Title

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Authors

Grismer, L Lee
del Pinto, Lelani
Quah, Evan SH
et al.

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Phylogenetic and multivariate analyses of *Gekko smithii* Gray, 1842 recover a new species from Peninsular Malaysia and support the resurrection of *G. albomaculatus* (Giebel, 1861) from Sumatra

L. Lee Grismer[1], Lelani del Pinto[1], Evan S. H. Quah[2,3], Shahrul Anuar[3,4], Michael Cota[5], Jimmy A. McGuire[6], Djoko T. Iskandar[7], Perry L. Wood Jr[8], Jesse L. Grismer[1]

1 *Department of Biology, La Sierra University, 4500 Riverwalk Parkway, Riverside, California 92515, USA*
2 *Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400, Kota Kinabalu, Sabah, Malaysia*
3 *School of Biological Sciences, Universiti Sains Malaysia, 11800 Minden, Penang, Malaysia*
4 *Center for Marine and Coastal Studies, Universiti Sains Malaysia, 11800 USM, Pulau Pinang, Malaysia*
5 *Natural History Museum, National Science Museum, Thailand*
6 *Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, Berkeley, California 94720, USA*
7 *The Indonesian Academy of Sciences, Jakarta 10110 Indonesia*
8 *Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109-1085, USA*

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Corresponding author: L. Lee Grismer (lgrismer@lasierra.edu)

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Abstract

An integrative taxonomic analysis of Sundaic populations of *Gekko smithii* from the Thai-Malaya Peninsula, Sumatra, and Borneo recovered four deeply divergent mitochondrial lineages that are separated by major geographic barriers (mountains and seaways). Furthermore, they bear a number of concordant statistically significant differences in meristic and morphometric features, morphospatial separation in multivariate space, and discrete differences in color pattern. *Gekko smithii sensu stricto* is restricted to southern Thailand south of the Isthmus of Kra and Peninsular Malaysia west of the Banjaran (mountain range) Titiwangsa, being that the type locality is on Penang Island, Penang. *Gekko hulk* **sp. nov.** is a new species from extreme southern Thailand and Peninsular Malaysia east of the Banjaran Titiwangsa and five east coast islands—the type locality being Pulau (island) Tioman, Pahang. *Gekko* cf. *albofasciolatus* is tentatively used to include Bornean populations west of the Iran Mountains in Sabah and Sarawak which, in the absence of molecular data, cannot unequivocally be separated morphologically from *G. albofasciolatus* from the type locality at Banjarmasin, Kalimantan, Indonesia east of the Iran Mountains. In the absence of molecular data, *G. albomaculatus* is resurrected to include mainland Sumatran, Nias Island, and Banyak Islands populations which, based on their morphology, cannot be separated from descriptions of *G. albomaculatus* from the type locality of Bangka Island, 15 km off the southeast coast of mainland Sumatra. Further integrative analyses of all Sumatran and Bornean populations are currently underway as well as the enigmatic Wallacean populations from Sulawesi. Data are presented that strongly suggest all references to *G. smithii* from Java stem from a 151 year-old misidentification of a specimen of *G. gecko* of unknown provenance. Additionally, there are no vouchered records of *G. smithii* from Myanmar. The phylogeographic patterns of Sundaic populations of the *G. smithii* complex are concordant with those of a plethora of other Sundaic lineages.

Key words

Gekkonidae, integrative taxonomy, phylogenetics, Sundaland, systematics

Introduction

The genus *Gekko* Laurenti, 1768 is an ecologically and morphologically diverse radiation of scansorial, nocturnal lizards comprising at least 82 species that collectively range throughout Southeast and East Asia to western Melanesia (Uetz et al. 2021; Wood et al. 2020a). Throughout its vast distribution, *Gekko* manifests a broad array of adaptive types ranging from large human commensals and granite boulder-adapted specialists, to highly cryptic arboreal species and parachuters (Rösler et al. 2011; Wood et al. 2020a). Based on an extensive integrative analysis, Rösler et al. (2011) constructed six phenotypic species groups within the genus *Gekko.* Two of these groups, *G. gecko* and *G. japonicus,* were recognized by Wood et al. (2020a) in a phylogenomic taxonomy that constructed seven subgenera and necessitated the synonymy of *Luperosaurus* Gray, 1845 and *Ptychozoon* Kuhl and van Hasselt, 1822 with *Gekko.* Included among the seven species of the subgenus *Gekko,* is *G. smithii* Gray, 1942*,* a large widespread, aggressive, scansorial, lowland, forest-adapted species and semi-human commensal found throughout much of Sundaland from southern Thailand south of the Isthmus of Kra through Peninsular Malaysia and Singapore to Sumatra, Borneo, and Sulawesi (Koch et al. 2009; Grismer 2011a,b) (Fig. 1). Chandramouli et al. (2021) indicated that *G. smithii* from Great Nicobar Island (erroneously reported as *G. gecko* by Biswas and Sanyal (1977)) was morphologically distinct and based on statistically significant differences, described it as *G. stoliczkai* Chandramouli, Gokulakrishnan, Sivaperuman, and Grismer, 2021 which we include here to be the eighth species of *G.* (*Gekko*). Reports of *G. smithii* from Java and Myanmar are likely erroneous (see below).

Integrative taxonomic analyses of many other species of Sundaic amphibians and reptiles were recovered as species complexes and whose pronounced phylogeo-

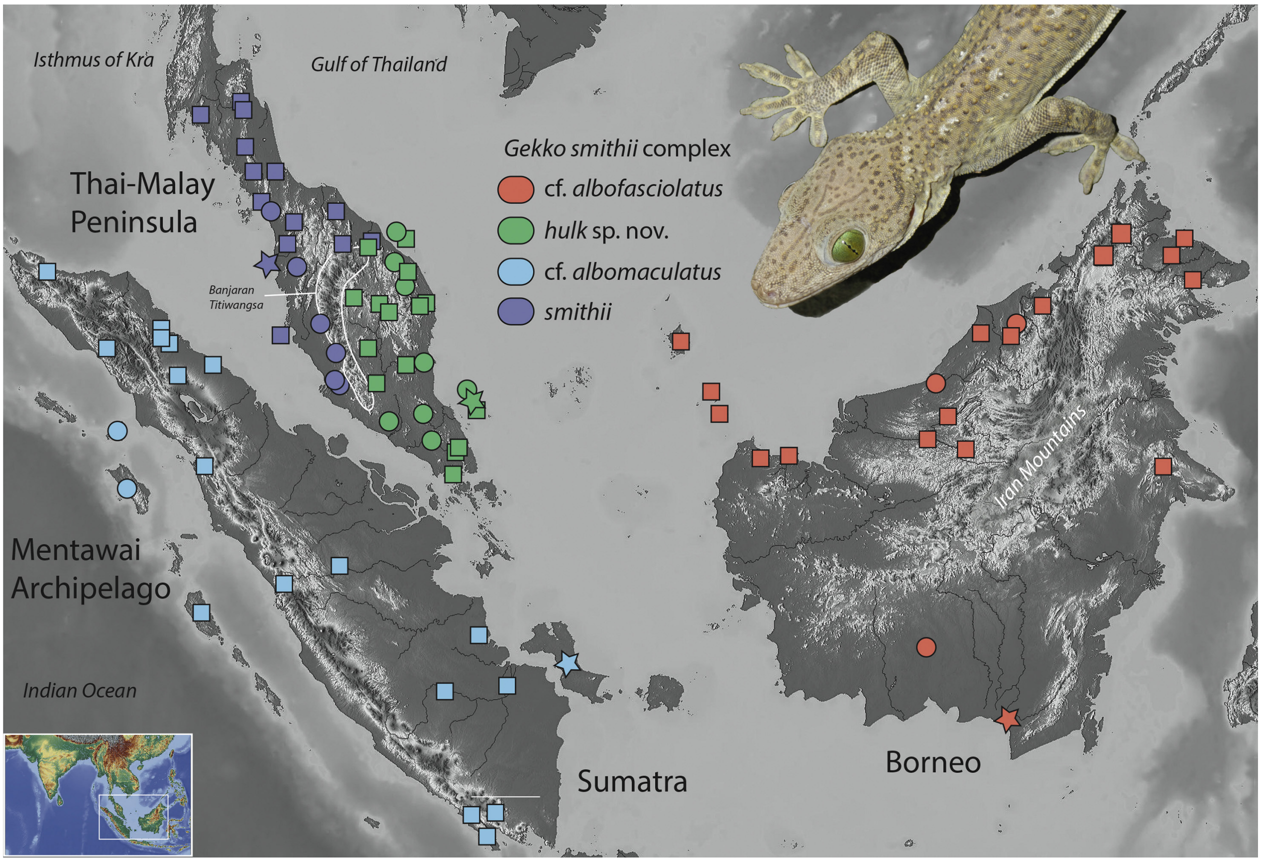

Figure 1. Distribution of the species of the *Gekko smithii* complex from throughout their respective Sundaic land masses. Circles denote the localities of specimens that were both examined first hand and are represented in the phylogeny (Fig. 2). Stars denote type localities. Squares denote localities of specimens or photographs examined here or verified from other publications as well as vouchered samples in the literature. Localities from non-peer reviewed literature or unverifiable online data were not included.

graphic sub-structuring across well-defined geographic features necessitated their taxonomic partitioning into multiple species (e.g., Grismer et al. 2013, 2014a,b, 2015, 2018a,b, 2019; Loredo et al. 2013; Matsui et al. 2014; Matsui 2019; Grismer and Quah 2015; Chan et al. 2016, 2017, 2018, 2020; Harvey et al. 2016; Grismer and Davis 2018; O'Connell et al. 2018, 2019; Quah et al. 2019, 2020, 2021a,b; Wood et al. 2020b). Therefore, we initiated the first integrative analysis of *G. smithii* based on morphology, color pattern, and genetic data derived from the mitochondrial gene NADH dehydrogenase subunit 2 (ND2). The analysis was focused primarily on the phylogeographic structure of populations on the Thai-Malay Peninsula and their associated islands—including the type locality on the west coast island of Penang that has remained unsampled since Gray's description in 1842. Although sampling was dense on the Thai-Malay Peninsula, we sequenced available tissue samples and examined representative specimens from Borneo and Sumatra for comparison. The phylogenetic analyses recovered significant mitochondrial divergences across well-established biogeographic boundaries within Peninsular Malaysia and between Peninsular Malaysia, Sumatra, and Borneo that were corroborated by statistically significant differences in body shape, scalation, color pattern, and morphospatial arrangement in multivariate space. As such, we consider *G. smithii* to be a species complex and adjust the taxonomy accordingly with the description of a new species from Peninsular Malaysia and the resurrection of one other from Sumatra.

Materials and methods

Species delimitation

The general lineage concept (GLC: de Queiroz 2007) adopted herein proposes that a species constitutes a population of organisms evolving independently from other such populations owing to a lack of gene flow. By "independently," it is meant that new mutations arising in one species cannot spread readily into another species (Barraclough et al. 2003; de Queiroz 2007). Integrative studies on the nature and origins of species are using an increasingly wider range of empirical data to delimit species boundaries (Coyne and Orr 1998; Fontaneto et al. 2007; Knowles and Carstens 2007; Leaché et al. 2009), rather than relying solely on morphology and traditional taxonomic methods. Under the GLC implemented herein, molecular phylogenies were used to recover monophyletic mitochondrial lineages of individuals (populations) in order to develop initial species-level hypotheses. Univariate and multivariate analyses of meristic and morphometric data were then used to search for statistically significant character differences and morphospatial patterns consistent with the phylogenetic delimitations of the species-level hypotheses—thus not conflating species *delimitation* with species *diagnosis*.

Phylogenetic analyses

We obtained 1267 base pairs of NADH dehydrogenase subunit 2 gene (ND2) and its flanking tRNAs from six specimens from GenBank and 60 newly sequenced specimens (Table 1) for phylogenetic analyses. *Gekko gecko* was used to root the tree based on R**ö**sler et al. (2011) and Siler et al. (2012). Total genomic DNA was isolated from liver or skeletal muscle stored in 95% ethanol using a SPRI magnetic bead extraction protocol (https://github.com/phyletica/lab-protocols/blob/master/extraction-spri.md). ND2 was amplified using a double-stranded Polymerase Chain Reaction (PCR) under the following conditions: 2.5 µl genomic DNA (~10–30 ng), 2.5 µl light strand primer (5 µM), 2.5 µl heavy strand primer (5 µM) (Table 2), 1.0 µl dinucleotide pairs (1.0 µM), 2.0 µl 5x buffer (2.0 µM), 1.0 MgCl 10x buffer (1.0 µM), 0.18 µl Taq polymerase (5u/µl), and 9.8s µl ultrapure H2O at n + 1. PCR reactions were executed on a Axygen Maxygene II gradient thermocycler under the following conditions: initial denaturation at 94˚C for 30 s, annealing at 52˚C for 30 s, followed by a cycle extension at 68˚C for 7 min for 33 cycles, followed by a final extension cycle run at 4°C for 35 s. All PCR products were visualized on a 1.0 % agarose electrophoresis gel. Successful targeted PCR products were outsourced to GENEWIZ® for PCR purification, cycle sequencing, and sequencing. Primers used for amplification and sequencing are presented in Table 2.

We used both maximum likelihood (ML) and Bayesian inference (BI) to estimate the phylogenetic relationships among the sampled geckos in our sequence alignment. A ML phylogeny was estimated using the IQ-TREE webserver (Nguyen et al. 2015; Trifinopoulos et al. 2016) preceded by the selection of substitution models using the Bayesian Information Criterion (BIC) in ModelFinder (Kalyaanamoorthy et al. 2017), which supported TPM2+F+G4 as the best fit model for the tRNAs, HKY+F+I for ND2 codon position one, TPM2u+F+G4 for position 2, and KKY+F for position 3. One-thousand bootstrap pseudoreplicates via the ultrafast bootstrap (UFB; Hoang et al. 2018) approximation algorithm were employed and nodes having UFB values of 95 and above were considered highly supported (Minh et al. 2013). A Bayesian inference (BI) analysis was carried out in MrBayes 3.2.3. (Ronquist et al. 2012) on XSEDE using the CIPRES Science Gateway (Cyberinfrastructure for Phylogenetic Research; Miller et al. 2010) employing default priors and models of evolution that most closely approximated those selected by the BIC and used in the ML analysis. Two independent Markov chain Monte Carlo (MCMC) analyses were performed, each with four chains, three hot and one cold. The MCMC simulation ran for 40 million generations, was sampled every 4000 generations, and the first 10% of each run were discarded as burn-in. Convergence and stationarity of all parameters from both runs were checked in Tracer v1.6 (Rambaut et al. 2014) to ensure effective sample sizes (ESS) were well above 200. Post-burn-in sampled trees from both runs were combined and a 50% majority-rule consensus tree was constructed. Nodes with Bayesian poste-

Table 1. Taxon sampling, locality data, and ND2 GenBank accession numbers from specimens used in the phylogenetic analyses.

Species	**Cat no.**	**Locality**	**Accession no.**
Gekko gecko	LSUHC 6813	Pulau Langkawi, Kedah, West Malaysia	OM420678
Gekko cf. *albofasciolatus*	FMNH 267868	Bintulu Division, Sarawak, East Malaysia	OM420649
Gekko cf. *albofasciolatus*	FMNH 269014	Bintulu Division, Sarawak, East Malaysia	OM420650
Gekko cf. *albofasciolatus*	FMNH 269015	Bintulu Division, Sarawak, East Malaysia	OM420651
Gekko cf. *albomaculatus*	MVZ 271122	Pulau Tuangku, Aceh, Sumatra	OM420692
Gekko cf. *albomaculatus*	MVZ 271123	Pulau Tuangku, Aceh, Sumatra	OM420693
Gekko cf. *albomaculatus*	MVZ 271125	Pulau Nias, North Sumatra, Sumatra	OM420677
Gekko hulk **sp. nov.**	LSUHC 8696	Pulau Perhentian Besar, Teregganu, West Malaysia	OM420680
Gekko hulk **sp. nov.**	LSUHC 8690	Pulau Perhentian Besar, Teregganu, West Malaysia	OM420679
Gekko hulk **sp. nov.**	LSUHC 6749	Endau Rompin, Johor, West Malaysia	OM420652
Gekko hulk **sp. nov.**	LSUHC 7651	Endau Rompin, Johor, West Malaysia	OM420654
Gekko hulk **sp. nov.**	LSUHC 7694	Endau Rompin, Johor, West Malaysia	OM420655
Gekko hulk **sp. nov.**	LSUHC 7702	Endau Rompin, Johor, West Malaysia	OM420656
Gekko hulk **sp. nov.**	LSUHC 7649	Endau Rompin, Johor, West Malaysia	OM420652
Gekko hulk **sp. nov.**	LSUHC 7650	Endau Rompin, Johor, West Malaysia	OM420653
Gekko hulk **sp. nov.**	LSUHC 9959	Gunung Lambak, Johor, West Malaysia	OM420657
Gekko hulk **sp. nov.**	LSUHC 6748	Endau Rompin, Johor, West Malaysia	JN019056
Gekko hulk **sp. nov.**	LSUHC 10585	Gunung Ledang, Johor, West Malaysia	OM420659
Gekko hulk **sp. nov.**	LSUHC 14015	Gunung Ledang, Johor, West Malayia	OM420658
Gekko hulk **sp. nov.**	LSUHC 7251	Pulau Tulai, Johor, West Malaysia	OM420705
Gekko hulk **sp. nov.**	LSUHC 5062	Pulau Tulai, Johor, West Malaysia	OM420696
Gekko hulk **sp. nov.**	LSUHC 5063	Pulau Tulai, Johor, West Malaysia	OM420697
Gekko hulk **sp. nov.**	LSUHC 3891	Pulau Tulai, Johor, West Malaysia	OM420694
Gekko hulk **sp. nov.**	LSUHC 6265	Pulau Tulai, Johor, West Malaysia	OM420699
Gekko hulk **sp. nov.**	LSUHC 5064	Pulau Tulai, Johor, West Malaysia	OM420698
Gekko hulk **sp. nov.**	LSUHC 6277	Pulau Tulai, Johor, West Malaysia	OM420701
Gekko hulk **sp. nov.**	LSUHC 6278	Pulau Tulai, Johor, West Malaysia	OM420702
Gekko hulk **sp. nov.**	LSUHC 7024	Pulau Tulai, Johor, West Malaysia	OM420703
Gekko hulk **sp. nov.**	LSUHC 7257	Pulau Tulai, Johor, West Malaysia	OM420706
Gekko hulk **sp. nov.**	LSUHC 6268	Pulau Tulai, Johor, West Malaysia	OM420700
Gekko hulk **sp. nov.**	LSUHC 7025	Pulau Tulai, Johor, West Malaysia	OM420704
Gekko hulk **sp. nov.**	LSUHC 5061	Pulau Tulai, Johor, West Malaysia	OM420695
Gekko hulk **sp. nov.**	LSUHC 6095	Pekan, Pahang, West Malaysia	JQ173534
Gekko hulk **sp. nov.**	LSUHC 7264	Pulau Tioman, Pahang, West Malaysia	OM420690
Gekko hulk **sp. nov.**	LSUHC 7263	Pulau Tioman, Pahang, West Malaysia	OM420689
Gekko hulk **sp. nov.**	LSUHC 4681	Pulau Tioman, Pahang, West Malaysia	OM420681
Gekko hulk **sp. nov.**	LSUHC 6278	Pulau Tioman, Pahang, West Malaysia	OM420702
Gekko hulk **sp. nov.**	LSUHC 5390	Pulau Tioman, Pahang, West Malaysia	OM420683
Gekko hulk **sp. nov.**	LSUHC 7299	Pulau Tioman, Pahang, West Malaysia	OM420691
Gekko hulk **sp. nov.**	LSUHC 6284	Pulau Tioman, Pahang, West Malaysia	OM420688
Gekko hulk **sp. nov.**	LSUHC 6890	Pulau Tioman, Pahang, West Malaysia	JN019055
Gekko hulk **sp. nov.**	LSUHC 5152	Pulau Tioman, Pahang, West Malaysia	OM420682
Gekko hulk **sp. nov.**	LSUHC 6283	Pulau Tioman, Pahang, West Malaysia	OM420687
Gekko hulk **sp. nov.**	LSUHC 5849	Pulau Tioman, Pahang, West Malaysia	OM420685
Gekko hulk **sp. nov.**	LSUHC 5399	Pulau Tioman, Pahang, West Malaysia	OM420684
Gekko hulk **sp. nov.**	LSUHC 6260	Pulau Tioman, Pahang, West Malaysia	OM420686
Gekko hulk **sp. nov.**	LSUHC 11977	Sungai Bubu, Terengganu, West Malaysia	OM420711
Gekko hulk **sp. nov.**	LSUHC 11976	Sungai Bubu, Terengganu, West Malaysia	OM420710
Gekko hulk **sp. nov.**	LSUHC 11206	Lata Belatan, Terengganu, West Malaysia	OM420663
Gekko cf. *albofasciolatus*	ID 8774	Gunung Mulu, Sarawak, East Malaysia	JN019054
Gekko smithii	LSUHC 10596	Sedim, Kedah, West Malaysia	OM420708
Gekko smithii	LSUHC 9626	Sedim, Kedah, West Malaysia	OM420707
Gekko smithii	LSUHC 12690	The Gap, Pahang, West Malaysia	OM420712
Gekko smithii	LSUHC 14005	The Gap, Pahang, West Malaysia	OM420713
Gekko smithii	LSUHC 13624	Penang Island, Penang, West Malaysia	OM420669
Gekko smithii	LSUHC 13625	Penang Island, Penang, West Malaysia	OM420670

