations are listed in the Materials and Methods.

	ZRC 2.1109 paratype	ZRC 2.111 paratype	ZRC 2.1111 paratype	USNM 26547 paratype	USNM 26548 paratype	USNM 26549 holotype
SVL	52.3	65.6	68	64.4	61.2	65.2
Supralabials	11	12	11	12	11	13
Infralabials	9	8	9	8	11	10
Ventral scales keeled (1) or not (0)	1	1	1	1	1	1
No. of precloacal pores	0	0	/	/	0	/
Precloacal pores continuous (1) or separated (0)	/	/	/	/	/	/
Precloacal pores elongate (1) or round (0)	/	/	/	/	/	/
No. of paravertebral tubercles	22	25	25	23	20	25
Tubercles linearly arranged (1) or more random (0)	w	w	0	w	w	w
Tubercles present (1) or absent (0) on flanks	w	w	0	0	0	0
Caudal tubercles in lateral furrow (1) or not (0)	0	0	0	0	0	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	1	1	1	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	1	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	0
Subcaudals keeled (1) or not (0)	1	1	1	1	1	1
Single median row of keeled subcaudals (1) or not (0)	post	post	post	post	post	post
Caudal tubercles encircle tail (1) or not (0)	1	1	1	1	1	1
Enlarged median subcaudal scale row (1) or not (0)	post	post	post	post	post	post
Postcloacal spurs	2	3	/	3	2	2
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0
Subtibial scales keeled (1) or not (0)	1	1	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0	0	0	0
No. of 4th toe lamellae	/	33	38	33	31	31
Sex	m	m	f	m	m	m
SVL	52.3	65.6	68.0	64.4	61.2	65.2
TL	/	/	/	77.0	/	81.5
TW	4.8	6.7	6.7	7.3	5.8	6.3

......continued on the next page

TABLE 15. (Continued)

	ZRC 2.1109 paratype	ZRC 2.111 paratype	ZRC 2.1111 paratype	USNM 26547 paratype	USNM 26548 paratype	USNM 26549 holotype
FL	9.7	12.0	11.9	12.8	12.1	13.4
TBL	12.6	16.7	15.3	15.0	14.0	14.2
AG	20.9	31.0	30.2	28.3	27.0	26.5
HL	13.5	17.7	17.6	17.5	16.8	17.7
HW	8.8	10.4	11.6	11.6	10.8	11.2
HD	5.6	8.8	7.2	7.0	7.0	6.9
ED	3.0	3.1	3.0	3.4	3.1	3.4
EE	3.8	5.0	5.3	5.5	4.4	4.7
ES	7.0	9.0	8.8	8.8	8.4	8.9
EN	5.5	/	6.8	6.6	6.4	6.8
IO	2.8	3.8	3.7	2.6	/	3.5
EL	1.2	1.5	1.3	1.6	1.0	1.6
IN	1.3	/	1.9	1.8	1.7	1.6

Distribution. *Cnemaspis sundagekko* sp. nov. is known only from the type locality of Pulau Siantan of the Anambas Archipelago, Riau Province, Indonesia (Fig. 4). We expect that it occurs on other nearby islands such as Pulau Matak as well. Mr. F. N. Chasen made collections on Pulau Jimaja to the west and did not report this species.

Natural History. Nothing has been reported on the natural history of this species. Being that it is the only species of *Cnemaspis* thus far known from the Anambas Archipelago we suspect it is a habitat generalist.

Comparisons. Within the Southern Seribuat clade, *Cnemaspis sundagekko* sp. nov. is differentiated from the species of the *nigridia* group (*C. dringi, C. nigridia* and *C. paripari*) by lacking as opposed to having precloacal pores; having fewer paravertebral tubercles (20–25 versus 265–43 collectively); having a single, enlarged, median row of keeled, subcaudal scales in the posterior portion of the tail as opposed to having smooth subcaudals throughout; having caudal tubercles that encircle the tail as opposed to lacking them; and having a greater number of subdigital lamellae on the fourth toe (33–38 versus 26–35 collectively). From the other species of the *kendallii* group (*C. baueri, C. bidongensis, C. kendallii, C. mumpuniae* sp. nov., *C. pemanggilensis,* and *C. peninsularis* sp. nov.), *C. sundagekko* sp. nov. differs from *C. pemanggilensis* by having a much smaller maximum SVL (68.0 mm versus 76.0 mm); fewer paravertebral tubercles (20–25 versus 30–37); a greater number of subdigital lamellae on the fourth toe (33–38 versus 27–34); and white caudal tubercles. From *C. mumpuniae* sp. nov. it differs in having a larger maximum SVL (68.0 mm versus 60.9 mm) and a greater number of lamellae on the fourth toe (33–38 versus 29–34). From *C. baueri, C. sundagekko* sp. nov. can be separated on the basis of having a greater number of subdigital lamellae on the fourth toe (33–38 versus 26–32) and a dorsal pattern lacking large black markings as opposed to having such markings. *Cnemaspis sundagekko* sp. nov. can be differentiated from *C. bidongensis* by having a larger maximum SVL (68.0 mm versus 58.1 mm); a greater number of subdigital lamellae on the fourth toe (33–38 versus 26–30); and the presence of white caudal tubercles. *Cnemaspis sundagekko* sp. nov. can be differentiated from *C. peninsularis* sp. nov. by having a larger maximum SVL (68.0 mm versus 60.0 mm); a greater number of subdigital lamellae on the first toe (33–38 versus 27–33); and posterior one-half of the tail in males being weakly banded as opposed to solid black. Lastly, from *C. limi,* C. *sundagekko* sp. nov. is separated by having a much smaller maximum SVL (68.0 mm versus 88.2 mm); fewer paravertebral tubercles (20–25 versus 25–35); a row of ventrolateral caudal tubercles; keeled as opposed to smooth subcaudal scales; and caudal tubercles that do not encircle the tail. *Cnemaspis sundagekko* sp. nov. can be differentiated from *C. sundainsula* sp. nov. by having a much smaller maximum SVL (68.0 mm versus 84.5 mm); 11–13 versus 9–11 supralabials; fewer paravertebral tubercles (20–25 versus 26–37); keeled as opposed to smooth subcaudals; caudal tubercles that encircle the tail; and a greater number of subdigital lamellae on the fourth toe (33–38 versus 26–31).

Relationships. Based on distribution, we hypothesize that *Cnemaspis sundagekko* sp. nov. is part of the Southern Sunda clade and within that clade, it aligns itself with the *kendallii* group by lacking precloacal pores and having caudal tubercles that encircle the tail (Table 6).

Discussion

Having a well-supported, multilocus phylogeny supporting an unambiguous, morphological taxonomy allows us to entertain other aspects of this group's evolutionary biology that were intractable prior to this analysis. Much of what can now be done is beyond the scope of this paper, however, below we provide a framework of initial hypotheses and observations that will guide future work—some of which is currently in progress.

Comments on biogeography

Cnemaspis has a unique distribution in that it is generally restricted to the areal, continental fringes of the Sunda Shelf and islands across the southern Sunda Plains (Fig. 1). This, coupled with the phylogenetic relationships and low vagility of its species, has potential in providing insight as to how the cyclical, transitory environmental and geographic history of Sundaland (e.g., Hall 1998, 2001, 2002, 2012; Bird *et al.* 2005; Outlaw & Voelker 2008; Reddy 2008; Cannon *et al.* 2009; Woodruff 2010; Cannon 2012; Morley 2012) has influenced the phylogeographic structure of this group (Grismer *et al*. 2011a). The intractable problem, however, is that key taxa for addressing such issues were most likely distributed across the varied habitats (see Bird *et al.* 2005) of the Sunda Plains which are now submerged. Thus, any biogeographical hypothesis generated can come only from refugial lineages on the areal fringes of this vast region.

The most striking feature concerning the phylogeny of *Cnemaspis* are the short branch lengths in the deeper regions of the tree between strongly supported clades and species groups that exist in allopatry or parapatry along well-established, biogeographic zones (Figs. 1–4). The exception being the Pattani clade's distribution within the southern portion of the Northern Sunda clade near the Thai-Malaysian border (Fig. 2). The distribution of the three sequentially basal lineages (the Ca Mau clade from southern Vietnam, the Pattani clade from southernmost Thailand, and the Southern Sunda clade from southern Sundaland) on the opposite sides of the Gulf of Thailand (Fig. 2) would suggest the origin of *Cnemaspis* was somewhere on the submerged Sunda Plains. The short branch lengths between the Pattani, Northern Sunda, and Southern Sunda clades may indicate a rapid, nearly simultaneous sequence of cladogenic events as inferred from the vertical alignment of their nodes (Figs. 2, 3, 4) followed by radiations into the current species groups.

The allopatry of the species groups within the Northern Sunda clade, in most cases, coincides with generally well-studied biogeographical transition zones. The Chao Phraya River basin in southern Thailand that separates the Tenasserim Mountains of western Thailand and Myanmar from the Cardomom Mountains of southern Thailand and Cambodia also separates the *chanthaburiensis* group from the *siamensis* group (Figs. 1, 2). The *siamensis* group is separated from the *argus* and *affinis* groups by the Kangar-Pattani Line near the Thai-Malaysian border. This lowland area (< 100 m) runs diagonally from southwest to northeast across the Thai-Malay Peninsula between the Banjaran Titiwangsa Mountains of Peninsular Malaysia in the south and the Sankalakhiri Mountains of Thailand to the north (Fig. 1). It was originally linked to the transition of Malay-type evergreen rain forest into the Thai-Burmese wet seasonal evergreen rain forest (see Van Steenis 1950; Wikramanayake *et al.* 2000; Woodruff 2003a) and of late has been shown to be an area of faunal exchange in number of groups of lizards, birds, and mammals (Reddy 2008; Woodruff & Turner 2009; Patou *et al.* 2010; Grismer 2011a). It has been posited, that this region was submerged in the Miocene (24–13 Ma) and again in the Pliocene (5.5–4.5 Ma), creating a 30–100 km wide seaway across the Thai-Malay Peninsula (Woodruff 2003a; however see Parnell 2013). The 17 species of the *argus* and *affinis* groups are confined to a relatively small portion of northern Peninsular Malaysia and broadly overlap but are only narrowly parapatric with *C. peninsularis* sp. nov. of the Southern Sunda clade at the Raub-Betong Suture Zone along the east side of the Banjaran Titiwangsa Mountains (Figs. 2–4).

The phylogeographic relationships within the species groups of each clade are reasonably well-resolved. Within the Northern Sunda clade, the *chanthaburiensis* group occurs along the northern margin of the Gulf of Thailand through the Cardamom Mountains of southern Thailand and Cambodia eastward to the mountainous regions on the Mekong Delta in southern Vietnam. It is separated from its possible sister lineage (support for this relationship is weak), the *siamensis* group of the northern Thai-Malay Peninsula by the wide, lowland plains of the Chao Phraya River Basin (Figs. 1, 3) which was flooded during the last Holocene highstand (Woodruff & Turner 2009). Within the *chanthaburiensis* group, the westernmost sister species *C. chanthaburiensis* and *C. neangthyi* are basal to the Vietnamese lineage containing *C. aurantiacopes, C. caudanivea, C. tucdupensis,* and *C. nuicamensis* approximately 300 km to the east (Figs. 1–3). The Vietnamese species are restricted to islands or habitat islands associated with the Mekong Delta (Grismer & Ngo 2007). Their well-resolved relationships suggest their phylogenetic structuring happened over a relatively long period of time and is likely tied to the interactions between the complex formation of the Mekong Delta (Thi *et al.* 2002) and cyclical changes in sea levels (Woodruff & Turner 2009; Woodruff 2010). The *siamensis* group is composed of a northern (at least two species) and southern (at least three species) lineage from opposite sides of the Isthmus of Kra (Fig. 2)—a well-known biogeographical barrier that separates a large number of species across a wide array of taxonomic groups (e.g., Hughes *et al.* 2003; Pauwels *et al.* 2003; Round *et al.* 2003; Woodruff 2003a,b; De Bruyn *et al.* 2005; Cattulo *et al.* 2008; Reddy 2008; Woodruff & Turner 2009; Parnell 2013).

Species of the *argus* and *affinis* groups occur on both sides of the Banjaran Titiwangsa Mountains—a prominent geographic feature separating the western one-third of Peninsular Malaysia and southern Thailand from the eastern two-thirds along the Raub-Bentong Suture Zone. It is likely this mountain range has played a significant role in the diversification within both these groups being that it separates the basal species of the *argus* group (*C. flavigaster*) from the remaining three species (*C. karsticola*, *C. argus,* and *C. perhentianensis*) in the northeast. In the *affinis* group, this mountain harbors four upland endemics (*C. narathiwatensis, C. stongensis* sp. nov., *C. temiah* sp. nov., and *C. flavolineata* from north to south); restricts six species to the west (*C. pseudomcguirei, C. affinis, C. harimau, C. shahruli, C. mcguirei,* and *C. grismeri*) and three species to the east (*C. hangus* sp. nov., *C. selamatkanmerapoh,* and *C. bayuensis*) with no discernable phylogeographic patterns amongst any of them (Figs. 2, 3).

The *affinis* group contains 13 species whose relationships to one another are well-resolved in the ND2 phylogeny and whose topology is represented in Figure 2 although the support for these relationships in the concatenated tree is weak. *Cnemaspis pseudomcguirei* from the Banjaran Bintang mountains represents the basal species lineage of this group and the sister species *C. affinis* from Penang Island and *C. harimau* from Gunung Jerai on the adjacent mainland represents one of the next two basal lineages (Fig. 2). During slightly lower sea levels, these two regions were in contact through a series of low mountains that now exist as a string of islands (Pulau Song, Pulau Bidan and Pulau Telur) lying between them. This same phylogeographic pattern is emerging in other taxa from these areas (Quah *et al.* in prep.).

The other basal lineage of that sister pair contains two clades; one containing the upland species *C. narathiwatensis* and its lowland sister species *C. shahruli* to the west and the other clade composing a polytomy of the remaining eight species (Fig. 2). Some of the species relationships within this polytomy, however, are resolved. *Cnemaspis mcguirei* from the upper regions of the Banjaran Bintang Mountains is the sister species of *C. grismeri* from the eastern base of the Banjaran Bintang and there is a lineage composed of three small, lowland, karst-dwelling species (*C. bayuensis, C. selamatkanmerapoh,* and *C. hangus* sp. nov., the latter two being sister species) from the northeast and an upland, granite-dwelling species *C. stongensis* sp. nov. that is the sister species of *C. bayuensis.*

The relationships and distribution of the species in the Southern Sunda clade illustrate how cyclical, environmental changes across broad expanses of time can generate sequential, cladogenic events in the same geographic area as evidenced by the position of these events in different places on the tree. The Southern Sunda clade is a polytomous group composed of three major lineages; *C. limi* from Tioman and Tulai islands*,* the *nigridia* group from northern Borneo, and the *kendallii* group ranging from southern Peninsular Malaysia and Singapore eastward through the Seribuat, Anambas, and Natunas archipelagos to Borneo. Eastern Peninsular Malaysia, the Seribuat and Anambas archipelagos, and the Natuna Archipelago and northwestern Borneo are each composed of separate, Upper Cretaceous-Late Paleocene northwest to southeast oriented arcs of granite plutons (Cobbing *et al.* 1992; Hutchinson 2009) on which many of the species of this group occur and may account for the origin of the three basal lineages in the Southern Sunda Clade (i.e. *C. limi,* the *nigridia* group, and *C. sundainsula* sp. nov). Speciation events within this clade are likely tied to cyclical changes in sea levels over the last 2.5 million years that would have isolated and reconnected these archipelagos with Peninsular Malaysia and Borneo through lowland, hilly areas and the intervening archipelagos at least 50 times (Woodruff 2010). Such events could serve as a "species-pump" generating sequential, cladogenic events on the same island arcs which could account for distantly related species occurring on the same islands (e.g., *C. limi* and *C. peninsularis* sp. nov. on Pulau Tioman and *C. sundainsula* sp. nov. and *C. mumpuniae* on Pulau Natuna Besar). A detailed biogeographic scenario at this point would be premature in that precise phylogenetic information from populations on geographically intermediate granite arcs (*C. sundagekko* sp. nov. from the Anambas and *C.* cf. *kendallii* from the Tambelan archipelagos, respectively) that would be crucial to any scenario are lacking. This issue will be addressed in a forthcoming paper following the acquisition of additional material from these islands.

Comments on diversity

The distribution of the known species of *Cnemaspis* (Figs. 1, 3, 4) is characterized by large, geographic discontinuities between species across vast regions as well as surprisingly low species diversity in other areas, suggesting that many species remain to be discovered. For example, in Southern Indochina, *C. laoensis* is currently a geographic outlier to the north, being separated from the nearest population of *C. chanthaburiensis* in southern Thailand by 600 km (Fig. 1). Given the rocky, mountainous terrain between these two species across southern Laos, Cambodia, and Vietnam we can surmise this hiatus is a collecting artifact as was demonstrated across southern Cambodia and Vietnam with the discovery of *C. aurantiacopes, C. nuicamensis, C. caudanivea, C. tucdupensis* (Grismer & Ngo 2007) and *C. neangthyi* (J. Grismer *et al.* 2010) between *C. chanthaburiensis* and *C. boulengerii* filling a hiatus of nearly 600 km. And still a hiatus of nearly 300 km remains between *C. neangthyi* and *C. nuicamensis* through suitable lowland, hilly, rocky habitat.

The highest diversity of *Cnemaspis* occurs on the Thai-Malay Peninsula (30 species) with 23 species in Peninsular Malaysia alone. This stands in sharp contrast to the four known species from Borneo (Grismer & Chan 2009), a landmass with nearly four times the surface area and a mountainous terrain with extensive areas of karst and granite formations exceeding those of Peninsular Malaysia. Furthermore, Borneo and Peninsular Malaysia were connected through a land-positive mountainous corridor (the remnants of which are the Natuna, Anambas, and Seribuat archipelagos) as little as 14 thousand years ago (Sathimurthy & Voris 2006.). Despite the number of overlapping and repetitive pocket guides and popular books on the herpetofauna of northern Borneo (see references in Grismer & Chan 2009), only recycled, anecdotal information on *Cnemaspis* has emerged. We posit that if research on *Cnemaspis* in Borneo were to commence, its diversity would exceed that of Peninsular Malaysia. We also suspect that *Cnemaspis* will eventually be found on the large, environmentally diverse island of Sumatra.

Comments on parallel evolution

The various species of *Cnemaspis* range across a relatively broad array of ecosystems and microhabitats. Some species are strictly lowland forms that do not range above 600 m in elevation, some are upland forms not occurring below 600 m, and others may extend from sea level to 1000 m so long as the appropriate microhabitat is present. Many species are substrate specialists that prefer only one type of rock surface (limestone or granite), others are vegetational specialists or habitat generalists, and one species, *C. chanthaburiensis,* is strictly terrestrial and can be found beneath and within logs and beneath rocks. Across all these environmental gradients, many species are nocturnal, others are diurnal, and some are both. The phylogenetic hypothesis of *Cnemaspis* indicates substrate preferences, activity periods, elevational zonation, and the presence of ocelli has evolved in parallel multiple times (Fig. 5). We note here that the most common combination of traits for *Cnemaspis* is to be a diurnal, granite-dwelling, lowland species lacking ocelli (19 of 44 species examined for which molecular data were available; Table 16). Ancestral state reconstructions based on maximum likelihood analyses will be used to test hypotheses concerning the evolutionary origins and trends among these different parameters are currently in progress (Wood & Grismer in prep.).

TABLE 16. Activity period, substrate preference (microhabitat), elevation (upland > 600 m), and presence or absence of ocelli (eyespots) in the species of *Cnemaspis* for which we had sufficient data or observations.

