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Phylogeny, taxonomy, and zoogeography of the genus *Gekko* Laurenti, 1768 with the revalidation of *G. reevesii* Gray, 1831 (Sauria: Gekkonidae)

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Abstract

A review of the taxonomy, phylogeny, and zoogeography of all currently recognized *Gekko* species is provided based on morphology (including size, scalation, color, and pattern) and mitochondrial and nuclear DNA sequence data. We distinguish six morphological (phenotypic) species groups within the gekkonid genus *Gekko*: the *G. gecko*, *G. japonicus*, *G. monarchus*, *G. petricolus*, *G. porosus*, and *G. vittatus* groups, all of which receive support from molecular phylogenetics. The taxon *G. reevesii*, formerly evaluated as a synonym of *G. gekko*, is revalidated herein at specific rank. Furthermore, a preliminary identification key of all currently recognized *Gekko* taxa is provided.

Key words: gecko, morphology, phylogeny, taxonomy, molecular phylogenetics, species groups, revalidation, *Gekko reevesii*, biogeography

Introduction

The genus *Gekko* is a moderately species-rich genus of the Gekkonidae sensu stricto (Gamble *et al.* 2008a), comprising 45 named species, all of which have their native distributions in the Old World, from India eastwards to Melanesia. Members of the genus are typical of the family in possessing large eyes with transparent brilles, vertical pupils, and clutches of two calcareous-shelled eggs. They may be diagnosed within the Gekkonidae by their broad fingers and toes, all bearing undivided scansors and the absence of claws on digit I of the manus and pes. *Gekko* species are egg gluers, exhibit brood care, and include some of the most vocal of all geckos.

Biological knowledge of *Gekko* species is highly variable. Whereas, for example, morphology, ethology, reproduction, ecology and distribution are well known for species such as *G. badenii*, *G. gecko, G. grossmanni, G. monarchus*, *G. petricolus*, *G. smithii,* and *G. vittatus*, these data are only poorly known or completely lacking in other *Gekko* species. The best known species in the genus is *G. gecko*, which is regularly used as a research subject in interdisciplinary studies and experiments. Valuable basic knowledge about the biology of reptiles in general has been obtained by studying this species, for example in the fields of adhesion mechanisms (Autumn *et al.* 2002), endocrinology (Chiu *et al.* 1970, Chiu & Phillips 1971, 1972), ethology (e.g., Gonzales *et al.* 1990; Losos 1990; Brillet & Paillette 1991; Bruce & Neary 1995 a, b; Tang *et al.* 2001), genetic divergence (Liu *et al*. 2000; Zhang *et al.* 2006; Qin *et al.* 2007), karyology (e.g., Cohen *et al.* 1967; Solleder & Schmidt 1984; Wu & Zhao 1984; Sharma & Kasid 1992; Du *et al.* 2002), morphology (e.g., Russell 1975, 1981, 1982; Maderson & Chiu 1981; Ma & Xia 1990; Russell & Bauer 1990; Moore *et al.* 1991; Hoogland *et al.* 1994; Loew 1994; Köppel & Authier 1995; Zhang *et al.* 1997; Zaaf *et al.* 2001; Chan *et al.* 2006), mitogenomics (Han & Zhou 2005; Zhou *et al.* 2006), neurobiology (e.,g, Northcutt & Butler 1974; Stoll & Voorn 1985; Hoogland & Vermeulen-Vander Zee 1990, 1993, 1995; Smeets & Jomker 1990; Smeets *et al.* 2001;), physiology (e.g., Werner 1972; Chiu *et al.* 1985; Sievert & Hutchison 1988; Mirwald & Perry 1991; Rumping & Jayne 1996; Andrews & Bertram 1997), and vision (Yokoyama & Blow 2001).

The taxonomic history of the genus *Gekko* began with Laurenti 1768 (species typica *Lacerta gecko* Linnaeus, 1758, by tautonymy), who provided a diagnosis based, in part on Seba's (1734) statements and illustrations. By the end of the 19th century, only eight species were recognized in the genus *Gekko* (see Boulenger 1885). Subsequently, through the comprehensive research of Taylor (see Adler 1989) in the Philippines (1920–1921) and in Thailand (1958–1960), the number of species in the genus *Gekko* increased markedly (five *Gekko* species were described during that period, of which four are still valid). Three additional species were later described from the Philippines by Brown and Alcala between 1962 and 1978.

In the most recent overview on gekkonid taxonomy, Kluge (2001) listed 28 species in the genus *Gekko*. Since 2004, fourteen additional *Gekko* species have been described: *G. ernstkelleri*, *G. scientiadventura*, and *G. canhi* (Rösler *et al.* 2005, 2006, 2010), *G. shibatai* and *G. vertebralis* (Toda *et al.* 2008), *G. nutaphandi* (Bauer *et al.* 2008), *G. russelltraini*, *G. takouensis*, and *G. canaensis* (Ngo *et al.* 2009; Ngo & Gamble 2010, 2011), *G. crombota* and *G. rossi* (Brown *et al.* 2008, 2009), *G. carusadensis* (Linkem *et al.* 2010), *G. vietnamensis* (Nguyen 2010) as well as *G. lauhachindaei* (Panitvong *et al.* 2010). In addition, some taxa listed as synonyms by Kluge (2001) have subsequently been revalidated (*G. melli*; Rösler *et al.* 2005) or their taxonomic status is still insufficiently resolved (*G. liboensis*, *G. mindorensis*, *G. scabridus*; Ferner *et al.* 2001, Kluge 2001, Zhao & Adler 1993). Nguyen *et al.* (2010) recently synonymized *G. ulikovskii* with *G. badenii*.

The phylogeny of the genus *Gekko* remains poorly known and largely unresolved. Some species groups have been dealt with morphologically (Günther 1994; Grossmann 2006; Rösler *et al.* 2006), cytomorphologically (Wu & Zhao 1984; Chen *et al.* 1986; Ota 1989a; Ota *et al.* 1990; Shibaike *et al.* 2010), or by molecular methods (Toda *et al.* 2008; Brown *et al.* 2009). The only attempt to clarify the intrageneric relations of all *Gekko* species known at that time was by Russell (1972). However, the latter author also included species which are now considered as belonging to a different genus (*Luperosaurus*, see Russell 1979a) and, of course, his review did not include the numerous recently described *Gekko* taxa.

Thus, because a comprehensive infrageneric systematic review of all *Gekko* representatives is still lacking, we herein present, as a basis for future phylogenetic studies, especially molecular phylogenies, a review of the currently recognized members of the genus *Gekko*. We also provide a first grouping based on morphological characters, present a preliminary multi-gene phylogeny of the genus, and discuss the biogeographic implications of this phylogeny. Further, we reinvestigate the status of the "black tokay" of China and Vietnam and provide evidence for its recognition as a valid species, *G. reevesii*.

Material and methods

Molecular data. Sequences were generated or obtained from Genbank for 45 specimens of 18 described and two undescribed species of *Gekko* (see Appendix 1). Representatives of two species of *Lepidodactylus* and two of *Gehyra* were used as outgroups based on earlier indications of their close relationship to *Gekko* (Russell 1972; Feng *et al.* 2007; Gamble *et al.* 2008a,b). The data set consists of multiple mitochondrial and nuclear genes: the complete sequence of the mitochondrial NADH dehydrogenase subunit 2 (ND2; 1,029–1,041 bp), along with partial or complete sequences of 5 adjacent tRNAs (287–307 bp), plus partial exon sequences of the nuclear genes recombination activating gene 1 (RAG-1; 1,035–1,038 bp) and phosducin (PDC; 395 bp).

For generation of new sequences, genomic DNA was isolated from ethanol-preserved tissue samples using a Qiagen DNeasy tissue and blood kit under manufacturers' protocols. PCR was performed in 25 µL reactions, with primer sequences retrieved from the literature (Jackman *et al.*, 2008). Standard reaction conditions included an initial denaturation at 95°C (2 min), followed by 32–34 cycles of denaturation at 95°C (35 s), annealing at 50°C (35 s), and extension at 72°C (initially 150 s, with 4 s added per cycle). Annealing temperature was lowered for poor-yielding samples. Purification of amplified PCR products was via AMPure magnetic bead system (Agencourt Bioscience). The sequencing reaction employed dye-terminator chemistry, with cycle sequencing followed by purification via the CleanSeq magnetic bead system (Agencourt Bioscience). Capillary electrophoresis and analysis were performed using an ABI 3700 sequencer. Resulting chromatograms were inspected by eye and compared against their reverse complements in BioEdit (Hall 1999) to detect call errors, followed by translation to check for premature stop codons. Sequences were then aligned using Clustal (Thompson *et al.* 1994), and manually corrected to take into account codon deletions and tRNA secondary structure. The separate gene sequences were then concatenated into a single data set for analyses.