Species	Cat no.	Locality	Accession no.
Gekko smithii	LSUHC 13626	Penang Island, Penang, West Malaysia	OM420671
Gekko smithii	LSUHC 13627	Penang Island, Penang, West Malaysia	OM420672
Gekko smithii	LSUHC 9157	Lata Iskandar, Pahang, West Malaysia	OM420667
Gekko smithii	LSUHC 9158	Lata Iskandar, Pahang, West Malaysia	OM420668
Gekko smithii	LSUHC 9153	Lata Iskandar, Pahang, West Malaysia	OM420664
Gekko smithii	LSUHC 9154	Lata Iskandar, Pahang, West Malaysia	OM420665
Gekko smithii	LSUHC 9155	Lata Iskandar, Pahang, West Malaysia	OM420666
Gekko smithii	LSUHC 15041	Perlis State Park, Perlis, West Malaysia	OM420673
Gekko smithii	LSUHC 15042	Perlis State Park, Perlis, West Malaysia	OM420674
Gekko smithii	LSUHC 15052	Perlis State Park, Perlis, West Malaysia	OM420675
Gekko smithii	LSUHC 15053	Perlis State Park, Perlis, West Malaysia	OM420676
Gekko smithii	LSUHC 6542	Kepong, Selangor, West Malaysia	JQ173535
Gekko smithii	LSUHC 15084	Kepong, Selangor, West Malaysia	OM420662
Gekko smithii	none	Ulu Gombok, Selangor, West Malaysia	FJ487868
Gekko smithii	LSUHC 6606	Kepong, Selangor, West Malaysia	OM420661
Gekko smithii	LSUHC 6564	Kepong, Selangor, West Malaysia	OM420660
Gekko smithii	none	Captive specimen no data	JN019057
Gekko smithii	LSUHC 15085 (JAM 1712)	Selangor, West Malaysia	OM420709

Table 2. Primers used for amplification and sequencing reactions for the ND2 gene and the flanking tRNA's.

Primer name	Primer reference		Sequence
L4437	(Macey et al. 1997)	EXTERNAL	5' -AAGCTTTCGGGCCCATACC- 3'
H5934	(Macey et al. 1997)	EXTERNAL	5' -AGRGTGCCAATGTCTTTGTGRTT- 3'

rior probabilities (BPP) of 0.95 and above were considered highly supported (Huelsenbeck et al. 2001; Wilcox et al. 2002). After removing the outgroup, MEGA7 (Kumar et al. 2016) was used to calculate uncorrected pairwise sequence divergence among and within species using the complete deletion option which removes missing data and gaps.

Morphological analyses

Morphometric data 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. Data taken were snout-vent length (SVL), taken from the tip of the snout to the vent; tail width (TW), measured at the base of the tail; axillia-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), measured 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), measured from the top of the head posterior to the eyes to the bottom of the lower jaw; internarial distance (IN), measured across the snout between the dorsal margins of the external nares; orbital diameter (OD), the horizontal diameter of the bony orbit; eye to ear distance (EE), measured from the anterior margin of the auricular opening to the posterior margin of the eyeball; snout-eye length (SE), measured from anteriormost margin of the eyeball to the tip of snout; nares-eye length (NE), measured from the anterior margin of the eyeball to the posterior margin of the external nares; auricular opening (TD), measured as the horizontal distance of the ear opening; interorbital distance (IO), measured across the narrowest part of the frontal bone between the orbits; forearm length (FL), measured from the distal edge of the elbow when flexed 90° to the wrist; and crus length (CL), measured from the distal edge of the knee when flexed 90° to the ankle. The tail width (TW) measured at the base of the tail where it contacts the body.

Meristic characters evaluated were scales across frontal bone (FS), counted as the number of scales across the frontal bone at the midline of the orbits; supralabials (SL) and infralabials (IL) counted from the angle of the jaw to the rostral and mental scales, respectively; chin scales (CS), counted as the number of enlarged scales medial to and contacting the infralabials; ventral scales counted across the belly between the ventrolateral body folds midway between the limb insertions (VS); midbody scales counted across the dorsum between the ventrolateral body folds (MB); paravertebral tubercles (PVT) counted as the number of longitudinally arranged tubercles between an imaginary line between the middle of the limb insertions; longitudinal rows of tubercles (LRT) counted across the dorsum between the ventrolateral body folds midway between the limb insertions; subdigital lamellae on the first (TL1) and fourth (TL4) toes; precloacal pore-bearing scales in males (PP); and cloacal spurs (CSP). Codes for natural history collections follow Sabaj (2020). Specimens examined and the raw data used in the analyses are in Table S1.

Statistical analyses

Seven of the 86 preserved specimens of *Gekko smithii* from the Thai-Malay Peninsula used in this study were not represented in the molecular phylogenetic analyses. These speciemens were place in a specific mitochondrial lineage based on their geographic proximity to that lineage. Following this, all individuals were subjected to a Discriminant Function Analysis (DFA) using the MASS Package in R (Ripley et al. 2018) based on a concatenated data set of eight meristic and 14 adjusted (see below) morphometric characters to assess the probability of the placement of each individual into a particular mitochondrial lineage based on geography. DFA uses linear combinations of untransformed data to characterize and separate predefined groups and explicitly attempts to model the differences between them. The predict() command was used to calculate the posterior probability for lineage membership of each individual. A second discriminant analysis was performed using the principal component loadings from the principal component analysis (see below) as a cross-validation for each individual's lineage membership.

All characters conformed to parametric test assumptions of normality (Shapiro-Wilk test, $p < 0.05$) and homogeneity of variances (F-test, $p > 0.05$). One-way analyses of variance (ANOVA) were conducted on characters to search for the presence of statistically significant mean differences ($p < 0.05$) across the data set. Characters bearing statistical differences were subjected to a TukeyHSD *post hoc* test to ascertain which population pairs differed significantly from each other for those particular characters. Boxplots were generated for discrete meristic characters in order to visualize the range, mean, median, and degree of differences between species pairs bearing statistically different mean values and violin plots with embedded boxplots were generated for continuous morphometric characters to visualize the same plus the distribution frequency of the data. All statistical analyses were performed in R [v3.4.3].

The morphospatial relationships of each species relative to one another and the clustering of the sampled individuals were visualized using multivariate ordination analyses on the appropriate combinations of data (meristic and morphometric). These analyses were employed as a multivariate assessment to determine if the respective data sets were morphospatially consistent with one another and the putative species boundaries delimited by the molecular phylogenetic analyses and diagnosed and defined by the univariate analyses (see below). It should be made clear these are not species delimitation analyses. Principal component analysis (PCA) implemented by the prcomp() command in R was employed to analyze the morphometric data. PCA is a dimension reducing analysis that decreases the complexity of a data set by finding a subset of input variables that contain the most relevant information (i.e. the greatest variance in the data) while de-emphasizing those characters that do not, thus increasing the overall accuracy of the model by eliminating noise and the potential of overfitting (Agarwal et al. 2007). This unsupervised analysis (i.e. data points (specimens) are not *a priori* assigned to species) that recovers morphospatial relationships among the sampled individuals (i.e. data points) and how well they form clusters that may or may not be aligned with the putative species boundaries delimited by the phylogenetic analyses. To ensure that allometric biases in the raw data were appropriately removed prior to analysis, hatchlings were omitted from the data set and the raw data were adjusted using the following equation: $X_{adj}=\log(X)-\beta[\log(SVL)-\log(SVL_{mean})]$, where X_{adj}=adjusted value; X=measured value; β=unstandardized regression coefficient for each population; and SVL_{mean}=overall average SVL of all populations (Thorpe 1975, 1983; Turan 1999; Lleonart et al. 2000)—accessible in the R package *GroupStruct* (available at https://github.com/chankinonn/GroupStruct). The morphometrics of each species were adjusted separately and then concatenated prior to analysis so as not to conflate intra- with interspecific variation (Reist 1985; McCoy et al. 2006).

Discriminant analysis of principal components (DAPC) from the ADEGENET package in R (Jombart et al. 2015) was performed on the morphometric data set. The DAPC is a supervised analysis that places individuals from each predefined population into separate clusters (i.e. plots of points) bearing the smallest within-group variance that produce linear combinations of centroids having the greatest between-group variance (i.e. linear distance; Jombart et al. 2010). DAPC relies on scaled data from an internal PCA as a prior step to ensure that variables analyzed are not correlated and number fewer than the sample size. Dimension reduction of the DAPC prior to plotting is accomplished by retaining the first set of PCs that account for approximately 90% of the variation in the data set (Jombart and Collins 2015) as determined from a scree plot generated as part of the analysis. Retaining too many PCs forces false structure to appear in the data while retaining too few, runs the risk of missing true structure.

A principal coordinate analysis (PCoA)—conceptually similar to a PCA—using a Gower (dis)similarity index was employed on a concatenated meristic and adjusted morphometric data set. The dissimilarity matrix is used as the input to the analysis, not the original variables themselves. Therefore, information concerning the original variables cannot be recovered. Because this unsupervised multivariate analysis is based on a (dis)similarity index constructed from Euclidean distances between data points, it is appropriate for data sets containing discrete characters (scale counts) because it does not require the data to fulfill the assumptions of linearity (as does PCA) or unimodality (Marhold 2011; Paliy and Shankar 2016), thus allowing more flexible handling of mixed data sets. Furthermore, it is insensitive to null values in the data frame (i.e. missing data) so informative characters such as precloacal pores, which occur only in males, may not have to be removed from the analysis.

Non-parametric permutation multivariate analyses of variance (PERMANOVA) from the VEGAN package in R (Oksanen et al. 2018) were used *a priori* to determine if the centroid locations of each species in the PCoA and PCA data sets were statistically different (Skalski et al.

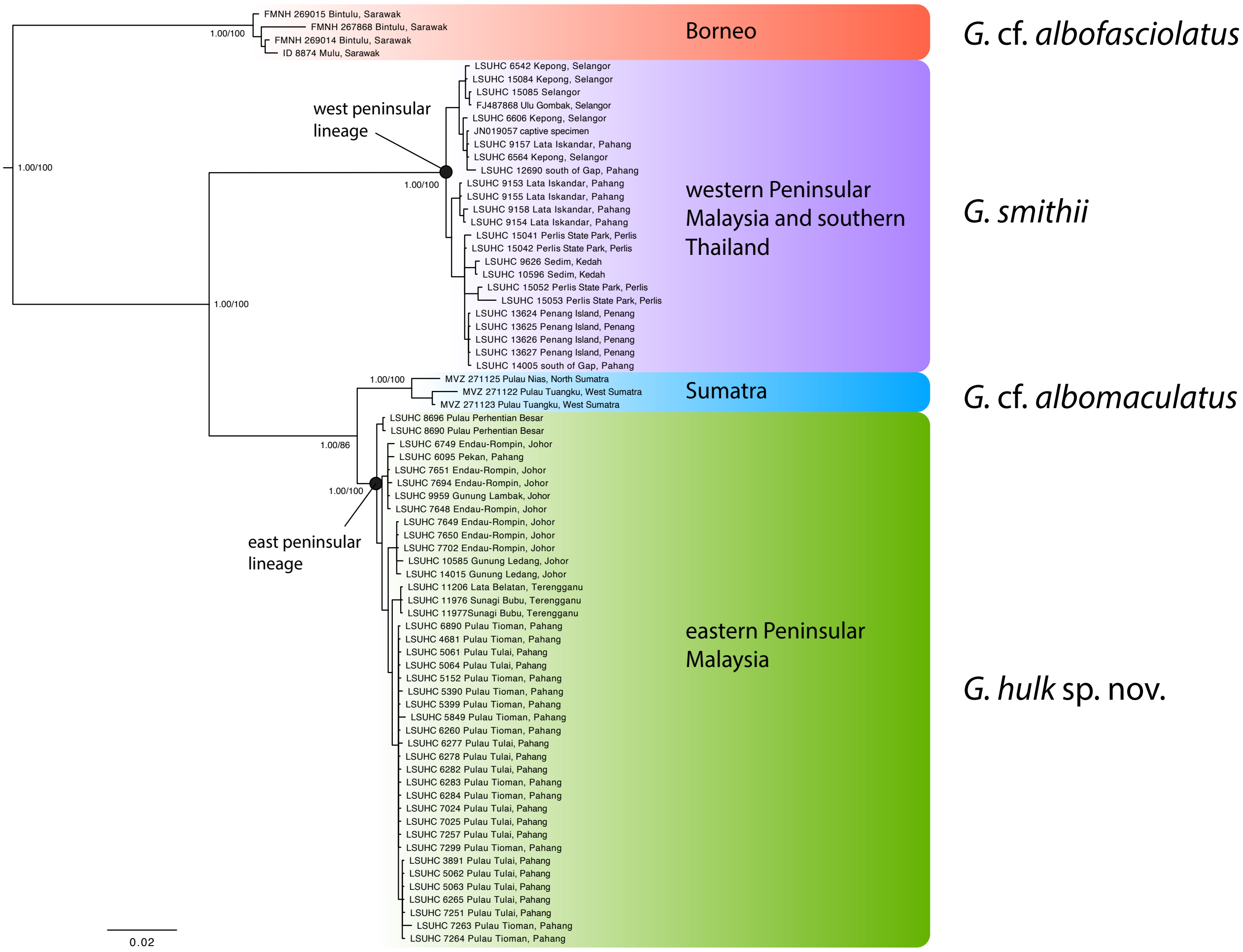

Figure 2. Maximum likelihood topology of the *Gekko smithii* complex based on 1267 base pairs of ND2 and its flanking tRNAs with BPP and UFB values, respectively, at the nodes.

2018). The analyses are based on the prior calculation of the distance between any two data points in a Gower (dis) similarity matrix from the PCoA data set and a Euclidean (dis)similarity matrix from the PCA data set, using 5000 permutations. The analyses are not based on the output of the PCoA or PCA and are thus independent of them. A pairwise *post hoc* test calculates the differences between all combinations of species pairs, generating a Bonferroni-adjusted p-value and an F ratio. $p < 0.05$ is considered significant and larger F-ratios indicate more pronounced group separation. A rejection of the null hypothesis (i.e. centroid positions and/or the spread of the data points are no different from random) signifies a significant difference among groups.