	Activity period		**Substrate preference**				**Elevation**		**Ocelli location**		
	nocturnal	diurnal	limestone	granite	vegetation	terrestrial	upland	lowland	shoulders	head	neck
Ca Mau clade											
boulenegerii		X		X				X			
psychedelica		X		X				X			
Pattani clade											
monachorum		X	X					X			
biocellata		X	X					X	X	X	X
niyomwanae	X		X					X			
kumpoli	X			X				X	X		
Northern Sunda clade											
***chanthaburiensis* group**											
chanthaburiensis	X					X	X	X			
neangthyi	X		X					X			
aurantiacopes	X			X				X			
caudanivea		X		X				X			
nuicamensis		X		X				X			
tucdupensis		X		X				X			
***siamensis* group**											
siamensis	X				X			X			
huaseesom	X		X					X			
chanardi		X		X	X			X			
omari sp. nov.		X			X			X			
roticanai		X			X		X	X			
kamolnorranathi	X			X	X	X		X			
punctatonuchalis	X			X				X	X		X
vandeventeri	X			X	X						
***argus* group**											
flavigaster		X	X	X				X			
argus		X		X			X	X			
karsticola		X	X					X			
perhentianensis		X		X				X			
***affinis* group**											
pseudomcguirei		X			X		X		X		
harimau	X			X			X	X	X		
affinis		X		X			X		X		
shahruli	X			X	X			X	X		
temiah sp. nov.		X			X		X				
flavolineata		X			X		X				
hangus sp. nov.		X	X					X			
selamatkanmerapoh		X	X					X			
stongensis sp. nov.	X			X			X	X			
bayuensis		X	X					X			
mcguirei		X		X			X		X		
grismeri		X	X					X	X		
narathiwatensis		X		X			X	X			
Southern Sunda clade											
limi		X		X			X	X			
***nigridia* group**											
nigridia		X		X				X			
paripari		X	X					X			
***kendallii* group**											
kendallii		X		X	X		X	X			
sundainsula sp. nov.		X		X				X			
pemanggilensis		X		X				X			
baueri		X		X				X			
mumpuniae sp. nov.		X		X	X			X			
bidongensis		X		X	X			X			
peninsularis sp. nov.		X	X	X	X		X	X			

Comments on genetic divergence with Cnemaspsis

The genetic divergence based on ND2 seen among species of *Cnemaspis* greatly exceeds that seen among species within other gekkotan genera such as *Hemiphyllodactylus, Phyllopezus, Pseudogekko, Ptychozoon, Cyrtodactylus.*

Comments on integrative taxonomy

A general assumption concerning integrative taxonomic analyses is that currently recognized, widespread species are composed of morphologically cryptic species whose detection is possible only through the use of molecular analyses (see Grismer *et al.* 2013b for a discussion). On the contrary, the majority of integrative analyses result in demonstrating that diagnostic, morphological characters were present but overlooked by the last author(s) to revise the group and their subsequent discovery was simply prompted by the results of a molecular analysis (see references in Grismer *et al.* 2013b). Prior to 2003, *Cnemaspis* was known from 10 species. Between 2003 and this study, we and associated authors described 34 of the then 44 known species on the basis of morphology and color pattern alone (Das & Grismer 2003; Grismer & Das 2006; Grismer & Ngo 2007; Chan & Grismer 2008; Grismer & Chan 2008, 2009, 2010; Grismer *et al.* 2008a,b, 2009, 2010a,b,c; Grismer 2009; Chan *et al.* 2010; J. Grismer *et al.* 2010; Wood *et al.* 2013). The analysis herein indicated the only error made was that a geographically outlying specimen from southern Thailand (included as part of the type series of *C. chanardi*) and continental populations of *C. roticanai* actually constituted a new species, *C. omari* sp. nov., which turned out to be the sister species of *C. roticanai sensu stricto.* This mistake was made because Grismer *et al.* (2010a) and Grismer & Chan (2010) did not have all the material available on hand to compare. The molecular analysis indicated these were different taxa (Fig. 2), prompting a reexamination herein by comparing all the material together and in so doing, we discovered additional, diagnostic, morphological characters. Thus, integrative taxonomic analyses are not necessarily revealing cryptic species but rather highlighting less than efficient morphological analyses.

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Chapter 4: Three new karst-dwelling *Cnemaspis* Strauch, 1887 (Squamata; Gekkonidae) from Peninsular Thailand and the phylogenetic placement of *C. punctatonuchalis* and *C. vandeventeri*

Three new karst-dwelling *Cnemaspis* Strauch, 1887 (Squamata; Gekkonidae) from Peninsular Thailand and the phylogenetic placement of *C. punctatonuchalis* and *C. vandeventeri*

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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 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 postcloaclal 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

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continued field research in poorly known areas of the Thai-Malay Peninsula, especially those that are threatened and often overlooked as biodiversity hot spots.

Subjects Genetics, Taxonomy, Zoology
Keywords Limestone forests, *chanthaburiensis* group, *siamensis* group, Malay peninsula

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 & Turner, 2009*; *Gorog, Sinaga & Engstrom, 2004*; *Pauwels et al., 2003*; *Hughes, Round & Woodruff, 2003*; *Woodruff, 2003*; *Grismer et al., 2014d*; *Grismer, 2011*). One feature that is often overlooked 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., 2014c*; *Grismer et al., 2014b*; *Schilthuizen et al., 2005*; *Schilthuizen et al., 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 & Whitten, 1999*; *Komo, 1998a*; *Komo, 1998b*; *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 floral endemism there are also high levels of invertebrate endemism associated with karst formations (e.g., *Holloway, 1986*; *Vermeulen & 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, Duckworth & Timmins, 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*; *Grismer et al., 2008b*; *Grismer* et al., 2009; Grismer et al., 2013b; Grismer et al., 2012; Grismer et al., 2014e; Grismer et al., 2014c; Grismer et al., 2013a; Grismer et al., 2016a; Wood Jr et al., 2013) and two new snakes (Grismer et al., 2014b; E Quah, 2017, unpublished data). 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; Grismer et al., 2015; Pauwels et al., 2013; Grismer et al., 2012; Ellis & 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 & Pauwels, 2012; Pauwels et al., 2013; Grismer et al., 2016a; Sacha, 2015, and references therein). The genus *Cyrtodactylus* is a monophyletic assemblage of 224 species (Uetz, Freed & Hošek, 2016) that have a broad range throughout Asia to the western Pacific (Wood Jr et al., 2012). This diverse group of nocturnal geckos occupies a broad suite of microhabitats (eg. karst and granite caves, granite boulders, leaf-litter, limestone forests etc.) with a number of specialists in distantly related clades. One group of convergent specialists that has recently received attention are the karst and cave dwelling ecomoprhs in the *condorensis* and *intermedius* species complexes (Grismer et al., 2015, and references therein). These granite and karst-dwelling *Cyrtodactylus* are often found syntopically with the Rock Geckos in genus *Cnemaspis* and can pose as a potential competitor.

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 (Fig. 8 in Grismer et al., 2014d) are brightly colored and a number of species dispersed throughout the phylogenetic tree are nocturnal with multiple independent transitions (Fig. 5 in Grismer et al., 2014d). Like *Cyrtodactylus*, *Cnemaspis* are also found on a variety of substrates (e.g., 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; Grismer et al., 2012; Grismer et al., 2014e; Grismer et al., 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, Prachuap Khiri Khan, 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 *Cyrtodactlyus*. 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 (Fig. 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/. The LSID for this publication is: urn:lsid:zoobank.org:pub:987831FC-F4BA-4409-A43C-9929F913E9F9. The online version of this work is archived and available from the following digital repositorie: 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^{TM} tissue kit (Valencia, CA, USA). The mitochondrial gene NADH dehydrogenase subunit 2 (ND2) and the flanking tRNAs (~1,335 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′-AAGCAGTTGGGCCCATACC-3′), 1.0 µl (10 µM) reverse primer H5934 (5′-AGRGTGCCAATGTCTTTGTGRTT-3′), 1.0 µl deoxynucleotide pairs (1.5 µM), 2.0 µl 5x buffer (1.5 µM), 1.0 MgCl 10x buffer (1.5 µM), 0.18 µl Promega Taq polymerase (5 u/µl), and 7.5 µl H2O, primers are from *Macey et al. (1997)*. All PCR reactions were executed in an Eppendorf Mastercycler gradient theromocycler 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 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′-TAGCCYTCTCYTCYATYGCCC-3′) and CyrtintR1 (5′-ATTGTKAGDGTRGCYAGGSTKGG-3′) from (*Siler et al., 2010*) on the ABI Big-Dye Terminator v3.1 Cycle Sequencing Kit in an ABI GeneAmp PCR 9700 thermal cycler.

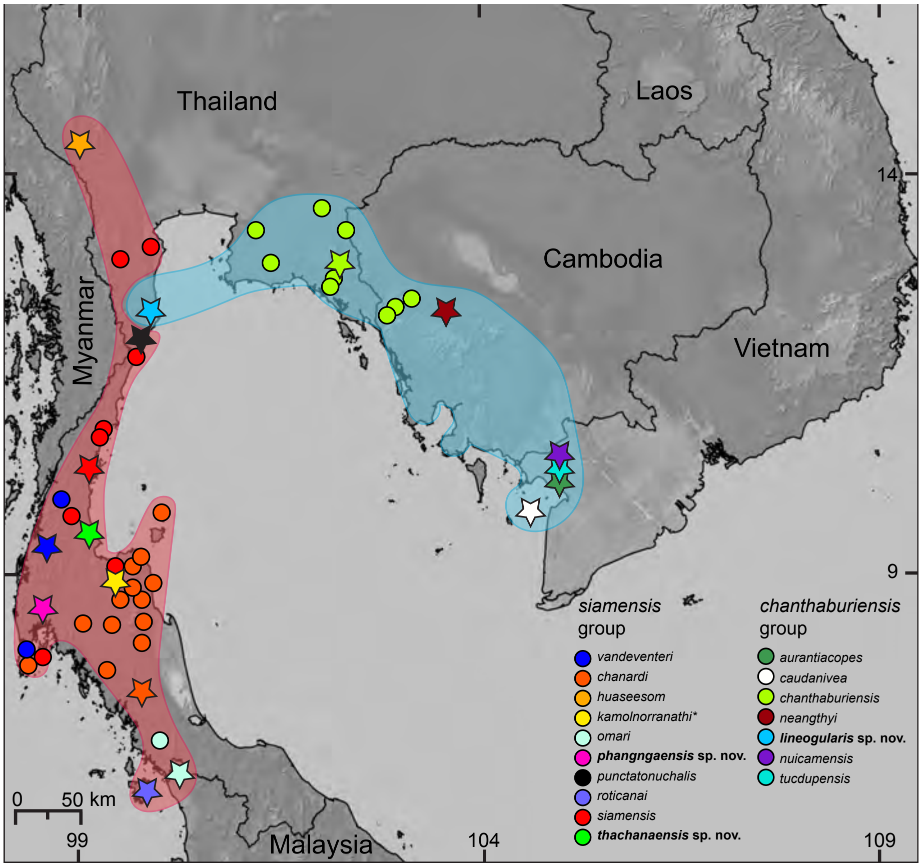

Figure 1 **Distribution of the species of *Cnemaspis* in the *chanthaburiensis* and *siamensis* groups.** Stars indicate type localities, colored dots represent additional localities for the respective species, and the colored outlines correspond to colored clades in Fig. 2. The asterisk (*) identifies a species not included in the molecular analysis and is hypothesized to be in the *siamensis* group based on its distribution (*Grismer et al., 2014d*).

Cycle sequencing reactions were purified with Sephadex 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 & 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 & Crandall, 1998*), using the Bayesian Information Criterion (BIC). The best fit

Table 1 Models of molecular evolution used for the ML and BI analyses.

Gene	Model selected	Model applied for ML	Model applied for BI
ND2			
1st pos	GTR+I+Γ	GTR+I+Γ	GTR+I+Γ
2nd pos	GTR+I+Γ	GTR+I+Γ	GTR+I+Γ
3rd pos	GTR+I+Γ	GTR+I+Γ	GTR+I+Γ
tRNAs	TrN+I+Γ	GTR+I+Γ	HKY+I+Γ

models of evolution are in presented in Table 1. The partitioned ML analyses was performed using RAxML HPC v7.5.4 (*Stamatakis, 2006*), 1,000 bootstrap pseudoreplicates via therapid hill-climbing algorithm (*Stamatakis, Hoover & Rougemont, 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 PLWJ 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 paravertebral row and the lateral, caudal furrow on the dorsolateral margin of the tail; lateral row—the row immediately below the lateral, caudal furrow; and ventrolateral row—the row below the lateral row on the ventrolateral margin of the tail below the lateral caudal furrow. When present, this row is usually restricted to the anterior 25% (or less) of the tail. Occasionally there may be a row of tubercles within the lateral, caudal furrow.

RESULTS

The phylogenetic analyses place both *C. punctatonuchalis* and *C. vandeventeri* in the *siamensis* group (Fig. 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 Prachuap Khiri Khan, 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 (Fig. 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 (Fig. 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

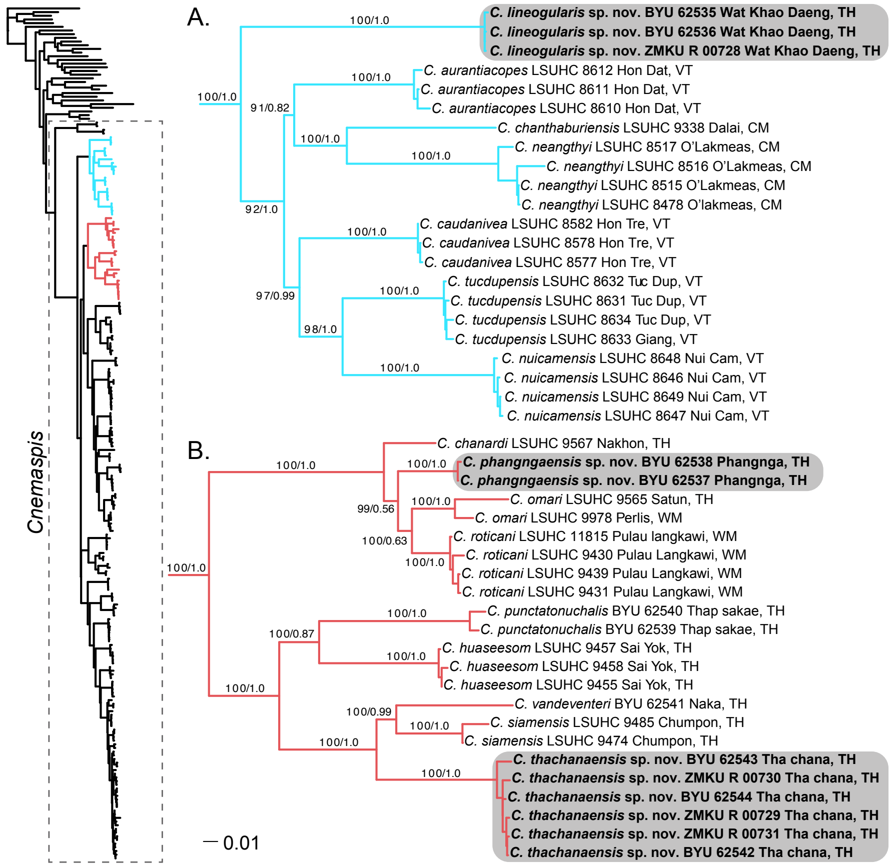

Figure 2 Phylogenetic relationships of the *chanthaburiensis* (A) and the *siamensis* (B) groups. Right, Maximum Likelihood tree from RAxML (−ln L 60818.390304) for all species of *Cnemaspis* and outgroups with bootstrap support values (BS) and Bayesian posterior probabilities (PP), respectively. Country abbreviations for the tip labels are as follows: CM, Cambodia; TH, Thailand; WM, West Malaysia; VT, Vietnam. All new species are highlighted with grey boxes and the genus *Cnemaspis* is highlighted using a box with dashed lines in the main tree.

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 bares 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 and 2B) 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.

Table 2 Pairwise uncorrected p-distances based on 1,335 bp of ND2 and associated tRNAs calculated in MEGA v6.06 (Tamura et al., 2013) within the *chanthaburiensis* group. Within species distances are presented in bold text and between species distances are presented below the diagonal.

	C. lineogularis sp. nov.	*C. aurantiacopes*	*C. caudanivea*	*C. chanthaburiensis*	*C. neangthyi*	*C. nuicamensis*	*C. tucdupensis*
C. lineogularis sp. nov.	**0.003**						
C. aurantiacopes	0.200	**0.011**					
C. caudanivea	0.195	0.136	**0.002**				
C. chanthaburiensis	0.217	0.161	0.167	–			
C. neangthyi	0.230	0.161	0.169	0.156	**0.001**		
C. nuicamensis	0.207	0.158	0.160	0.175	0.179	**0.002**	
C. tucdupensis	0.206	0.149	0.140	0.171	0.166	0.140	**0.006**

Table 3 Pairwise uncorrected p-distances based on 1,335 bp of ND2 and associated tRNAs calculated in MEGA v6.06 (Tamura et al., 2013) within the *siamensis* group. Within species distances are presented in bold text and between species distances are presented below the diagonal.

	C. thachanaensis sp. nov.	*C. phangngaensis* sp. nov.	*C. omari*	*C. chanardi*	*C. punctatonuchalis*	*C. vandeventeri*	*C. huaseesom*	*C. roticani*	*C. siamensis*
C. thachanaensis sp. nov.	**0.003**								
C. phangngaensis sp. nov.	0.260	**0.002**							
C. omari	0.282	0.112	**0.042**						
C. chanardi	0.243	0.114	0.118	–					
C. punctatonuchalis	0.211	0.250	0.264	0.255	–				
C. vandeventeri	0.144	0.252	0.266	0.240	0.211	–			
C. huaseesom	0.208	0.237	0.282	0.262	0.170	0.201	**0.004**		
C. roticani	0.275	0.088	0.090	0.117	0.256	0.268	0.274	**0.002**	
C. siamensis	0.134	0.250	0.278	0.255	0.194	0.123	0.194	0.281	–

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

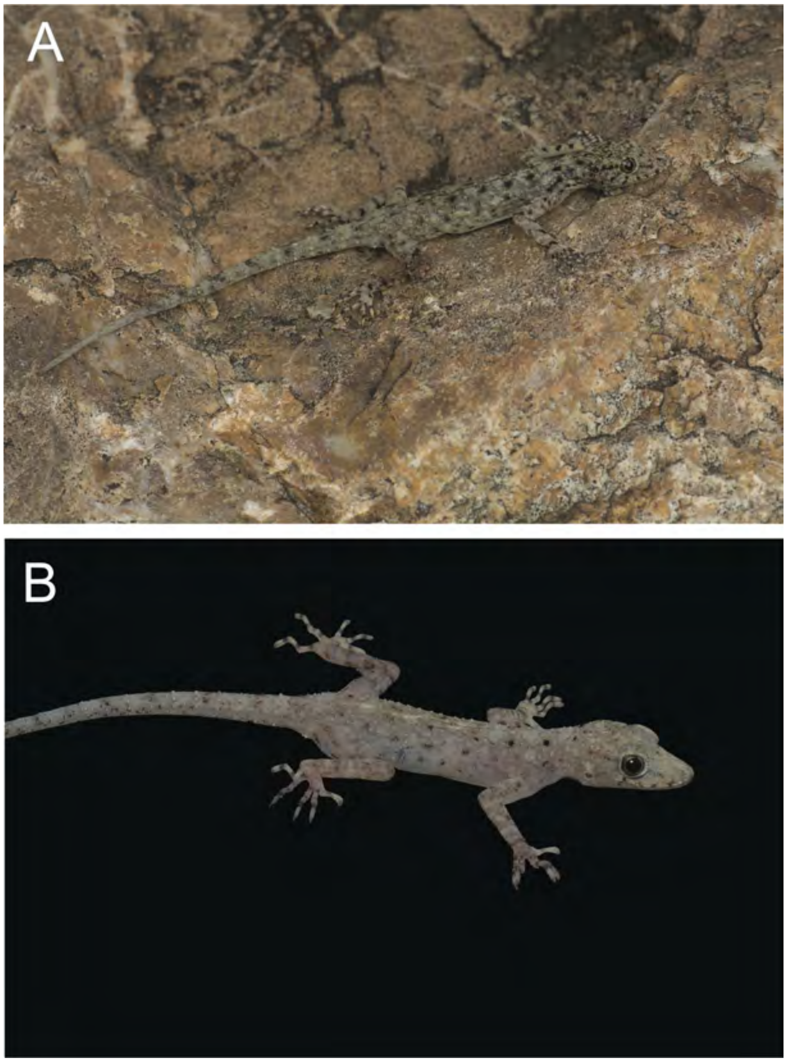

Figure 3 (A) male holotype BYU 62535 and (B) female paratype ZMKU R 00728 of *Cnemaspis lineogularis* sp. nov.