Bayesian, likelihood, and parsimony methods were employed for phylogenetic analyses. PhyML (Guindon & Gascuel 2003) and jModelTest 0.91 (Posada 2008) were used to estimate parameters for all standard models of evolution, with the Akaike Information Criterion (AIC) used to identify the best-fitting model of evolution. Based on the AIC, the TIM1 + I + Γ model was suggested. Due to software limitations, the similar GTR + I + Γ model was employed for the Bayesian and likelihood analyses. For all analyses, alignment gaps were treated as missing data, and pairwise deletion of sites was employed.

The Bayesian analysis was run in MrBayes 3.1.2 (Huelsenbeck & Ronquist 2001). Two parallel runs with three heated and one cold chain were run for 1,500,000 generations, with a sampling frequency of 100 generations per sample. The data were divided into four partitions (ND2, tRNA, RAG-1, PDC), with all parameters unlinked across the partitions. A burnin of 3,000 samples (300,000 generations) was used to discard the region of increasing likelihood values. The average standard deviation of split frequencies (finished at 0.005) and potential scale reduction factors (all values approaching 1.00) were consulted to ensure that the chains ran for an adequate length of time. Branch support was assessed using posterior probabilities. The likelihood analysis was performed using RAxML 7.2.6 (Stamatakis 2006). The same partitions employed in the Bayesian analysis were used in the likelihood analysis. One hundred independent searches were employed to find the most likely tree, and branch support was assessed with 1,000 nonparametric bootstrap replicates. For the parsimony analysis, a close neighbor interchange search was implemented in MEGA 4 (Kumar *et al.* 2008), with 30 random addition replicates and 1,000 nonparametric bootstrap replicates.

Morphological data. Morphological data were derived from literature sources and from observations on preserved specimens of *G. badenii*, *G. canhi*, *G. ernstkelleri*, *G. gecko*, *G. grossmanni*, *G. hokouensis*, *G. japonicus*, *G. melli*, *G. mindorensis*, *G. monarchus*, *G. palmatus*, *G. petricolus*, *G. russelltraini*, *G. scientiadventura*, *G. siamensis*, *G. smithii*, *G. subpalmatus*, and *G. vittatus* (see Appendix 2). Investigated specimens are deposited in the following museum collections: BMNH = The Natural History Museum, London; CPHR = private collection of Herbert Rösler; IEBR = Institute of Ecology and Biological Resources, Hanoi; MNHN = Muséum national d'Histoire naturelle, Paris; MTD = Senckenberg Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Dresden; NMW = Naturhistorisches Museum Wien; VNUH = Vietnam National University Hanoi; ZMB = Institut für Systematische Zoologie, Museum für Naturkunde der Humboldt-Universität zu Berlin; ZFMK = Zoologisches Forschungsmuseum Alexander Koenig, Bonn; ZSM = Zoologische Staatssammlung München.

Abbreviations are as follows: SVL = snout-vent length, TL = tail length, AG = distance between axilla and groin, LT = thigh length (from knee to middle of body), HL = maximum head length (from tip of snout to hind margin of ear), HW = maximum head width, HH = maximum head height, SE = distance from snout tip to front of eye, EE = distance between hind margin of eye and hind margin of ear, ED = maximum eye diameter, EAD = maximum ear diameter, RW = maximum rostral width, RH = maximum rostral height, MW = maximum mental width, ML = maximum rostral length, DTL = dorsal tubercle length (in one of two central rows in the middle of the back), DTW = dorsal tubercle width, LTL = lateral tubercle length, LTW = lateral tubercle width.

SPL = supralabials, SBL = sublabials (or infralabials), N = nasals (in direction from rostral to labial: nasorostrals, supranasals, postnasals), I = internasals (scales between nasorostral in contact with rostral), SC7SPL = scales crosswise between seventh supralabials, IO = interorbitals, CS = ciliary spines, PM = postmentals, GP = gulars bordering the postmentals, DTR = dorsal tubercle rows, GSDT = granules surrounding dorsal tubercles, SMC = scales along underside of body from mental to the front of cloacal slit, SR = scales around the middle of the body, V = ventrals, TT = thigh tubercles, LF1 = subdigital lamellae under the first finger, LF4 = subdigital lamellae under the fourth finger, LZ1 = subdigital lamellae under the first toe, LZ4 = subdigital lamellae under the fourth toe, PP = precloacal pores (only in males), PS = precloacal scales (only in females), PAT = postcloacal tubercles, T1W = tubercles in the first caudal whorl, T5W = tubercles in the fifth caudal whorl, S3W = dorsal scale rows in the middle of the third caudal whorl, SC = subcaudals along underside of tail from cloacal slit to tail tip.

We also used the presence or absence of digital webbing for our phenotypic grouping. We estimated webbing as being present, when it was discernible for at least 1/3 of finger and toe length.

Coloration was described according to the standard plates published by PANTONE MATCHING SYSTEMS® (Printed in USA) and we report the respective PANTONE catalogue number in parentheses.

Statistical significance in morphological and morphometric differences in the evaluation of *G. reevesii* were evaluated using t-Tests (Lozán & Kausch 1998).

Results

Molecular results

The final alignment measured 2,881 bp (1,041 bp ND2, 353 bp tRNAs, 395 bp PDC, 1,038 bp RAG-1). Of these, 1,317 sites were variable, and 1,017 were parsimony-informative. A single most parsimonious tree was found, with a length of 5,509 steps. The score of the best likelihood tree from 100 independent inferences was –ln L 27044.334952.

The monophyly of *Gekko* is strongly supported (Figure 1). A chiefly Philippine clade was retrieved with strong support as the sister to remaining members of the genus. Within this clade *G. athymus* from Palawan was sister to the remaining taxa sampled. *Gekko mindorensis* and. *G. monarchus* are sister taxa and together are sister to a clade including *G. porosus* and several recently described or identified species from islands in the Luzon Strait. Large-bodied *Gekko*, represented by *G. gecko* and *G. smithii*, are sister to a well supported clade of East Asian species and these groups together are allied to Vietnamese and Thai species plus the easternmost taxon, *G. vittatus*.

All species represented by multiple samples were found to be monophyletic. Divergences were shallow within *G. vittatus* with the greatest difference occurring between a specimen from Palau and those from the Louisiade Archipelago, Solomons and Vanuatu. Likewise, little variation is seen in *G. mindorensis* or *G. monarchus*, although levels of divergence between populations in these species exceed that between two putatively new species identified by Brown *et al.* (2009). Both *G. smithii* and *G. gecko* exhibit much deeper intraspecific divergences, with a Sarawak *G. smithii* significantly outside of West Malaysian samples. In *G. gecko*, samples from East Timor to China were nearly identical, with Myanmar and Thai samples substantially different.