Results

The ML and BI analyses recovered trees with identical strongly supported topologies delimiting four major lineages separated by relatively long branch lengths that correspond to distinct geographic regions (Fig. 2). Surprisingly, individuals from the Thai-Malay Peninsula do not form a monophyletic group but are separated into west and east peninsular lineages on opposite sides of the Banjaran Titiwangsa that divide the northern three-quarters of Peninsular Malaysia into eastern and western halves and to a great extent, separate Peninsular Malaysia from southern Thailand (Fig. 1). The east peninsular lineage occurs on at least five east coast islands, the adjacent continental lowlands, southern Peninsular Malaysia, and Singapore (Grismer 2011a,b), and is the sister lineage to a clade of individuals from islands off the west coast of Sumatra including Nias (a deep-water island) and Tuangku (of the Banyak Islands) (Fig. 1), and presumably the rest of Sumatra (see below). The west peninsular lineage is the sister lineage to the eastern peninsular lineage plus the Sumatran lineage and occurs on at least two islands off the west coast of the Malay Peninsula (Grismer 2011b) and ranges northward through southern Thailand to the Isthmus of Kra (Fig. 1). Individuals from Borneo comprise the sister lineage to all other included *G. smithii* populations. Uncorrected pairwise sequence divergences among all lineages ranges from 2.5% between the Sumatran and east peninsular lineage to 13.3% between both the Sumatran and west peninsular and Bornean lineages. The east and west peninsular lineages are 4.8% divergent (Table 3). The phylogenies recovered here corroborate the limited mito-nuclear phylogeny of Rösler et al. (2011) in that their Bornean sample was recovered as the closest relative

Table 3. Percent uncorrected pairwise sequence divergence for species of the *Gekko smithii* complex calculated from 1267 base pairs of the mitochondrial gene ND2 and flanking tRNAs.

	cf. *albofasciolatus*	*hulk* **sp. nov.**	cf. *albomaculatus*	*smithii*
cf. *albofasciolatus*	**0.012**	0.128	0.133	0.133
hulk **sp. nov.**	0.128	**0.007**	0.025	0.048
cf. *albomaculatus*	0.133	0.025	**0.015**	0.133
smithii	0.133	0.048	0.133	**0.023**

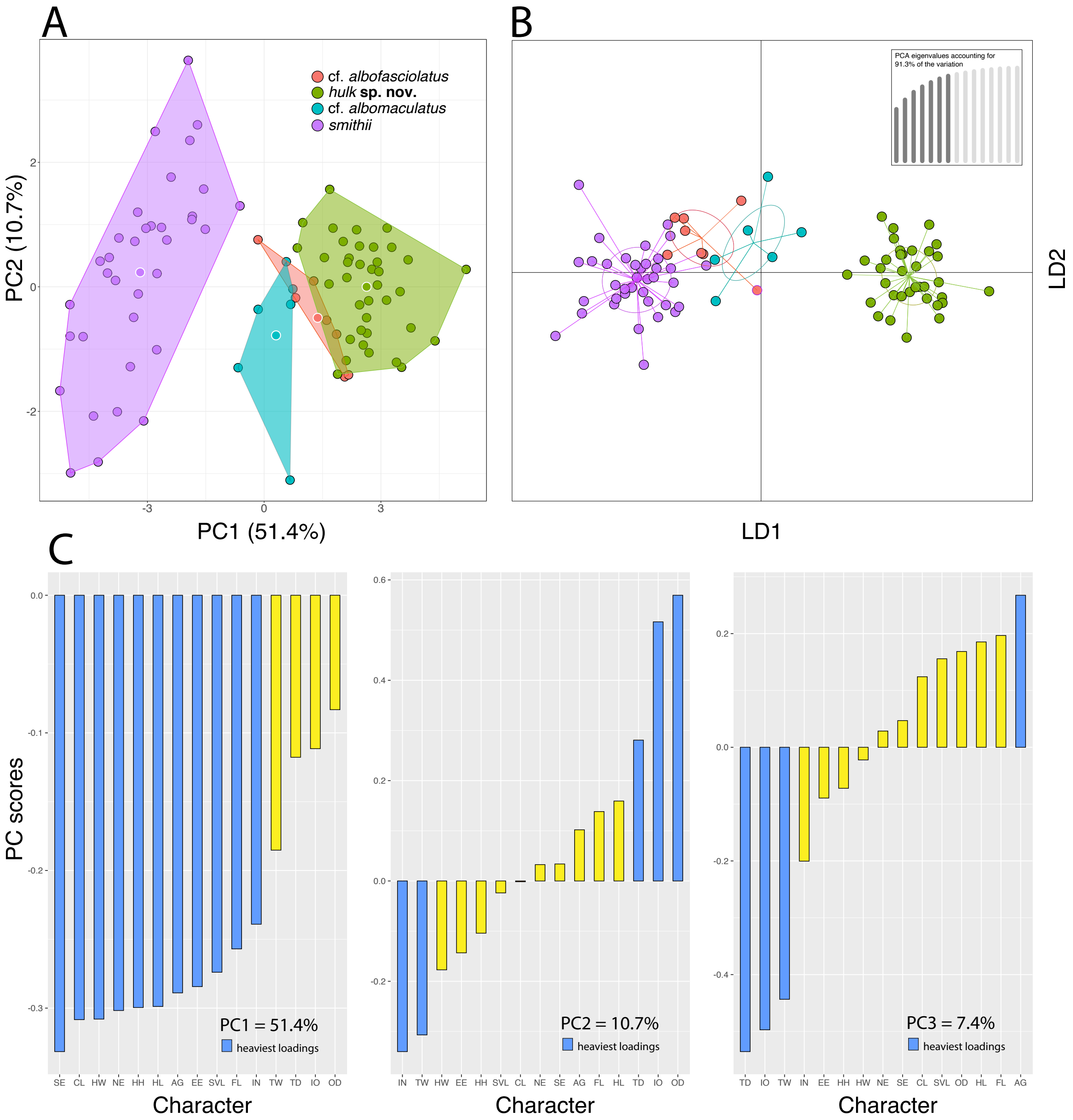

Figure 3. A, PCA and B, DAPC of morphometric data of the species of the *Gekko smithii* complex. C. Bar plots of PCA loading scores of PC1–PC3.

to sister lineages from eastern (Pahang and Johor states) and western (Selangor state) Peninsular Malaysia.

The DFA and DAPC placed nearly all Thai individuals for which there were no sequence data with all the sequenced individuals from the west peninsular lineage with a 99–100% posterior probability (PsP). The only exception was THNHM 01841 from the Hala-Bala Wildlife Sanctuary, Narathiwat in southeastern Thailand which

Table 4. Summary statistics and principal component analysis scores for the *Gekko smithii* complex. Abbreviations are listed in the Materials and methods.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15
Standard deviation	2.7774	1.2686	1.0521	0.9805	0.8919	0.8035	0.6850	0.6636	0.6195	0.5293	0.4392	0.3830	0.3579	0.2928	0.2008
Proportion of variance	0.5143	0.1073	0.0738	0.0641	0.0530	0.0430	0.0313	0.0294	0.0256	0.0187	0.0129	0.0098	0.0085	0.0057	0.0027
Cumulative proportion	0.5143	0.6216	0.6954	0.7594	0.8125	0.8555	0.8868	0.9162	0.9417	0.9604	0.9733	0.9831	0.9916	0.9973	1.0000
Eigenvalue	7.7139	1.6094	1.1069	0.9613	0.7955	0.6456	0.4693	0.4403	0.3838	0.2802	0.1929	0.1467	0.1281	0.0858	0.0403
SVL	–0.2670	–0.0713	–0.2095	0.0708	–0.1368	0.1959	–0.0262	0.7912	–0.4339	0.0327	–0.0134	–0.0011	–0.0360	–0.0101	0.0056
HH	–0.3108	0.1252	0.0566	–0.2202	0.0012	–0.1208	0.1317	0.0136	–0.0030	–0.5180	0.6112	0.2228	0.0683	0.2174	–0.2458
HL	–0.3130	–0.1084	–0.1615	0.0913	–0.0211	0.2363	0.0117	–0.3320	–0.1645	–0.2507	–0.3411	–0.1758	–0.5291	0.3518	–0.2199
HW	–0.3019	0.2881	0.0488	–0.1983	0.0018	0.2507	–0.1829	–0.1517	–0.0452	–0.0191	0.0033	–0.0115	–0.1359	–0.7773	–0.1990
IN	–0.2455	0.3503	0.1525	–0.0695	–0.2712	–0.0030	0.0768	0.3192	0.6867	0.1069	–0.1851	–0.2018	–0.0935	0.1732	–0.1042
IO	–0.1120	–0.4619	0.5028	–0.2884	–0.1288	0.1457	0.5758	–0.0181	–0.0831	0.2170	0.0125	–0.0307	–0.0673	–0.0875	–0.0331
TD	–0.1209	–0.2948	0.5368	0.5117	–0.2618	0.0651	–0.4826	–0.0036	0.0627	–0.1438	0.0921	0.0542	0.0626	–0.0239	–0.0473
EE	–0.2132	–0.0887	0.1304	0.2195	0.8088	0.0081	0.0194	0.1704	0.2056	0.1073	0.1866	–0.0653	–0.2876	–0.0312	0.1461
NE	–0.3204	0.0005	0.0143	0.0732	0.3104	0.1812	0.0833	–0.0722	–0.0044	–0.0081	–0.3876	0.1053	0.7122	0.1017	–0.2674
SE	–0.3431	0.0153	–0.0478	–0.0375	–0.1196	0.1176	0.0811	–0.1184	0.0847	–0.2592	–0.1184	0.1768	0.0788	–0.0428	0.8378
OD	–0.0831	–0.5050	–0.1428	–0.6109	0.0846	–0.0621	–0.5166	0.0734	0.2085	–0.0195	–0.0570	–0.0893	0.0512	0.0591	0.0027
FL	–0.2209	–0.2934	–0.2339	0.2314	–0.0827	–0.6963	0.2218	0.0365	0.1004	–0.1775	–0.1879	–0.0441	–0.0185	–0.3491	–0.1168
CL	–0.3220	0.0301	–0.1229	0.0794	–0.1117	–0.0752	–0.0393	–0.2255	–0.1487	0.3058	0.3715	–0.6873	0.2391	0.0775	0.1193
AG	–0.3023	–0.0817	–0.2673	0.0982	–0.1522	–0.0131	–0.0620	–0.1804	0.1052	0.5943	0.1739	0.5806	–0.1111	0.1024	–0.0816
TW	–0.1972	0.3236	0.4231	–0.2267	0.0878	–0.5115	–0.2066	–0.0064	–0.4049	0.1756	–0.2471	0.0935	–0.0992	0.1771	0.0898

was placed in the Sumatran lineage with a 79.5% PsP and in the west peninsular lineage with a 20.2% PsP. The DAPC placed it in the west peninsular lineage with a 100% PsP. All other individuals from the east peninsular lineage, Sumatra, and Borneo grouped together with a 98.9–99.9%, 83.0–99.6%, and 88.2–99.1% PsP, respectively. These data were taken as statistical justification for downstream statistical comparisons among the four major lineages. Given the results of both analyses, we consider the placement of THNHM 01841 in the Sumatran lineage as an anomaly. For downstream analyses, it was considered part of the west peninsular lineage and its placement therein is discussed below.

The PCA and DAPC (Fig. 3) were congruent with the PCoA (Fig. 4) in showing separation among the lineages although PERMANOVA analyses revealed the PCA was slightly more discriminating (Table 5). All three analyses recovered complete separation between the east and west peninsular lineages along the collective ordination of the first two axes and all recovered reasonably complete separation of the Bornean and Sumatran lineages from the west peninsular lineage. Principle component (PC) 1 of the PCA accounted for 51.4% of the variation in the data set and loaded most heavily for head size (HH, HL, HW, EE, NE) and crus length (CL) (Table 4; Fig. 3). PC2 accounted for an additional 10.7% of the variation and loaded most heavily for interorbital distance (IO) and orbital diameter (OD). The PERMANOVA analyses indicated that all the centroid locations in the PCA are statistically significantly different from one another (Table 5). The only centroid locations not significantly different in the PCoA were between the Bornean and east peninsular lineages and the Bornean and Sumatran lineages (*p*-adjusted = 0.25 and 1.00, respectively). Although significant, the centroid placement in the PCA of the Bornean and Sumatran lineages was far more similar ($F = 3.39$; *p*-adjusted = 0.02) than that between the east and west peninsular lineages ($F = 102.02$; *p*-adjusted = 0.0001). This was mirrored in the PCoA, bearing an F ratio of 1.12 (*p*-adjusted = 1.00) between the Bornean and Sumatran lineages and an F ratio of 53.62 (*p*-adjusted = 0.0001) between the east and west peninsular lineages.

The ANOVA analyses and subsequent Tukey-HSD *post hoc* tests of the meristic and morphometric data sets recovered various combinations of statistically different mean values between various combinations of lineage pairs at varying levels of significance (Fig. 5; Tables 6, 7, 8, 9). The analyses recovered the west peninsular lineage and the Bornean lineage as being the most significantly divergent species pair in both the meristic and morphometric data set. The east and west peninsular lineages were also significantly

Table 5. PERMANOVA summary statistics for the centroid placement between all species pairs from the PCA and PCoA analyses. Shaded cells denote insignificant adjusted *p*-values.

Lineage pairs	***F* ratio**	**R^2**	***p*-value**	**adjusted *p*-value**
PCA statistics				
cf. *albofasciolatus* vs *hulk* **sp. nov.**	5.53231	0.11399	0.00014	0.00084
cf. *albofasciolatus* vs cf. *albomaculatus*	3.38702	0.23542	0.00411	0.02471
cf. *albofasciolatus* vs *smithii*	14.8605	0.26602	2.00E-05	0.00011
hulk **sp. nov**. vs cf. *albomaculatus*	13.74370	0.24655	2.00E-05	0.00012
hulk **sp. nov**. vs *smithii*	102.01761	0.58624	2.00E-05	0.00012
cf. *albomaculatus* vs *smithii*	8.29619	0.17177	6.00E-05	0.00036
PCoA statistics				
cf. *albofasciolatus* vs *hulk* **sp. nov.**	1.83536	0.04387	0.04194	0.25163
cf. *albofasciolatus* vs cf. *albomaculatus*	1.11739	0.21835	0.50000	1.00000
cf. *albofasciolatus* vs *smithii*	6.80440	0.22089	0.00032	0.00191
hulk **sp. nov**. vs cf. *albomaculatus*	5.34969	0.11796	0.00018	0.00107
hulk **sp. nov**. vs *smithii*	53.62436	0.47194	2.00E-05	0.00011
cf. *albomaculatus* vs *smithii*	3.93881	0.14098	0.00046	0.00275

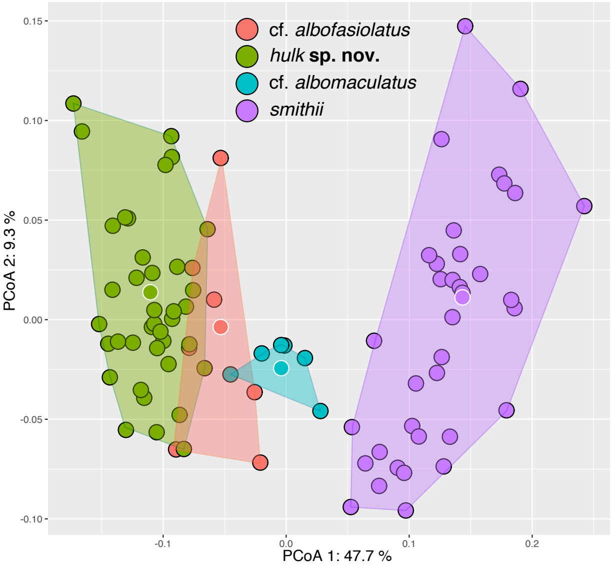

Figure 4. PCoA of concatenated meristic and morphometric data of species of the *Gekko smithii* complex.

well-separated in both data sets. Nonetheless, despite many of these characters having statistically different mean values between the eastern and western lineages, their ranges overlap considerably, rendering them uninformative as discretely diagnostic characters. Numeric and morphometric trends in these characters among all the lineages are illustrated in Figure 6.

Geckos from the west peninsular lineage have a considerable amount of dark dorsal blotching in the interspaces between the transversely aranged white spots which often tend to form bands (Fig. 7). Dorsal blotching is faint to absent in geckos from the east peninsular lineage or appears as fine dark speckling. Geckos from the west peninsular lineage also have a thin dark nuchal loop running from the back of one eye to the back of the other eye. The nuchal loop is usually absent in geckos from the east peninsular lineage, and if present, it is very faint and usually does not contact the eyes. The white dorsal spots on the body of geckos from the west peninsular lineage tend to be larger and surround the dorsal tubercles or border them posteriorly, whereas in geckos from the east peninsular lineage, the spots are usually very small and restricted to the tubercles and/or border them anteriorly.

Given that the multivariate and univariate diagnoses corroborate the geographically structured phylogenetic delimitation of distinct allopatric mitochondrial lineages within *Gekko smithii* across prominent biogeographic barriers (i.e. mountain ranges and seaways), we hypothesize these are non-reticulating lineages that should be designated as separate species. Because Penang Island is the type locality for *Gekko smithii* (Gray 1842), individuals in the western peninsular lineage retain that name and a new name is proposed for the eastern peninsular lineage. Based on the descriptions of *Platydactylus albomaculatus* Giebel (Giebel, 1861) from Bangka Island, Sumatra, the specific epithet *albomaculatus* is available for the Sumatran populations (see discussion below). Based on the description of *Gecko albo-fasciolatus* (Günther, 1867) from Banjermassin (= Banjarmasin), Kalimantan, Indonesian Borneo (see Rösler et al. 2011), the specific epithet *albofasciolatus* is available for the Bornean populations (see discussion below).

Taxonomy

Gekko smithii Gray, 1842

Figures 7, 8

Gecko Smithii: Gray 1842:57; Stoliczka 1870:161

Platydactylus Stentor: Cantor 1847:624

Gecko Smithii: Duméril 1856:449; Anderson 1871:150; Müller 1882:124

Gecko Stentor: Günther 1864:103; Boulenger 1889:143, 1890:103, 1912:51 (in part); Müller 1895:832 (in part); Flower 1896:867 (in

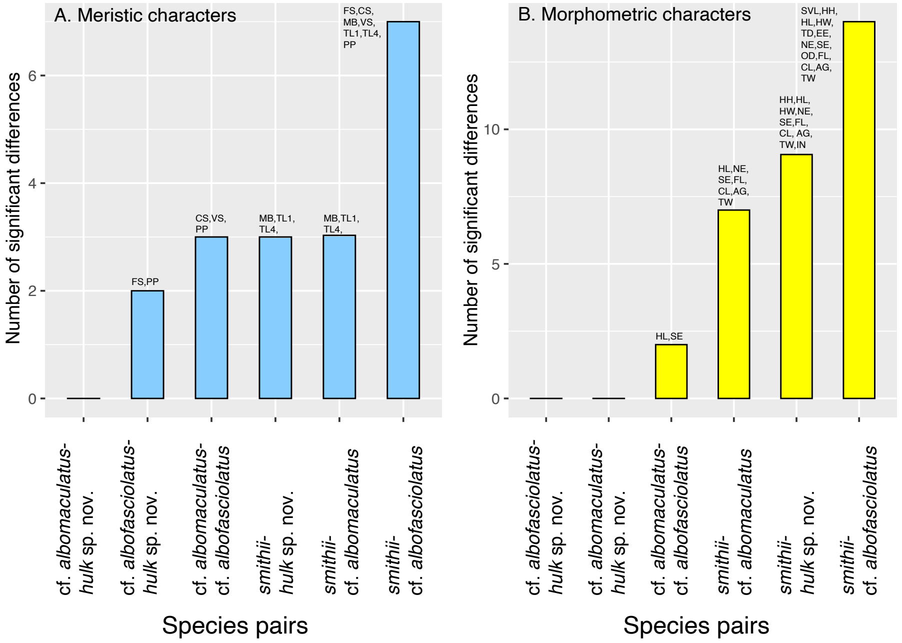

Figure 5. A. Bar graph showing the number of meristic characters bearing statistically significant mean differences between each species pair. B. Bar graph showing the number of mensural characters bearing statistically significant mean differences between each species pair.