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

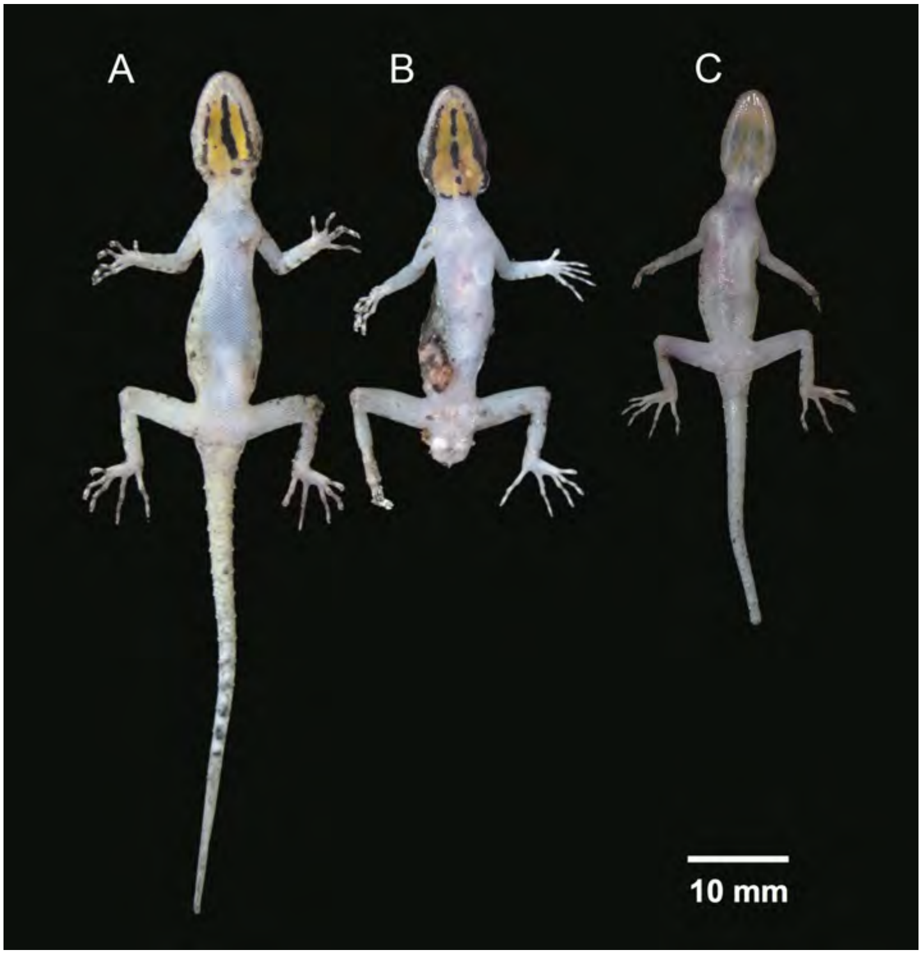

Figure 4 Ventral coloration and sexual dichromatism in the type series of *Cnemaspis lineogularis* sp. nov. (A) adult male holotype BYU 62535, (B) adult male paratype BYU 62536, (C) adult female paratype ZMKU R 00728.

region yellow-orange, thick, black lineate markings in males, absent in females; subcaudal region 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

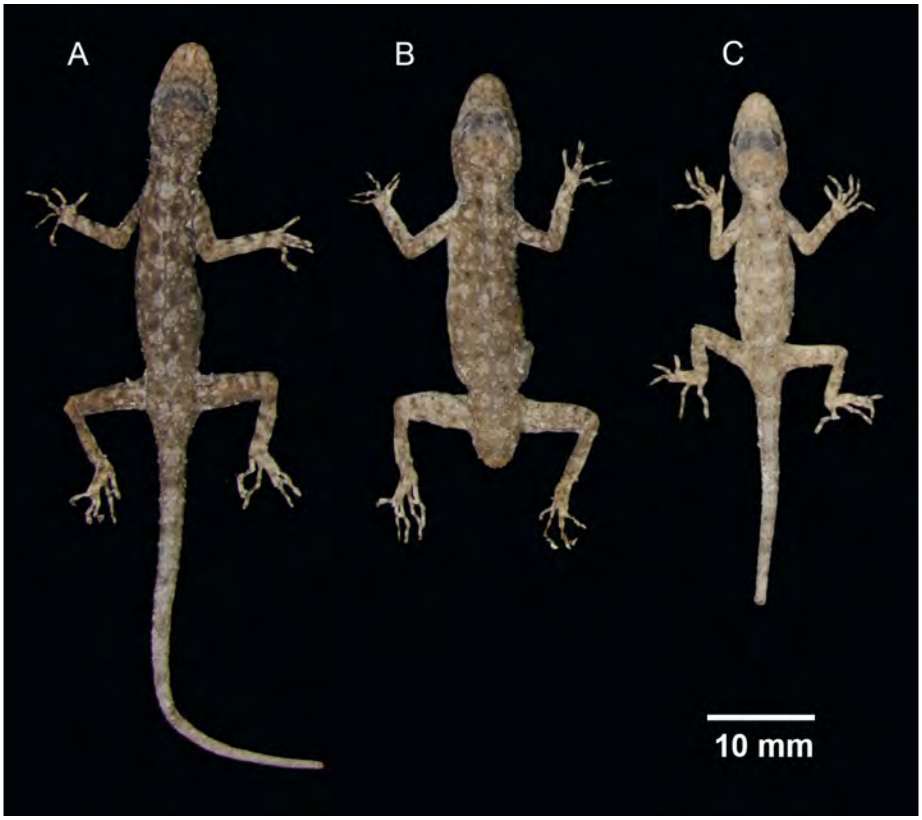

Figure 5 **Dorsal view of the type series of *Cnemaspis lineogularis* sp. nov.** (A) adult male holotype BYU 62535, (B) adult male paratype BYU 62536, (C) adult female paratype ZMKU R 00728.

groove; rostral bordered 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

Table 4 **Mensural and meristic character states for the type series of *Cnemaspis lineogularis* sp. nov.** All measurements taken are in millimeters and the abbreviations are defined in the materials and methods.

	BYU 62535 Holotype	**BYU 62536 Paratype**	**ZMKU R 00728 Paratype**
Supralabials	9	9	9
Infralabials	8	8	8
Ventral scales keeled (1) or smooth (0)	0	0	0
No. of precloacal pores	0	0	0
Precloacal pores continuous (1) or separated (0)	/	/	/
Precloacal pores elongate (1) or round (0)	/	/	/
No. of paravertebral tubercles	13	13	13
Tubercles linearly arranged (1) or more random (0)	1	1	1
Tubercles present (1) or absent (0) on lower flanks	0	0	0
Lateral caudal furrows present (1) or absent (0)	1	/	1
Caudal tubercles in lateral furrow (1) or not (0)	0	/	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	/	1
Lateral caudal tubercle row present (1) or absent (0)	1	/	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	/	1
Subcaudals keeled (1) or smooth (0)	0	/	0
Single median row of keeled subcaudals (1) or smooth (0)	0	/	0
Caudal tubercles encircle tail (1) or not (0)	0	/	0
Enlarged median subcaudal scale row (1) or not (0)	1	/	1
No. of postcloacal tubercles in males	1	1	/
Enlarged femoral scales present (1) or absent (0)	1	1	1
Shield-like subtibial scales present (1) or absent (0)	0	0	0
Subtibial scales keeled (1) or smooth (0)	0	0	0
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0
No. of 4th toe lamellae	29	27	29
SVL	38	35	29
TL	48	b	24
TW	2.9	/	2.66
FL	6.5	6.3	4.34
TBL	7.3	7.1	5.27
AG	17.5	15.7	10.6
HL	9.6	9.6	5.95
HW	6.4	6.3	5
HD	3.7	3.56	3.1
ED	2.5	1.78	1.71
EE	2.68	2.9	2.19
ES	5	4.2	3.54
EN	3.7	3.2	2.88
IO	3.1	2.5	1.99

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Table 4 (*continued*)

	BYU 62535 Holotype	BYU 62536 Paratype	ZMKU R 00728 Paratype
EL	0.7	0.3	0.4
IN	1.2	1.2	0.89
Sex	m	m	f

Notes.
m, male; f, female; /, data unavailable or absent; b, broken.

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, multicariante, becoming smaller posteriorly; ventral scales of thigh smooth; subtibial 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 anteriormost 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 (Figs. 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.

Table 5 **Diagnostic color pattern characters separating various species of *Cnemaspis* from one another following Grismer et al., 2014d.**

	***chanthaburiensis* group**								***siamensis* group**									
	***lineogularis* sp. nov.**	***chanthaburiensis***	***neangthyi***	***laoensis****	***aurantiacopes***	***caudanivea***	***nuicamensis***	***tucdupensis***	***phangngaensis* sp. nov.**	***thachanaensis* sp. nov.**	***siamensis***	***huaseesom***	***chanardi***	***omari***	***roticanai***	***punctatonuchalis***	***vandeventeri***	***kamolnorranathi****
Dorsal color pattern sexually dimorphic	yes	no	no	/	yes	no	no	no	yes	yes	no	yes	no	no	yes	yes	no	no
Ventral pattern sexually dimorphic	yes	yes	no	/	yes	no	no	no	yes	yes	yes	yes	yes	/	yes	yes	yes	/
Head yellow	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no
Reddish blotches on head and body	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Dense yellow reticulum on occiput and side of neck	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on occiput and nape	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on shoulder	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Dual ocelli on shoulder	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Ocelli on brachium and side of neck	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	yes	no	no
Thin, white, nuchal loop	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Large, black round spots on nape and anterior of body	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no
Thin yellow reticulum on side of neck	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Yellowish, prescapular crescent	no	no	no	no	no	no	no	no	yes?	no	no	no	yes	yes	yes	no	yes	var
Forelimbs yellow	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no
Hind limbs yellow	no	no	no	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no
Reddish blotches or bands on limbs	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Forearms and forelegs orange	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no	no
Dorsal ground color magenta	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no

(*continued on next page*)

Table 5 (*continued*)

	chanthaburiensis group								*siamensis* group									
	lineogulari sp. nov.	*chanthaburiensis*	*neangthyi*	*laoensis**	*aurantiacopes*	*caudanivea*	*nuicamensis*	*tucdupensis*	*phangngaensis* sp. nov.	*thachanaensis* sp. nov.	*siamensis*	*huaseesom*	*chanardi*	*omari*	*roticanai*	*punctatonuchalis*	*vandeventeri*	*kamolnorranathi**
Dorsal ground reddis color	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Uniform brown ground color	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Light vertebral	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n
Yellow postscapular	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n	n
Black, squarish, paired, paravertebral dorsal markings	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no
Small, light, round spots on flanks	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Black flanks with distinct yellowish spots	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Yellow or white bars on flanks	no	no	no	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no
Original tail	n	n	n	n	n	n	n	n	n	n	n	va	n	n	n	n	n	n
Original tail	n	n	n	n	ye	n	n	n	n	n	n	n	n	n	n	n	n	n
Regenerated tail	n	n	n	/	n	/	n	n	/	n	n	n	n	n	ye	/	n	n
Regenerated tail	n	n	n	/	n	/	n	n	/	n	n	n	n	n	n	/	n	n
White, dorsal caudal tubercles	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no
Caudal bands	n	ye	ye	ye	ye	ye	ye	ye	ye	ye	ye	ye	ye	ye	ye	ye	ye	ye
Wide black and yellow bands on tail	no	no	no	no	no	yes	no	yes	no	no	no	no	no	no	no	no	no	no
Thin, yellow caudal bands anteriorly	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no	no

(*continued on next page*)

Table 5 (*continued*)

	chanthaburiensis group								*siamensis* group									
	lineogularis sp. nov.	*chanthaburiensis*	*neangthyi*	*laoensis**	*aurantiacopes*	*caudanivea*	*nuicamensis*	*tucdupensis*	*phangngaensis* sp. nov.	*thachanaensis* sp. nov.	*siamensis*	*huaseesom*	*chanardi*	*omari*	*roticanai*	*punctatonuchalis*	*vandeventeri*	*kamolnorranathi**
Posterior portion of original tail white	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no
Posterior portion of original tail black	no	no	no	no	no	no	no	yes	/	no	no	no	no	no	no	no	no	no
Disticnt black and white caudal bands at least posteriorly	no	no	no	no	no	no	no	no	/	no	no	no	no	no	no	no	no	no
Gular region orange	yes	yes	no	/	yes	no	no	yes	no	yes	no	no	no	no	no	/	yes	no
Gular region yellow	no	no	no	/	no	no	no	no	yes	no	yes	yes	yes	yes	yes	/	no	no
Lineate gular markings	yes	no	no	/	yes	no	yes	no	no	yes	yes	no	no	no	no	/	no	no
Throat yellow	no	no	no	/	no	no	no	no	no	no	yes	yes	no	no	no	no	no	no
Throat orange	no	yes	no	/	yes	no	no	yes	no	yes	no	no	no	no	no	yes	no	no
Pectoral region yellow	no	no	no	/	no	no	no	no	no	no	yes	yes	no	no	yes	/	no	no
Pectoral region orange	no	no	no	/	yes	no	no	yes	no	no	no	no	no	no	no	/	var	no
Abdomen yellow	no	no	no	/	no	no	no	no	yes	no	no	no	yes	yes	yes	/	no	no
Abdomen orange	no	yes	no	/	yes	no	no	yes	no	no	no	no	no	no	no	/	yes	no
Ventral surfaces of forelimbs orange	no	no	no	/	yes	no	no	yes	no	no	no	no	no	no	no	/	yes	no
Ventral surfaces of forelimbs yellow	no	no	no	/	no	no	no	no	no	no	no	yes	no	no	no	/	no	no
Ventral surfaces of hind limbs orange	no	no	no	/	yes	no	no	yes	no	no	no	no	no	no	no	/	yes	no
Ventral surfaces of hind limbs yellow	no	no	no	/	no	no	no	no	no	no	no	no	yes	yes	yes	/	no	no
Subcaudal region yellow	no	no	no	/	no	no	no	no	yes	no	no	yes	yes	yes	yes	no	no	no
Subcaudal region orange	no	yes	no	/	no	no	yes	no	no	no	no	no	no	no	no	yes	yes	no
At least posterior half of subcaudal region white	no	no	no	no	no	yes	no	no	no	no	no	no	no	no	no	no	no	no

Notes.

/, data unavailable; *, indicate species that are not included in the molecular analyses.

Table 6 Diagnostic morphological characters separating *C. lineogularis* from species of *Cnemaspis* in the *chanthaburiensis* group.

	***lineogularis* sp. nov.**	***chanthaburiensis***	***neangthyi***	***laoensis****	***aurantiacopes***	***caudanivea***	***nuicamensis***	***tucdupensis***
Maximum SVL	38	42.2	54.0	40.9	58.4	47.2	48.2	51.0
Supralabials	9	8–10	11–13	9	9–11	8,9	7–9	8–10
Infralabials	8	7–10	10–12	7	8–10	7,8	6–7	7–9
Ventral scales keeled (1) or smooth (0)	0	0	0	0	0	0	0	0
No. of precloacal pores	0	6–9	2	/	0	0–2	3–6	0
Precloacal pores continuous (1) or separated (0)	/	1	1	/	/	0	0	/
Precloacal pores elongate (1) or round (0)	/	0,1	0	/	/	0,1	0,1	/
No. of paravertebral tubercles	13	21–25	20–26	22	23–31	20–24	16–21	16–22
Tubercles linearly arranged (1) or more random (0)	1	1	1	0	1	1	1	w,1
Tubercles present (1) or absent (0) on lower flanks	0	1	1	1	1	0	1	1
Lateral caudal furrows present (1) or absent (0)	1	1	1	1	1	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	0	1	1	1	0	0, ant	0, ant	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	0	1	0	1	1	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	0	1	0, ant	0, ant	0
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	0	0	0	0	0	0	0	0
Subcaudals keeled (1) or smooth (0)	0	0	0	0	0	0	0	0
Single median row of keeled subcaudals (1) or smooth (0)	0	0	0	0	0	0	0	0
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	1	0, post, w	1	w	1	0,w	1	w

(*continued on next page*)

Table 6 (*continued*)

	***lineogularis* sp. nov.**	***chanthaburiensis***	***neangthyi***	***laoensis****	***aurantiacopes***	***caudanivea***	***nuicamensis***	***tucdupensis***
No. of postcloacal tubercles in males	1	1–3	1	2,3	1,2	1,2	2–4	0–3
Enlarged femoral scales present (1) or absent (0)	1	0	0	0	0	0	0	0
Shield–like subtibial scales present (1) or absent (0)	0	0	0	0	0	1	0	0
Subtibial scales keeled (1) or smooth (0)	0	0,1	1	1	1	0,w	0	0
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0	0	0	1	0,w	0	1
No. of 4th toe lamellae	27–29	22–29	22–25	29	27–31	23–30	27–33	26–32
Sample size ($n =$)	3	8	5	1	17	9	10	11

Notes.

w, weak; ant, anterior; post, posterior; *, species that are not included in the molecular analyses; /, data unavailable or absent.

Character abbreviations follow those of *Grismer et al. (2014d)*.

Figure 6 (A) habitat and (B) microhabitat of *Cnemaspis lineogularis* sp. nov.

Etymology. The specific epithet *lineogularis* is derived from the Latin adjective *linues* 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 (Figs. 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 (Fig. 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 somroiyot* with which it is hypothesized to be syntopic with. This is a commonly observed pattern among syntopic pairs 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 and 6 for additional comparisons). *Cnemaspis lineogularis* sp. nov. differs from *C. chanataburiensis*, *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. loaensis*, *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. loaensis*, *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. nuicamensies* 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 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, Mueang Phangnga District, Phangnga Province, Thailand (8.442344°N, 98.514869°E; 12 m a.s.l.), 26 July 2016, by PLW, LLG, CA, MC, MSG, MLM.

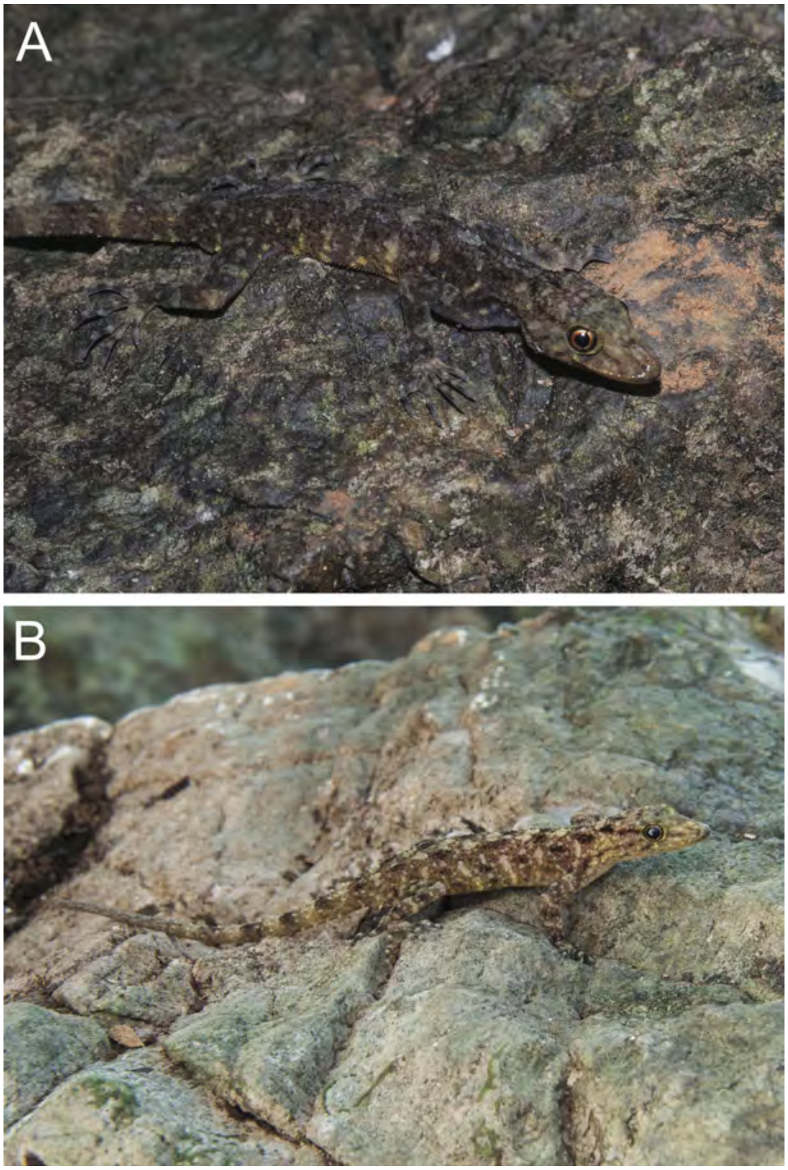

Figure 7 (A) adult male holotype BYU 62538 and (B) female paratype BYU 62537 of *Cnemaspis phangngaensis* sp. nov.