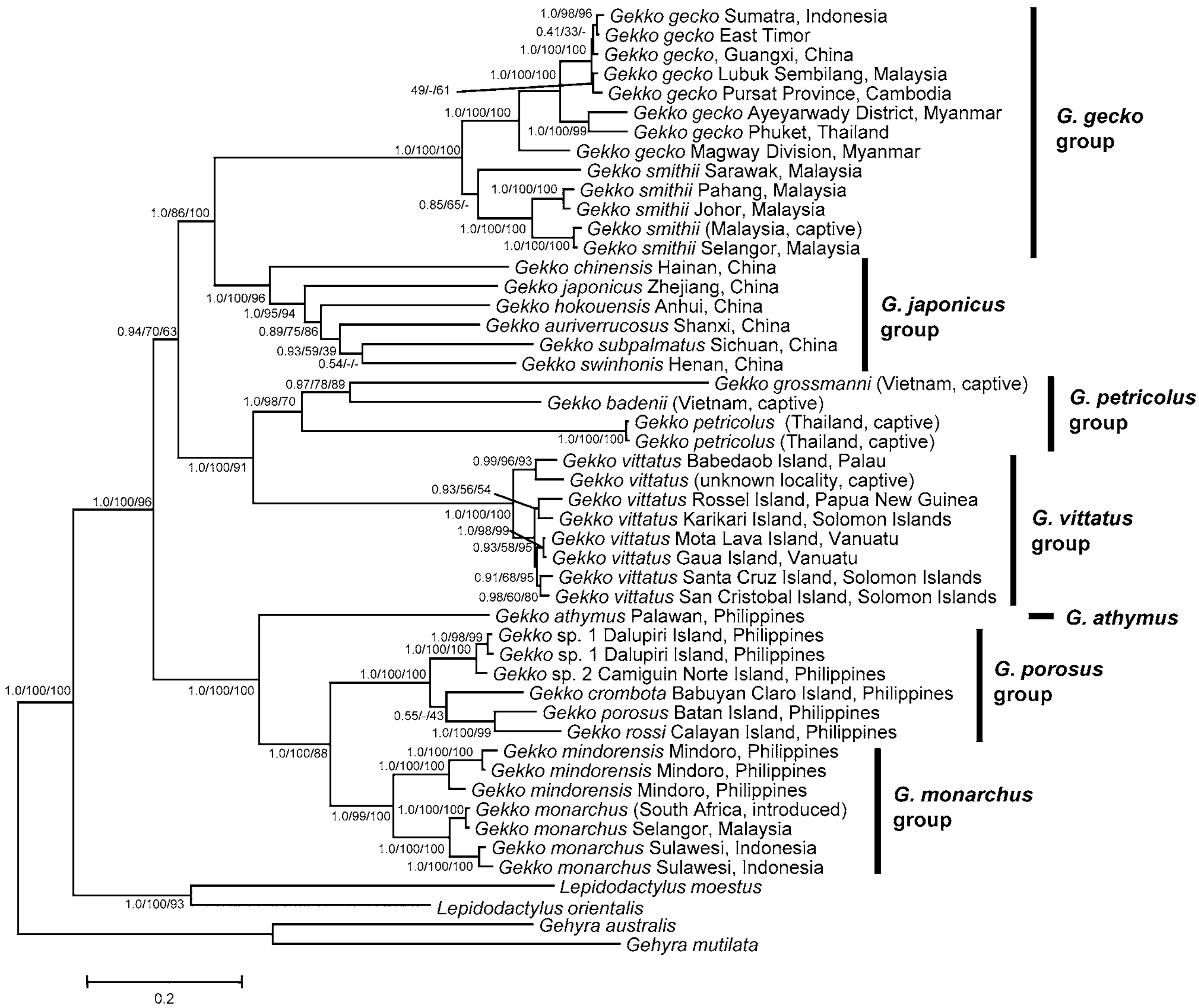

FIGURE 1. Bayesian phylogeny of *Gekko*, based on nucleotide sequences of the mitochondrial *ND2* gene and nuclear *RAG-1* and *PDC* genes (2881 bp). Support values (Bayesian pp/ML bootstrap/MP bootstrap) are given at nodes. Species groups proposed herein are indicated.

Diagnostic traits of the genus *Gekko* Laurenti, 1768

Gekko species are characterized by the following combination of traits: SVL 50–191 mm; snout-vent length the same or smaller than tail length; head dorsoventrally depressed, but to different degrees depending on species; head distinctly set off from neck; snout concave in region of the paired nasals and single frontal; body cylindrical to slightly dorsoventrally depressed; belly flat; hind limbs larger than fore limbs; tibia longer than forearm; webbing between toes from rudimentary to distinct; head, body, limbs and tail without significant skin flaps; tail base not or only slightly thickened; tail base round or slightly dorsoventrally depressed; unregenerated tail with more or less distinct whorls.

Rostral wider than long; nares with or without rostral contact, mostly surrounded by 3 (2–4) nasals; ciliary spines present or lacking; rostral wider than mental; two enlarged postmentals present in most cases; tubercles on head, body, limbs and dorsal tail surface present or lacking; dorsals granular; ventrals flat, imbricate; lateral folds slightly developed (i.e., discernible transition from large and flat ventrals towards smaller and more or less raised lateral scales); lateral folds without tubercles (except for *G. vittatus*); toes apically extended, with undivided, broadened subdigital lamellae; fingers and toes except for digit I of both manus and pes with apical, dorsal claws; dorsum of finger I and toe I with apically enlarged scale; subcaudals distinctly enlarged (medially subdivided in different degrees according to species), arranged in a longitudinal row; subcaudals with repeating arrangement of two slightly and one greatly widened plates or with subcaudals slightly or not widened.

Hemipenis elongate, apically divided and with two lobes of same size; sulcus spermaticus bordered by voluminous skin bulges; small to large calyces with smooth or denticulated seams (Unterhössel 1902; Zhang 1986; Utsunomiya *et al.* 1996; Shang 2001; Rösler *et al.* 2005).

Eyes covered by transparent brille; pupil vertical when iris is closed; anteriorly and posteriorly denticulated pupil margins.

Base coloration mainly brown in different degrees, combined with gray, yellow, green and red, only a few species with uniform gray, brown or green base coloration. Head with or without pattern (most often Y- or W-shaped patterns). Dorsum mainly with bands or flecks, some species also show symmetrical or asymmetrical light dorsal blotches. Striped pattern rare (e.g., *G. vittatus*). Tail more or less banded. Juveniles usually with distinct, strongly contrasting light and dark tail bands.

Embryo with paired egg teeth in apical contact (Sluiter 1893; Woerdeman 1919).

Natural history and distribution

Most *Gekko* species inhabit trees or rocks. They are nocturnal and predominantly adapted to pristine environments, but some of them also are synanthropic species. One or two eggs are laid per clutch. Eggs are glued to hard substrates such as wood and stones (e.g., Mell 1929). Depending on the species, brood care may be practiced (e.g., Grossmann 2008a).

Gekko species mainly inhabit the Indo-Malayan Realm. Due to human-mediated introduction *G. gecko* is established elsewhere and other species are regularly introduced via ports around the world (Bauer & Baker 2008; Bauer & Branch 2004), although most populations have not been naturalized. About one half of the *Gekko* representatives are exclusively distributed on the Asian mainland (Bangladesh, Cambodia, China, India, Korea, Laos, Myanmar, Nepal, Thailand, Malaysia, Singapore, Vietnam); remaining species occur on the islands of Indonesia, Japan, Papua New Guinea, Philippines, Republic of Palau, Taiwan, the Solomons, Vanuatu, as well as in Brunei (Borneo) and East Timor. Few *Gekko* species occur on the mainland as well as on islands.

Taxonomic review and phenotypic grouping of *Gekko* members

We propose six species groups within the genus *Gekko*. Each corresponds to a clade retrieved by the molecular phylogeny. Assignment to groups, especially for species not included in the molecular phylogeny, was guided by a combination of characters including size, scalation, color, pattern, and geographic distribution. For an overview of specific and group characters see Tables 1–2.

TABLE 1. Measurements, scalation, and distribution of *Gekko* species.

1—maximum snout-vent length (in mm); 2—number of supralabials; 3—number of sublabials; 4—nostril touching rostral; 5—number of nasals; 6—number of internasals; 7—number of interorbitals; 8—size of postmentals (enlarged or not); 9—number of dorsal tubercle rows; 10—number of scales along underside of body from mental to beginning of cloacal slit; 11—number of scales around midbody; 12—number of ventrals; 13—throat and lateral folds with tubercles; 14—number of subdigital lamellae under the first toe; 15—number of subdigital lamellae under the fourth toe; 16—toes webbed; 17—tubercles on fore limbs; 18—tubercles on hind limbs; 19—number of precloacal pores (only in males); 20—number of postcloacal tubercles; 21—

tubercles on dorsal surface of tail; 22—subcaudals enlarged; 23—ground coloration of dorsum; 24—marking on upper side of head; 25—back flecked or blotched; 26—banded back; 27—striped back; 28—banded tail; 29—distribution.

"1" = presence of character state; 0 = absence of character state; ? = data unavailable; under character 23: (l) = coloration in live specimens; p = coloration in preserved specimens. Species of uncertain taxonomic status are marked with an asterisk (*).

[1] Size and scalation from 23 specimens from Java, Indonesia (see Appendix 1); [2] Only females known; [3] Size an scalation from lectotypes ZMB 27659 A and ZMB 27659 B; [4] Size and scalation from 35 specimens from Vietnam (see Appendix 1); [5] Size and scalation from 42 specimens from China and Vietnam (see Appendix 1); [6] dorsal tubercles present; [7] Size and scalation from 18 specimens from New Guinea and Ambon Island (see Appendix 1).