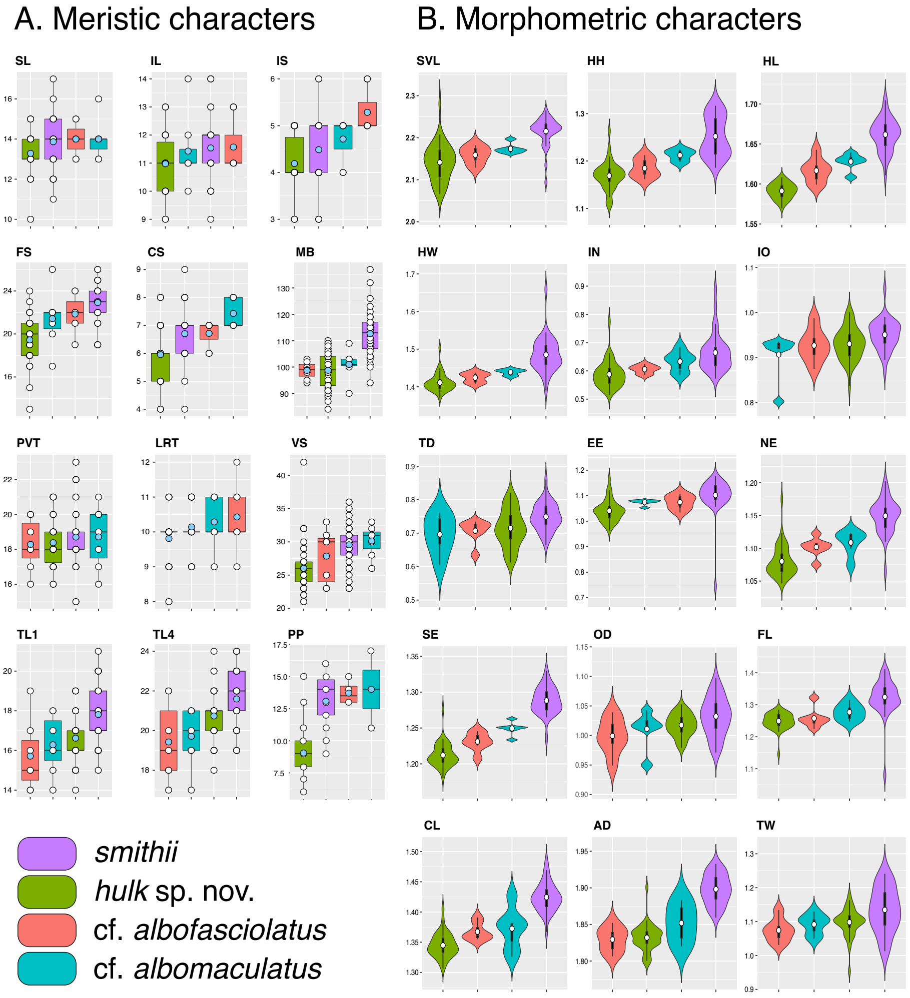

Figure 6. A. Box plots of meristic characters showing the range, mean (blue dot), and 50% quartile (rectangle) for each character. White dots are y-axis values. B. Violin plots of mensural characters embedded with boxplots showing the range, frequency, mean (white dot), and 50% quartile (black rectangle) for each character. Violin plots are vertically oriented mirror-imaged frequency diagrams.

Table 6. Summary statistics from ANOVA and TukeyHSD tests of meristic data. difference = the average difference between species. lower and upper = confidence interval of the average differences. Shaded cells denoted species pairs bearing significantly different mean values.

Infralabials (IL)	**difference**	**lower**	**upper**	**p adj**		**Longitudinal tubercle rows (LRT)**	**diff**	**lower**	**upper**	**p adj**
cf. *albofasciolatus-hulk* **sp. nov**.	–0.5952	–1.7145	0.5241	0.5074		cf. *albofasciolatus-hulk* **sp. nov**.	–0.2857	–1.0020	0.4305	0.7238
cf. *albomaculatus-hulk* **sp. nov**.	–0.1429	–1.6084	1.3227	0.9941		cf. *albomaculatus-hulk* **sp. nov**.	–0.1429	–1.0806	0.7949	0.9784
smithii-hulk **sp. nov**.	–0.0309	–1.1610	1.0992	0.9999		*smithii-hulk* **sp. nov**.	–0.6178	–1.3409	0.1054	0.1213
cf. *albomaculatus*-cf. *albofasciolatus*	0.4524	–0.6669	1.5717	0.7157		cf. *albomaculatus*-cf. *albofasciolatus*	0.1429	–0.5734	0.8591	0.9535
smithii-cf. *albofasciolatus*	0.5644	–0.0538	1.1825	0.0863		*smithii*-cf. *albofasciolatus*	–0.3320	–0.7276	0.0635	0.1318
smithii-cf. *albomaculatus*	0.1120	–1.0181	1.2420	0.9938		*smithii*-cf. *albomaculatus*	–0.4749	–1.1980	0.2482	0.3198
Internasals (IS)						**Ventral scales (VS)**				
cf. *albofasciolatus-hulk* **sp. nov**.	–0.5952	–1.7145	0.5241	0.5074		cf. *albofasciolatus-hulk* **sp. nov**.	–1.8333	–5.5633	1.8967	0.5736
cf. *albomaculatus-hulk* **sp. nov**.	–0.1429	–1.6084	1.3227	0.9941		cf. *albomaculatus-hulk* **sp. nov**.	2.2857	–2.5980	7.1694	0.6125
smithii-hulk **sp. nov**.	–0.0309	–1.1610	1.0992	0.9999		*smithii-hulk* **sp. nov**.	1.7104	–2.0554	5.4762	0.6352
cf. *albomaculatus*-cf. *albofasciolatus*	0.4524	–0.6669	1.5717	0.7157		cf. *albomaculatus*-cf. *albofasciolatus*	4.1190	0.3891	7.8490	0.0244
smithii-cf. *albofasciolatus*	0.5644	–0.0538	1.1825	0.0863		*smithii*-cf. *albofasciolatus*	3.5438	1.4837	5.6038	0.0001
smithii-cf. *albomaculatus*	0.1120	–1.0181	1.2420	0.9938		*smithii*-cf. *albomaculatus*	–0.5753	–4.3411	3.1905	0.9782
Frontal bone scales (FS)						**Subdigital lamellae on first toe (TL1)**				
cf. *albofasciolatus-hulk* **sp. nov**.	–2.4048	–4.5951	–0.2144	0.0256		cf. *albofasciolatus-hulk* **sp. nov.**	0.9048	–0.6002	2.4098	0.3986
cf. *albomaculatus-hulk* **sp. nov**.	–0.4286	–3.2965	2.4393	0.9795		cf. *albomaculatus-hulk* **sp. nov**.	0.5714	–1.3991	2.5419	0.8725
smithii-hulk **sp. nov**.	1.0618	–1.1496	3.2732	0.5925		*smithii-hulk* **sp. nov**.	2.0965	0.5771	3.6160	0.0028
cf. *albomaculatus*-cf. *albofasciolatus*	1.9762	–0.2142	4.1666	0.0920		cf. *albomaculatus*-cf. *albofasciolatus*	–0.3333	–1.8383	1.1717	0.9379
smithii-cf. *albofasciolatus*	3.4665	2.2568	4.6763	0.0000		*smithii*-cf. *albofasciolatus*	1.1918	0.3606	2.0229	0.0017
smithii-cf. *albomaculatus*	1.4903	–0.7211	3.7018	0.2972		*smithii*-cf. *albomaculatus*	1.5251	0.0056	3.0445	0.0488
Chin scales (CS)						**Subdigital lamellae on fourth toe (TL4)**				
cf. *albofasciolatus-hulk* **sp. nov**.	–0.7619	–1.7015	0.1777	0.1538		cf. *albofasciolatus-hulk* **sp. nov**.	1.3095	–0.1772	2.7963	0.1043
cf. *albomaculatus-hulk* **sp. nov**.	0.7143	–0.5160	1.9446	0.4299		cf. *albomaculatus-hulk* **sp. nov**.	0.2857	–1.6609	2.2323	0.9806
smithii-hulk **sp. nov**.	–0.0116	–0.9603	0.9371	1.0000		*smithii-hulk* **sp. nov**.	2.1660	0.6650	3.6670	0.0016
cf. *albomaculatus*-cf. *albofasciolatus*	1.4762	0.5365	2.4158	0.0005		cf. *albomaculatus*-cf. *albofasciolatus*	–1.0238	–2.5105	0.4629	0.2788
smithii-cf. *albofasciolatus*	0.7503	0.2314	1.2693	0.0016		*smithii*-cf. *albofasciolatus*	0.8565	0.0354	1.6776	0.0375
smithii-cf. *albomaculatus*	–0.7259	–1.6745	0.2228	0.1945		*smithii*-cf. *albomaculatus*	1.8803	0.3793	3.3813	0.0079
Midbody scales (MB)						**Precloacal pores (PP)**				
cf. *albofasciolatus-hulk* **sp. nov**.	0.0238	–7.8616	7.9092	1.0000		cf. *albofasciolatus-hulk* **sp. nov**.	–4.6912	–7.8552	–1.5271	0.0015
cf. *albomaculatus-hulk* **sp. nov**.	2.2857	–8.0387	12.6102	0.9379		cf. *albomaculatus-hulk* **sp. nov**.	0.2500	–4.0986	4.5986	0.9987
smithii-hulk **sp. nov**.	13.9614	6.0002	21.9226	0.0001		*smithii-hulk* **sp. nov**.	–0.6136	–3.7085	2.4812	0.9512
cf. *albomaculatus*-cf. *albofasciolatus*	2.2619	–5.6235	10.1473	0.8760		cf. *albomaculatus*-cf. *albofasciolatus*	4.9412	1.3757	8.5067	0.0033
smithii-cf. *albofasciolatus*	13.9376	9.5826	18.2926	0.0000		*smithii*-cf. *albofasciolatus*	4.0775	2.2389	5.9161	0.0000
smithii-cf. *albomaculatus*	11.6757	3.7145	19.6369	0.0013		*smithii*-cf. *albomaculatus*	–0.8636	–4.3678	2.6406	0.9117

part), 1899:634 (in part); Annandale 1906:92; De Rooij 1915:57 (in part)
Gecko Stentor: Theobald 1876:72
Gekko stentor: Brongersma 1934:165
Gekko smithi: Smith 1935:113 (in part); Taylor 1963:803 (in part); Biswas 1984:477 (in part)
Gecko smithii: Mertens 1946:16
Gekko gecko: Biswas and Sanyal 1977:111 (in part)
Gekko smithii: Wermuth 1965:40 (in part); Kluge 1967:135 (in part); Grossmann and Ulber 1990:9; Kluge 1991:10 (in part); Ota et al. 1991:147; Manthey and Grossmann 1997:234 (in part); Grismer 2011a:127 (in part), 2011b:469 (in part)
Gekko albofasciolatus: Ota et al. 1991:150 (in part)
Gekko (*Gekko*) *smithii*: Wood et al. 2020a:7 (in part)
Gekko cf. *smithii*: Chandramouli et al. 2021:108 (in part)

Non-technical books, field guides, and pockets guides are not listed

Diagnosis. *Gekko smithii sensu stricto* herein after referred to as *G. smithii* unless noted otherwise can be separated from all other species of *Gekko* in the *G. smithii* species complex by having the combination of a maximum SVL of 191.1 mm, 11–17 supralabials, 9–14 infralabials, 3–6 internarial scales, 19–26 frontal scales, 4–9 chin scales, 94–137 midbody scales, 17–23 paravertebral tubercles, 8–11 longitudinal rows of tubercles, 23–35 ventral scales, 15–20 1st toe subdigital lamellae, 19–24 4th toe lamellae; 13–15 precloacal pores in males (absent in females); enlarged subcaudal scales; thin, white nuchal band at base of occiput composed of closely spaced spots; thin dark nuchal band contacting the eyes; large white ocelli surrounding dorsal tubercles or bordering them posteriorly in six or seven transverse rows; and a thick dark reticulum to diffuse banded dorsal pattern (Tables 9, 10).

Distribution. *Gecko smithii* ranges from southern Thailand south of the Isthmus of Kra from at least Khao Phanom Bencha National Park in Krabi and Khao Nan National Park in Nakhon Si Thammarat Province to the northern border of the Banjaran Titiwangsa in southeastern Thailand and northwestern Peninsular Malaysia. Its range continues southward along the west side of the Banjaran Titiwangsa to at least the state of Selangor but very likely farther as well (Figs 1, 7).

Stoliczka (1870) reports "*Gecko Smithii*" from Java based on a juvenile specimen (SVL 86.3 mm) specimen sent to him but not collected by him. However, his description of the color pattern is well within the range of variation of both *G. smithii* and *G. gecko.* Stoliczka (1870) stated his specimen had 12 longitudinal rows of "small flattened sub-equal granules [=longitudinal rows of dorsal tubercles], slightly varying in size on the posterior part of the body and especially at the sides". The dorsal tubercles of species in the *smithii* complex are distinctly raised and sub-conical in adults but less so in juveniles. Furthermore, of the 93 specimens of the *smithii* complex examined here, only one specimen from Borneo had 12 rows dorsal tubercles. The others ranged from 8–11. Awal Riyanto (pers com. in lit. 2021) says he nor

Supralabials (SL)					**Paravertebral tubercles (PVT)**				
cf. *albofasciolatus-hulk* **sp. nov**.	–0.7143	–1.9074	0.4789	0.4024	cf. *albofasciolatus-hulk* **sp. nov**.	0.0952	–1.6545	1.8450	0.9990
cf. *albomaculatus-hulk* **sp. nov**.	0.0000	–1.5622	1.5622	1.0000	cf. *albomaculatus-hulk* **sp. nov**.	0.4286	–1.8624	2.7195	0.9612
smithii-hulk **sp. nov**.	–0.1351	–1.3398	1.0695	0.9911	*smithii-hulk* **sp. nov**.	0.4170	–1.3496	2.1835	0.9261
cf. *albomaculatus*-cf. *albofasciolatus*	0.7143	–0.4789	1.9074	0.4024	cf. *albomaculatus*-cf. *albofasciolatus*	0.3333	–1.4164	2.0831	0.9591
smithii-cf. *albofasciolatus*	0.5792	–0.0798	1.2381	0.1055	*smithii*-cf. *albofasciolatus*	0.3218	–0.6446	1.2881	0.8194
smithii-cf. *albomaculatus*	–0.1351	–1.3398	1.0695	0.9911	*smithii*-cf. *albomaculatus*	–0.0116	–1.7781	1.7550	1.0000

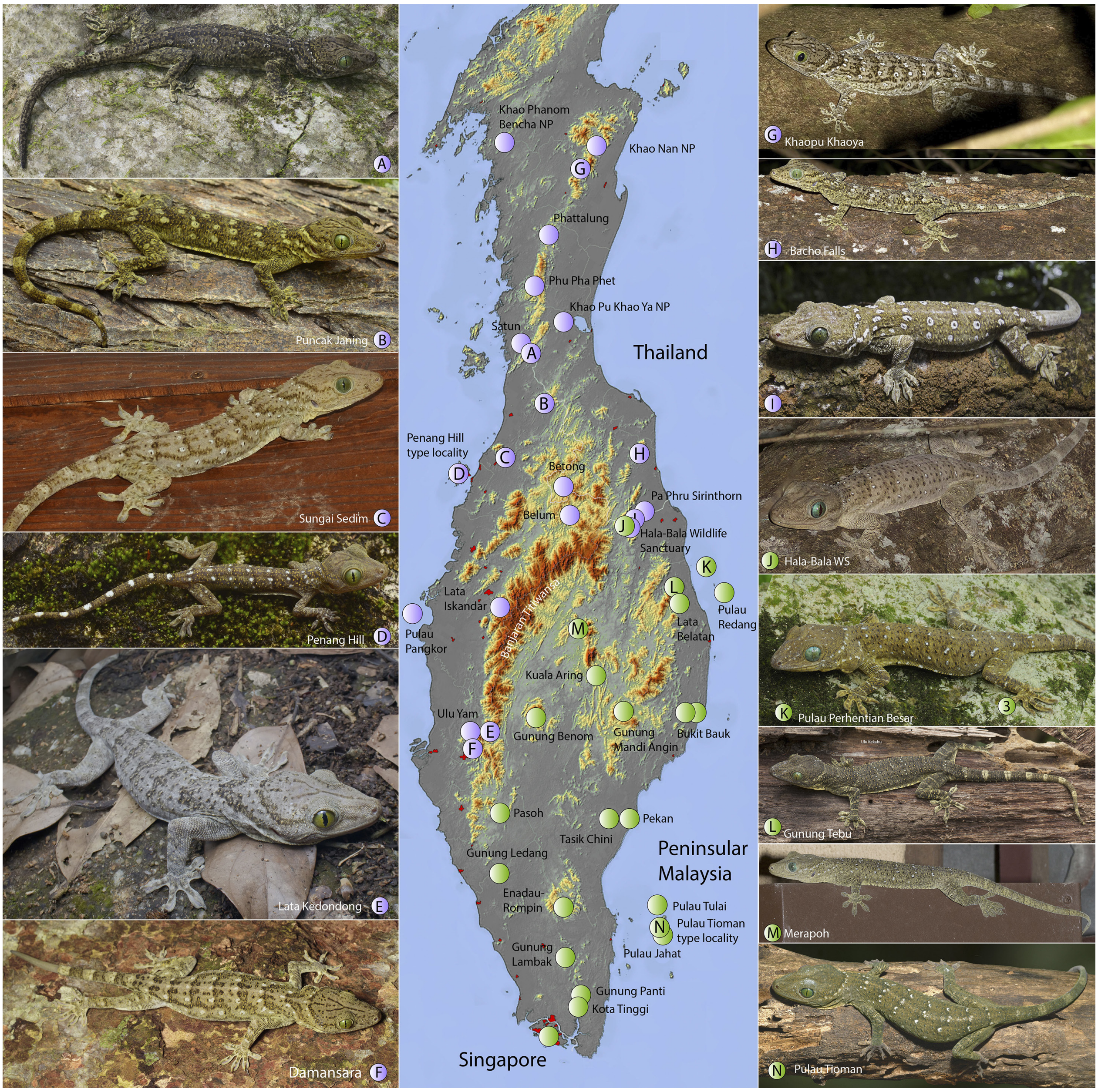

Figure 7. Distribution and color pattern variation in *Gekko smithii* and *G. hulk* **sp. nov**. on the Thai-Malay Peninsula. A. *Gekko smithii* (LSUHC 15052) from Perlis State Park, Perlis, Peninsular Malaysia. B. *Gekko smithii* (LSUDPC 12884) from Puncak Janing, Kedah, Peninsualr Malaysia. C. *Gekko smithii* (LSUHC 9626) from Sedim, Kedah, Peninsular Malaysia. D. *Gekko smithii* (LSUDPC 12869) from Penang Hill (type locality), Penang, Peninsular Malaysia. E. *Gekko smithii* (LSUDPC 12886) from Lata Kedondong, Selangor, Peninsular Malaysia. F. *Gekko smithii* (LSUDPC 12887) from Kota Damansara, Selangor, Peninsular Malaysia. G. *Gekko smithii* (LSUDPC 11174) from Khaopu Khaoya, Nakhon Si Thamarat Province, Thailand. H. *Gekko smithii* (LSUDPC 11173) from Bacho Falls, Narathiwat Province, Thailand. I. *Gekko smithii* (LSUDPC 12878) from the Weang District, Narathiwat Province, Thailand. J. *Gekko hulk* **sp. nov**. (LSUDPC 12880) from the Hala-Bala Wildlife Sanctuary, Narathiwat Province, Thailand. K. *Gekko hulk* **sp. nov**. (LSUHC 8696) from Pulau Perhentian Besar, Terengganu, Peninsular Malaysia. L. *Gekko hulk* **sp. nov.** (LSUDPC 7991) from Gunung Tebu, Terengganu, Peninsular Malaysia. M. *Gekko hulk* **sp. nov**. (LSUDPC 12897) from Merapoh, Pahang, Peninsular Malaysia. N. *Gekko hulk* **sp. nov**. (LSUDPC 12897) from Pulau Tioman, Pahang, Peninsular Malaysia. Photographs by L. Lee Grismer (A, K, L, N), Evan S. H. Quah (B, C, D), Kurt H. P. Guek (E), Steven Wong (F), Henrick Bringsøe (G, H); Parinya Pawangkhanant (I), Ian Dugdale (J), and Nick Baker (M). Unannotated circles denote localities of specimens or photographs examined here or verified from other publications as well as vouchered samples in the literature.