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;

Figure 8 **Ventral coloration and sexual dichromatism of *Cnemaspis phangngaensis* sp. nov.** (A) male holotype BYU 62538 and (B) female paratype BYU 62537.

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 (Tables 5–7).

Figure 9 **Dorsal coloration of the type series of *Cnemaspis phangngaensis* sp. nov.** (A) male holotype BYU 62538 and (B) female paratype BYU 62537.

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 dorsoposteriorly; 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, 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; subtibial scales keeled, 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, 29 (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; 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 darker 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

Table 7 **Mensural and meristic character states for the type series of *Cnemaspis phangngaensis* sp. nov.** All measurements are taken in millimeters and the abbreviations are defined in the materials and methods.

	BYU 62538 holotype	**BYU 62537 paratype**
Supralabials	10	10
Infralabials	10	10
Ventral scales keeled (1) or smooth (0)	1	1
No. of precloacal pores	4	0
Precloacal pores continuous (1) or separated (0)	1	/
Precloacal pores elongate (1) or round (0)	0	/
No. of paravertebral tubercles	22	22
Tubercles linearly arranged (1) or more random (0)	1	1
Tubercles present (1) or absent (0) on lower flanks	0	0
Lateral caudal furrows present (1) or absent (0)	1	1
Caudal tubercles in lateral furrow (1) or not (0)	0	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	1	1
Subcaudals keeled (1) or smooth (0)	1	1
Single median row of keeled subcaudals (1) or smooth (0)	1	1
Caudal tubercles encircle tail (1) or not (0)	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	0
No. of postcloacal tubercles in males	2	/
Enlarged femoral scales present (1) or absent (0)	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0
Subtibial scales keeled (1) or smooth (0)	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	0
No. of 4th toe lamellae	29	30
SVL	42	41
TL	23b	44
TW	3.3	3.2
FL	6.37	6.6
TBL	8.26	8.23
AG	19.28	17.6
HL	11.6	11.1
HW	6.79	6.56
HD	4.1	4.1
ED	2.4	2.4
EE	3.1	3.1
ES	5.17	4.86
EN	3.9	4.2
IO	2.6	2.9

(*continued on next page*)

Table 7 (*continued*)

	BYU 62538 holotype	BYU 62537 paratype
EL	1	0.99
IN	2.85	2.75
Sex	m	f

Notes.
m, male; f, female; /, data unavailable or absent; b, broken.

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 m above the limestone forest floor adjacent to the nearby karst formation. Individuals were also observed active during the day, but avoided being caprtured be 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. roticani* (Fig. 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 8). *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 paraveterbral 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 *roticani* by having more supralabial scales (10 vs. 8,9 and 8,9, respectively). *C. phangngaensis* sp. nov. differs from *C. chanardi* by having fewer precloacal pores (4 vs. 6–8). *Cnemaspis phangngaensis* sp. nov. differs from *C. roticani* 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

Table 8 Diagnostic morphological characters separating species of *Cnemaspis* from one another in the *siamensis* group.

	phangngaensis sp. nov.	*thachanaensis* sp. nov.	*siamensis*	*huaseesom*	*chanardi*	*omari*	*roticanai*	*punctatonuchalis*	*vandeventeri*	*kamolnorranathi**
Maximum SVL	42	39	39.7	43.5	40.1	41.3	47.0	49.6	44.7	37.8
Supralabials	10	10,11	8,9	7–10	7–10	8,9	8,9	8	8,9	8,9
Infralabials	10	9–11	6–8	6–9	6–8	7,8	7,8	7,8	7–9	7,8
Ventral scales keeled (1) or smooth (0)	1	1	1	0	1	1	1	0	1	0,w
No. of precloacal pores	4	0	0	5–8	6–8	4	3–6	0	4	7
Precloacal pores continuous (1) or separated (0)	1	/	/	1	0	0	0	/	0	1
Precloacal pores elongate (1) or round (0)	0	/	/	0	0	0	0	/	0	1
No. of paravertebral tubercles	22	15–19	19–25	18–24	20–30	22–29	25–27	24–27	25–29	19–24
Tubercles linearly arranged (1) or more random (0)	1	1	0	w,0	0	w,0	0	w	0	w
Tubercles present (1) or absent (0) on lower flanks	0	1	1	1	1	w,1	1	1	0	1
Lateral caudal furrows present (1) or absent (0)	1	1	1	1	1	1	1	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	0	0	0	1	0	0	1	0	0	1
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	1	0	0	0	0	0	1	0	0
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	0	1	1	0	ant	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	1	1	0	0	0	0	0	0	0	0
Subcaudals keeled (1) or smooth (0)	1	1	1	0	1	1	1	0	1	1
Single median row of keeled subcaudals (1) or smooth (0)	1	1	0	0	0	0	0	0	w	w
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	0	1	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	0	1	0	1	0	w	1	1	w

(*continued on next page*)

Table 8 (*continued*)

	***phangngaensis* sp. nov.**	***thachanaensis* sp. nov.**	***siamensis***	***huaseesom***	***chanardi***	***omari***	***roticanai***	***punctatonuchalis***	***vandeventeri***	***kamolnorranathi****
No. of postcloacal tubercles in males	2	0	1,2	1,2	1	1	1,2	1–3	1–3	1,2
Enlarged femoral scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0
Shield–like subtibial scales present (1) or absent (0)	0	0	0	0	0	0	0	0	0	0
Subtibial scales keeled (1) or smooth (0)	1	1	1	0	1	1	1	0	1	0,1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	0	1	0	0	0	0	0	0	0	0
No. of 4th toe lamellae	29	24	24–26	21–31	25–30	25–28	26–29	29–31	24–28	24–28
Sample size	2	6	12	5	25	4	8	5	3	3

Notes.

w, weak; ant, anterior; post, posterior; *, species that are not included in the molecular analyses; /, data unavailable or absent.
Character abbreviations follow that of *Grismer et al. (2014d)*.

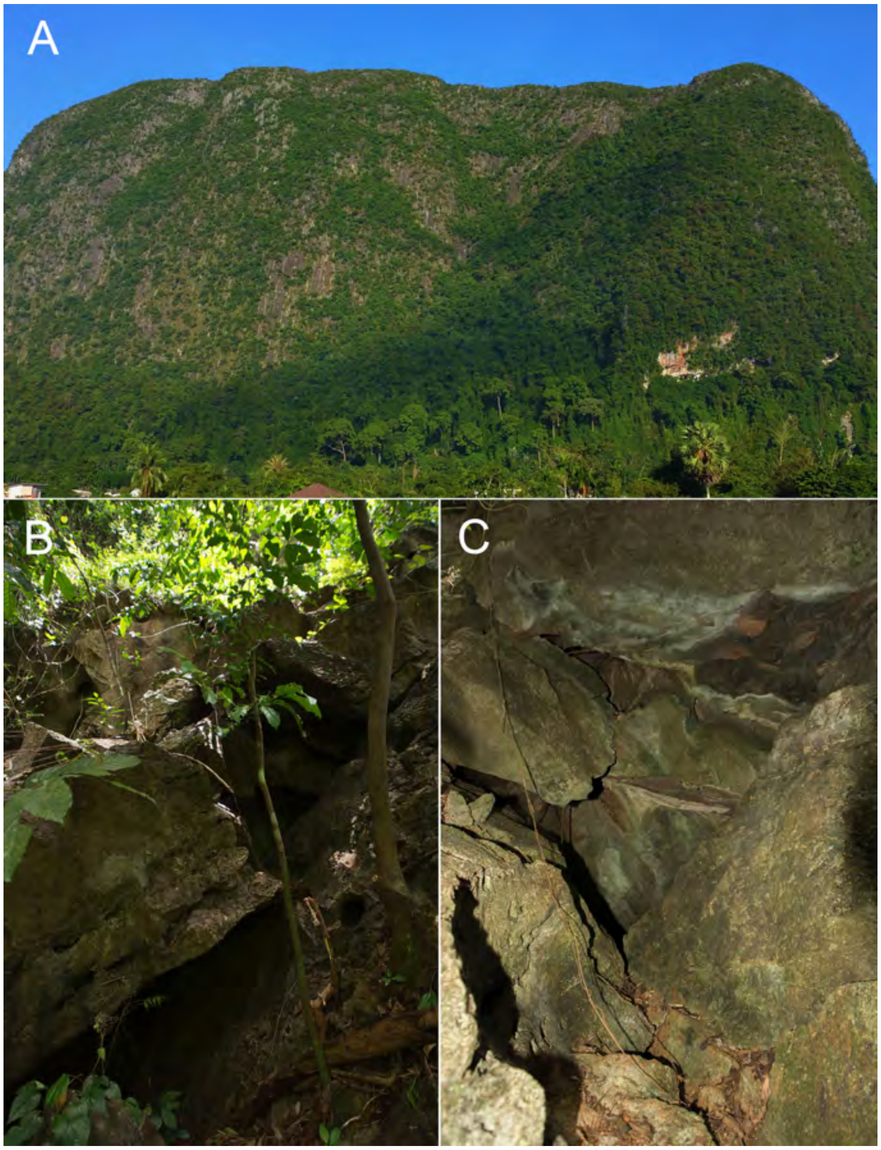

Figure 10 (A) general karst and limestone forest near the type locality of *Cnemaspis phangngaensis* sp. nov. (B) karst microhabitat where *C. phangngaensis* occurs.

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 (Tables 5 and 8).

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, Surat Thani Province, 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 9).

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; frontalrostralis sulcus shallow; canthus rostralis nearly absent, smoothly rounded; eye large (ED/HL 0.22); extra-brillar, 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 dorsoposteriorly; 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; enlargerd

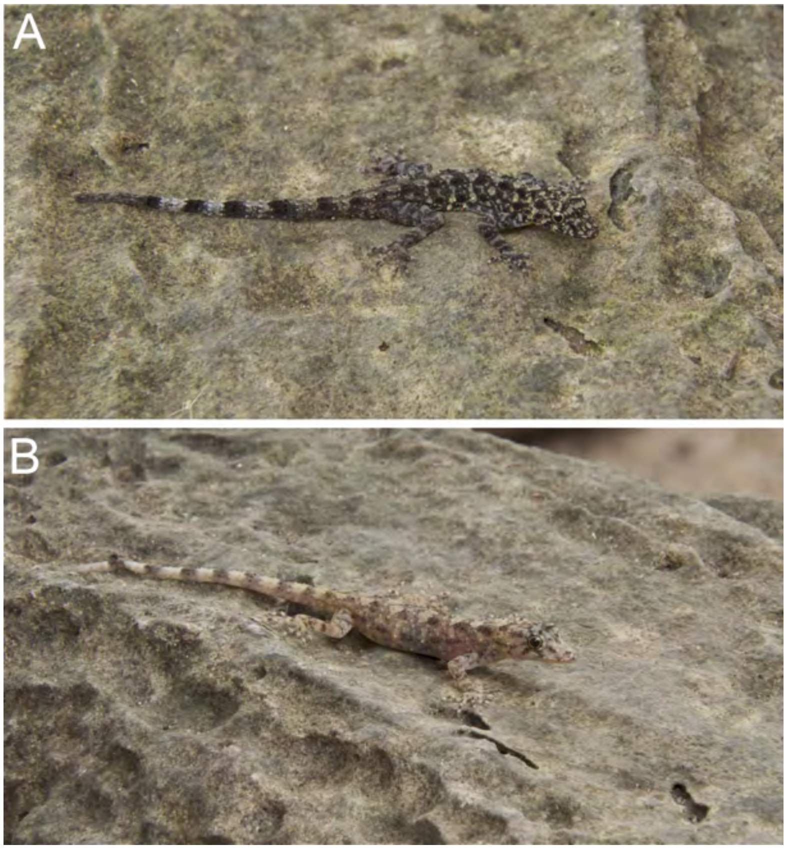

Figure 11 Coloration of *Cnemaspis thachanaensis* sp. nov. (A) male holotype BYU 62544 and (B) BYU 62542 female paratype.

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; subtibial 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

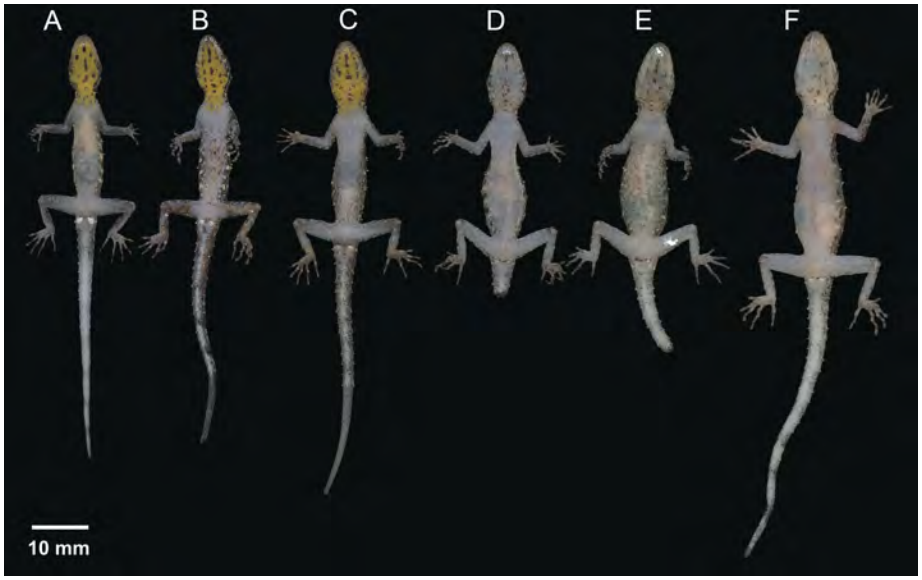

Figure 12 Ventral coloration and sexual dichromatism of the type series of *Cnemaspis thachanaensis* sp. nov., males: (A) BYU 62543, (B) BYU 62544 (holotype), (C) ZMKU R 00731, females: (D) ZMKU R 00729, (E) ZMKU R 00730, (F) BYU 62542.

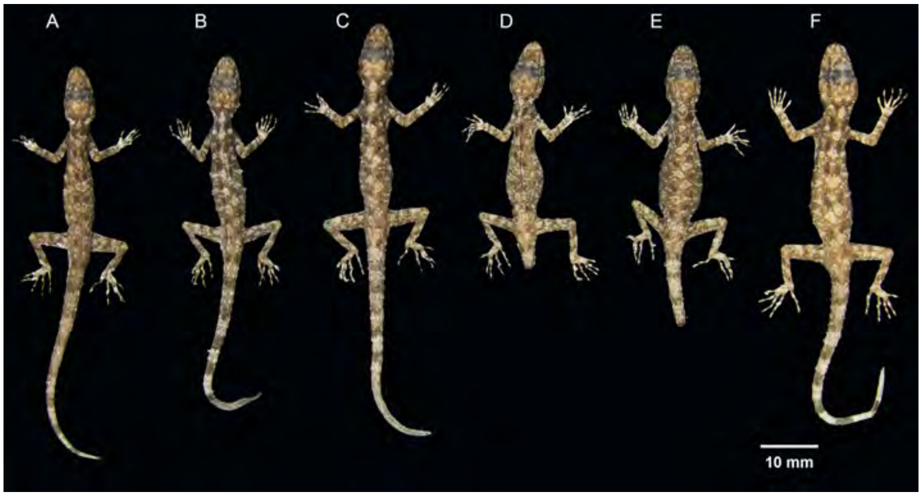

Figure 13 Dorsal coloration of the type series of *Cnemaspis thachanaensis* sp. nov., males: (A) BYU 62543, (B) BYU 62544 (holotype), (C) ZMKU R 00731, females: (D) ZMKU R 00729, (E) ZMKU R 00730, (F) BYU 62542.

Table 9 **Menusural and meristic character state for the type series of *Cnemaspis thachanaensis* sp. nov.** All measurements are taken in millimeters and the abbreviations are defined in the materials and the methods.

	BYU 62544 holotype	ZMKU R 00731 paratype	BYU 62543 paratype	BYU 62542 paratype	ZMKU R 00729 paratype	ZMKU R 00730 paratype
Supralabials	10	11	10	10	10	10
Infralabials	10	11	10	10	9	9
Ventral scales keeled (1) or smooth (0)	1	1	1	1	1	1
No. of precloacal pores	0	0	0	/	/	/
Precloacal pores continuous (1) or separated (0)	/	/	/	/	/	/
Precloacal pores elongate (1) or round (0)	/	/	/	/	/	/
No. of paravertebral tubercles	15	19	15	17	15	16
Tubercles linearly arranged (1) or more random (0)	1	1	1	1	1	1
Tubercles present (1) or absent (0) on lower flanks	1	1	0	1	1	1
Lateral caudal furrows present (1) or absent (0)	1	1	1	1	1	1
Caudal tubercles in lateral furrow (1) or not (0)	0	0	0	0	0	0
Ventrolateral caudal tubercles anteriorly (1) or not (0)	1	1	1	1	1	1
Lateral caudal tubercle row present (1) or absent (0)	1	1	1	1	1	1
Caudal tubercles restricted to a single paravertebral row on each side (1) or not (0)	1	1	1	1	1	1
Subcaudals keeled (1) or smooth (0)	1	1	1	1	1	1
Single median row of keeled subcaudals (1) or smooth (0)	1	1	1	1	1	1
Caudal tubercles encircle tail (1) or not (0)	0	0	0	0	0	0
Enlarged median subcaudal scale row (1) or not (0)	0	0	0	0	0	0
No. of postcloacal tubercles in males	0	0	0	/	/	/
Enlarged femoral scales present (1) or absent (0)	1	1	1	0	0	0
Shield-like subtibial scales present (1) or absent (0)	0	0	0	0	0	0
Subtibial scales keeled (1) or smooth (0)	1	1	1	1	1	1
Enlarged submetatarsal scales on 1st toe (1) or not (0)	1	1	1	1	1	1
No. of 4th toe lamellae	24	23	24	25	23	23
SVL	33	37	34	39	35	35
TL	41	44r	43	46	6b	16b
TW	3.6	3.91	3.32	4	3.4	3.7
FL	5.97	5.68	5.39	5.83	5	5.9
TBL	6.8	7.3	6.19	7.14	6.9	6.5
AG	14.55	16	13.1	17.72	14.49	15.6
HL	9.79	10.3	9.74	11.49	9.37	9.8
HW	5.55	6.27	5.3	6.6	5.45	5.7
HD	3.64	4.1	3.8	4.32	3.9	3.8
ED	2.21	2.4	2	2.36	2.04	1.9
EE	2.85	2.79	2.6	2.79	2.67	3
ES	4.4	4	3.6	4.29	4.29	4.57
EN	2.5	1.18	2.6	3.1	2.79	3.7
IO	2.58	2.97	2.3	3.29	3.1	2.8

(*continued on next page*)

Table 9 (*continued*)

	BYU 62544 holotype	**ZMKU R 00731 paratype**	**BYU 62543 paratype**	**BYU 62542 paratype**	**ZMKU R 00729 paratype**	**ZMKU R 00730 paratype**
EL	0.76	0.82	0.67	1	0.71	0.75
IN	2.1	2.8	2.4	2.2	2.29	2.2
Sex	m	m	m	f	f	f

Notes.
m, Male; f, Female; /, Data unavailable or absent; b, Broken; r, regenerated.