Cited references are as follows: 1—Alcala (1986); 2—Baker (1928); 3—Bauer (1994); 4—Boulenger (1885); 5—Boulenger (1907); 6—Brown & Alcala (1962); 7—Brown & Alcala (1978); 8—Darevsky & Orlov (1994); 9—Das (2007); 10—Denzer & Manthey (1991); 11—De Rooij (1915); 12—Gaulke (2003); 13—Goris & Maeda (2004); 14—Grossmann (2004a); 15—Grossmann (2004b); 16—Grossmann (2006); 17—Grossmann & Ulber (1990); 18—Günther (1864); 19—Günther (1867); 20—Günther (1994); 21—Harbig (2006); 22—Houttuyn (1782); 23—Liu & Zhou (1982); 24—Loveridge (1948); 25—Lue *et al.* (1999); 26—Manthey & Grossmann (1997); 27—Matsui & Okada (1968); 28—McCoy (2006); 29—Means (1996); 30—Mertens (1955); 31—Nekrasova & Szczerbak (1993); 32—Ngo *et al.* (2009); 33—Ngo & Gamble (2010); 34—Okada (1956); 35—Oshima (1912); 36—Ota & Nabhitabhata (1991); 37—Ota *et al.* (1991); 38—Ota *et al.* (1995); 39—Rösler (2001); 40—Rösler (2005a); 41—Rösler & Tiedemann (2007); 42—Rösler *et al.* (2005); 43—Rösler *et al.* (2006); 44—Rösler *et al.* (2010); 45—Smith (1923); 46—Smith (1935); 47—Song (1985); 48—Stejneger (1932); 49—Szczerbak & Nekrasova (1994); 50—Taylor (1919); 51—Taylor (1922a); 52—Taylor (1922b); 53—Taylor (1925); 54—Taylor (1962); 55—Taylor (1963); 56—Toda *et al.* (2008); 57—Tytler (1864); 58—Utsunomiyta *et al.* (1996); 59—Veselý (1999); 60—Vogt (1922); 61—Zhao *et al.* (1999); 62—Zhou & Li (1982b); 63—Zhou & Liu (1982); 64—Ziegler (2002); 65—own data, 66—Brown *et al.* (2008) ; 67—Nguyen N. S. (2010) ; 68—Zhou & Wang (2008) ; 69—Bauer *et al.* (2008) ; 70—Linkem *et al.* (2010) ; 71—Brown *et al.* (2009) ; 72—Panitvong *et al.* (2010); 73—Ota (1989b); 74—Shibata (1981); 75—Teynié & David (2010); 76—Ngo & Gamble (2011).

Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
*G. albofasciolatus**	165.1	13	11	0	?	?	?	0	10	?	?	26	0	?	?
G. athymus	119.9	11–15	11–13	1	3	1	50–54	0	0	?	122–140	30–36	0	14–16	18–22
G. auriverrucosus	69	9–11	9–11	0	3	0–1	25	0	16–20	?	?	?	0	6–8	6–8
G. badenii	108	11–15	9–14	1	3	1	30–46	1	12–17	136–145	128–137	29–35	0	12–14	15–22
G. canaensis	108.5	14–17	11–15	1	3	1	32–34	1	10–14	?	86–93	30–32	0	14–16	17–19
G. canhi	99.2	14	10–12	1	3	1	49–50	1	11–12	168–170	205–227	49–51	0	13–16	14–17
G. chinensis	72	10–14	9–13	1	2–3	1	35–48	1	10	?	118–140	?	0	8–10	9–12
G. crombota	117.9	13–15	11	1	3	1	?	1	18–22	?	145–164	38–42	0	12–13	15–18
G. ernstkelleri	92.1	11–16	10–11	1	3–4	1–2	39–45	1	14–15	159–181	147–162	41–48	0	15–17	17–19
G. gecko gecko [1]	161	11–15	9–14	0	3–6	0–3	16–28	0	11–13	135–142	81–105	30–34	0	14–19	19–23
G. gecko azhari [2]	155	12–13	10–11	0	4	1	20–23	0	15	?	90–97	?	0	17–18	22–24
G. gecko reevesii [3]	173	10–14	9–13	0	3–6	0–1	17–29	0	12–18	133–141	82–103	28–32	0	13–19	18–24
G. gigante	104.7	11–13	10–12	1	3	1	40–46	1	12–18	?	180–190	41–50	0	12–16	16–20
G. grossmanni	89.4	11–13	9–12	1	3	0–1	38–46	1	8–12	139–165	116–135	26–31	0	11–15	17–20
G. hokouensis	70	10–14	8–11	1	3	1–2	30–33	0	12–18	153–174	119–130	36–43	0	8–11	15–18
G. japonicus	74	9–13	8–13	1	3	0–1	32–35	0	9–14	169–188	130–144	39–44	0	10–12	14–16
G. kikuchii	80	13	10	1	3	1	?	?	18	?	?	?	0	13	14
*G. liboensis**	85	12	11	1	3	0	40	0	10	?	?	?	0	8	9
G. melli [4]	84.6	10–13	9–12	1	3	1	35–39	0	0	147–158	?	43–49	0	10–11	12–14
*G. mindorensis**	88.2	11–13	9–11	1	3	1	30–40	1	16–19	166–174	151–155	38–40	0	10–13	12–15
G. monarchus	100	10–13	9–13	1	3	1	34–35	1	16–24	167–179	148–177	30–43	0	10–12	16–17

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Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
G. monarchus	100	10–13	9–13	1	3	1	34–35	1	16–24	167–179	148–177	30–43	0	10–12	16–17
G. nutaphandi	116	12–14	10	0	3	1	24	1	14	?	?	30–31	0	12	15
G. palawanensis	65.7	12–14	10–12	1	3	1	?	1	10–20	?	152–164	40–44	0	13–16	16–19
G. palmatus [5]	82.5	11–15	9–13	1	3	0–2	33–47	1	6–12	172–199	139–156	34–50	0	10–14	11–17
G. petricolus	101	12–15	10–12	1	3	0–1	34–41	1	15–18	146–156	113–121	27–32	0	12–14	16–18
G. porosus	96.7	12–13	9	1	3	1	?	1	15–17	?	155–160	35–44	0	?	14–16
G. russelltraini	82.9	12–16	11–13	1	?	?	30–34	1	12–16	?	90–107	28–30	0	15–16	17–19
G. romblon	89.2	11–14	10–12	1	3	1	36–38	1	12–15	?	145–150	37–42	0	12–14	12–16
*G. scabridus**	77	9–11	9–11	1	3	1–2	30	0	17–21	?	?	?	0	6–9	7–9
G. scientiadventura	73	12–14	9–13	1	3	0	41–51	1	0	118–140	139–143	38–48	0	12–15	14–17
G. siamensis	150	13–21	10–12	0	4	0	28–34	1	14–19	156	121–132	33–37	0	13–15	11–20
G. shibatai	70.9	10–13	10–14	1	3	0–1	37–52	0	5–14	?	114–134	?	0	?	9–16
*G. similignum**	58.9	12–14	11	1	3	1	46–48	0	11	?	144–153	?	0	11–13	12–14
G. smithii	191	12–17	10–14	0	4–6	1–2	31–43	0	8–13	151–167	89–141	29–39	0	16–20	19–23
G. subpalmatus	72	8–12	7–12	1	3	1	32	0	0	?	?	48	0	7–9	7–10
G. swinhonis	66	7–12	7–11	1	?	?	23–24	0	6–8	?	?	40	0	6–9	6–9
G. taibaiensis	69	9–10	8–10	1	?	?	28	?	?	?	?	?	0	6–7	7–8
G. takouensis	107	13–16	10–13	1	3	?	27–34	1	14–17	?	83–90	30–34	0	14–16	18–20
G. tawaensis	71	13	15	1	?	2	?	0	0	?	?	?	0	10	12
G. vertebralis	69.2	10–15	10–15	1	3	0–2	35–50	0	2–12	?	112–139	?	0	?	9–17
G. verreauxi	155	11–15	9–11	1	4	0	?	0	11	?	?	?	0	16–18	20–22
G. vietnamensis	100	11–12	10–11	1	?	?	?	?	?[9]	?	?	28–30	0	?	18–20
G. vittatus [7]	140	12–15	11–16	1	3–4	0–2	25–31	0	22–31	176–222	129–155	30–39	1	13–17	18–26
G. wenxianensis	59	12	11	1	?	1	?	?	10	?	?	42–44	0	6	9
G. yakuensis	72	12–13	9–13	1	3	1	?	0	?	?	?	?	0	10	15

Table 1 continued

Taxon	16	17	18	19	20	21	22	23	24	25	26	27	28
*G. albofasciolatus**	?	?	?	16	?	?	0	reddish-olive (p)	1	1	1	?	?
G. athymus	1	?	?	20–24	?	0	1	dark grayish-brown (p)	0	0	1	0	?
G. auriverrucosus	0	1	1	8–11	2–3	1	1	pale gray (p)	0	0	1	0	1
G. badenii	0	0	0	10–15	2	1	1	yellow-brown to dark green-gray (l)	0	0	1	0	0
G. canaensis	0	0	0	14–18	2	1	1	gray with tan to brown overtones (l)	0	1	0	0	1
G. canhi	0	0	1	5	2–3	0	1	gray-green (l)	0	1	1	0	1
G. chinensis	1	1	1	17–27	1	1	1	dark olive-gray to brown-olive (l)	0	1	0	0	1
G. crombota	0	1	1	58–74	1	1	1	dark purplish-gray to yellowish-brown	0	1	1	0	1
G. ernstkelleri	0	0	1	36–48	2	1	1	olive to brown-olive (l)	0	1	0	0	1