any of his colleagues working in Java have ever seen *G. smithii*. Photographic material and specimens we have examined from Java cataloged as *G. smithii* in the Zoological Museum Amsterdam, now officially part of Naturalis Biodiversity Center in Leiden, are *G. gecko*. We believe reports of *G. smithii* from Java stem from the possible misidentification of this species by Stoliczka (1870) as no new naturally occurring populations have been reported or observed to our knowledge. The less likely scenario exists, however, that Stoliczka described a juvenile

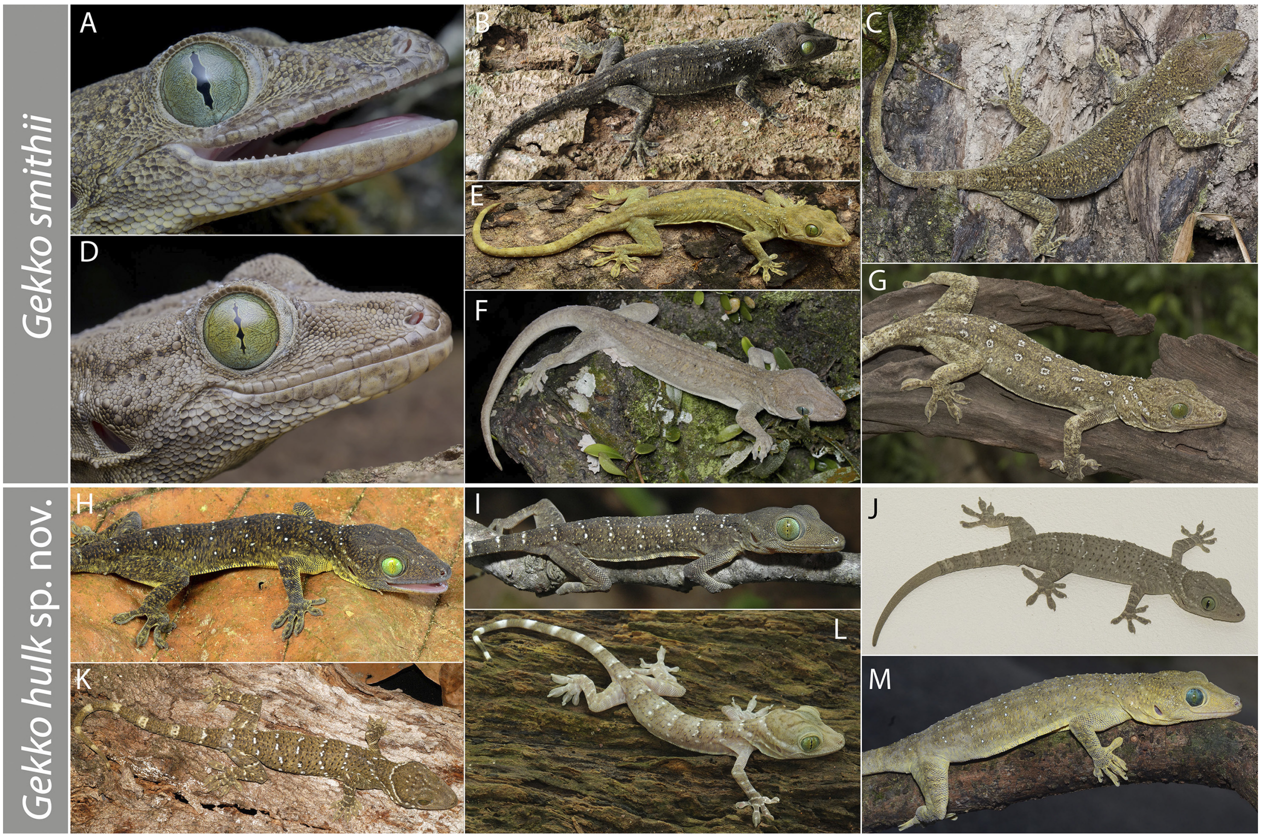

Figure 8. Geographic variation in *Gekko smithii* (A–G) and *G. hulk* **sp. nov**. (H–M). A. *Gekko smithii* (LSUDPC 12899) from Ulu Yam, Selangor, Peninsular Malaysia. B. *Gekko smithii* (LSUHC 4959) from Pulau Pangkor, Perak, Peninsular Malaysia. C. *Gekko smithii* (LSUDPC 12898) from Ulu Yam, Selangor, Peninsular Malaysia. D. *Gekko smithii* (LSUDPC 12895) from Kota Damansara, Selangor, Peninsular Malaysia. E. *Gekko smithii* (LSUDPC 12903) from Bukit Panchor, Penang, Peninsular Malaysia. F. *Gekko smithii* (LSUDPC 12902) from Ulu Yam, Selangor, Peninsular Malaysia. G. *Gekko smithii* (THNHM 01844) from Phu Pha Phet, Satun, Province, Thailand. H. *Gekko hulk* **sp. nov.** (LSUDPC 12912) from Lata Kekabu, Setiu, Terengganu, Peninsular Malaysia. I. *Gekko hulk* **sp. nov.** (LSUDPC 8696) from Endau-Rompin, Johor, Peninsular Malaysia. J. *Gekko hulk* **sp. nov**. (LSUDPC 12953) from the Hala-Bala Wildlife Sanctuary, Narathiwat Province, Thailand. K. *Gekko hulk* **sp. nov**. (LSUHC 5152) from the Tekek-Juara Trail, Pulau Tioman, Pahang, Peninsular Malaysia. L. *Gekko hulk* **sp. nov**. (LSUHC 5873) from Kota Tinggi, Peninsular Malaysia. M. *Gekko hulk* **sp. nov**. (LSUDPC 12955) from Hutan Lipur Sekayu, Terengganu, Peninsular Malaysia. Photographs by Kurt H. P. Guek (A, C, D, F), L. Lee Grismer (B, K, L), Evan S. H. Quah (E, H), Michael Cota (G, J), M. A. Muin (I) and Syed A. Rizal (M).

G. albomaculatus from Bangka island, Indonesia as he notes "I have also added a complete description of the rare *Gecko smithii*, Gray, a specimen of which was sent to me from Java, and that of what appears to be a full grown specimen of *Tetragonosoma* [*Lycodon*] *effrene,* CANT., from the island Banca." The ambiguity in this sentence could mean these two species were sent to him from Java but were collected on Bangka Island.

Stoliczka (1870) reported *Gekko smithii* (as *Gecko stentor*) from the coastal cities of Chittagong, Bangladesh and Akyab (= Sittwe = Sittway, Rakhine [Arakan] State), Myanmar which was followed by Theobald (1876), Annandale (1906), Boulenger (1912), and Taylor (1963). Smith (1935) stated "I do not know of any specimens to prove that this Gecko inhabits Burma, as has been stated." Ota et al. (1991) examined a specimen (MCZ 3120) putatively from "Burma: Rangoon" (=Myanmar, Yangon). MCZ has no other data on this specimen and the only species of *Gekko* we have seen in Yangon and throughout all of Myanmar over the last five years of field work has been *Gekko gecko.* Furthermore, the herpetological surveys in Myanmar by the California Academy of Sciences (www.calacademy.org/research/herpetology/myanmar) which resulted in the collection of over 14,000 specimens, found no *Gekko smithii.* We do not consider this species as part of the Burmese herpetofauna. However, the type material of *Gekko gecko azhari* Mertens, 1955 from Barkal, Chittagong Hill Tracts, Bangladesh does bear some resemblance to *G. smithii* in head shape, gular scales, and dorsal tubercle shape (Rösler 2001). Mahony et al. (2009) reported on 23 additional specimens from throughout the Chittagong Division that they considered *G. g. azhari.*

Variation in color pattern. The dorsal body tubercles of *Gekko smithii* from northernmost Peninsular Malaysia and Thailand north of the Kangar-Pattani Line (generally running from Gunung Jerai, Kedah, Peninsular Malaysia to Songkhla, Songkhla, Thailand) are surrounded by a large white ocellus whereas in southern populations, the ocelli are smaller and may only border the tubercles posteriorly (Figs 7, 8). Although the latter creates a general resemblance to *G. hulk* **sp. nov.**, the small white spots in

Table 7. Summary statistics from ANOVA and TukeyHSD tests of morphometric data. difference = the average difference between species. lower and upper = confidence interval of the average differences. Shaded cells denoted species pairs bearing significantly different mean values.

Snout-vent length (SVL)	**difference**	**lower**	**upper**	**p adj**		**Tympanum diameter (TD)**	**difference**	**lower**	**upper**	**p adj**
cf. *albofasciolatus*-*hulk* **sp. nov**.	-0.0317	-0.0854	0.0219	0.4086		cf. *albofasciolatus*-*hulk* **sp. nov**.	0.0239	-0.0594	0.1073	0.8730
cf. *albomaculatus*-*hulk* **sp. nov**.	-0.0031	-0.0762	0.0700	0.9995		cf. *albomaculatus*-*hulk* **sp. nov**.	0.0139	-0.0997	0.1275	0.9883
smithii-*hulk* **sp. nov** .	0.0490	-0.0060	0.1040	0.0971		*smithii*-*hulk* **sp. nov**.	0.0622	-0.0232	0.1476	0.2294
cf. *albomaculatus*-cf. *albofasciolatus*	0.0287	-0.0250	0.0823	0.4979		cf. *albomaculatus*-cf. *albofasciolatus*	-0.0100	-0.0934	0.0733	0.9888
smithii-cf. *albofasciolatus*	0.0807	0.0572	0.1043	0.0000		*smithii*-cf. *albofasciolatus*	0.0383	0.0017	0.0748	0.0370
smithii-cf. *albomaculatus*	0.0521	-0.0029	0.1070	0.0697		*smithii*-cf. *albomaculatus*	0.0483	-0.0371	0.1337	0.4481
Head height (HH)						**Eye-ear distance (EE)**				
cf. *albofasciolatus*-*hulk* **sp. nov**.	-0.0195	-0.0673	0.0283	0.7054		cf. *albofasciolatus*-*hulk* **sp. nov**.	-0.0188	-0.0744	0.0369	0.8101
cf. *albomaculatus*-*hulk* **sp. nov**.	0.0257	-0.0394	0.0908	0.7258		cf. *albomaculatus*-*hulk* **sp. nov**.	0.0118	-0.0640	0.0876	0.9764
smithii-*hulk* **sp. nov**.	0.0490	0.0000	0.0979	0.0499		*smithii*-*hulk* **sp. nov**.	0.0494	-0.0076	0.1064	0.1123
cf. *albomaculatus*-cf. *albofasciolatus*	0.0452	-0.0026	0.0930	0.0703		cf. *albomaculatus*-cf. *albofasciolatus*	0.0306	-0.0251	0.0862	0.4736
smithii-cf. *albofasciolatus*	0.0685	0.0475	0.0894	0.0000		*smithii*-cf. *albofasciolatus*	0.0681	0.0437	0.0925	0.0000
smithii-cf. *albomaculatus*	0.0233	-0.0257	0.0722	0.5957		*smithii*-cf. *albomaculatus*	0.0376	-0.0194	0.0946	0.3127
Head length (HL)						**Nares-eye distance (NE)**				
cf. *albofasciolatus*-*hulk* **sp. nov**.	-0.0129	-0.0348	0.0089	0.4091		cf. *albofasciolatus*-*hulk* **sp. nov**.	-0.0143	-0.0464	0.0178	0.6436
cf. *albomaculatus*-*hulk* **sp. nov**.	0.0216	-0.0083	0.0514	0.2354		cf. *albomaculatus*-*hulk* **sp. nov**.	0.0144	-0.0293	0.0580	0.8216
smithii-*hulk* **sp. nov**.	0.0574	0.0350	0.0798	0.0000		*smithii*-*hulk* **sp. nov**.	0.0534	0.0206	0.0862	0.0004
cf. *albomaculatus*-cf. *albofasciolatus*	0.0345	0.0126	0.0564	0.0006		cf. *albomaculatus*-cf. *albofasciolatus*	0.0287	-0.0034	0.0607	0.0957
smithii-cf. *albofasciolatus*	0.0704	0.0608	0.0800	0.0000		*smithii*-cf. *albofasciolatus*	0.0677	0.0536	0.0818	0.0000
smithii-cf. *albomaculatus*	0.0359	0.0135	0.0583	0.0004		*smithii*-cf. *albomaculatus*	0.0390	0.0062	0.0719	0.0135
Head width (HW)						**Snout-eye distance (SE)**				
cf. *albofasciolatus*-*hulk* **sp. nov**.	-0.0164	-0.0570	0.0242	0.7117		cf. *albofasciolatus*-*hulk* **sp. nov**.	-0.0102	-0.0329	0.0126	0.6415
cf. *albomaculatus*-*hulk* **sp. nov**.	0.0176	-0.0377	0.0730	0.8349		cf. *albomaculatus*-*hulk* **sp. nov**.	0.0266	-0.0044	0.0576	0.1171
smithii-*hulk* **sp. nov**.	0.0461	0.0045	0.0877	0.0243		*smithii*-*hulk* **sp. nov**.	0.0614	0.0381	0.0847	0.0000
cf. *albomaculatus*-cf. *albofasciolatus*	0.0340	-0.0066	0.0746	0.1313		cf. *albomaculatus*-cf. *albofasciolatus*	0.0368	0.0141	0.0596	0.0004
smithii-cf. *albofasciolatus*	0.0625	0.0446	0.0803	0.0000		*smithii*-cf. *albofasciolatus*	0.0716	0.0616	0.0816	0.0000
smithii-cf. *albomaculatus*	0.0284	-0.0132	0.0700	0.2819		*smithii*-cf. *albomaculatus*	0.0347	0.0114	0.0581	0.0012
Internarial distance (IN)						**Orbit diameter (OD)**				
cf. *albofasciolatus*-*hulk* **sp. nov**.	-0.0133	-0.0739	0.0474	0.9387		cf. *albofasciolatus*-*hulk* **sp. nov**.	0.0181	-0.0218	0.0580	0.6323
cf. *albomaculatus hulk* **sp. nov**.	0.0413	-0.0413	0.1240	0.5541		cf. *albomaculatus*-*hulk* **sp. nov**.	0.0249	-0.0295	0.0792	0.6253
smithii-*hulk* sp. nov.	0.0426	-0.0195	0.1048	0.2784		*smithii*-*hulk* **sp. nov**.	0.0380	-0.0028	0.0789	0.0772
cf. *albomaculatus*-cf. *albofasciolatus*	0.0546	-0.0060	0.1152	0.0923		cf. *albomaculatus*-cf. *albofasciolatus*	0.0068	-0.0331	0.0467	0.9696
smithii-cf. *albofasciolatus*	0.0559	0.0293	0.0825	0.0000		*smithii*-cf. *albofasciolatus*	0.0200	0.0025	0.0375	0.0192
smithii-cf. *albomaculatus*	0.0013	-0.0608	0.0634	0.9999		*smithii*-cf. *albomaculatus*	0.0132	-0.0277	0.0541	0.8302

Interorbital distance (IO)					**Forearm length (FL)**				
cf. *albofasciolatus-hulk* **sp. nov.**	0.0258	-0.0298	0.0815	0.6135	cf. *albofasciolatus-hulk* **sp. nov.**	-0.0063	-0.0553	0.0427	0.9864
cf. *albomaculatus-hulk* **sp. nov.**	0.0201	-0.0557	0.0959	0.8967	cf. *albomaculatus-hulk* **sp. nov.**	0.0094	-0.0574	0.0762	0.9822
smithii-hulk **sp. nov.**	0.0457	-0.0113	0.1028	0.1588	*smithii-hulk* **sp. nov.**	0.0764	0.0262	0.1266	0.0009
cf. *albomaculatus*-cf. *albofasciolatus*	-0.0057	-0.0614	0.0499	0.9930	cf. *albomaculatus*-cf. *albofasciolatus*	0.0157	-0.0333	0.0648	0.8318
smithii-cf. *albofasciolatus*	0.0199	-0.0045	0.0443	0.1482	*smithii*-cf. *albofasciolatus*	0.0827	0.0612	0.1042	0.0000
smithii-cf. *albomaculatus*	0.0256	-0.0314	0.0826	0.6380	*smithii*-cf. *albomaculatus*	0.0670	0.0167	0.1172	0.0044
Crus length (CL)					**Axilla-groin distance (AG)**				
cf. *albofasciolatus-hulk* **sp. nov.**	-0.0236	-0.0595	0.0123	0.3136	cf. *albofasciolatus-hulk* **sp. nov.**	0.0094	-0.0186	0.0374	0.8128
cf. *albomaculatus-hulk* **sp. nov.**	0.0105	-0.0384	0.0594	0.9416	cf. *albomaculatus-hulk* **sp. nov.**	0.0317	-0.0065	0.0699	0.1365
smithii-hulk **sp. nov.**	0.0597	0.0229	0.0964	0.0004	*smithii-hulk* **sp. nov.**	0.0821	0.0534	0.1108	0.0000
cf. *albomaculatus*-cf. *albofasciolatus*	0.0341	-0.0018	0.0700	0.0681	cf. *albomaculatus*-cf. *albofasciolatus*	0.0223	-0.0057	0.0503	0.1634
smithii-cf. *albofasciolatus*	0.0833	0.0676	0.0990	0.0000	*smithii*-cf. *albofasciolatus*	0.0727	0.0604	0.0850	0.0000
smithii-cf. *albomaculatus*	0.0492	0.0124	0.0859	0.0042	*smithii*-cf. *albomaculatus*	0.0504	0.0217	0.0791	0.0001
Tail width (TW)									
cf. *albofasciolatus-hulk* **sp. nov.**	0.0094	-0.0186	0.0374	0.8128					
cf. *albomaculatus-hulk* **sp. nov.**	0.0317	-0.0065	0.0699	0.1365					
smithii-hulk **sp. nov.**	0.0821	0.0534	0.1108	0.0000					
cf. *albomaculatus*-cf. *albofasciolatus*	0.0223	-0.0057	0.0503	0.1634					
smithii-cf. *albofasciolatus*	0.0727	0.0604	0.0850	0.0000					
smithii-cf. *albomaculatus*	0.0504	0.0217	0.0791	0.0001					

G. hulk **sp. nov.**, when not confined to the tubercles, tend to border them anteriorly. Although not as adept at substrate matching as *G. gecko* (see Figs 374–378 in Grismer 2011a), considerable variation has been observed wherein some individuals of *G. smithii* from Penang and Selangor states have very faded dark dorsal markings (Fig. 8F). Although rare, other geckos from Selangor state may resemble east peninsular lineage geckos in lacking a dark nuchal loop and having a darkly speckled dorsum (Fig. 8C). Iris color can also range from turquoise to lime green in the same population (Figs 8A, 8D) and along with ground color (which can vary from yellow to dark gray (Figs 8B, 8E)), is not a diagnostic character (contra Grossmann 2006). See Tables 9 and 10 for variation in morphology.

Natural history (adapted from Grismer 2011a,b). *Gekko smithii* is an arboreal nocturnal species that is well-established in all types of primary and secondary forests. It is particularly well-suited for inhabiting occupied and abandoned human dwellings along forest edges where it is most easily observed. In forested habitats, geckos occur on the trunks of large trees and boulders from where males are commonly heard calling during the day and early in the evening.