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 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 (Figs. 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 (Fig. 12). Select body measurements and additional variation in squamation are presented in Table 9.

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

Distribution. This species is only know 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 (Fig. 14).

Figure 14 (A) karst and limestone forest near the type locality of *Cnemaspis thachanaensis* sp. nov. (B) karst microhabitat of *Cnemaspis thachanaensis* sp. nov.

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 know to sleep on vegetation at night (*Grismer et al., 2010*; *Grismer et al., 2014d*, P Wood, pers. obs., 2016). 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. kamolnorranthi* and place it in *C. thachanaensis* sp. nov. 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. kamolnorranthi* 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* (Fig. 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 caudal tubercles restricted to a single paravertebral row on each side; having a single median row of keeled subcaudal scales; lacking a single enlarged subcaudal scale row; lacking postcloaclal 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. 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 (Tables 5 and 8).

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 roticani* 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 within 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)* and

Grismer et al. (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* (Fig. 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) and Grismer et al. (2014d), however the hypothesis that it may be more closely related to the group with the prescapular crescent is not supported by our phylogenetic hypothesis and could represent an instance of convergent evolution of the prescapular crescent. This in 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 (P Wood et al., 2016, unpublished data).

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 & Voris, 2006; Woodruff, 2010). Further investigation into the biogeographic patterns for *Cnemaspis* are in preparation (P Wood et al., 2016, unpublished data), and with the continued discovery of new species of *Cnemasapis* 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.

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Perry Lee Wood Jr conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- L. Lee Grismer conceived and designed the experiments, performed the experiments, wrote the paper, reviewed drafts of the paper.
- Anchalee Aowphol, César A. Aguilar, Micheal Cota, Marta S. Grismer and Matthew L. Murdoch performed the experiments, reviewed drafts of the paper.
- Jack W. Sites Jr contributed reagents/materials/analysis tools, reviewed drafts of the paper.

Animal Ethics

The following information was supplied relating to ethical approvals (i.e., approving body and any reference numbers):

Brigham Young University's Institutional Animal Care and Use Committee (IACUC) has approved the animal use protocol for this study (protocol # 160401).

Field Study Permissions

The following information was supplied relating to field study approvals (i.e., approving body and any reference numbers):

We received a collecting permit from the National Research Council Thailand (NRCT) to PLW and AA (No. 0002/7606).

DNA Deposition

The following information was supplied regarding the deposition of DNA sequences:

GenBank accession numbers KY091231–KY091244.

New Species Registration

The following information was supplied regarding the registration of a newly described species:

Publication ID:
urn:lsid:zoobank.org:author:E2AF9554-5062-48C6-84AA-FA50D720DEF7

Family: Gekkonidae, Genus: Cnemaspis, Species: *lineogularis*
urn:lsid:zoobank.org:act:8E3B21A4-93BF-4D08-B8D1-0A3EEF6BE44F

Family: Gekkonidae, Genus: Cnemaspis, Species: *phangngaensis*
urn:lsid:zoobank.org:act:6053C709-A409-4F65-B15C-8C647D7EDF1C

Family: Gekkonidae, Genus: Cnemaspis, Species: *thachanaensis*
urn:lsid:zoobank.org:act:3581C94E-6170-4F42-9159-E2B564B576F1

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Chapter 5: A Geologically-driven Rapid Radiation on the Sunda Shelf

A Geologically-driven Rapid Radiation on the Sunda Shelf

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Abstract

The geological complexity and the understudied biodiversity hot spot of Southeast Asia provides outstanding options for studying patterns and processes of diversification and evolution. Here we provide the most complete phylogeny of rock geckos based on a genomic dataset, coupled with well informed paleogeographic reconstructions, to generate hypotheses about the tempo and modes of diversification in this species-rich clade on the Sunda Shelf. We demonstrate that rock geckos had a significant rate shift in speciation correlating to dynamic geological episodes on the Sunda Shelf. We show that the temporal radiation of rock geckos coincides with the temporal diversification of other terrestrial vertebrates across Sundaland.

Introduction

Southeast Asia (SEA) is a complex, intriguing and vastly understudied region of the world[1]. The continental and insular landmasses of SEA comprise 4% of the earth's landmasses, yet contain 20–25% of the earth's biodiversity, making the Sundaic region (Sundaland) one of the world's biodiversity hotspots[2–10]. Sundaland is comprised of the Sunda Shelf and the Thai-Malay Peninsula, the large islands of Borneo, Java, Sumatra, and many smaller archipelagos (Figure S1). One of the most prominent features of Sundaland is the Sunda Shelf, a vast area of continental shelf composed of the Sunda Plains (currently submerged beneath the South China Sea), and the surrounding land-positive fringe regions of the Thai-Malay Peninsula, Sumatra, Borneo, and Java. Cyclical climatic and sea level fluctuations over the last 2.4 million years have facilitated range expansion and contraction/isolation of biotas[11,12], especially in the cooler montane rainforests[13,14], resulting in the formation of interglacial upland refugia[15,16]. Sea level fluctuations have also driven the formation and isolation of island archipelagos[8,17,18]. Due to this long and varied geological history, the majority of the biota of this vast landscape exists in a refugial state[2,4,7,12,19].

The older geological history of SEA has been impacted and shaped by dynamic Cenozoic tectonic forces[20,21], but the combined influence of Cenozoic geological processes and Quaternary climatic changes as drivers of the evolutionary history of the SEA biota is less clear and is often over-looked[19,22,23]. Recent advances in Cenozoic paleogeographic reconstructions of the Sunda Shelf[20,21,24] provide an excellent framework to test *a priori* hypotheses about the temporal/spatial drivers of diversification throughout this region.

Geckos of the genus *Cnemaspis* comprise a species-rich clade (55 species[25]) that is widely distributed throughout Sundaland (Figure S1), and study of this group may provide general insights into some of the diversification patterns throughout this region. Recent molecular phylogenetic studies based on a small number of mitochondrial and nuclear genes recover a well-supported monophyletic genus and resolve "recent history" relationships within some groups, but they lack sufficient signal to resolve the deeper nodes in this clade[25–27]. The distribution of *Cnemaspis* throughout Sundaland, its well-supported monophyly, low vagility, and unresolved deep relationships, make this clade a model system to test multiple nested biogeographic hypotheses.

Here we use a genomic dataset to construct a time-calibrated *Cnemaspis* phylogeny, and address the following questions: (1) are the unresolved polytomies in the genus "hard" or "soft"? (2) is there evidence for gradual or punctuated increases in the accumulation of species in *Cnemaspis*? And (3) do dynamic geological events across the Sunda Shelf at different time scales coincide with patterns of lineage diversification in *Cnemaspis*?

Results

The maximum likelihood (ML) analyses for the concatenated datasets (514, 440, and 105 loci) composed of the 50p, 60p, and 75p all recover *Cnemaspis* as monophyletic. Nodal support varied between the different ML analyses (Figure S2). For example, the 50p dataset had a longer alignment (267,912 bp/514 loci) compared to the 60p (231,027 bp/440 loci), and 75p (57,940bp/105 loci), but had missing individuals per locus compared to the other two datasets. The 50p dataset recovered a topology with higher support values than the 60p and 75p datasets (Figure S2), which is congruent with the results of other studies[28], so we present these results here, which generally recovers a topology concordant with similar levels of nodal support as the 60p and 75p datasets and analyses. A few well-supported nodes recovered in the BI analyses are not supported by the ML analyses, and other nodes well-supported by ML are not strongly supported in our BI trees (Figure S3A).

The concatenated and species tree analyses from A-II and SVDQ recover similar topologies with respect to some other well-supported deeper nodes, although some weakly supported relationships were recovered in the species tree analyses (Figure S3A,B, S4). Further, some interrelationships within the more nested (younger) clades are incongruent between the two analyses. Three samples (*C. affinis*, *C. hangus*, and *C. narathiawatensis*) were only represented by a single gene and their phylogenetic placement was ambiguous in the SVDQ analysis, therefore they were removed, but were included in the A-II analysis which recovered the same phylogenetic placement of these three species as the previous analyses (Figure S5). The quartets generated from the A-II analyses showed that 68.42% of all the quartets in the gene trees were also recovered in the species tree.

We recovered the Ca Mau clade as sister to all other *Cnemaspis* groups, which is concordant with previous studies[25,26], but the remaining relationships differ from previous studies[25,26]. We recover the Southern Sunda clade as the sister group to the remaining species of *Cnemaspis*, whereas previous studies recovered the Pattani clade as the sister group to all other *Cnemaspis* groups excluding the Ca Mau clade (Figure S3). However these deeper internodes in the previous studies were characterized by short branch lengths with no significant support. Here we resolved the deeper phylogenetic relationships in the concatenated analyses with well-supported nodes, whereas our other analyses recovered the same topology albeit with lower support values for the deeper nodes (i.e., PP=0.64, BS=70, and SVDB=70 for the deepest node and PP=0.92, BS=80, and SVDB=51 for the other, Figures S4A,B). To further investigate this issue we estimated the posterior probabilities at these problematic nodes and calculated the percentages of the quartets in the gene trees that agree with the respective branches ("quartet support") on these short internal nodes in the backbone of the *Cnemaspis* tree (Figure S4).

To further investigate these two problematic nodes we estimated the posterior at these problematic nodes and calculated the percentages of the quartets in the gene trees that agree with the respective branches ("quartet support") on these short internal nodes in the backbone of the *Cnemaspis* tree (Figure S4).

Our divergence analyses with the fossil and the root height calibrations estimated that crown Gekkota diverged from its common ancestor approximately 105.9 MYA, which is well within the estimates of previous analyses[29,30]. The common ancestor of the Ca Mau clade and the ancestor to all other *Cnemaspis* species diverged during the mid-Paleocene approximately 61.1 MYA (Figure 1A, S5). Within this "all other" clade, the Southern Sunda clade diverged from the ancestor of the remaining species ∼41.9 MYA (Figure 1A, S5). The former ancestor of the "remaining species" clade then diverged into the Malaysian Peninsula clade, while the ancestor to the Pattani and the Thai Peninsula/Indochina clade diverged approximately 39.2 MYA, and the ancestor to the (Pattani

+ Thai Peninsula/Indochina) clade diverged 37.3 MYA. In summary, all major clades (Southern Sunda(Malay Peninsula(Pattani + Thai Peninsula/Indochina))), diverged between 33.4–41.9 MYA (41.9/39.2/37.3/33.4 MYA, respectively).

BAMM[31] diversification analyses show a relatively high early average speciation rate (λ) for all *Cnemaspis*, increasing from 2 to 5.9 species/my (Figure S6A); exclusion of the Ca Mau clade increases the average speciation rate slighty from 5.9 to 6.37 species/my (Figure S6B). There was a positive extinction rate of μ=0.41 species/my for all *Cnemaspis*, and a slight increase in extinction around 60–40 MYA (Figure S6C). Exclusion of the Ca Mau clade increases this extinction rate almost imperceptibly from 0.41 to 0.42, so extinctions remain relatively constant through time (Figure S6D). We found strong evidence for a single rate shift in speciation along the branch leading to the species-rich *Cnemaspis* clade that is the sister group to the Ca Mau clade, with the core shift probability of 0.70 (Figure 1, S7). We then calculated the Bayes Factor (BF) by incorporating the rate shift at the branch subtending this large clade under the prior alone, and found strong evidence (BF = 40.9, based on Kass and Raftery 1995[32]) for a rapid radiation "Out of the Sunda Shelf" (OSS, Figure 1).

To further investigate the OSS idea, we estimated a LTT plot to test for a rapid radiation in *Cnemaspis*, and estimated net diversification rates in Geiger. The LTT plot showed a significant departure from the null CR model of speciation, with the greatest accumulation of species during the past $\sim$5–20 MYA and the with the OSS radiation starting much earlier (Figure S8A). This result has a significantly negative γ-statistic (γ= -1.847611; *p* = 0.04) based on the 20,000 simulated pure-birth constant rate trees for the MCCR test (Figure S8B); this is evidence of a significant increase in diversification rates (rapid radiation).

The BioGeoBears ancestral biogeographical range reconstruction analysis selected the DIVALIKE+J model as the best fit to our data (Table S2), and recovers an ancestral node for all *Cnemaspis* composed of (Ca Mau + Borneo + Peninsular Malaysia); the proto-Sunda Shelf. This analysis also recovered two vicariant and twelve jump-dispersal founder events. The ancestral node of all *Cnemaspis* represents a vicariant event that separated the Ca Mau area and Peninsular Malaysia+Borneo 61.1 MYA (Figure 1). Directly following the separation of the proto-Sunda Shelf, another vicariant event split the Borneo and Peninsular Malaysia highland areas (41.9 MYA), giving rise to the ancestral range for the Southern Sunda clade and the ancestor to the Peninsular Malaysia area. Within the Southern Sunda clade there are five jump-dispersal or founder events, the details of which will be the focus of another paper and not discussed here. The Peninsular Malaysia area has a founder event/jump dispersal event to Central Indochina 39.2 MYA, giving rise to the Borneo clade (Figure 1).

Discussion. Previous phylogenetic hypotheses of *Cnemaspis*[25,26] had unresolved short internodes, which obscured the relationships of the larger clades and limited biogeographic inferences pertaining to temporal patterns of diversification across the Sunda Shelf. Here we resolve the deeper nodes of the phylogeny with moderate to strong support for the for the species tree analyses (the concatenated dataset, Figure S3). Previous studies[25,26] recovered four major clades: Ca Mau, Pattani, Southern Sunda, and Northern Sunda, and in both the species tree and the concatenated analyses, we recovered the Ca Mau, Pattani, and the Southern Sunda clades, but also a paraphyletic Northern Sunda group *sensu* Grismer et al.[26] (Figure S3A,B). Here we designate the paraphyletic Northern Sunda group into two new clades, the Malaysian Peninsula and the Thai Peninsula/Indochina clades, respectively (Figure S3A,B).

The resolution of these short internal branches provide evidence that this is not a "hard" polytomy, but a "soft" polytomy that is evident of a rapid diversification within Cnemaspis "OSS". However, the concatenated analyses can be misleading because they ignore the individual gene histories and can even provide strong support for the wrong tree[33]. In comparison our species tree analyses recovered identical deeper relationships of *Cnemaspis* with moderate support for short internal branches. The quartet approach for those two branches indicate that a small percentage of the genetree quartets are congruent with the branches in the species tree (Figure S3A,B); this is evidence of high levels of incomplete lineage sorting (ILS), which is expected during times of rapid lineage accumulation[34,35]. ILS topologies (evidence of ancient lineage accumulations associated with short internodes) have been documented in a number of clades, including birds[36], rodents[37], and cichlid fishes[38]. Our LTT plot shows a statistically significant increase in speciation rate in the large *Cnemaspis* clade, consistent with the hypothesis of an accelerated lineage accumulation from $\sim$40 MYA throughout the clades geologically more recent history. In addition, the strong Bayes Factor (40.9) from the BAMM analysis and 70% probability (Figure 1A and S7) recovered a significant rate shift along the lineage leading to the large clade of *Cnemaspis*, which is contemporaneous with the initial increase in rapid lineage accumulation from the MCCRT and visually in the LTT (Figure S8A,B).

The biogeographic analyses suggest that *Cnemaspis* most likely originated on the proto-Sunda Shelf in the Paleocene (Figure 1A) and rapidly radiated during times of significant Eocene geological/vicariant events of Eastern Indochina (Ca Mau clade)[1,5,21,39]. These analyses also suggest that there were two major vicariant events during the early history of *Cnemaspis*; one each during the Paleocene and the late Eocene encompassing the vicariant events of the ancestral proto-Sunda Shelf, followed by the separation of the paleogeographic Peninsula Malaysian and Bornean highlands[5,21] (Figure 1C). All major clades of *Cnemaspis* except for the Ca Mau clade, then diversified rapidly between 41.9–37 MYA during the separation of the Malaysian and the Bornean highlands. The temporal diversification of *Cnemapsis* is not a novel event and many other flora and fauna including the banana family (Musaceae)[40], megophryid and rhacophorid frogs[41,42], dragon lizards[43], geckos[44,47], and the evolution of volant vertebrates in Southeast Asia[45], have revealed similar initial diversification conclusions and are often attributed to the collision of the Indian plate with Eurasia.

The initial diversification of *Cnemaspis* starts during the Paleocene, with a rapid diversification during the Eocene and the LTT plots identifies that there is significant increases in lineage accumulation during the more recent history (Miocene-Eocene). The Oligocene–Miocene diversification ($\sim$20–30 My) pattern shown in the LTT plots of *Cnemaspis* has also been documented in a number of other squamate reptiles, including agamid (Wood et al. in prep), gekkonids[46,47], and homolopsid snakes[48]. Other groups, including some plants in the custard apple family and palms[49,50], spiny frogs [42,51], ranid frogs[52] and marine gastropods[53], birds[54] also experienced increased diversification rates in SEA during the Oligocene-Miocene transition. Some hypotheses for these shared common patterns are contentious owing to competing hypotheses about the extent of connectivity of the Sunda Shelf islands[5], or its division by marine transgressions[10]. However, recent evidence favors the marine transgressions[10,55,56], though the extent, location and frequency of these are still unclear[48]. The possibility that *Cnemapsis* has undergone multiple rapid radiations is a realistic possibility with the BAMM analysis recovering an older rate shift in speciation and the LTT plots with a rapid increase in speciation during the Oligocene-Miocene transition and provides a competing hypothesis for the the rapid radiation of *Cnemaspis*.

This study provides a well-resolved phylogeny for nearly all species of Sundaland *Cnemaspis* and presents the phylogeny in a temporal perspective coupled with a rapid radiation corresponding to major geological events from the Paleocene to the Miocene. *Cnemaspis* most likely originated in the Paleocene and had initial rate shifts of rapid lineage accumulation starting in the Eocene with additional radiations in the more recent history during the Oligocene-Miocene transition. The number of dynamic geological events in the Paleocene and Miocene across the Sunda Shelf region provided dispersal corridors at different time intervals facilitating the dispersal and rapid speciation of *Cnemaspis*. Further generating alternative hypotheses pertaining to the patterns and processes of speciation and evolution across the Sunda Shelf.

Methods

Data collection. Complete sampling of all of the species of *Cnemaspis* is difficult based on their large distribution and many of the species are micro endemics with no available genetic material. We sampled one individual per species for almost all putative species of *Cnemaspis*, including two undescribed species (n=53), but not including *C. dringi*, *C. laoensis*, *C. sundagekko*, and *C. kamolnorranathi*, for which genetic samples are unavailable. We included 21 outgroup taxa based on[57] and a list of voucher specimens used in this study is presented in (Table S1).

Targeted sequence capture and UCE data collection. Targeted sequence capture data were collected using a dataset of RNA probes specific for iguanian lizards[58]. The commercially synthesized custom probes were designed to target 585 loci with 2X tiling (two 120 bp probes per locus) using MYbaits target enrichment kit (MYcroarray Inc., Ann Arbor, MI, USA). These probes targeted 541 ultraconserved elements (UCEs) that were used in the Tetrapods-UCE-5Kv1 probes[59] (describes in detail at http://www.ultraconserved.org), for details about the the probe design and selection see[60]. In addition to the UCEs we added 44 loci from the Squamate Tree of Life project (SToL)[61].

Genomic DNA was extracted from liver or skeletal muscle tissue stored in 95% ethanol using the animal DNA extraction protocol from a Qiagen DNeasy® tissue kit (Valencia, CA, USA). To check the quality of the DNA we ran electrophoreses gels to ensure that the DNA had a high molecular weight. All DNA samples (∼400 ng) that had high molecular weights were then sonicated with a targeted size peak of 400 bp on a Bioruptor Pico (Diagenode Inc.) for seven cycles of sonication for seven seconds then ninety seconds of rest. We then prepared DNA libraries using the Illumina TruSeq Nano DNA library preparation kit. The DNA library samples were then hybridized to the RNA-probes in presence of a blocking mixture composed of forward and reverse compliments of the Illumina TruSeq Nano adapters, with insoines in place of the indices, as well as salmon blocking and Chicken blocking mixtures (Chicken Hybloc, Applied Genetics Lab Inc.) to reduce repetitive DNA binding to beads. Libraries were then incubated with the RNA probes at

65°C for 24 hours. We enriched the post-hybridization libraries using TruSeq adapter primers with Phusion* High-Fidelity DNA Polymerase (New England Biolabs Inc.) for 22 cycles. Following PCR enrichment we cleaned the libraries with AMPure XP beads. Enriched DNA libraries were quantified using qPCR (Applied Biosystems Inc.) with primers targeting five loci mapping to the *Anolis carolinensis* genome. Final libraries were verified using the Agilent Tape-station 2200 (Agilent Technologies). The final sample libraries were pooled in equimolar ratios and sequenced using an Illumina HiSeq2500 at the DNAsc (DNA sequencing center) at Brigham Young University (BYU).