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Taxon	16	17	18	19	20	21	22	23	24	25	26	27	28
G. gecko gecko [1]	0	1	1	12–16	1–3	1	0	gray to bluish or brownish-gray (l)	1	1	1	0	1
G. gecko azhari [2]	0	1	1	? (6)	2–3	1	0	brown-olive (p)	1	1	0	0	1
G. gecko reevesii [3]	0	1	1	13–20	1–4	1	0	gray-green to dark-gray (l)	1	1	1	0	1
G. gigante	0	?	?	52–66	1	1	1	reddish-gray to brownish-gray (p)	?	1	1	0	1
G. grossmanni	0	0	0	8–14	2	0	1	gray-brown to brown (l)	1	1	1	0	1
G. hokouensis	0	0	0	5–9	1	0/1	1	gray-brown to lilac-brown (l)	0	1	0	0	1
G. japonicus	0	0/1	1	6–9	2–4	1	1	pale gray to gray-brown (l)	0	0	1	0	1
G. kikuchii	0	1	1	48	?	1	1	pale-brown toochre-brown (l)	0	1	0	0	1
*G. liboensis**	0	0	0	?	1	?	?	grayish tan (p)	0	0	1	0	?
G. melli [4]	1	0	0	?	1	0	1	olive-brown (p)	1	0	1	0	1
*G. mindorensis**	0	1	1	50–66	1–2	1	1	olive to brown-olive (l)	1	1	1	0	1
G. monarchus	0	1	1	32–40	2–3	1	1	lilac-brown to dark brown (l)	1	1	0	0	1
G. nutaphandi	0	1	1	17–22	1	1	0	grayish brown (p)	0	1	1	0	1
G. palawanensis	0	?	?	65–70	1	1	?	grayish to reddish-brown (p)	1	1	1	0	?
G. palmatus [5]	1	0	0	24–32	1	1	1	brown-olive to blackish green (l)	0	1	1	0	1
G. petricolus	0	0	1	9–11	1	1	1	gray-brown to yellow-brown (l)	0	1	0	0	1
G. porosus	0	?	?	74–80	?	1	1	tan to ligth brown (p)	0	1	1	0	1
G. russelltraini	0	?	?	8–11	2	?	1	yellow-brown (l)	0	1	0	0	1
G. romblon	0	1	1	70–84	?	1	1	gray-brown to blackish olive (l)	0	1	0	0	0
*G. scabridus**	0	1	1	10–15	1–3	1	1	pale brown (p)	0	1	1	0	1
G. scientiadventura	1	0	0	5–8	2–3	0	1	brownish to yellowish	1	1	0	0	1
G. siamensis	0	1	1	10–13	2	1	0	gray-brown to dark green	0	1	1	0	1
G. shibatai	0	0	0	0–3	1	1	1	chestnut (p)	0	1	0	0	1
*G. similignum**	1	0	0	17	1	1	1	dark-brown	0	1	0	0	1
G. smithii	0	1	1	7–17	1–4	1	0	yellow-green to dark green-gray (l)	1	1	0	0	1
G. subpalmatus	1	0	0	5–11	1	0	1	blackish green to blackish olive (l)	0	1	1	0	1
G. swinhonis	0	1	1	7–9	2–3	?	1	gray (p)	0	1	0	0	1
G. taibaiensis	?	?	?	4–6	?	?	?	?	0	1	1	0	1
G. takouensis	0	?	?	11–14	2–3	1	1	gray-brown (l)	0	1	0	0	1
G. tawaensis	0	0	0	0	1	0	1	gray-brown (l)	0	1	1	0	1
G. vertebralis	0	0	0	0–1	1–2	0	1	brownish (p)	0	1	0	0	?
G. verreauxi	0	1	1	11–13	1–2	1	0	gray-brown (l)	0	1	1	0	1
G. vietnamensis	0	?	?	0	1	?	1	dark-brown (l)	0	0	1	0	1
G. vittatus [7]	0	1	1	49–65	1–3	1	0	light to dark brown (l)	1	0	0	1	1
G. wenxianensis	0	0	1	6–8	2–3	?	?	brown (p)	0	1	0	0	1
G. yakuensis	0	0	0	6–8	1	1	1	bluish-gray (l)	0	1	0	0	1

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Table 1 continued

Taxon	29	References
*G. albofasciolatus**	Indonesia (Borneo)	19
G. athymus	Philippines (Palawan)	1, 6, 7, 66
G. auriverrucosus	China	63
G. badenii	Vietnam (Lao?)	8, 31, 49,65
G. canaensis	Vietnam	76
G. canhi	Vietnam	44
G. chinensis	China (Vietnam?)	38, 46, 61
G. crombota	Philippines (Babuyan Claro Island)	66
G. ernstkelleri	Philippines (Panay Island)	43, 66
G. gecko gecko [1]	China, India, Indonesia, Cambodia, Laos, Malaysia, Myanmar, Nepal, Philippines, Singapore, Thailand, Vietnam	9, 10, 14, 29, 40, 65
G. gecko azhari [2]	Bangladesh	30, 39, 65
G. gecko reevesii [3]	China, Vietnam	40, 61, 65
G. gigante	Philippines (Gigante Island)	1, 7, 66
G. grossmanni	Vietnam	20, 65
G. hokouensis	China, Japan, Taiwan	61, 65
G. japonicus	China, Japan, Korea	13, 61, 65
G. kikuchii	Taiwan (Lanyu Island)	3, 25, 35, 61
*G. liboensis**	China	62
G. melli [4]	China	41, 42, 60, 65
*G. mindorensis**	Philippines	1, 3, 7, 50, 51, 65, 66
G. monarchus	Brunei, Indonesia, Malaysia, Philippines, Thailand, Singapore	26, 36, 53, 55, 65
G. nutaphandi	Thailand	69
G. palawanensis	Philippines (Palawan)	1, 7, 53, 66
G. palmatus [5]	Vietnam	5, 65
G. petricolus	Cambodia, Laos, Thailand	21, 36, 54, 65
G. porosus	Philippines (Batan Island)	7, 52, 66
G. russelltraini	Vietnam	32, 65
G. romblon	Philippines (Tablas and Sibuyan)	1, 7, 12, 66
*G. scabridus**	China	23, 61
G. scientiadventura	Vietnam, Laos	42, 75
G. siamensis	Thailand	17, 36, 65
G. shibatai	Japan	56
*G. similignum**	China (Hainan Island)	38, 45
G. smithii	Brunei, India (Nicobars), Indonesia, Myanmar (?), Malaysia, East Timor, Thailand, Singapore	15, 16, 26, 36, 46, 65
G. subpalmatus	China	18, 61, 65

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Taxon	29	References
G. swinhonis	China	5, 18, 48, 61
G. taibaiensis	China	47, 61
G. takouensis	Vietnam	33
G. tawaensis	Japan	13, 34, 58
G. vertebralis	Japan	56
G. verreauxi	India (Andamans)	37, 57, 59
G. vietnamensis	Vietnam	67
G. vittatus [7]	Indonesia, Papua New Guinea, Palau, Vanuatu, Solomon Islands	2, 3, 4, 11, 22, 24, 28, 65
G. wenxianensis	China	68
G. yakuensis	Japan	13, 27, 73, 74

TABLE 2. *Gekko* species group characters. 1 = SVL (< 115 mm = 0, > 115 mm = 1); 2 = nostril in contact with rostral but not first supralabial (no = 0, yes = 1); 3 = nasals (three or less = 0, three or more = 1); 4 = postmentals (small = 0, large = 1); 5 = dorsal tubercles (available = 0, missing = 1); 6 = precloacal pores (24 or less = 0, 32 or more = 1); 7 = postcloacal tubercles (one = 0, one or more = 1); 8 = toes webbed (no = 0, yes = 1); 9 = tubercles on limbs (present = 0, absent = 1); 10 = tubercles on lateral fold (absent = 0, present = 1); 11 = subcaudals (enlarged = 0, not enlarged = 1).