Gekko albofasciolatus (Günther 1867)

Rösler et al. (2011) and Wood et al. (2020a) considered *Gekko albofasciolatus* a valid species within *G.* (*Gekko*). Rösler et al. (2011) provide a detailed history of the taxonomy *G. albofaciolatus* which is best repeated here in its original form: “In the original description of *Gecko albo-fasciolatus* (= *Gekko albofasciolatus*), Günther (1867) only provided a vague type locality Polynesia with a question mark. Smith (1935) subsequently stated ‘type loc. unknown, probably Malay Archipelago.’ Later, Wermuth (1965) wrote ‘Polynesia’ as the type locality with the addition (fide Smith 1935), that the species probably occurs in the Indo-Australian Archipelago. According to Günther (1872), *G. smithii* occurs in the north of Borneo (Labuan, now Sabah) and *G. albofasciolatus* in the South (Banjermassin, Martapoura). We herein restrict the type locality of *G. albofasciolatus* to Banjermassin (= Banjar-masin), Kalimantan, Indonesia. While commenting on *G. albofasciolatus*, Günther (1872:589) stated that he received three specimens from Dr. Bleeker from Borneo under different names (*Platydactylus pentonopus*, *Platydactylus borneensis*, and *Hemidactylus zosterophorus*). From Günther’s (1872) footnotes it is obvious that he allocated all of Bleeker’s specimens to *G. albofasciolatus*. Of Bleeker’s species, only *Platydactylus borneensis* had been recorded from Borneo. The names *P. borneënsis* (= *P. born-*

Table 8. Summary statistics of the adjusted morphometric data. sd = 1 standard deviation. N = sample size. Character abbreviations are in the Materials and methods.

smithii	**SVL**	**HH**	**HL**	**HW**	**IN**	**IO**	**TD**	**EE**	**NE**	**SE**	**OD**	**FL**	**CL**	**AG**	**TW**
mean (±sd)	2.21 (±0.036)	1.22 (±0.023)	1.66 (±0.018)	1.45 (±0.03)	0.63 (±0.04	0.95 (±0.027)	0.74 (±0.03)	1.09 (±0.023)	1.13 (±0.014)	1.27 (±0.013)	1.05 (±0.032)	1.33 (±0.043)	1.41 (±0.021)	1.91 (±0.019)	1.08 (±0.054)
range	2.13–2.25	1.19–1.27	1.63–1.68	1.39–1.5	0.59–0.74	0.91–0.99	0.69–0.79	1.06–1.14	1.11–1.15	1.24–1.29	0.99–1.1	1.26–1.41	1.37–1.44	1.88–1.93	1.01–1.15
N	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11
***hulk* sp. nov.**															
mean (±sd)	2.14 (±0.038)	1.17 (±0.026)	1.59 (±0.009)	1.41 (±0.019)	0.58 (±0.037)	0.93 (±0.036)	0.72 (±0.056)	1.04 (±0.038)	1.08 (±0.019)	1.21 (±0.013)	1.02 (±0.019)	1.25 (±0.026)	1.34 (±0.017)	1.83 (±0.015)	1.1 (±0.041)
range	2.07–2.21	1.11–1.23	1.57–1.61	1.37–1.46	0.52–0.66	0.84–1.0	0.61–0.82	0.96–1.13	1.05–1.12	1.18–1.23	0.98–1.05	1.15–1.28	1.31–1.39	1.8–1.86	0.95–1.18
N	38	38	38	38	38	38	38	38	38	38	38	38	38	38	38
cf. *albomaculatus*															
mean (±sd)	2.17 (±0.012)	1.21 (±0.011)	1.63 (±0.011)	1.44 (±0.007)	0.63 (±0.036)	0.91 (±0.051)	0.7 (±0.059)	1.07 (±0.011)	1.11 (±0.019)	1.25 (±0.009)	1.01 (±0.032)	1.28 (±0.025)	1.37 (±0.035)	1.85 (±0.026)	1.09 (±0.029)
range	2.16–2.2	1.2–1.22	1.61–1.64	1.43–1.44	0.59–0.68	0.8–0.94	0.6–0.76	1.05–1.08	1.07–1.12	1.23–1.26	0.95–1.04	1.25–1.31	1.33–1.43	1.82–1.88	1.05–1.13
N	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
cf. *albofasciolatus*															
mean (±sd)	2.16 (±0.02	1.18 (±0.019	1.62 (±0.015	1.42 (±0.013	0.61 (±0.014	0.93 (±0.036	0.71 (±0.034	1.07 (±0.027	1.10 (±0.014	1.23 (±0.013	1.00 (±0.03	1.26 (±0.031	1.37 (±0.014	1.83 (±0.016	1.07 (±0.034
range	2.13–2.18	1.16–1.21	1.6–1.64	1.41–1.44	0.59–0.62	0.87–0.99	0.63–0.73	1.03–1.11	1.08–1.12	1.21–1.25	0.95–1.04	1.22–1.32	1.35–1.39	1.81–1.85	1.03–1.13
N	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7

eensis) and *H. zosterophorus* were introduced by Bleeker (1857) without formal species descriptions (see also Bleeker 1860). The type locality of *Platydactylus borneensis* (non *Pentadactylus borneensis* Günther, 1864 = *Aeluroscalabotes felinus* Günther, 1864; non *Tarentola borneensis* Gray, 1845 = *Tarentola delalandii* Duméril & Bibron, 1836) is 'Bandjermasin' and the type locality of *Hemidactylus zosterophorus* is 'Padang (ook op Nias)'. In his critical review of Bleeker's type specimens, Boulenger (1887) did not consider the taxa *Platydactylus borneensis* and *Hemidactylus zosterophorus*. According to Bauer (1994), both names are species inquirenda and Kluge (2001) listed them as nomina nuda (see also Rösler 2000). Therefore, the names *Platydactylus borneensis* Bleeker, 1857 and *Hemidactylus zosterophorus* Bleeker, 1857, which are according to Günther's (1872) statements younger, subjective synonyms of *Gekko albofasciolatus* Günther, 1867, are not available. The same concerns Günther's (1872) name *Platydactylus pentonopus*. Boulenger (1885) synonymized *G. albofasciolatus* with *G. smithii* (see also Wermuth 1965; Kluge 1991, 1993; Bauer 1994; Rösler 2000). De Rooij (1915) obviously also followed Boulenger (1885), because she listed the distribution of *G. albofasciolatus* based on Günther (1872) under the species *G. smithii*. Recently, Kluge (2001) revalidated *G. albo-fasciolatus* at the specific rank, but Malkmus et al. (2002) and Das (2004) did not consider *G. albofasciolatus* as part of the Bornean herpetofauna."

Günther (1867) noted that *Gekko albofasciolatus* had a reddish-olive dorsum marbled with grayish and a uniformly whitish venter. Specimens with a reddish-olive dorsum with gray marbling also occur in Sabah (Fig. 9E) and preserved material examined from western and eastern Borneo all have uniform whitish venters, although in life, some have faint-yellow marbling which presumably fades after preservation. Günther (1867) also noted his specimen had "a narrow horseshoe-shaped band across the neck, the convexity being directed backwards". This is clearly in reference to the nuchal band which was not present in specimens we examined or in photographs we acquired (Fig. 9). Contra to Das (2004, 2007), all Bornean specimens we examined had the characteristic dark Y-shaped marking on the head common to *G. smithii* and geckos of the eastern peninsular lineage (Figs 7, 8, 9). Grossmann (2006) illustrated a specimen from eastern Kalimantan (i.e. eastern Borneo) with a brown vertebral stripe and small white dorsal flecks. All adult Bornean specimens examined herein, have small white flecks and variable degrees of dorsal striping and ground color (Fig. 9). Therefore, dorsal color pattern is not a reliable character separating populations from Borneo west of the Iran Mountains and populations east of the Iran Mountains. Rösler et al. (2011) noted that northern Bornean populations might be different on the basis of Günther's *G. albofasciolatus* (eastern

Figure 9. Distribution and color pattern variation in *Gekko albofasciolatus* and *G.* cf. *albofasciolatus* in Borneo A. LSUDPC 12916 from Gunung Mulu, Sarawak, East Malaysia. B. LSUDPC 12918 from Gunung Mulu, Sarawak, East Malaysia. C. LSUDPC 12919) from Kelay Subdistrict, Kalimantan, Indonesia. D. LSUDPC 1293 from Kalimantan, Indonesia. E. LSUDPC 12949 from Kinabatangan River, Sabah, East Malaysia. F. LSUDPC 12924 from Lambir, Sarawak, East Malaysia. G. LSUDPC 12925 from Lambir, Sarawak, East Malaysia. H. LSUDPC 12929 from Gunung Gading, Sarawak, East Malaysia. Unannotated circles denote localities of specimens or photographs examined here or verified from other publications as well as vouchered samples in the literature. Photographs by Alan Watson www.alanwatsonfeatherstone.com (A), Wolfgang Grossmann (B, H), C. J. Franklin (C), Mistar Kamsi (D), Chien C. Lee (E), and Nick Baker (F,G).

Table 9. Summary statistics of the meristic data. sd = 1 standard deviation. N = sample size. Character abbreviations are in the Materials and methods.

	SL	IL	IN	FS	CS	MB	PVT	LRT	VS	TL1	TL4	PP
smithii												
mean (±sd)	13.7 (±1.48)	11.6 (±1.28)	4.5 (±0.75)	22.6 (±2.06)	6.7 (±1.03)	112.9 (±9.73)	19.1 (±1.94)	9.7 (±0.61)	29.2 (±3.17)	17.6 (±1.39)	21.4 (±1.5)	13.2 (**±1.95**)
range	11–17	9–14	3–6	19–26	4–9	94–137	17–23	8–11	23–35	15–20	19–24	13–15
N	27	27	27	27	27	27	27	27	27	27	27	23
***hulk* sp. nov.**												
mean (±sd)	13.3 (±0.94)	11 (±0.92)	4.2 (±0.55)	19.5 (±2.1)	6 (±0.91)	98.7 (±6.82)	18.4 (±1.31)	10.1 (±0.57)	26.0 (3.74)	16.6 (±1.27)	20.7 (±1.23)	8.7 (±1.85)
range	10–15	9–13	3–5	13–24	4–8	84–110	16–21	9–11	22–28	14–19	18–24	6–13
N	42	42	42	42	42	42	42	42	42	42	42	16
cf. *albomaculatus*												
mean (±sd)	14 (±1.00)	11.4 (±1.27)	4.7 (±0.49)	21.4 (±2.7)	7.4 (±0.53)	101 (±5.69)	18.7 (±1.8)	10.3 (±0.76)	30.1 (±2.41)	16.3 (±1.5)	19.7 (±1.5)	14.0 (±3.00)
range	13–16	10–14	4–5	17–26	7–8	90–109	16–21	9–11	26–33	14–18	17–21	11–17
N	7	7	7	7	7	7	7	7	7	7	7	3
cf. *albofasciolatus*												
mean (±sd)	14 (±0.82)	11.6 (±0.98	5.3 (±0.49)	21.9 (±1.77)	6.7 (±0.49)	98.7 (±3.35)	18.3 (±1.5)	10.4 (±0.98)	27.9 (±4.1)	15.7 (±1.8)	19.4 (±1.99)	13.6 (±0.96)
range	13–15	11–13	5 or 6	19–24	6 or 7	94–103	16–20	9–12	23–33	14–19	17–22	13–15
N	7	7	7	7	7	7	7	7	7	7	7	4

Borneo) having 26 rows of ventral scales versus 29–39 in *G. smithii* s.l. However, specimens examined from northern Borneo (N = 7) have 23–33 scale rows and a specimen examined from eastern Kalimantan at Kelay (Fig. 9C) has 27 scale rows. Therefore, at this point, other than the spotted nuchal band, there are no morphological or color pattern differences between *G. albofasciolatus* populations east of the Iran Mountains and populations west of the Iran Mountains (i.e. from the Malaysian states of Sarawak and Sabah and the Sultanate of Brunei). The molecular data clearly indicate that the Bornean samples from Sarawak are not conspecific with *G. smithii* s.s. or any other lineage (Fig. 2). Therefore, the name *albofasciolatus,* is available for Bornean populations. However, owing to an absence of molecular data from eastern populations, all populations west of the Iran Mountains are referred to as *G.* cf. *albofasciolatus* pending the outcome of a molecular analysis. We believe this approach is justified based on the fact that the Banjaran Titiwangsa of Peninsular Malaysia separate *G. smithii* and the east peninsular lineage and the Iran Mountains may be doing the same with populations from Borneo. Investigations on Bornean populations are currently underway (Grismer et al. unpubl.)

Resurrection of *Gekko albomaculatus* (Giebel, 1861)

Figure 10

Platydactylus albomaculatus: Giebel 1861:58; Boulenger 1889:143; Müller 1941:188

Gecko stentor: Boulenger 1885:185 (in part); 1890:103 (in part); de Rooj 1915:57 (in part)

Gecko fascoilatus: Boettger 1886:256

Gekko stentor: Brongersma 1934:165 (in part)

Gekko smithii: Ota, Hikida, and Matsui 1991:150 (in part); Kluge 1991:10 (in part), 2001:11 (in part); Ota and Nabhitabhata 1991:503 (in part); Grossmann and Mudrack 2004:627 (in part); Koch, McGuire, Arida, Riyanto, and Hamidy 2009:172 (in part); Rösler, Bauer, Heinicke, Greenbaum, Jackman, Nguyen, and Ziegler 2011:10 (in part)

Non-technical books, field guides, and pockets guides are not listed

Gray (1842) described *Gecko Smithii* from “Prince of Wales’ Island” (= Penang Island, Penang, Peninsular Malaysia). Cantor (1847)—apparently unaware of Gray’s previous description—created the junior synonym, *Platydactylus Stentor,* by describing additional material from “Pinang” (the Malay and Thai phonetic spelling of Penang) Island. Giebel (1861) described three new species of *Platydactylus*, one of which was *P. albomaculatus* from “Insel Bangka” (= Bangka Island, Bangka Belitung Province, Sumatra, Indonesia). Based on the descriptions of Gray (1842) and Cantor (1847), Günther (1864) removed Cantor’s *P. Stentor* from the genus *Platydactylus* and placed it in the genus “*Gecko”*. Günther (1864), however,

Table 10. Diagnostic character states (shaded cells) separating *Gekko hulk* **sp. nov.** from the other species of *G.* (*Gekko*). Data on *G. gecko*, *G. nutaphandi*, *G. reevesi*, *G. siamensis*, *G. stoliczkai*, and *G. verreauxi* come from Grossmann and Ulber (1990), Ota and Nabhitabhata (1991), Bauer et al. (2008), Rosler et al. (2011), and Chandramouil et al. (2021).

	albofasciolatus	***alblomaculatus***	***gecko***	***hulk* sp. nov.**	***nutaphandi***	***reevesi***	***siamensis***	***smithii***	***stoliczkai***	***verreauxi***
max SVL	165.1	157.4	185	161.3	117	173	150	191	128.4	155
precloacal pores (males)	13–15	11–17	12–16	6–13	17–22	13–20	10–13	13–15	13–15	11–13
rostral scale contacting nares	no	no	no	no	no	no	no	no	no	yes
occiput scales smaller than snout scales	yes	yes	no	yes	yes	no	yes	yes	yes	yes
longitudinal rows of tubercles	9–12	9–11	9–18	9–11	14	12–18	16–19	8–11	10–12	10–14
subcaudals enlarged	yes	yes	no	yes	yes	no	yes	yes	yes	yes
iris color	green	green	gold/copper/olive/brown	turquoise/green	red	gold/copper/olive/brown	green	turquoise/green	green	golden
solid, thin, white nuchal band	no	yes	no	no	no	no	no	no	no	no

made no mention of *P. albomaculatus,* and thus that name remained valid and his taxonomy was followed by several prominent authors of the time (e.g. Boulenger 1889, 1890, 1912; Müller 1895 first report from Sulawesi; Flower 1896, 1899; de Rooij 1915 and Smith 1930). Boettger (1886) synonymized *Gecko Stentor* Cantor from "Insel Nias" with (*Gecko*) *fasciolatus* (sic) Günther (1867). Additionally, Stoliczka's (1870) description of a specimen from Java as *Gecko Smithii* was most likely based on a specimen of *Gekko gecko*. It wasn't until Smith (1935) stated "Gray's description of *Gekko smithi,* brief though it is, cannot well apply to any other Gecko coming from Penang; I therefore reinstate his name, which has priority over *stentor.*" that *Platydactylus Stentor* formally became recognized as a junior synonym of *G. smithi.* Smith (1935) stated that *G. smithi* ranged throughout the Malay Peninsula as far north as Pattani [Thailand] and the Malay Archipelago. Grossmann and Ulber (1990) reverted to the original spelling of the specific epithet "*smithii*" following Mertens (1946).

Comparing the short description of the two syntypes of *Platydactylus albomaculatus* by Giebel (1861) and the slightly more detailed redescription of a lectotype (the larger of the two syntypes) by Müller (1941), we cannot differentiate them from the specimens examined from Sumatra, islands off the west coast of Borneo, or *G. smithii*. They can be putatively separated from the eastern peninsular lineage by the male having 15 precloacal pores as opposed to 6–13 (n=16) and having dark blotching on the body as opposed to its absence or reduction to fine speckling (Fig. 10G). Müller (1941) noted that the lectotype had a dark-brown horseshoe-shaped band on the back of the head running from eye to eye that was bordered posteriorly by a row of moderately large white blotches. Only some Sumatran specimens have a dark nuchal band and the white blotches are often fused, forming a thin white band that is unique to specimens from Sumatra and its adjacent islands (Fig. 10). Bangka Island is Indonesia's ninth largest island and lies less than 15 km off the southeastern coast of Sumatra from where *G.* "*smithii*" have been reported (e.g. de Rooij 1915; Fig. 10). The seaway between Bangka Island and mainland Sumatra is less than 25 m deep and these landmasses had broad intermittent subaerial connections with one another, Peninsular Malaysia, and Borneo over the last 10 million years (Hall 2013). Nonetheless, lacking sequence data from topotypic material and mainland Sumatra, the possibility exists, however unlikely, that the Bangka Island population is not conspecific with other Sumatran populations. The molecular data clearly indicate that the Nias and Banyak Islands populations are not *G. smithii* or any other lineage. Therefore, based on current geography and geographic history, we refer to these insular populations and mainland Sumatran populations as *G.* cf. *albomaculatus*. Investigations on these populations are currently underway (Grismer et al. unpubl.).

Figure 10. Distribution and color pattern variation in *Gekko albomaculatus* and *G.* cf. *albomaculatus* in Sumatra A. LSUDPC 12933 from Gunung Leuser NP, North Sumatra, Sumatra, Indonesia. B. LSUDPC 12934 (JAM 10261) from Pulau Nias, Sumatra, Indonesia. C. LSUDPC 12940 from Andalas University, Sumatra Barat, Sumatra, Indonesia. D. LSUDPC 12944 from Kecamatan Ngambur, Lampung, Sumatra, Indonesia. E. LSUDPC 12952 from Sum, Sumatra, Indonesia. F. LSUDPC 12924 from Sumber Rejio, Bengkuat Belimbing, Sumatra, Indonesia. G. Syntypes of *G. albomaculatus* from Banka Island, Sumatra, Indonesia. Unannotated circles denote localities of specimens or photographs examined here or verified from other publications as well as vouchered samples in the literature. Photographs by Andrea Molyneaux (A), Jimmy A. McGuire (B), Eric N. Smith (C, E), C. J. Franklin (D), Photo from Creative Commons Attribution Share Alike (F), and Frank Tillack (G).