Bioinformatics and data processing. The raw DNA sequence reads were demultiplexed based on unique dual-indexed sequence tags using Casava (Illumina). We pre-processing the raw sequences reads with a custom Rscript (Illumina prep function github: XXXXX) to reformat the sequences names with the proper sequence adapters to make them compatible input files for PHYLUCE[62] and illumiprocessor[63]. We used illumiprocessor v 2.0.7[63] to batch process the demultiplexed sequence reads and trim adapter contamination in preparation for Trimmomatic[64] to remove low-quality reads, adapter sequences and low-quality end reads. We assembled clean reads for each species using Trinity[65] and used the PHYLUCE pipeline[62] to assemble loci across species (TableS1). Multiple sequence alignments were performed for each locus using MAFFT[66] and PHYLUCE[62] was used to assemble loci across species and long ragged-ends were trimmed to reduce missing or incomplete data. Phylogenomic algorithms for both concatenated and species tree approaches provide the highest branch support values when including loci with up to 50% of the missing taxa[28], and excluding all missing data from the dataset might be a problematic guideline for setting a standard of missing data. We assembled three different datasets (50p, 60p, and 75p), whereas each loci per dataset must contain 50%, 60%, and 75% of the taxa respectively. All datasets were assembled using the PHYLUCE[62] pipeline for all down stream analyses.

We obtained targeted sequence capture data from 541 UCE and 44 SToL loci for 71 individuals (Table S1) with three species that were not successful during the hybrid enrichment (*C. affinis*, *C. hangus*, *C. narathiawatensis*) and were removed from downstream analyses. The lack of success for these two samples could be caused from inefficiently during the hybridization step or low sequencing effort[34]. We combined the recombination activating protein 1 (RAG1) from the SToL capture dataset in combination with the RAG1 dataset of Grismer et al. 2014[26], as they are contiguous sequences and allowed us to incorporate the three species that were not successful during the hybrid enrichment, completing a dataset of all inclusive species of *Cnempasis* where genetic material is available (53 of 56). Summary data for the 541 UCE and the 44 SToL loci were calculated using scripts available at https://github.com/dportik/Alignment Assessment[67] (Figure S3A–E). Frequency distributions for proportions of the genomic data are presented on a per locus basis for 69 of the 71 individuals sequenced and we found a positive correlation between the number of informative sites and the alignment length (R^2=0.0854, p< 0.0000, Figure S3F). The final alignments were composed 21 outgroup and 53 ingroup taxa for 514 loci.

Phylogenomic analyses. We inferred phylogenetic relationships within *Cnemaspis* using unpartitioned Maximum Likelihood (ML), Bayesian Inference (BI), and coalescent based species tree methods. All analyses were rooted based on the most distant relative (*Correlophus cilliatus* and *Lialis burtonis*) following Gamble et al.[57], allowing to test for the monophyly of *Cnemaspis* with respect to the other outgroup species. For the concatenated ML analyses we used the IQ-TREE software[68] with the model of molecular evolution set to GTR+Γ and nodal support estimated with 1000 bootstrap pseudoreplicates via the ultrafast bootstrap approximation algorithm[69]. The BI analyses were estimated using ExaBayes[70] based on four runs for 100,000 generations each, after which convergence was assessed using the *postProcParam* command; we assumed stationarity if ESS values were $\geq$200, and computed a consensus tree using the *consense* command in ExaBayes. Nodal support for the concatenated analysis are posterior probabilities (PP) and IQ-TREE rapid bootstraps (BS), respectively, and nodes with (PP) and IQ-TREE rapid bootstraps (BS), respectively, and nodes with PP$\geq$0.95 and BS$\geq$90 are considered to be well-supported[69,71,72].

We estimated a species tree from 514 UCE/sequence capture loci by first estimating gene trees for each locus using a search of 200 iterations for the best tree, and the resulting gene trees with the highest respective likelihood score were used as the input trees for downstream species tree analyses in ASTRAL-II (A-II)[73]. In addition to the initial branch support values provided from the species tree, which is considered to be more reliable[74], we estimated nodal support using 100 bootstrap replicates for each gene generated in RAxML v7.5.5[75], and then used the default site-only resampling[76] in A-II[73], which is based on the quadripartitions and not the more often used branch bipartitions[74]. To further investigate specific nodes/branches in the deeper nodes for the *Cnemaspis* nodes we calculated quartet support values in A-II[73]. The quartet support values are the posterior estimate at a given branch where each genetree quartet agrees with the respective branch.

To estimate a species tree without first estimating gene trees, we used the program SVDQuartets (SVDQ)[77], as implemented in a test version of Paup*v4.0a150[78]. This algorithm randomly samples quartets using a coalescent model and and a quartet amalgamation heuristic to generate a species tree, and has proven useful and accurate for estimating species trees from complete alignments of large genomic datasets[79]. We evaluated all possible quartet scores from the entire alignment using the multispecies coalescent tree model, and performed 100 bootstrap replicates to calculate nodal support. The program Quartet MaxCut v2.1.0[80] was used to construct a species tree from the sampled quartets.

To estimate times of divergence within the genus *Cnemaspis* and their relatives we used a constrained concatenated ExaBayes UCE tree based on 514 loci (267,912 bp) as the guide tree in MCMCtree in PAML v4.9[81]. We used one fossil calibration and a root height for the crown gekkotans. The fossil calibration was based on the divergence between *Sphaerodactylus roosevelti* and *S. townsendi* as estimated from an amber-preserved fossil *Sphaerodactylus* from Hispanola dated 15–20 million years ago (MYA)[82]. We set the root height of crown gekkotans with an upper bound of 125 MYA and a lower bound of 95 my based on previously used constraints[30,83–86]. The divergence times were estimate using the program MCMCtree in PAML v4.9[81]. Divergence times were estimated with the independent rates model and the Birth-Death process for species sampling.

The size of our data set precluded implementation of a full Markov chain Monte Carlo (MCMC) iteration, so we used an approximate likelihood algorithm[87,88]. We first calculated maximum-likelihood estimates for the branch lengths, a gradient vector and Hessian matrix, using the internal programs BaseML and CodeML in PAML v4.9[81]. The most complex model available in MCMCtree was applied (HKY+Γ) with four categories, which allows for rate variation among nucleotides. The second step in our analysis used the MCMC algorithm to estimate the divergence times on the given guide tree, and the estimated gradient vectors along with the Hessian matrices were used to generate the Taylor expansion for the log-likelihoods[89]. The incorporation of these approximate likelihood estimates on large datasets decreases the computational time and makes these analyses tractable. These analyses were run for 10^6 generations, sampling every 10^3 generations, and with a 10% burnin. The MCMC outputs were loaded into Tracer v1.6[90] to assess convergence, and stationarity was assumed when effective sample sizes were ≥ 200.

Diversification and ancestral area reconstructions. To test for rapid rates of diversification in *Cnemaspis*, and to estimate speciation and extinction rates, we used the Bayesian Analysis of Macroevolutionary Mixtures (BAMM) program v2.5[31], which detects and quantifies rate heterogeneity along the branches of a phylogenetic tree. We analyzed our complete dataset (ingroup + outgroup terminals), and then a *Cnemaspis*-only dataset separately, to be sure that younger rate shifts were not being obscured by the inclusion of the much older outgroups. All BAMM analyses were run for 10^6 generations and event data were sampled every 10^3 generations, and we simulated the prior distribution of the number of rate shifts using default priors. BAMM accommodates unsampled taxa by incorporating a nonrandom incomplete taxon sampling correction into the likelihood equation. We discarded 10% of the generations as burnin after assessing convergence in BAMMtools[31,91,92]. We checked effective sample sizes using the CODA package[93] and assumed convergence if ESS >300. The rate shifts, speciation rates, extinction rates, and rate-through-time curves were summarized and visualized using the R v3.1.2[94] package BAMMtools[92] and all speciation and extinction rates are mean rates and not constant through time.

Independently of BAMM we plotted fluctuation rates of a dated phylogeny and visualized the diversification history of *Cnemaspis* via construction of a lineage-through-time (LTT) plot. LTT plots and their associated statistics have been used for testing simultaneous radiations versus constant rates of speciation[95,96]. We constructed a LTT plot from the time-calibrated tree generated in MCMCtree using the R package ape v4.0[97], and tested for a significant departure from the null hypothesis (a constant rate of cladogenesis in *Cnemaspis*) using a Monte Carlo constant rates test (MCCRT[98,99]) of diversification, as implemented in the R package Laser v2.4-1[100]. The net diversification rate statistic (γ) was estimated for the time-calibrated MCMCtree using Ape v4.0. To account for missing taxa we simulated 20,000 constant rate pure-birth trees with random pruning to mimic incomplete sampling, until the empirical number of taxa was reached (n = 53[55]). The estimatedγ-statistic was used to compare the relative positions of the nodes in the phylogeny to the expected distribution under a constant rate of speciation model of diversification. A negatively significantγ-statistic $<$-1.645[98] is expected to be a good measure of a rapid radiation.

To estimate ancestral areas at nodes of the *Cnemaspis* time tree, we first pruned the tree to include only *Cnemaspis*, and we then designated biogeographic regions throughout the distribution of *Cnemaspis* across Southeast Asia. We designated 13 biogeographic regions (Figure 1B) that either: (1) correspond to all of the islands in a given archipelago; (2) were previously designated regions from the literature (see below); or (3) were previously recovered clades of *Cnemaspis* and do not correspond to any political boundaries. This last group includes: (A) Pulau Bidong; (B) Seribuat Archipelago, Malaysia; (C) Ca Mau Islands, Vietnam; (D) Borneo; (E) Sumatra, Indonesia; (F) Peninsular Malaysia (from the southern portion of the Kangar-Pattani line south including Singapore); (G) Pattani (from the northern border of the Kangar-Pattani line north to the southern part of the Isthmus of Kra); (H) Central Indochina (from the northern border of the Isthmus of Kra east of the Salween River, and west of the Mekong River, and the greater Mekong Delta region[47]); (I) Langkawi Archipelago, Malaysia; (J) Natuna Archipelago, Indonesia; (K) Perhentian Archipelago, Malaysia; (L) Pulau Pinang, Malaysia; and (M) Hon Tre Island, Vietnam.

To infer the ancestral ranges of *Cnemaspis* we used a probabilistic-statistical modeling approach in the R[94] package BioGeoBEARS[101], to test alternative diversification. BioGeoBEARS uses the Akaike information criteria (AIC) in a statistical model fitting approach to select the best fit model for ancestral geographic range reconstructions for the data. We tested four models in BioGeoBEARS, including: (1) a likelihood version of the maximum parsimony model Dispersal-Vicariance Analysis DIVA ('DVIALIKE') model[102]); (2) the Dispersal-Extinction Cladogenesis (DEC) model[103,104] which has a common conceptual frame work with traditional with the DIVA model of ancestral character reconstructions, in which biogeographic areas are coded as discrete characters and species' ranges are coded as binary presence/absence data, and the ranges evolve along the phylogenetic branches by lineage movement (dispersal from one area to another) and local extinction[105]; and (3) the Bayesian-based BayArea ('BAYAREALIKE') model[106] which extends the application of more realistic problems involving large numbers of biogeographic areas by marginalizing over all possible biogeographic histories[106].

In combination with these models we also incorporated a jump-dispersal or founder event speciation parameter (+J), was incorporated; this step has been shown to be useful for datasets of insular clades107. We used a discrete character presence/absence matrix for the above 13 biogeographic regions for each species, based on specimen-verified locality data in Grismer et al. 201426 and Wood et al. 201725. We used likelihood ratio tests of the null (without +J) versus the alternative models (with +J) to see if we could reject scenarios without founder event speciation. All analyses were unconstrained, allowing each individual to have the same probability of colonizing among all adjacent areas or biogeographic regions. The maximum number of areas was set to three, with only four species occupying more than one biogeographic region with none of them occupying more than two.

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Supplemental Material

Table S1: Specimens used for the UCE/sequence capture dataset. Voucher number abbreviations are as follows: BYU, Monte L. Bean Life Science Museum, Brigham Young University; LSUHC, La Sierra University Herpetological Collection; MZB, Museum Zoologicum Bogoriense, Cibinung, Java, Indonesia; TG, Tony Gamble; USMHC, Universiti Sains Malaysia Herpetological Collection at the Universiti Sains Malaysia, Penang, Malaysia; UTAF, University of Texas at Austin field series; ZMKU R, Zoological Museum Kasetsart University, Thailand.

Samples	**Vouchers**	**Contigs**	**Total bp**	**Mean length**	**Max length**	**Contigs >1kb**	**UCE loci**	**SToL loci**	**Total loci**
Cnemaspis argus	LSUHC 8612	2002	607473	303.4330669	1408	8	248	18	266
Cnemaspis aurantiacopes	LSUHC 10835	3462	1386836	400.5880994	8927	42	399	6	405
Cnemaspis baueri	LSUHC 7302	2415	1116726	462.4124224	15591	73	500	30	530
Cnemaspis bayuensis	LSUHC 9072	12143	4474430	368.4781356	16786	253	398	21	419
Cnemaspis bidongensis	LSUHC 11445	928	283314	305.2952586	1726	4	148	2	150
Cnemaspis biocellata	LSUHC 8789	20759	6934324	334.0394046	15381	535	439	21	460
Cnemaspis boulengerii	LSUHC 9278	3498	1363916	389.9130932	2580	32	356	18	374
Cnemaspis caudanivea	LSUHC 8577	1640	507069	309.1884146	4959	14	272	8	280
Cnemaspis chanardi	LSUHC 9567	3471	1463922	421.7579948	12791	49	460	26	486
Cnemaspis chanthaburiensis	LSUHC 9338	2478	741780	299.346247	3348	18	245	13	258
Cnemaspis flavigaster	LSUHC 8835	5730	2229867	389.1565445	9156	156	470	22	492
Cnemaspis flavolineata	LSUHC 8079	1374	456270	332.0742358	2841	19	301	9	310

Table S1…

Cnemaspis grismeri	LSUHC 9733	1267	386531	305.0757695	2013	10	189	7	196
Cnemaspis harimau	LSUHC 9667	4113	1544414	375.4957452	12675	43	467	26	493
Cnemaspis huaseesom	LSUHC 9458	3493	1323571	378.9209848	8723	48	391	14	405
Cnemaspis karsticola	LSUHC 9055	14910	4727367	317.060161	15629	100	464	25	489
Cnemaspis kendallii	LSUHC 9178	4517	1524574	337.5191499	12950	39	486	22	508
Cnemaspis kumpoli	LSUHC 8848	17075	5431575	318.1010249	16943	119	499	26	525
Cnemaspis limi	LSUHC 3902	2027	960099	473.6551554	13894	38	449	31	480
Cnemaspis lineogularis	ZMKU R 00728	5522	2032636	368.0977907	15801	80	341	16	357
Cnemaspis mahsurae	LSUHC 11828	1556	712900	458.1619537	4105	42	465	26	491
Cnemaspis mcguirei	LSUHC 8853	10527	3566139	338.7611855	13705	98	419	22	441
Cnemaspis monachorum	LSUHC 10807	3132	1164791	371.9000639	8766	51	504	30	534
Cnemaspis mumpuniae	MZBLace 10166	35748	11306444	316.2818619	16474	447	489	31	520
Cnemaspis neangthyi	LSUHC 8515	4421	1575057	356.2671341	2766	61	374	18	392
Cnemaspis nigridia	LSUHC 9170	10096	3230439	319.9721672	11559	82	405	15	420
Cnemaspis niyomwanae	LSUHC 9568	7072	2628614	371.6931561	15750	151	479	32	511
Cnemaspis nuicamensis	LSUHC 8649	7264	2643370	363.9000551	14478	104	480	30	510
Cnemaspis omari	LSUHC 9978	6784	2677116	394.6220519	6463	163	369	19	388
Cnemaspis paripari	LSUHC 9186	5327	1931742	362.6322508	13851	68	485	25	510

Table S1…

Cnemaspis pemanggilensis	LSUHC 8014	4614	1397381	302.8567404	3369	35	184	7	191
Cnemaspis peninsularis	USMHC 0228	16150	5426317	335.9948607	13227	293	501	30	531
Cnemaspis perhentianensis	LSUHC 8700	7232	2104491	290.9970962	14284	38	228	10	238
Cnemaspis phangngaensis	BYU 62537	1909	735157	385.1005762	4799	18	179	17	196
Cnemaspis pseudomcguirei	LSUHC 9145	11139	3349907	300.7367807	12114	74	309	16	325
Cnemaspis psychedelica	LSUHC 9244	5401	1561206	289.0586928	10028	12	338	13	351
Cnemaspis punctatonuchalis	LSUHC 12453	8015	2499492	311.8517779	7981	79	249	13	262
Cnemaspis rajabasa	ENS 7766	3978	1171332	294.4524887	7678	14	170	10	180
Cnemaspis roticanai	LSUHC 11815	2484	1076916	433.5410628	4918	47	420	26	446
Cnemaspis selamatkanmerapoh	LSUHC 11015	2848	861428	302.4676966	4031	7	224	8	232
Cnemaspis shahruli	LSUHC 9613	1158	479578	414.1433506	12904	9	369	23	392
Cnemaspis siamensis	LSUHC 9474	289	86914	300.7404844	1323	1	85	3	88
Cnemaspis sp. nov. 1	LSUHC 9569	646	249515	386.24613	645	0	483	20	503
Cnemaspis sp. nov. 2	LSUHC 9570	7034	2409882	342.6047768	6942	66	368	9	377
Cnemaspis thachanaensis	ZMKU R 00729	4887	1739130	355.8686311	6503	97	269	13	282
Cnemaspis stongensis	LSUHC 11089	2445	801773	327.9235174	5654	33	156	3	159
Cnemaspis sundainsula	MZBLace 10156	335	99276	296.3462687	864	0	124	5	129
Cnemaspis temiah	LSUHC 9817	857	281424	328.3827305	3665	6	239	6	245

Table S1…

Cnemaspis tucdupensis	LSUHC 8631	913	271781	297.67908	2228	6	35	1	36
Cnemaspis vandeventeri	LSUHC 12449	1327	677694	510.6963075	8817	12	435	22	457
Outgroups									
Agamura persica	TG0188	60658	18572940	306.1911042	7486	512	458	27	485
Coleonyx variegatus	TG0179	19048	6926627	363.6406447	16872	495	322	12	334
Correlophus ciliatus	TG2314	1105	465188	420.9846154	3170	10	345	18	363
Cyrtopodion scaber	TG0109	24800	7740463	312.1154435	15488	108	387	26	413
Gehyra mutilata	LSUHC 12328	20639	6797555	329.3548622	15735	278	416	17	433
Gonatodes ocellatus	TG1855	12256	4476060	365.2137728	16771	180	299	12	311
Gonatodes vittatus	TG1845	6004	1752371	291.8672552	6241	24	207	11	218
Hemidactylus mabouia	TG2142	340	102614	301.8058824	1125	4	82	0	82
Hemidactylus turcicus	TG2125	12806	4709784	367.7794784	15493	539	311	14	325
Lialis burtonis	TG2114	8832	3349236	379.2160326	10226	215	305	13	318
Paroedura picta	TG2139	7764	2879736	370.9088099	16201	202	416	24	440
Phelsuma laticauda	TG1616	7866	2881395	366.3100687	4116	131	286	7	293
Phyllodactylus wirshingii	TG2385	12546	4171741	332.5156225	11606	127	471	32	503
Sphaerodactylus macrolepis	TG2147	4257	1284436	301.7232793	3209	25	273	10	283
Sphaerodactylus roosevelti	TG2384	6433	1918054	298.1585574	10116	37	285	12	297

Table S1…

Sphaerodactylus townsendi	TG2150	23647	7673801	324.5147799	22498	387	490	31	521
Stenodactylus cf. *sthenodactylus*	TG0185	6393	2236146	349.7803848	10310	73	391	24	415
Teratoscincus keyserlingii	TG2382	3529	1552260	439.8583168	8079	117	466	31	497
Teratoscincus przewalskii	TG233	16085	5652107	351.3899285	15606	287	498	34	532
Thecadactylus rapicauda	TG1864	32594	10374532	318.29576	16664	351	401	14	415
Tropiocolotes cf. *tripilotanus*	TG2354	1823	756570	415.0137137	4172	37	462	28	490

Table S2: The results of the model fitting from the ancestral area reconstructions in BioGeoBears. d= is the rate of dispersal or range expansion, e= is the extinction rate, and j= is the jump-dispersal rate.