	1	2	3	4	5	6	7	8	9	10	11
Gekko gecko group	1	0/1	1	0/1	0	0	1	0	0	0	1
Gekko japonicus group	0	0/1	0	0/1	0/1	0/1	0/1	0/1	0/1	0	0/1
Gekko monarchus group	0	1	0	0	0	1	0/1	0	0	0	0
Gekko petricolus group	0	1	0	0	0	0	1	0	0	0	0
Gekko porosus group	1	1	0	0	0	1	0	0	0	0	0
Gekko vittatus group	1	1	1	1	0	1	1	0	0	1	1
G. athymus	1	1	0	0	0	0	?	1	?	0	1
G. vietnamensis	0	1	?	?	0	0	0	0	?	0	1

Gekko gecko group
(Figure 2)

Species. *G. albofasciolatus* Günther, 1867; *G. gecko* (Linnaeus, 1758) (Figure 2A); *G. nutaphandi* Bauer, Sumontha & Pauwels, 2008; *G. siamensis* Grossmann & Ulber, 1990 (Figure 2B); *G. smithii* Gray, 1842 (Figure 2C); *G. verreauxi* Tytler, 1864 (Figure 2D); *Gekko* sp. "Tioman"; *Gekko* sp. "Sulawesi"; *Gekko* sp. "Togian."

Characters. 150.0–191.0 mm SVL; nares, except for *G. verreauxi*, not in contact with rostral; nasals 3–6; postmentals relatively slow (largest in *G. siamensis*), dorsal tubercle rows 10–19; precloacal pores 10–16; postcloacal tubercles 2–4 (rarely single); webbing between fingers and toes lacking; tubercles present on fore and hind limbs; lateral fold without tubercles; subcaudals enlarged, in two parallel rows; iris yellow, green, blue or brick red; Y-shaped head pattern usually discernible; light (white), more or less transversally arranged, symmetrical dorsal and lateral blotches.

Distribution. From India and Nepal to China, southwards to Indonesia (Indoaustralian Archipelago) (Figure 3B); *G. albofasciolatus* is endemic to Borneo; *G. verreauxi* is endemic to the Andaman Islands; *Gekko* sp. "Tioman" is endemic to Tioman Island; *Gekko* sp. "Sulawesi" is endemic to Sulawesi; *Gekko* sp. "Togian" is endemic to Togian and Batudaka. Allochthonous populations of *Gekko gecko* exist in the Caribbean, in Belize, on Hawaii and in Florida (Kraus 2009).

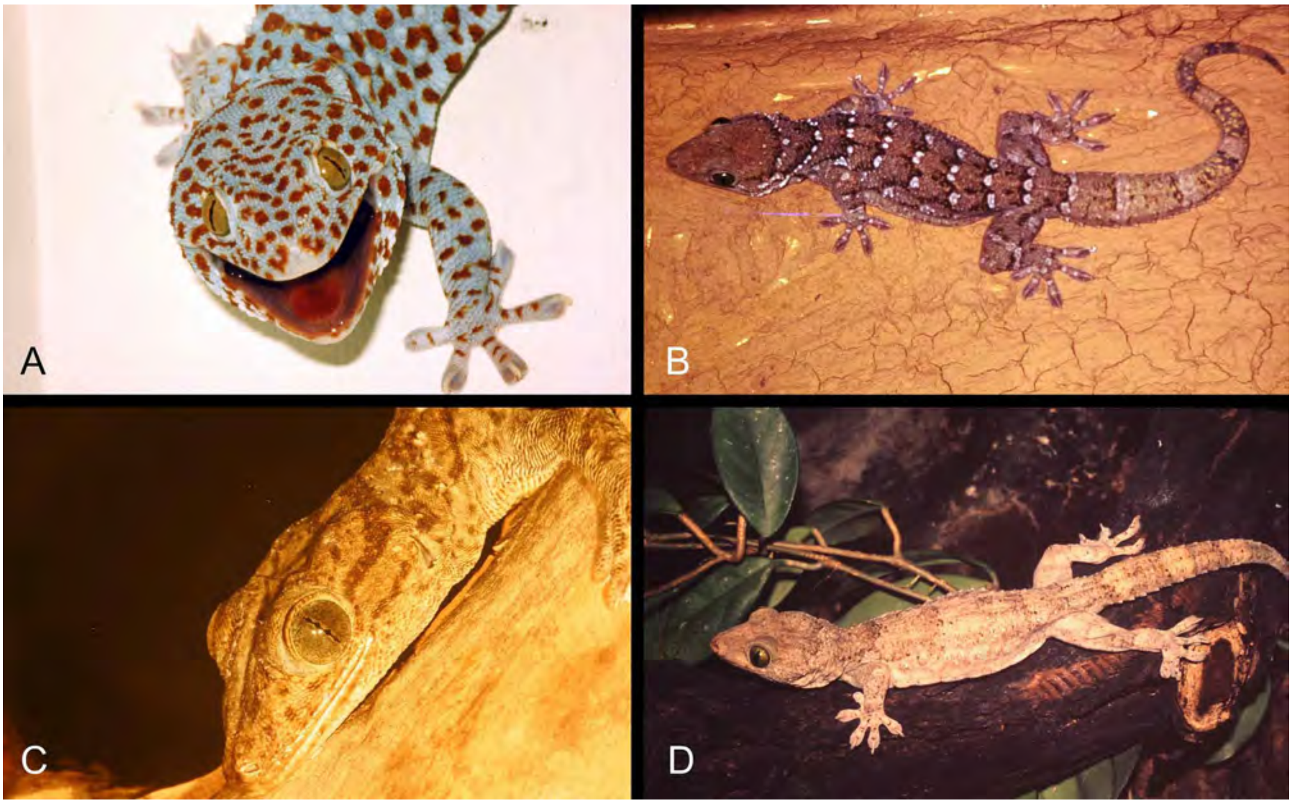

FIGURE 2. A. *Gekko gecko* (*G. gecko* group), photo by H. Rösler; B. Male *G. siamensis* (*G. gecko* group), Thailand, photo by H. Rösler; C. *G. smithii* (*G. gecko* group), Malaysia, photo by H. Rösler; D. *G. verreauxi* (*G. gecko* group), Andaman Islands, photo by M. Vesely.

Remarks. 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 (= Banjarmasin), 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. borneensis*) and *H. zosterophorus* were introduced by Bleeker (1857) without formal species descriptions (see also Bleeker 1860). The type loaclity 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. albofasciolatus* at the specific rank, but Malkmus *et al.* (2002) and Das (2004) did not consider *G. albofasciolatus* as part of the Bornean herpetofauna. According to its original description (Günther 1867), *G. albofasciolatus* differs from *G. smithii* by a different coloration of the dorsum (reddish-olive, marbled with grayish in *G. albofasciolatus*) and the venter (lower parts uniform whitish in *G. albofasciolatus*). Both species correspond well with respect to size and characteristic scalation (e.g., nares not in contact with rostral; postmentals relatively short; number of supralabials and sublabials; dorsal tubercle rows; precloacal pores) as well as in head and back pattern. A distinguishing feature at present is the number of ventrals (26 in *G. albofasciolatus* versus 29–39 in *G. smithii*). However, further specimen-based studies are needed to confirm whether *G. albofasciolatus* in fact deserves specific recognition.

Concerning *G. smithii*, Das (2004, 2007) depicted specimens from Borneo, which did not show a Y-shaped head pattern, as is characteristic for specimens from Thailand and Malaysia (see also figures in Chan-ard *et al.* 1999; Grossmann 2006). A specimen from eastern Kalimantan showed a brown vertebral stripe and very small white dorsal flecks (Grossmann 2006). Lim & Lim (1999) recorded *G. smithii* for the first time from Tioman Island, Malaysia (see Grossmann & Tillack 2004, 2005), which has been followed by Hien *et al.* (2001), and Grismer *et al.* (2002, 2004). However, the Pulau Tioman form differs from *G. smithii* sensu stricto according to Grossmann (2006) in eye coloration (turquous blue versus mossy green) and in ground coloration (gray brown versus green) and has been considered distinctive by Grismer (2006). In life, the form from Tioman more closely resembles *G. verreauxi*, from which it differs in the lighter eye coloration (emerald green in *G. verreauxi*) and the position of the nostril. We therefore suspect the form from Tioman Island to represent a distinct species and thus refer to it as *Gekko* sp. ”Tioman”. Additionally, Koch *et al.* (2009) published the first records of *G. smihii* from Sulawesi and Pulau Togian as well as from Pulau Batudaka. These authors argued against human introduction and rather believed that a natural dispersal from the Sunda shelf had occurred. Slight differences of the forms from Sulawesi and Togian compared with *G. smithii* s. str. were explained by Koch *et al.* (2009) as incipient divergence stemming from isolation, but they could not exclude the possibility that a cryptic species complex exists. Accordingly, we herein treat these both forms tentatively under the names *Gekko* sp. "Sulawesi" and *Gekko* sp. "Togian".