Gekko hulk sp. nov.

Figures 7, 11, 12, 13

Gecko Stentor: Boulenger 1889:184 (in part), 1912:51 (in part); Müller 1895:832 (in part); Flower 1896:867 (in part), 1899:634 (in part); Laidlow 1901:306; de Rooij 1915:57 (in part)

Gekko smithi: Smith 1935:113 (in part); Taylor 1963:803 (in part); Jeffery 1997:145

Gekko smithii: Grossmann and Ulber 1990:9 (in part); Kluge 1991:10 (in part); Ota et al. 1991:147 (in part); Manthey and Grossmann 1997:234 (in part); Lim and Lim 1999: 143; Hien et al. 2001:14; Grismer et al. 2004:252; Grismer et al. 2002:27; Grismer et al. 2004:252; Grossmann and Tillack 2004:45, 2005:58; Grismer et al. 2006:160; Grismer 2011a:127 (in part), 2011b:469 (in part); Shahrudin 2013:83 (in part)

Gekko albofasciolatus: Kluge 1991:10 (in part)

Gekko albomaculatus: Kluge 1991:10 (in part)

Gekko sp. Rösler et al. 2011:11

Gekko (*Gekko*) *smithii*: Wood et al. 2020a:7 (in part)

Non-technical books, field guides, and pockets guides are not listed

Holotype. Adult male LSUHC 6284 from the Tekek-Juara trail on Pulau Tioman, Pahang, Peninsular Malaysia (2.821021°N 104.179596°E; 462 m) collected by Jesse L. Grismer, Perry L. Wood, Jr., and L. Lee Grismer on 2 July 2004.

Paratypes. All paratypes are from Peninsular Malaysia and were collected by various personnel from La Sierra

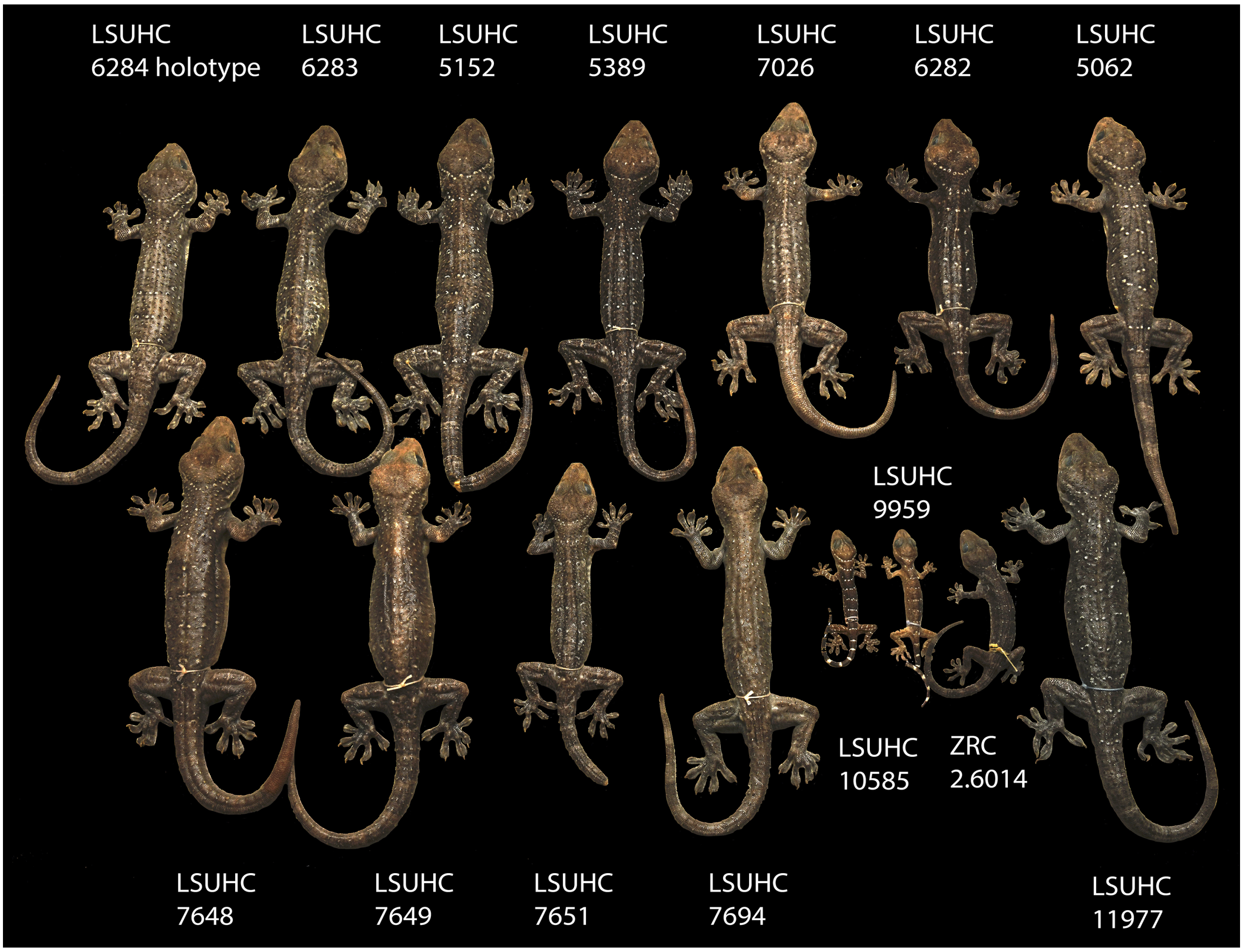

Figure 11. Type series of *Gekko hulk* **sp. nov**. from Peninsular Malaysia.

University, Universiti Sains Malaysia, Universiti Kebangsaan Malaysia, and the Department of Wildlife and National Parks Malaysia. Adult female LSUHC 6283 bears the same data as the holotype. Adult females LSUHC 5152 and 5399 from the upper Tekek-Juara trail on Pulau Tioman, Pahang (2.821021°N 104.179596°E; 462 m) collected on 3 March 2003. Adult female LSUHC 7026 from Pulau Tulai, Johor (2.909920°N 104.105315°E; 11 m) collected on 14 September 2004. Adult male LSUHC 5062 from Pulau Tulai, Johor (2.909920°N 104.105315°E; 11 m) collected on 17 August 2002. Adult male LSUHC 7648 from Endau-Rompin, Peta, Visitor center, Johor (2.530818°N 103.414191°E; 42 m) collected on 25 August 2005 by Perry L. Wood, Jr., Kin Onn Chan, and L. Lee Grismer. Adult female LSUHC 7649 and 7651 from Endau-Rompin, Peta, Visitor center, Johor (2.530818°N 103.414191°E; 42 m) collected on 25 August 2005 by Perry L. Wood, Jr., Kin Onn Chan, and L. Lee Grismer. Adult female LSUHC 7694 from Endau-Rompin, Peta, Sungai Semawak, Johor (2.529150°N 103.401173°E; 36 m) collected on 29 August 2005 by Perry L. Wood, Jr., Kin Onn Chan, Norhayati Ahmad, and L. Lee Grismer. Juvenile female LSUHC 10585 from Gunung Ledang, Johor (2.529150°N 103.401173°E; 36 m) collected on 31 May 2008, collector unknown 2008. Juvenile female LSUHC 9959 from Gunung Lambak, (2.029934°N 103.353323°E; 255 m). Juvenile male ZRC 2.6014 from FRIM, Pasoh, Negeri Sembian (2.968545°N 102.297043°E; 255 m) collected on 27 November 2008. Adult male LSUHC 1197 from Sungai Bubu, Terengganu (4.997105°N 102.953106°E; 174 m) collected on 1 September 2009 by L. Lee Grismer and Kin Onn Chan.

Diagnosis. *Gekko hulk* **sp. nov**. can be separated from all other species of *Gekko* in the *G. smithii* species complex by having the combination of a maximum SVL of 161.3 mm, 10–15 supralabials, 9–13 infralabilas, 3–5 internarial scales, 13–24 frontal scales, 4–8 chin scales, 84–110 midbody scales, 16–21 paravertebral tubercles, 9–11 longitudinal rows of tubercles, 22–28 ventral scales, 14–19 1st toe subdigital lamellae, 18–24 4th toe lamellae; 6–13 precolacal pores in males (absent in females); subcaudals enlarged; thin, white nuchal band at base of occiput composed of closely spaced spots; thin dark nuchal band absent or faded and never contacting eyes; small white ocelli confined to dorsal tubercles or their anterior margin in six or seven transverse rows; and no thick dark reticulum on body (Tables 9, 10).

Description of holotype (Fig. 12). Adult male SVL 147.5 mm; head moderate in length (HL/SVL 0.28), width (HW/HL 0.65), somewhat flattened, distinct from neck, triangular in dorsal profile; lores concave slightly anteriorly, weakly inflated posteriorly; prefrontal region concave; canthus rostralis rounded; snout elongate (SE/HL 0.41), rounded in dorsal profile; eye large (OD/HL 0.26), pupil vertical, margins crenulated; ear opening elliptical, obliquely oriented, moderate in size; eye to ear distance slightly less than diameter of eye; rostral rectangular, bordered posteriorly by large left and right supranasals and smaller azygous postrostral, bordered laterally by first supralabials; external nares seated anteriorly in nasal scale bordered anteriorly by rostral, dorsally by large anterior and smaller posterior supranasals, posteriorly by three small postnasals, ventrally by first and second supralabials; five internasals; 12 (R,L) rectangular supralabials, first supralabial slightly larger than second; 12(R) 10(L) infralabials tapering smoothly to angle of jaw; scales of rostrum and lores flat, larger than flat scales on top of head and occiput; scales of occiput intermixed with distinct, small tubercles; superciliaries elongate, largest dorsally; mental not enlarged, subtriangular, bordered laterally by first infralabials and posteriorly by left and right trapezoidal postmentals contacting medially for 60% of their length posterior to mental; one row of slightly enlarged, elongate chin scales extending posteriorly to fifth (R) and sixth (L) infralabial; gular and throat scales small, flat, juxtaposed, grading posteriorly into larger, smooth, imbricate, pectoral scales which grade into larger ventral scales.

Body slightly flattened, relatively long (AG/SVL 0.51) with well-defined ventrolateral folds; dorsal scales small, flat, juxtaposed, interspersed with larger, smooth subconical, regularly arranged tubercles; 110 longitudinal rows of scales at midbody; 17 paravertebral tubercles, those at midbody surrounded by 9–12 smaller scales; 10 longitudinal rows of tubercles at midbody; body tubercles extend from occiput onto base of tail forming transverse rows, terminating near end of original tail; smaller tubercles in temporal and postocular regions; 25 longitudinal rows of flat, imbricate, ventral scales much larger than dorsal scales between body folds; and eight large, pore-bearing, precloacal scales.

Forelimbs moderately robust, relatively short (FL/SVL 0.13); large, imbricate scales of upper arm and anterior surface of forearm larger than those on posterior surface which are interspersed with large tubercles; palmar scales flat, subimbricate; digits well-developed, inflected at penultimate interphalangeal joints, arising from digital pad; subdigital lamellae wide, transversely expanded forming digital pad; claws well-developed, claw base sheathed by a dorsal and lateral scale; digit I clawless; hind limbs more robust than forelimbs, moderate in length (CL/SVL 0.16), covered anteriorly by large, flat, imbricate scales, dorsally and posteriorly by much smaller flat, juxtaposed scales interspersed with large, subconical tubercles; ventral scales of hind limbs large, flat, imbricate, abruptly contacting small postfemoral scales; femoral pores absent; plantar scales flat, subimbricate; digits well-developed, inflected at penultimate interphalangeal joints, arising from digital pad; distal subdigital lamellae wide, transversely expanded forming digital pad; 15 transverse lamellae beneath digit I, 19 transverse lamellae beneath digit IV; claws well-developed, claw base sheathed by a dorsal and lateral scale; digit I clawless; small amount of webbing between digits I–IV.

Tail original, 139.0 mm in length, tapering to a point; dorsal scales flat, square, bearing transverse rows of six large, subconical tubercles; tubercle rows separated by six or seven transverse rows of dorsal scales; large, paired, median, transversely expanded subcaudal scales; and base of tail bearing hemipenal swellings, each with two conical postcloacal tubercles.

Color pattern (Figs 11, 12). Ground color of all dorsal surfaces yellowish-brown bearing slightly darker faint mottling; top of head bearing small white spots and dark-colored, diffuse Y-marking; thin white nuchal band composed of closely spaced spots extends from one ear opening to other, edged anteriorly by faint, dark-colored nuchal band running between postocular regions; incomplete series of obliquely aligned, small white spots immediately anterior to forelimb insertions parallel the white nuchal spots; series of five rows of transversely arranged, widely separated, small white spots between limb insertions, another between hind limb insertions; white spots on body generally confined to tubercles or border them anteriorly; limbs bearing incomplete, thin white bands; white spots on base of each digit and one or two more on each digit; venter beige, mottled with faint dark-colored markings, weakest in gular region, most dense in subcaudal region; and center of iris gold, transitioning distally to green then turquoise.

Variation (Figs 7, 8). Color pattern variation in *Gekko hulk* **sp. nov.** is not as extensive as that in *G. smithii.* The hue and intensity of the ground color changes from day to night and is generally lighter and less bold during evening hours. The description here is of the daytime coloration. The dorsal ground color in life can be dark brownish green, light-green, tan or yellowish brown. There are no thick, dark-colored reticulations on the dorsum although some specimens have faint, brown markings. The white dorsal spots are small and typically confined to the tubercles although in some specimens they may border the tubercles anteriorly or both. The light-colored caudal bands can vary in both width and boldness. In one specimen from Pulau Tioman (LSUHC 5152; Fig. 8K), the white nuchal spots form a solid band as in *G. albomaculatus*. The color pattern of hatchlings and juveniles is more boldly marked. Variation in morphology is presented in Tables 11 and 12.

Distribution. *Gekko hulk* **sp. nov.** ranges from at least the southeastern corner of southernmost Thailand in the Hala-Bala Wildlife Sanctuary, Narathiwat Province, southward east of the Banjaran Titiwangsa through Peninsular Malaysia to Singapore. It approaches the west coast of Peninsular Malaysia south the Banjaran Titiwangsa at Gunung Ledang, Johor. It is known from the east coast islands of Perhentian Besar and Redang, Terengganu in the north and from the islands of Tulai and Jahat, Johor and Tioman, Pahang in the south (Figs 1, 7).

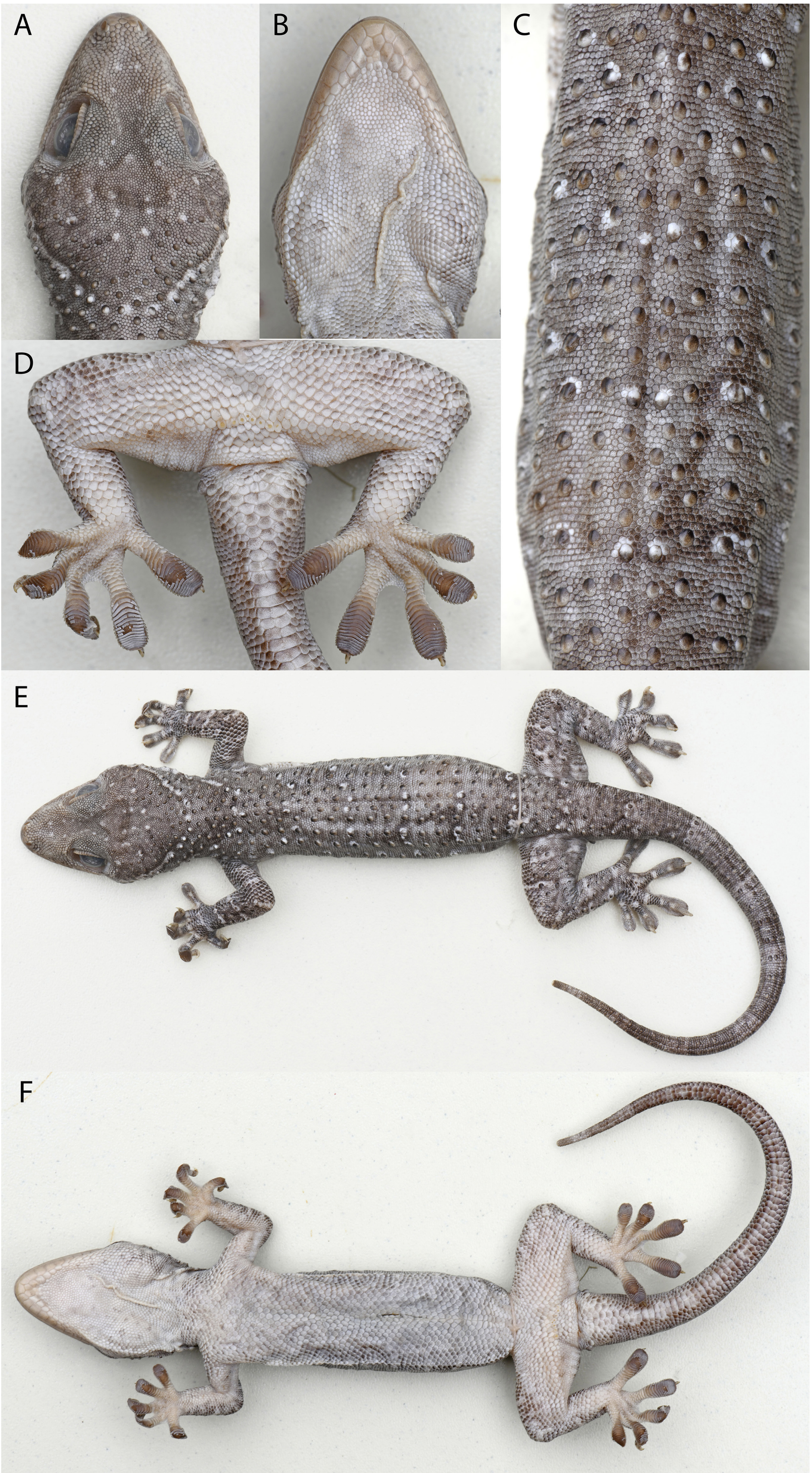

Figure 12. Holotype of *Gekko hulk* **sp. nov**. (LSUHC 6284) from the Tekek-Juara Trail, Pulau Tioman, Pahang, Peninsular Malaysia. A. Top of head. B. Gular region. C. Dorsum. D. Precloacal region and ventral surfaces of the hind limbs and tail. E. Complete dorsal view. F. Complete ventral view.

Table 11. Raw morphometric data of the type series of *Gekko hulk* **sp. nov**. from Peninsular Malaysia. All measurements are in millimeters. Abbreviations are in the Materials and methods.