	LnL	numparams	d	e	j	AICc	AICc wt
DEC	-123.2	2	0.19	0.73	0	250.7	1.0e-09
DEC+J	-108.1	3	0.062	0.72	0.018	222.7	0.0012
DIVALIKE	-114.4	2	0.20	1.0e-12	0	233.1	6.7e-06
DIVALIKE+J	-101.4	3	0.061	1.0e-12	0.016	209.3	1.00
BAYAREALIKE	-146.6	2	0.20	2.92	0	297.4	7.2e-20
BAYAREALIKE+J	-122.4	3	0.047	2.94	0.017	251.4	7.2e-10

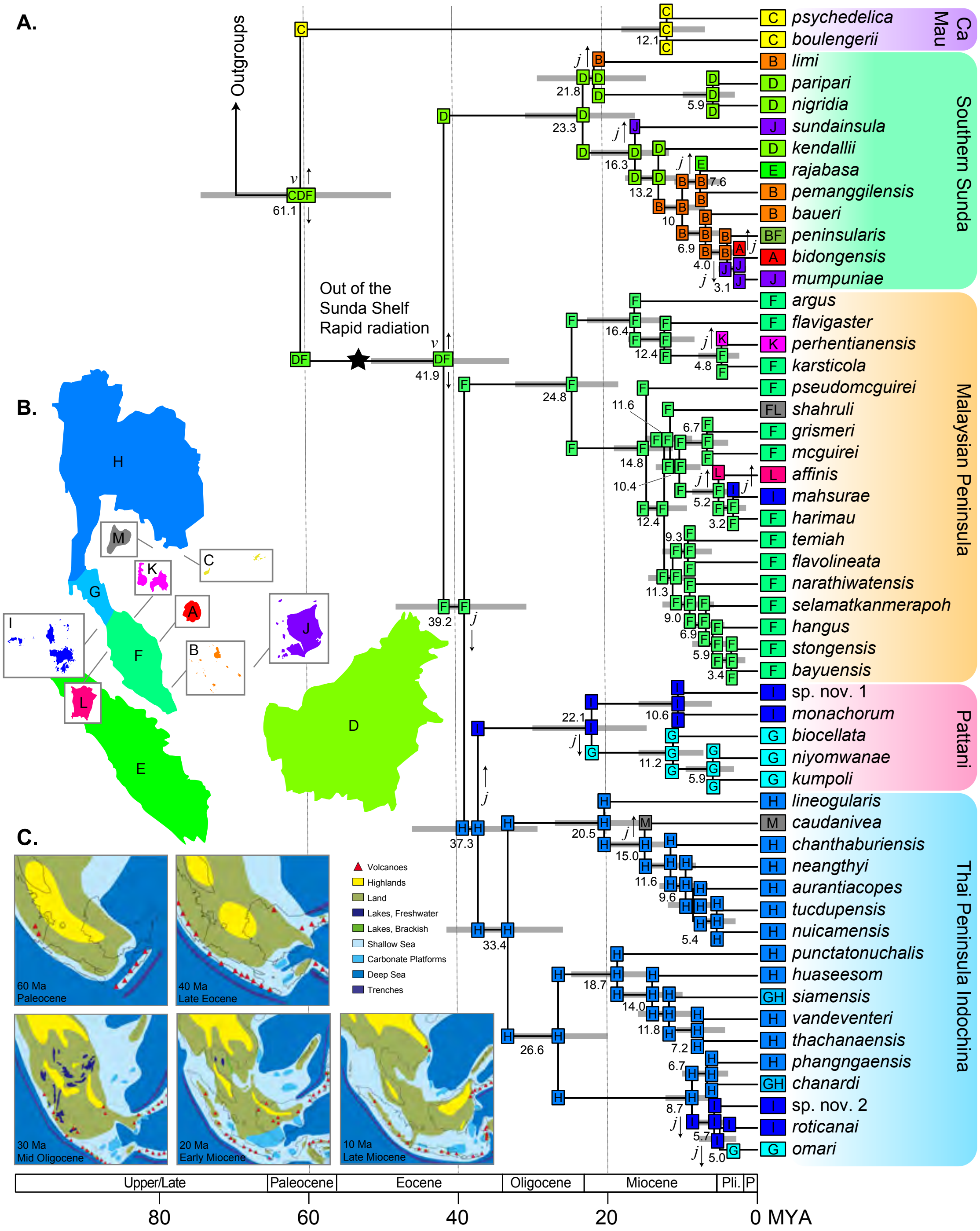

Figure 1: A. Chronogram of *Cnemaspis* based on a concatenated ExaBayes analysis of 514-locus guide tree (full tree in supplemental Figure S5). Numbers near the nodes are mean divergence time estimates from fossil and root height calibrations implemented in MCMCtree. The topology and all nodal support values are identical to Figure S4. Unconstrained ancestral area reconstructions inferred from the *DIVALIKE+J* model in BioGeoBears [1]. The black star indicates the rate-shift detected from the BAMM analysis (Probability=70%). B. Biogeographic regions for the ancestral range reconstructions (abbreviations described in the materials and methods). Arrows indicate a dispersal or vicariant event from one biogeographic region to another, j= jump-dispersal or founder event and v=vicariant event. C. Paleogeographic reconstructions are modified from Hall[2, 3].

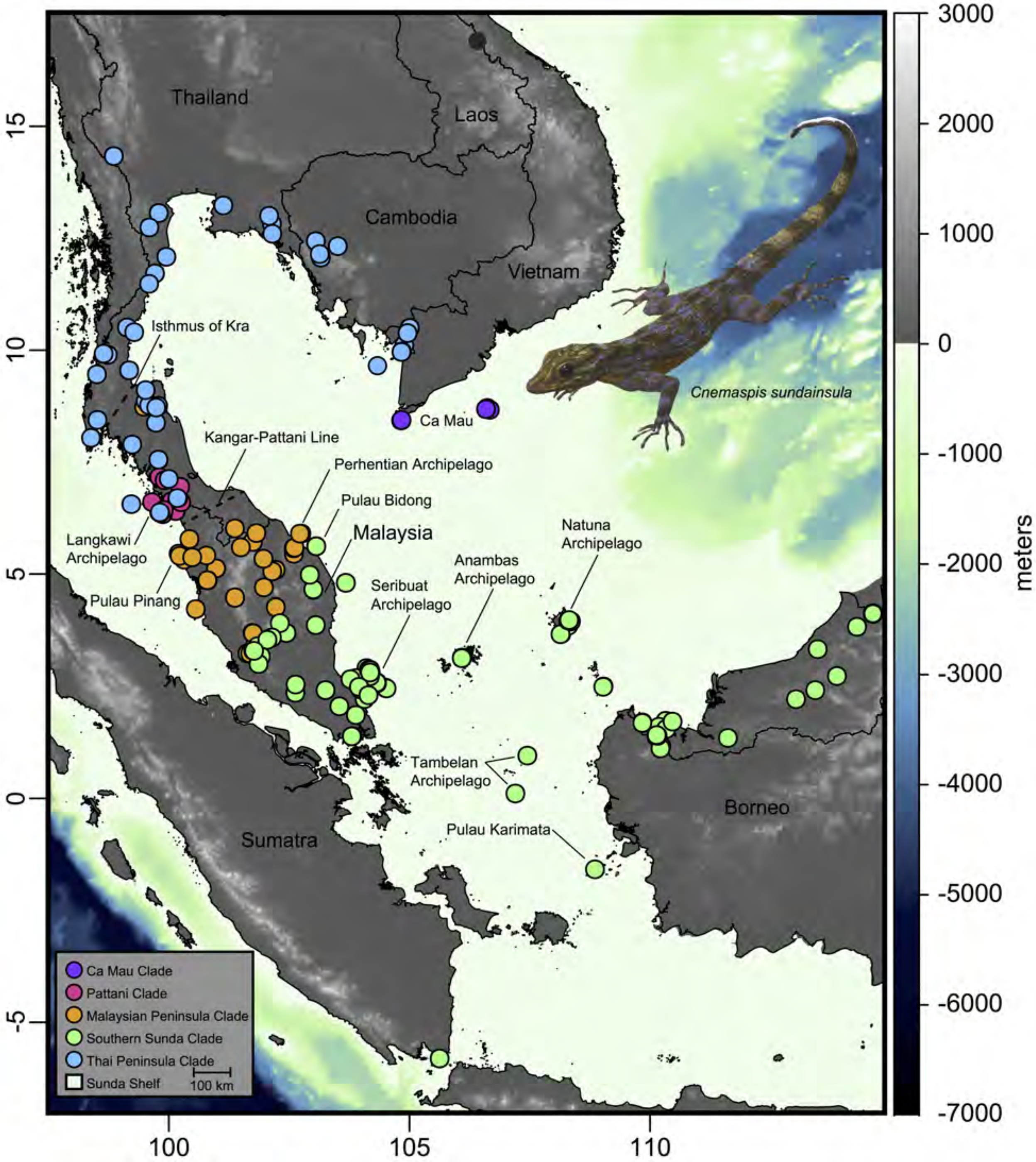

Figure S1: Distribution of the genus Cnemaspis based on Grismer et al. 2014[4]; colors identify major clades. The black circle is *C. laoensis* and its placement into one of the major clades is unknown due to the lack of genetic material. The map is generated using a global one arc-minute grid obtained from the General Bathymetric Chart of the Oceans (GEBCO).

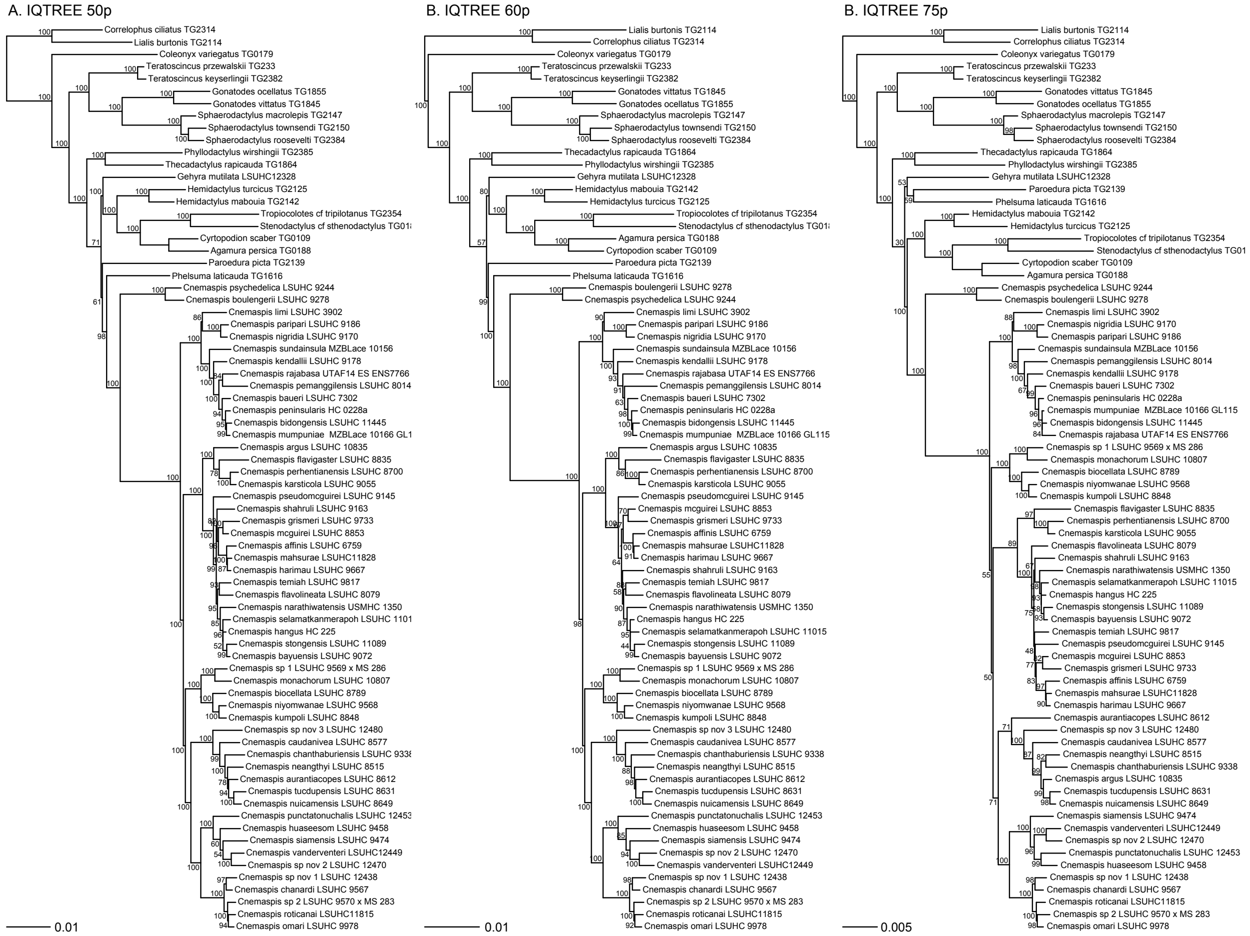

Figure S2: Maximum Likelihood trees estimated in IQTREE[5, 6] using three different sized datasets: A. 50p (267,912 bp/514 loci), B. 60p (231,027 bp/440 loci), C.75p (57,940bp/105 loci).

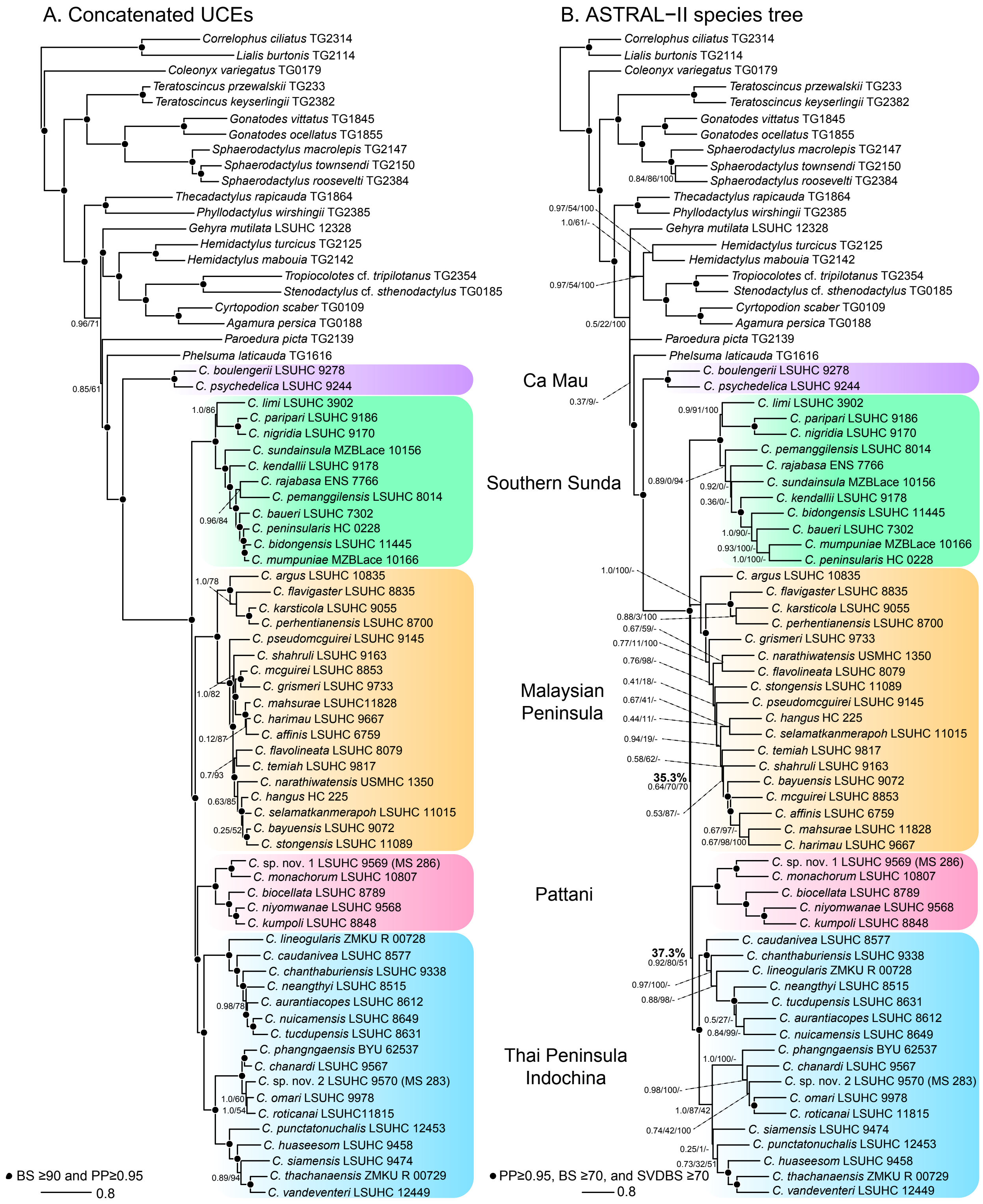

Figure S3: Phylogenomic relationships of *Cnemaspis* based on 514 loci (267,912 bp). Major clades are colored based on the distributions used in Figure 1. A. Concatenated ExaBayes analysis with ExaBayes PP and IQ-TREE BS support values respectively. B. Astral-II species tree with PP, BS (from RAxML bootstraps) and SVDBS support values respectively. The numbers in bold on the species tree represent the percentage of genetree quartets that are congruent with a given branch (the quartet approach).

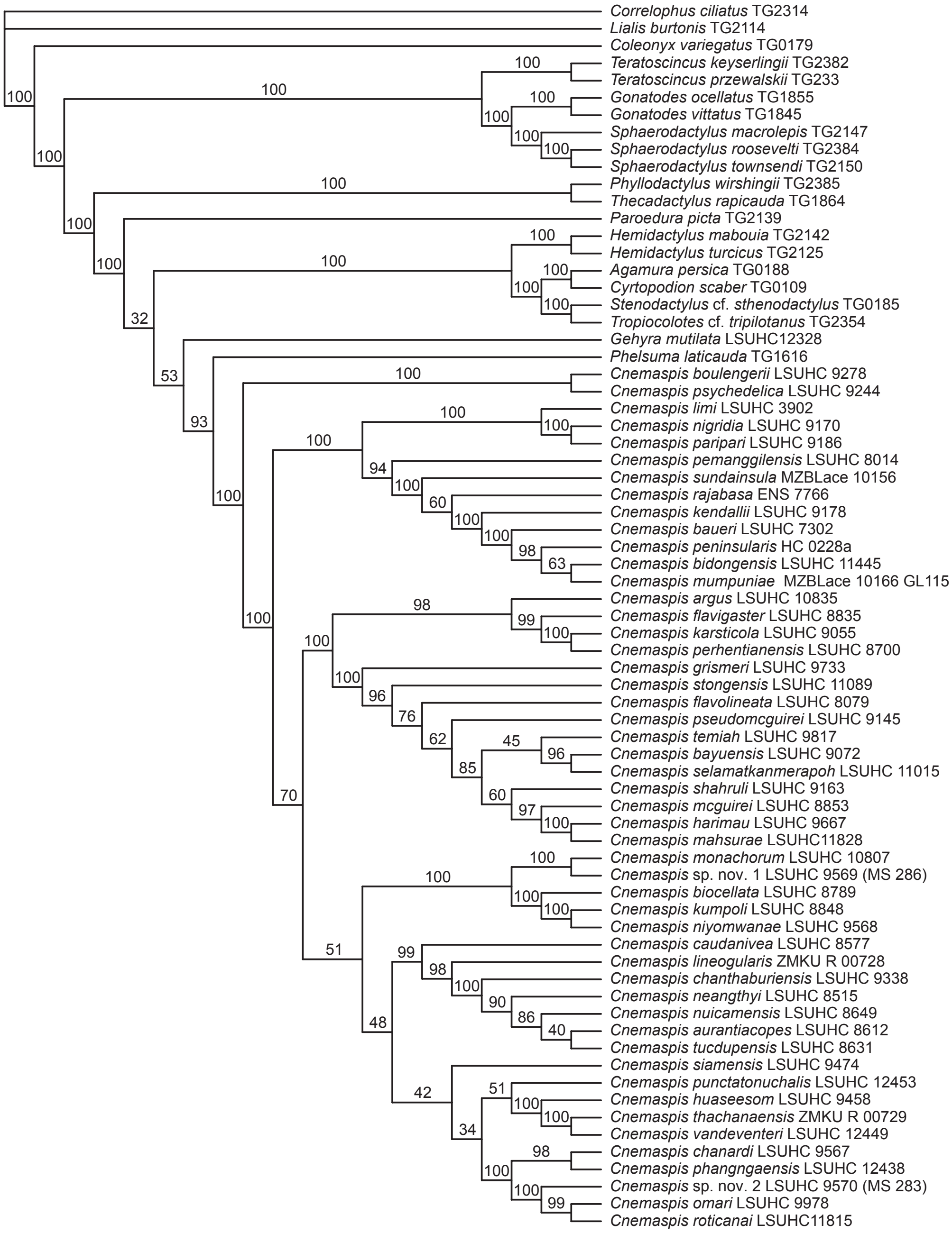

Figure S4: SVDQuartets consensus species tree with bootstrap consensus support values (SVDBS).