We herein consider the species of the *Gekko gecko* group a monophyletic unit. Species displaying green to blue or brick red iris (i.e., *G. albofasciolatus*, *G. nutaphandi*, *G. siamensis*, *G. smithii*, *G. verreauxi*, *Gekko* sp. ”Tioman“, *Gekko* sp. ”Sulawesi“, *Gekko* sp. ”Togian“) and more-or-less green ground coloration seem to be closely allied. For remarks on *Gekko gecko* and congeners see below.

Gekko japonicus group

(Figures 4, 5A)

Species. *G. auriverrucosus* Zhou & Liu 1982; *G. canhi* Rösler, Nguyen, Doan, Ho & Ziegler 2010; *G. chinensis* Gray, 1842; *G. hokouensis* Pope, 1928 (Figure 4B); *G. japonicus* (Schlegel, 1836) (Figure 4A); *G. liboensis* Zaho & Li, 1982; *G. melli* Vogt, 1922; *G. palmatus* Boulenger, 1907 (Figure 4C); *G. scabridus* Liu & Zhou, 1982; *G. scientiadventura* Rösler, Ziegler, Vu, Herrmann & Böhme, 2004 (Figure 4D); *G. shibatai* Toda, Sengoku, Hikida & Ota, 2008; *G. similignum* Smith, 1923; *G. subpalmatus* Günther, 1864; *G. swinhonis* Günther, 1864; *G. taibaiensis* Song, 1985; *G. tawaensis* Okada, 1956; *G. vertebralis* Toda, Sengoku, Hikida & Ota, 2008 (Figure 5A); *G. wenxianensis* Zhou & Wang, 2008; *G. yakuensis* Matsui & Okada, 1968.

Characters. 58.9–99.2 mm SVL; nares in contact with rostral (except for *G. auriverrucosus*); nasals 3 (rarely 2 in *G. chinensis*); postmentals relatively small (e.g., *G. similignum*), largest in *G. canhi*, *G. chinensis*, *G. palmatus*, *G. scientiadventura*; 0–21 dorsal tubercle rows; 0–32 precloacal pores; postcloacal tubercles 1–4; webbing between fingers and toes weakly developed to extensive (*G. chinensis*, *G. melli*, *G. palmatus*, *G. scientiadventura*, *G. similignum*, *G. subpalmatus*); tubercles present on fore and hind limbs, hind limbs only, or lacking all together; lateral fold without tubercles; subcaudals enlarged, in a longitudinal row (in *G. yakuensis* medially subdivided); head pattern present or not, without figure-shape (UU- to W-shaped in *G. melli* and W-shaped in *G. scientiadventura*); vertebral region with relatively large, light flecks, blotches or bands.

Distribution. China, Japan, Korea, Taiwan, and Vietnam including offshore islands; possibly Laos (Figure 3A).

Remarks. The *Gekko japonicus* group is very complex. Different morphological features of the species of this group (e. g., nares in contact with rostral or not, broad webbing between fingers and toes or not, dorsal tubercles absent or present, tubercles on limbs absent or present, see Table 2) demonstrate that this genetically well-defined clade is highly morphologically variable (see Figure 1).

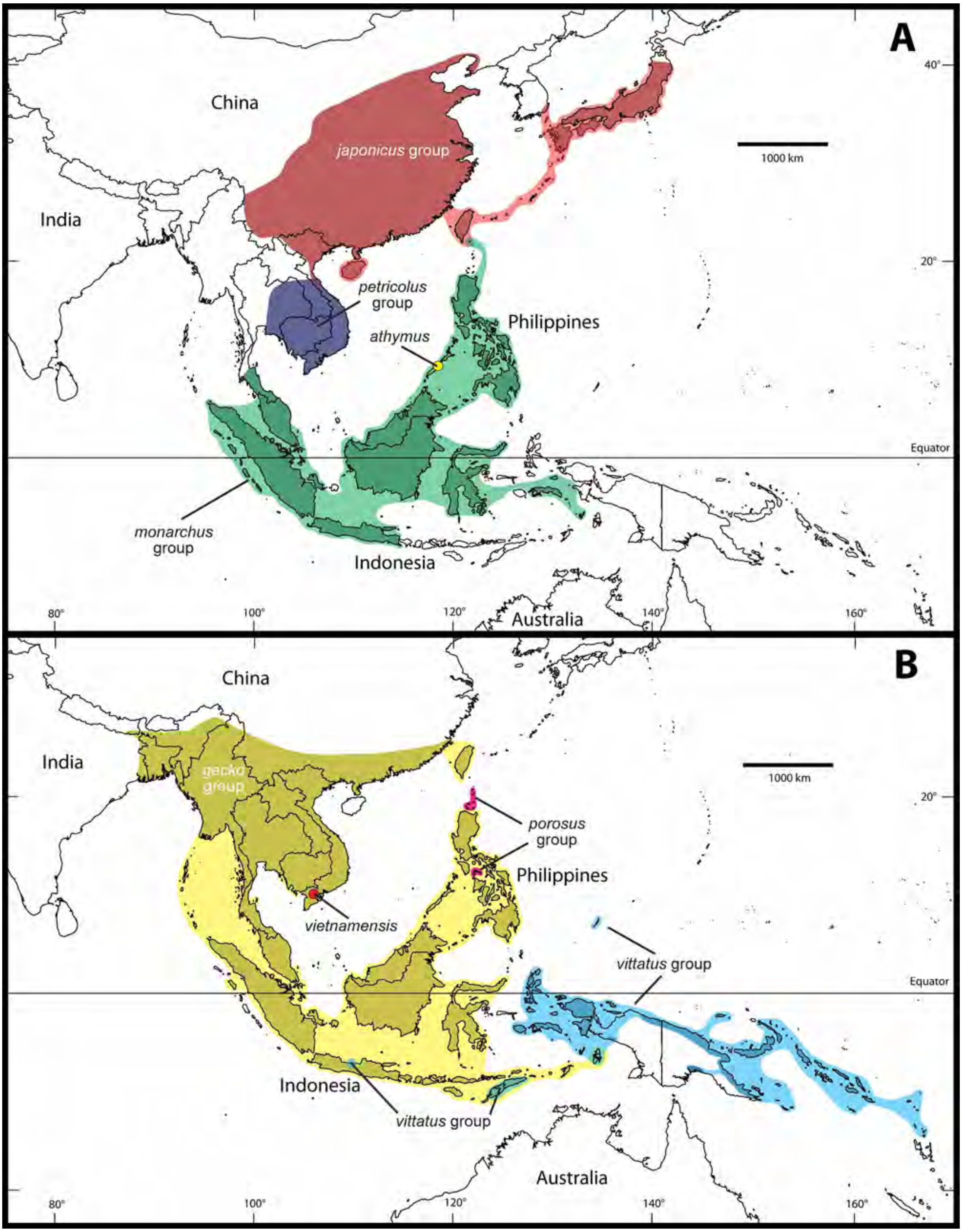

FIGURE 3. Map of East and Southeast Asia and the Indo-Australian Archipelago showing the approximate distribution of (A) the *Gekko japonicus*, *G. petricolus*, and *G. monarchus* groups and *G. athymus* and (B) the *G. gecko*, *G. porosus*, and *G. vittatus* groups and *G. vietnamensis*.