Locality	LSUHC cat. no.	Sex	SVL	HH	HL	HW	IN	IO	TD	EE	NE	SE	OD	FL	CL	AG	TW
Pulau Tioman	holotype 6284	M	147.5	15.9	41.7	27.2	3.7	8.2	6.3	10.8	12.2	16.9	11.0	19.8	23.8	75.8	12.8
Pulau Tioman	5399	F	149.2	14.3	42.4	27.8	4.3	8.7	6.2	11.8	13.0	18.0	10.8	20.0	22.9	77.5	15.2
Pulau Tioman	6283	F	161.3	15.0	44.2	28.1	4.4	9.7	7.0	13.8	13.4	18.4	10.3	21.0	25.3	81.3	12.9
Pulau Tioman	5152	F	157.2	16.7	41.1	28.6	4.4	9.0	4.5	10.9	12.6	17.9	11.4	20.2	25.6	75.7	16.7
Pulau Tioman	7263	F	141.2	15.3	39.9	26.2	3.6	9.4	5.1	10.0	13.0	16.4	11.2	14.3	22.3	67.8	13.1
Pulau Tioman	6890	M	158.4	16.9	44.0	28.3	3.7	9.6	5.2	12.4	14.7	18.1	11.3	19.7	25.2	77.4	14.5
Pulau Tioman	5151	M	146.5	16.3	39.8	27.2	3.6	9.7	5.0	10.0	12.2	17.3	11.3	19.6	24.2	71.1	15.3
Pulau Tioman	4681	M	149.0	16.6	42.4	25.9	3.6	8.9	5.3	12.2	12.4	16.7	10.3	18.7	24.8	70.0	13.7
Pulau Tioman	5390	F	117.0	11.9	33.3	21.1	3.3	7.3	4.5	11.9	10.8	13.6	9.0	15.4	19.1	58.8	10.2
Pulau Tioman	7299	F	149.9	15.9	41.3	27.1	4.3	8.3	5.3	12.9	12.3	16.9	10.5	19.3	26.2	72.7	14.6
Pulau Tioman	6260	F	121.4	12.9	35.7	20.8	3.8	7.2	5.3	10.2	10.9	15.1	9.2	16.8	21.1	60.9	11.3
Pulau Tioman	5849	M	122.6	13.8	36.2	23.1	3.3	8.3	5.0	10.2	11.9	15.4	9.6	17.6	20.8	60.3	10.8
Pulau Tioman	7264	F	133.4	14.5	39.5	25.0	3.7	8.4	6.1	12.4	12.5	16.7	10.9	18.8	22.8	67.5	12.1
Pulau Tulai	4694	F	127.5	12.9	36.5	23.9	3.9	7.7	6.2	9.7	10.9	14.9	10.1	15.9	20.2	58.6	11.6
Pulau Tulai	6282	M	134.5	13.6	39.1	25.8	4.5	9.7	6.4	10.9	12.0	16.6	10.3	17.6	19.8	68.8	12.7
Pulau Tulai	7026	F	143.0	15.3	39.4	27.3	4.4	8.7	4.8	11.0	13.1	16.7	10.3	17.9	23.1	69.2	13.6
Pulau Tulai	4697	F	138.1	14.7	38.7	27.0	4.5	8.6	4.2	11.0	11.8	15.8	10.4	18.8	21.7	66.4	12.7
Pulau Tulai	6278	F	117.1	11.8	33.4	21.5	3.5	7.6	5.4	8.5	11.0	13.9	10.3	15.2	18.8	54.0	11.7
Pulau Tulai	5063	F	133.0	14.7	38.3	24.4	3.9	8.6	5.2	9.8	11.0	16.1	10.2	18.1	20.8	68.0	11.7
Pulau Tulai	5062	M	139.6	16.4	39.5	27.7	4.4	9.2	5.2	11.8	12.7	17.1	11.4	17.2	21.9	65.4	12.5
Pulau Tulai	6265	F	128.5	13.7	37.0	25.7	3.8	7.5	5.2	10.3	11.1	15.3	10.5	15.9	20.9	64.6	12.2
Pulau Tulai	6277	F	141.1	15.6	38.8	29.2	3.8	8.8	4.1	10.7	12.1	16.5	10.7	18.2	21.9	68.6	14.1
Pulau Tulai	7025	M	136.6	15.1	38.1	25.9	3.7	8.9	6.1	10.5	11.6	16.1	10.2	17.4	21.3	62.6	12.4
Pulau Tulai	7257	F	137.6	14.3	39.4	25.4	3.6	8.4	5.3	10.5	11.8	16.1	10.7	17.1	22.4	66.6	12.9
Pulau Tulai	3891	F	127.1	13.4	37.2	23.5	3.6	8.1	4.8	10.6	11.1	14.9	9.9	17.8	20.6	64.1	10.5
Pulau Tulai	5059	F	121.5	14.2	36.5	23.2	3.5	9.3	5.3	10.2	10.8	15.4	10.4	17.0	20.8	60.5	11.1
Pulau Tulai	7024	M	135.6	14.7	40.1	26.5	3.9	9.8	5.1	11.1	11.9	16.7	9.8	16.6	21.6	65.6	12.4
Pulau Tulai	5061	F	137.3	15.8	38.5	24.8	4.0	9.0	4.9	10.9	11.6	16.2	10.1	17.2	22.2	70.5	13.2
Pulau Tulai	3990	M	148.8	16.2	42.9	26.4	4.8	9.3	5.7	12.2	13.0	17.6	10.8	17.9	22.2	67.5	11.4
Pulau Tulai	5060	M	124.7	15.4	37.0	25.2	3.6	9.3	5.5	12.3	11.2	15.5	10.6	16.6	20.9	60.5	13.7
Pulau Tulai	7251	F	143.9	15.0	38.8	25.4	3.9	9.2	6.2	11.1	11.6	16.6	10.3	17.5	21.8	72.1	12.0
Endau Rompin	7649	F	143.5	15.9	40.2	27.1	3.7	8.6	5.7	11.4	12.1	16.6	11.0	16.9	21.7	72.0	11.8
Endau Rompin	7694	F	143.0	14.9	39.5	25.4	3.7	8.2	4.5	10.8	11.7	16.3	9.7	18.9	22.2	70.5	13.3
Endau Rompin	7651	M	116.4	11.9	34.3	21.2	3.4	7.2	4.1	8.9	11.2	13.5	9.7	15.3	19.1	58.4	10.5
Endau Rompin	7702	F	67.1	7.3	20.5	12.6	2.3	4.5	2.7	4.9	6.2	8.3	4.7	7.8	9.8	33.4	4.8
Endau Rompin	7650	F	61.2	6.1	19.5	11.8	2.3	4.9	2.4	4.4	5.1	7.4	5.1	8.0	9.6	32.0	4.6
Endau Rompin	7648	M	151.5	16.8	43.0	30.7	3.5	8.0	4.3	12.9	13.7	17.8	10.5	20.0	23.5	75.3	14.3
Gunung Lambak	9959	M	56.9	6.4	17.9	11.3	1.1	3.7	2.0	3.6	4.9	6.7	5.3	7.0	9.0	27.9	3.1
Gunung Ledang	10585	F	54.6	5.3	17.1	10.6	1.8	4.0	2.2	3.8	4.4	6.7	4.9	7.1	8.9	26.1	3.0

Table 12. Meristic data of the type series of *Gekko hulk* **sp. nov**. from Peninsular Malaysia. Abbreviations are in the Materials and methods.

Locality	LSUHC cat. no.	Sex	SL	IL	FS	CS	MB	PVT	LRT	VS	TL1	TL4	PP	CSP
Pulau Tioman	holotype 6284	M	12	10	18	6	110	17	10	25	15	19	8	4
Pulau Tioman	5399	F	14	12	21	5	104	18	10	22	17	21	0	4
Pulau Tioman	6283	F	14	11	18	6	95	18	10	26	16	20	0	4
Pulau Tioman	5152	F	12	10	18	5	91	17	10	21	16	21	0	4
Pulau Tioman	7263	F	15	13	18	6	90	16	9	22	18	22	0	2
Pulau Tioman	6890	M	14	12	19	7	98	19	11	27	17	21	7	4
Pulau Tioman	5151	M	14	12	21	6	109	19	10	23	19	24	8	4
Pulau Tioman	4681	M	15	12	20	5	91	20	10	21	16	20	7	6
Pulau Tioman	5390	F	13	11	17	7	106	21	11	26	17	21	0	4
Pulau Tioman	7299	F	14	11	18	6	105	19	10	27	15	19	0	2
Pulau Tioman	6260	F	14	11	21	7	108	21	11	32	17	21	0	4
Pulau Tioman	5849	M	13	11	22	7	91	21	11	22	16	21	6	4
Pulau Tioman	7264	F	12	9	20	5	93	17	11	26	16	21	0	4
Pulau Tulai	4694	F	13	11	19	8	104	17	9	27	19	23	0	2
Pulau Tulai	6282	M	13	11	18	6	101	19	10	24	16	20	10	4
Pulau Tulai	7026	F	12	10	21	6	98	18	10	25	17	21	0	2
Pulau Tulai	4697	F	12	10	17	6	98	18	11	27	16	20	0	4
Pulau Tulai	6278	F	13	11	18	6	102	17	10	24	17	21	0	2
Pulau Tulai	5063	F	13	11	17	6	99	17	10	25	16	20	0	4
Pulau Tulai	5062	M	13	11	20	5	106	18	10	27	15	19	6	2
Pulau Tulai	6265	F	13	11	21	7	109	19	10	28	17	21	0	2
Pulau Tulai	6277	F	14	12	19	6	106	17	10	26	17	22	0	2
Pulau Tulai	7025	M	14	12	23	6	96	17	10	24	19	22	9	2
Pulau Tulai	7257	F	13	11	20	7	95	18	9	23	16	20	0	2
Pulau Tulai	3891	F	13	11	20	5	102	18	10	26	18	22	0	2
Pulau Tulai	5059	F	14	12	22	6	104	18	10	25	16	21	0	2
Pulau Tulai	7024	M	14	12	21	6	100	20	10	24	17	21	8	4
Pulau Tulai	5061	F	14	11	19	6	98	19	10	27	17	21	0	2
Pulau Tulai	3990	M	13	10	22	6	104	21	10	23	17	20	9	3
Pulau Tulai	5060	M	13	10	15	7	92	18	10	26	19	23	9	4
Pulau Tulai	7251	F	13	11	21	5	101	19	11	29	19	22	0	4
Endau Rompin	7649	F	14	9	20	8	191	19	11	32	16	20	0	4
Endau Rompin	7694	F	13	11	18	6	102	18	10	29	15	19	0	4
Endau Rompin	7651	M	13	11	19	5	105	16	11	26	18	22	10	4
Endau Rompin	7702	F	10	10	13	4	89	19	9	23	16	20	0	0
Endau Rompin	7650	F	13	10	20	5	87	19	10	26	15	19	0	2
Endau Rompin	7648	M	13	10	21	7	95	19	11	30	14	18	11	6
Gunung Lambak	9959	M	13	10	18	6	84	18	10	24	16	20	10	0
Gunung Ledang	10585	F	14	11	24	5	89	18	10	23	16	21	0	2

Contact zone with *Gekko smithii* (Fig. 7). As noted above, the DFA placed THNHM 01841 from the Hala-Bala Wildlife Sanctuary, Waeng District, Narathiwat, Province, Thailand in *Gekko* cf. *albomaculatus* with a 79.5% PsP and in *G. smithii* with a 20.2% PsP. The DAPC placed it in *G. smithii* with a 100% PsP. THNHM 01841 bears the color pattern of the northern populations of *G. smithii* having white ocelli surrounding the tubercles (e.g. Figs 7I, 8G) although the ocellei are somewhat reduced in width (Fig. 13). However, photographs of two other specimens from the Hala-Bala Wildlife Sanctuary that were not examined, have the typical *G. hulk* **sp. nov.** color pattern with small white spots generally restricted to the tubercles (LSUDPC 12880 and 12953; Figs 7J and 8J, respectively). Examination of a specimen of *G. smithii* from Pa Phru Sirinthorn Research Station, Su-ngai Kolok District, Narathiwat (THNHM 01844) and a photograph of another specimen of *G. smithii* from Waeng, Narathiwat (LSUDPC 12877, Fig. 7I) approximately 32 km and 13 km to the north of the Hala-Bala Wildlife Sanctuary, respectively, also have the typical northern *G. smithii* color pattern. Both the DFA and DAPC placed THNHM 01844 in *G. smithii* with a 100% PsP. These data indicate the *G. smithii* and *G. hulk* **sp. nov.** are very likely to be sympatric in the Hala-Bala Wildlife Sanctuary and that the color pattern of THNMH 01841 may be the result of hybridization. A genomic data set is currently being developed to further investigate this contact zone.

Figure 13. THNHM 01841 from the Hala-Bala Wildfife Sanctuary, Narathiwat Province, Thailand. Photographs by Michael Cota.

Etymology. The specific epithet "*hulk*" is a noun in apposition in reference to "The Incredible Hulk", who is a fictional character and superhero created by Stan Lee and artist Jack Kirby in 1962 and appears in the Marvel Comics publications. When angry, The Incredible Hulk becomes a large, green-skinned, muscular beast possessing great physical strength and a very aggressive temperament—all characteristics of *Gekko hulk* **sp. nov**.

Comparisons. Wood et al. (2020a) erected the subgenus *Gekko* (*Gekko*) based on the phylogenetic relationships of the holotype of *G. hulk* **sp. nov.** (LSUHC 6284) and its inferred close relationship to the generotype species *G. gecko* (Rösler et al. 2011) in order to contain the species *G. albofasciolatus; G. gecko* (Linnaeus, 1758); *G. nutaphandi* Bauer, Sumontha, and Pauwels, 2008; *G. reevesii* (Gray, 1831); *G. siamensis* Grossmann and Ulber, 1990; *G. smithii* s.s.; and *G. verreauxi* Tytler, 1864. To this we add *G. albomaculatus, G. hulk* **sp. nov.**, and *G. stoliczkai.* Although several authors have used dorsal ground color as a diagnostic character (e.g. Rösler et al. 2011; Otal et. al. 1991), it is too variable in all species to be of diagnostic significance (see above). Chandramouli et al. (2021) noted several statistically significant differences in meristic and morphometric characters between *G. smithii* s.l. and *G. stoliczkai.* No data or formal analysis has ever been forwarded to argue that *Gekko taylori* Ota and Nabhitabhata, 1991 is a junior synonym of *G. siamensis.* Thus, the former remains in *G.* (*Gekko*) pending the outcome of current investigations (Grismer unpubl).

Gekko hulk **sp. nov.** can be separated from other species of the subgenus *G.* (*Gekko*) by a number of discrete characters (Table 10). *Gekko hulk* **sp. nov.** differs from *G. gecko* and *G. smithii* by having a much smaller maximum SVL (161.3 versus 185.0 and 191.0, respectively) and from *G. nutaphandi* (SVL 117.0) and *G. stoliczkai* (SVL 128.4) by having a larger maximum SVL. It differs from *G. verreauxi* by having the rostral scale in contact with the external nares as opposed to them being separated by a small scale. *Gekko hulk* **sp. nov.** differs from *G. gecko* and *G. reevesi* by having occipital scales and those on the top of the head smaller than the scales on the rostrum as opposed to them being the same size and having enlarged versus small subcaudal scales. It differs from *G. reevesi* by having 9–11 versus 12–18 longitudinal rows of dorsal tubercles. Male *G. hulk* **sp. nov.** differ from *G. albofasciolatus, G. nutaphandi, G. reevesi, G. smithii,* and *G. stoliczkai* in having fewer precloacal pores (6–13) as opposed to 13–15, 17–22, 13–20, 13–15, and 13–15, respectively. *Gekko hulk* **sp. nov.** has a turquoise/green iris which separates it from *G. gecko* and *G. reevesi* that have a gold/copper to olive/brown iris, from *G. nutaphandi* which has a bright-red iris, and from *G. verreauxi* which has a golden iris. It differs from *G. albomaculatus* by not having a thin, white, solid nuchal band (except for one specimen from Pulau Tioman). *Gekko hulk* **sp. nov.** differs from *G. albofasciolatus* by having as opposed to lacking a white nuchal band. *Gekko hulk* **sp. nov.** differs from *G. smithii* in that the small white dorsal spots, if not confined to the tubercles, tend to border them anteriorly, whereas in *G. smithii,* the dorsal tubercles are surrounded by a large white ocellus in northern populations and the smaller ocelli in the southern populations only tend to border the tubercles posteriorly. *Gekko hulk* **sp. nov.** has a number of significantly different mean meristic and morphometric values as well as significantly different morphospatial placement that separate it from *G. albofaciolatus, G. albomaculatus,* and *G. smithii* (Figs 3–6; Tables 6–9).

Natural history. Much like other species of *Gekko* (*Gekko*)*, G. hulk* **sp. nov.** is an arboreal nocturnal species that is well-established in all types of primary and secondary forests as well as buildings on forest edges. We observed lizards 3–4 m above the ground on the trunks of large trees on Gunung Tebu (Fig. 14) and heard males calling in the afternoon. On Pulau Tioman, we observed individuals 4–5 m above the ground on tree trunks, in tree cavities, and on cement light poles. On Pulau Tulai, lizards were seen on trees during the day but collected off the metal stair railing at night. On Perhentian Besar, geckos occur is high densities and are more common on granite boulders where they take refuge between boulders and in

Figure 14. Microhabitats of *Gekko hulk* **sp. nov**. on Peninsular Malaysia. A. Granite boulder microhabitat on Pulau Perhentian Besar, Terengganu. B. Forest microhabitat of the type locality along the Tekek-Juara Trail, Pulau Tioman, Pahang. Strangler Fig microhabitat along Sungai Mentawak, Pulau Tioman, Pahang. Photographs by L. Lee Grismer.

rock cracks. Lizards are far less common on tree trunks. Grismer (2011b) reports finding eggs attached to the undersides of boulders on Pulau Perhentian Besar during September and a gravid female was collected during July on Pulau Tioman.

Discussion

Several integrative taxonomic analyses of Peninsular Malaysian genera and species across a number of taxonomic groups have consistently found the Banjaran Titiwangsa to be an effective geographic barrier separating sister clades and sister species (Grismer et al. 2013, 2014a,b, 2015, 2018a,b, 2019; Chan et al. 2017, 2018; Wood et al. 2020b). Therefore, it is not surprising that a lineage such as the *Gekko smithii* complex that had not been examined in depth since its description in 1842, shows the same biogeographic pattern. Also, the relationships of several Peninsular Malaysian taxa such as *G. hulk* **sp. nov.** being more closely related to Sumatran lineages as opposed to other Peninsular Malaysian or Bornean lineages is also not uncommon (Loredo et al. 2013; Matusi et al. 2014, 2019; Chan et al. 2016, 2017, 2018, 2020; Harvey et al. 2016; Grismer and Davis 2018; O'Connell et al. 2018, 2019). The shared episodic environmental fluctuations of these major Sundaic landmasses since the Miocene accounts for a plethora of overlapping and distinct combinations of concordant phylogeographic patterns across a broad range of taxa (de Bruyn et al. 2013, 2014 and references therein). When the results from integrative taxonomic analyses of more groups become available—especially those that include the vast number of unstudied lineages from Sumatra (Eric Smith pers. com. in lit. 2017) and Indonesian Borneo—these patterns will likely become even more commonplace.

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