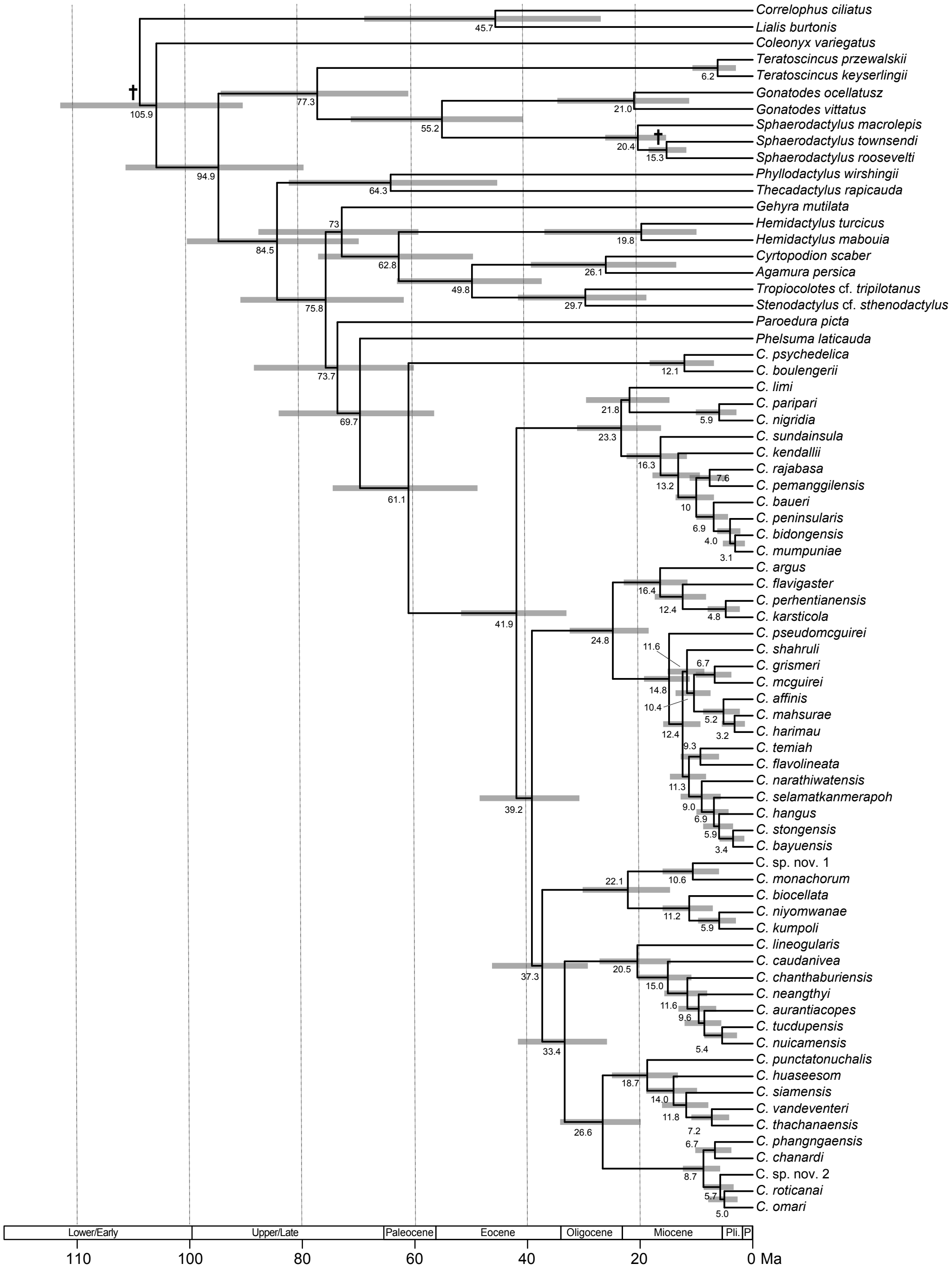

Figure S5: Numbers near the nodes are mean divergence time estimates from fossil and root height calibrations implemented in MCMCtree. The cross symbols indicate outgroup nodes with calibration points. Plio=Pliocene, P= Pleistocene.

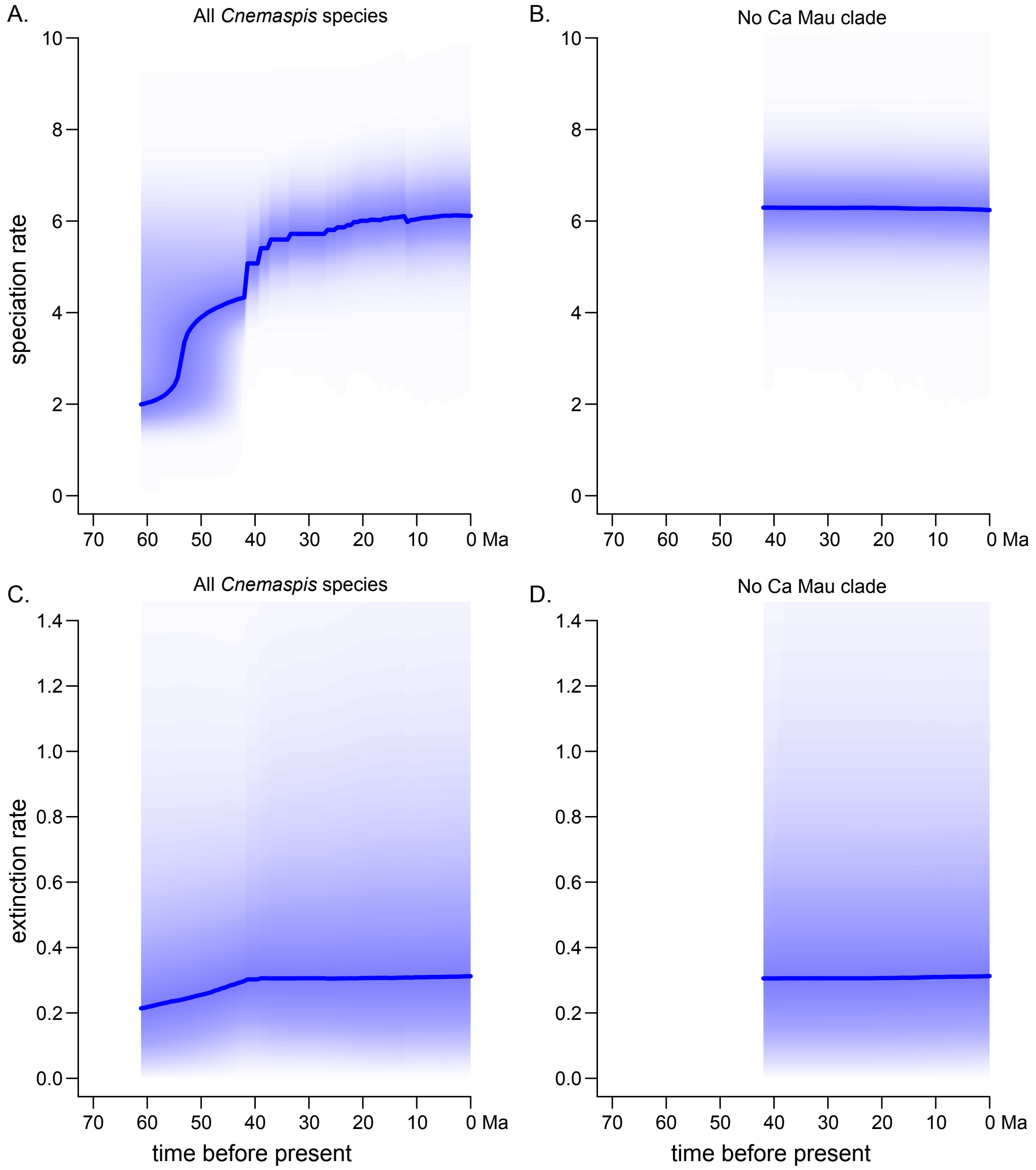

Figure S6: Estimated net speciation and extinction rates for *Cnemaspis* from BAMM outputs based on the time-calibrated tree. A. The rate shift for *Cnemaspis* estimated to be between 60–40 Ma with a higher magnitude of change from 2 to approximately 5.9 (λ=5.905598). B. The net speciation rate of *Cnemaspis* with the exclusion of the Ca Mau clade (the net speciation rate is constant λ=6.373306). C. Extinction rate for all of *Cnemaspis* with a small increase in extinction between 60–40 Ma (μ=0.41). D. Extinction rates with exclusion of the Ca Mau clade appear to be constant through time (μ=0.42).

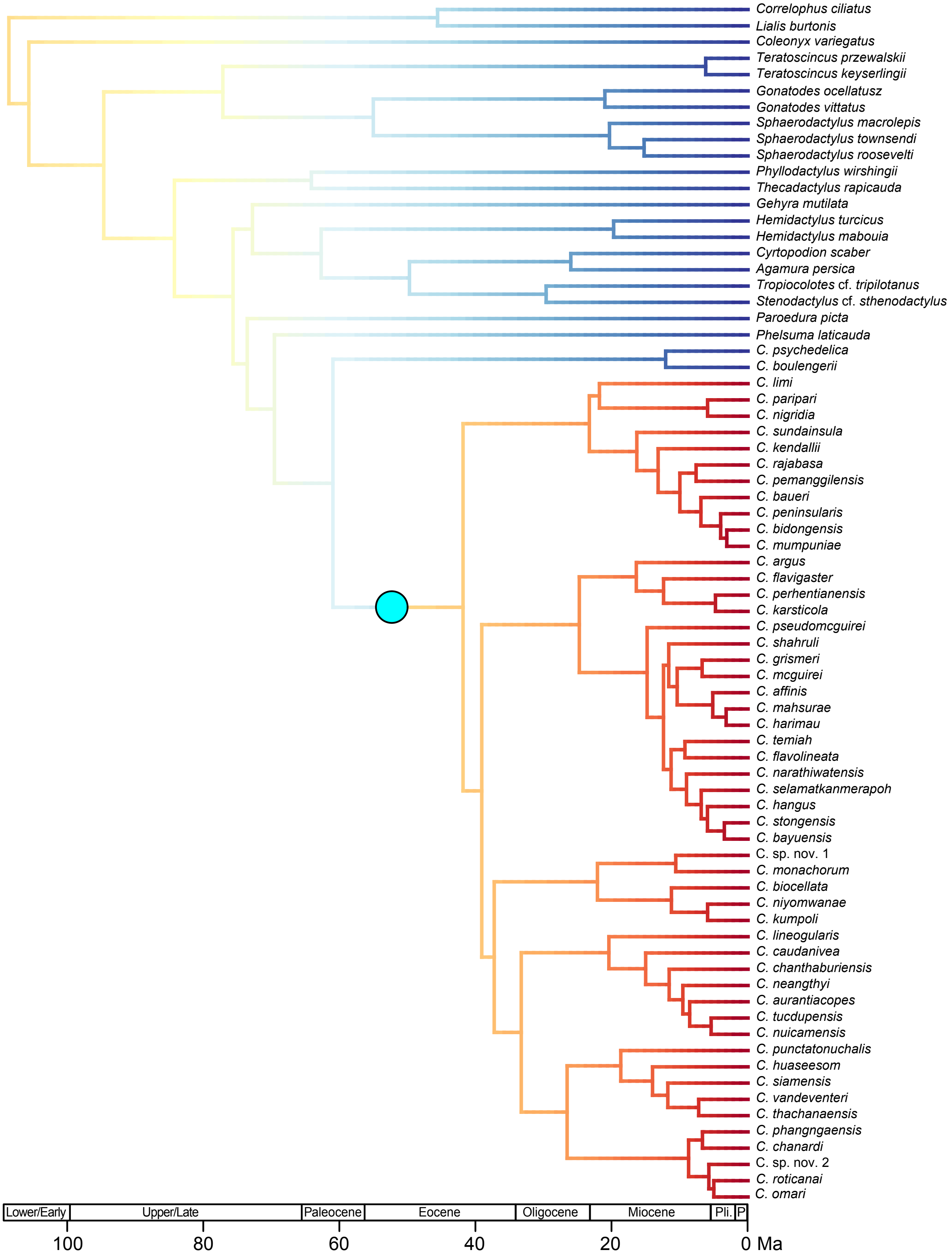

Figure S7: The BAMM tree with a single rate shift (blue circle, probability=0.70) associated with a rapid radiation of *Cnemaspis* with the exclusion of the Ca Mau clade.

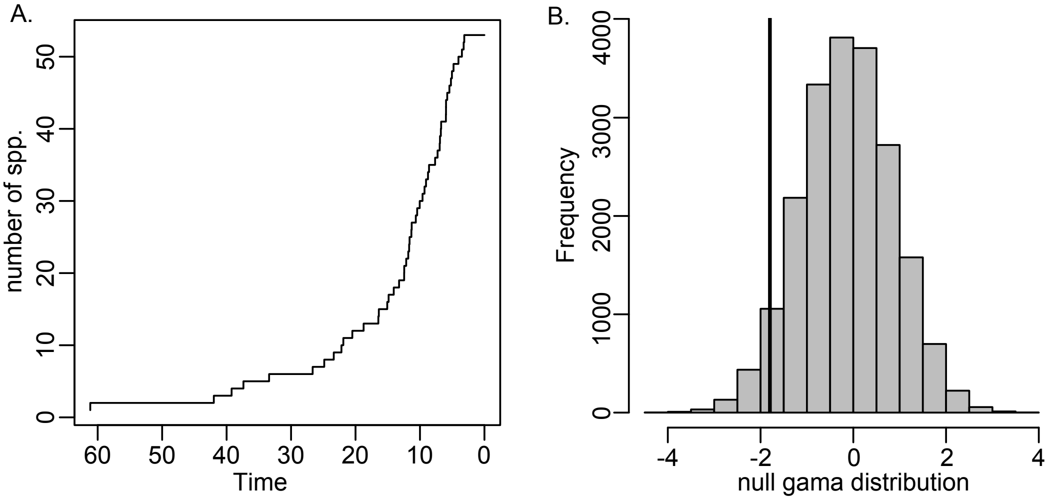

Figure S8: A. Lineage through time plot based on the time-calibrated tree generated from MCMCtree. B. Null gamma distribution from the 20,000 simulated pure-birth constant rate trees from the MCCRT with the observed gamma statistic for the empirical tree (γ = -1.847611, p-value = 0.041, critical value = -1.758) represented as the vertical solid black line[7].

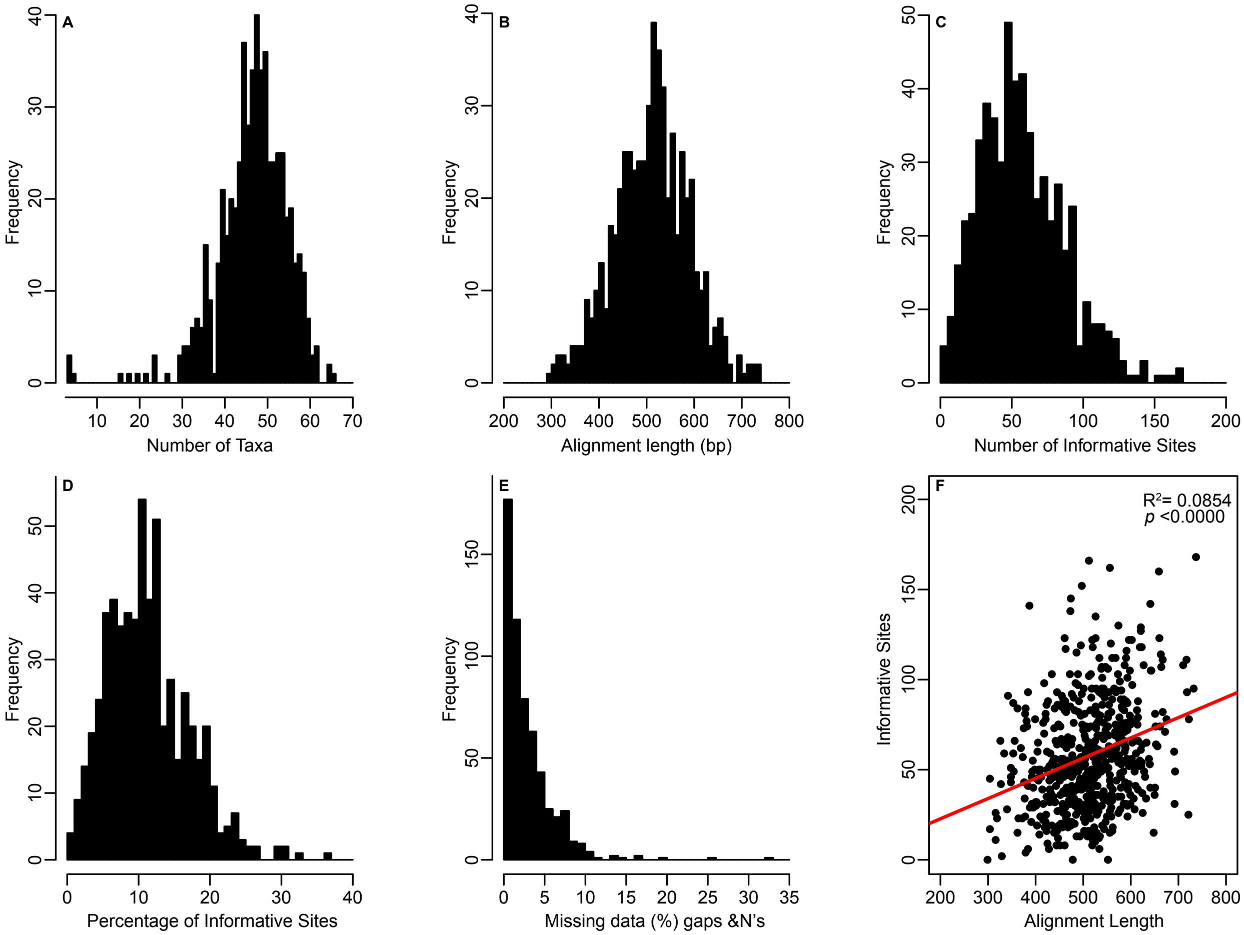

Figure S9: Summary statistics from the raw Illumina reads. A. Number of taxa in the alignment. B. Alignment length C. The number of informative sites. D. Percentage of informative sites. E. The percentage of missing data, gaps and N's. F. Alignment length with respect to informative sites; there is a significant positive correlation between the alignment length and the number of informative sites.

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