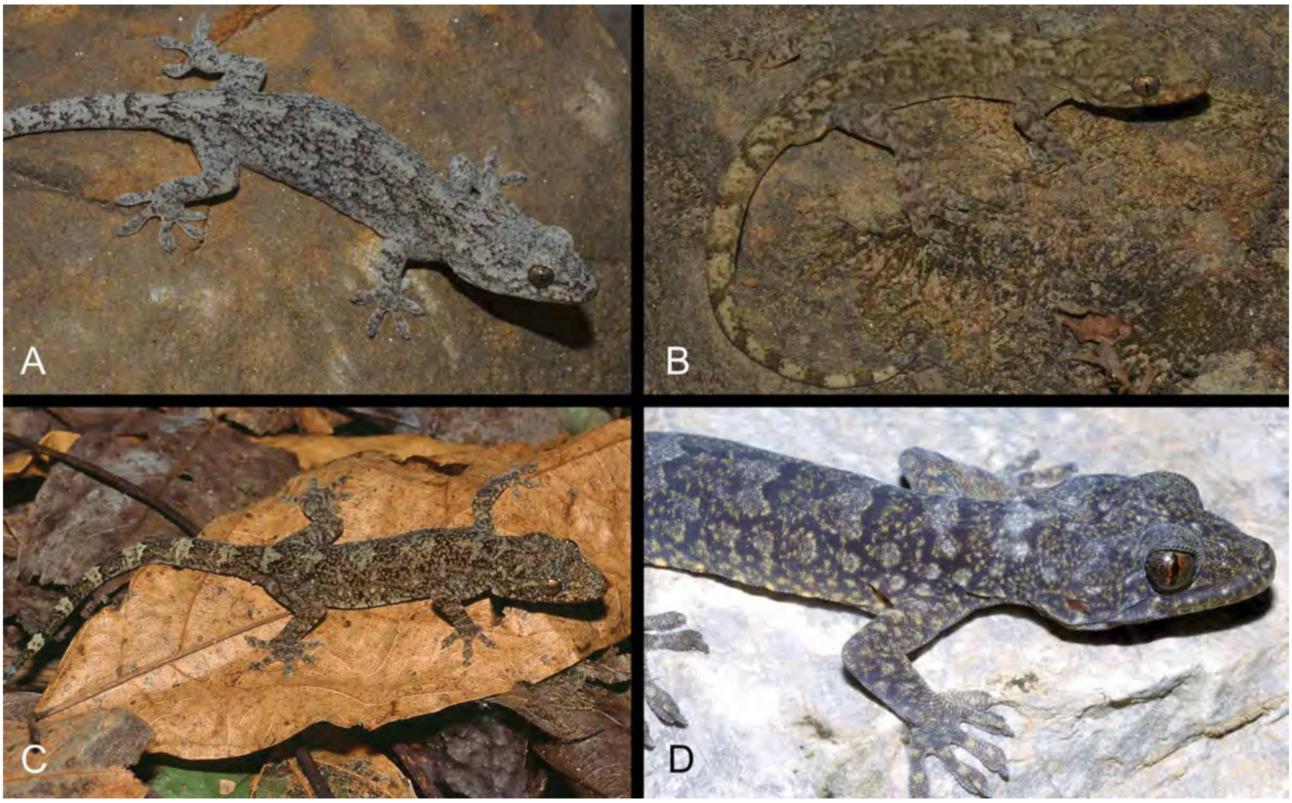

FIGURE 4. A. Female *Gekko japonicus* (*G. japonicus* group), photo by J. Boone; B. Male *G. hokouensis* (*G. japonicus* group), photo by J. Boone; C. *G. palmatus* (*G. japonicus* group), Quang Binh Province, Vietnam, photo by T. Ziegler; D. *G. scientiadventura* (*G. japonicus* group), Quang Binh Province, Vietnam, photo by T. Ziegler.

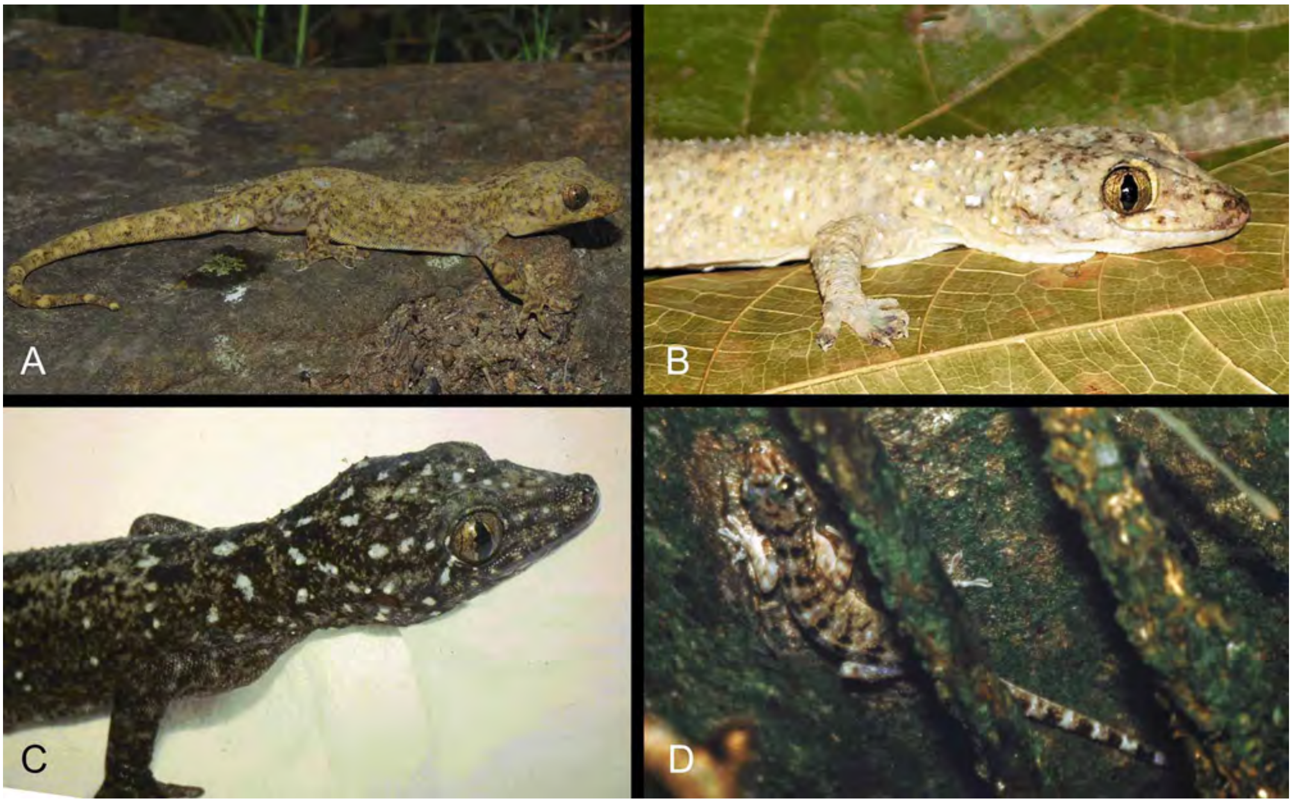

FIGURE 5. A. Male *Gekko vertebralis* (*G. japonicus* group), photo by J. Boone; B. *G. monarchus* (*G. monarchus* group), Banggai Islands, Indonesia, photo by A. Koch; C. *G. ernstkelleri* (*G. monarchus* group), Panay Island, Philippines, photo by M. Gaulke; D. *G. mindorensis* (*G. monarchus* group), Cebu Island, Philippines, photo by M. Gaulke.

Numerous authors have listed *Gekko chinensis* as a representative of Vietnam's herpetofauna (e.g., Bourret 1937b, 1940a, 1943; Zhao & Adler 1993; Welch 1994; Bobrov 1995a; Rösler *et al.* 2005). According to Nguyen *et al.* (2005), *G. chinensis* is widely distributed in the north of the country, whereas *G. palmatus* is only recorded from the two northern provinces of Lang Son and Vinh Phuc (see also Nguyen & Ho 1996). However, according to Ziegler *et al.* (2006) and based on new locality records (see Appendix 1) the distribution of *G. palmatus* in Vietnam in fact extends from several northern provinces southward to central Vietnam in Quang Binh Province. Taking into account the records given for *G. chinensis* by Nguyen & Ho (1996), the latter species must occur in sympatry with *G. palmatus* at least in the northern Vietnamese provinces of Bac Giang, Bac Kan, Cao Bang, Lang Son, Quang Ninh, and Vinh Phuc. However, all *Gekko* studied by us from these provinces proved to be *G. palmatus* and none had the diagnostic characters of *G. chinensis*. This also makes the records of *G. chinensis* from Hai Duong and Ninh Binh provinces (see Nguyen & Ho 1996) questionable and they are probably based on misidentifications of *G. palmatus*. Bobrov & Semenov (2008) listed all previous identifications of *G. chinensis* from Vietnam as *G. palmatus*. Ota *et al.* (1995) believed *G. chinensis* and *G. palmatus* to represent allopatric taxa (see also Matsui & Ota 1995). Concordant with the latter authors we herein suggest that the known occurrence of *G. chinensis* is limited to China (southern provinces of Fujian, Guangdong, Guangxi, Guizhou, Hong Kong, Sichuan, and Yunnan) whereas that of *G. palmatus* is only in northern and central Vietnam (Bac Giang, Bac Kan, Cao Bang, Hai Duong, Hai Phong, Lang Son, Ninh Binh, Quang Binh, Quang Ninh, and Vinh Phuc provinces). Further collections or study of museum specimens are needed to clarify the identification of populations along the China-Vietnam border and whether *G. chinensis* and *G. palmatus* occur in sympatry.

The distinguishing character of broad toe webbing in *G. palmatus* versus a narrower webbing in *G. chinensis*, which can regularly be found in the older literature (e.g., Boulenger 1907; Smith 1935; Bourret 1937b), may have conspicuously added to the above listed confusion and misidentifications, because it represents an ambiguous diagnostic character (Ota *et al.* 1995). Smith (1935: 114) even concluded that *G. palmatus* is "possibly a racial form of *G. chinensis*." However, *G. palmatus* and *G. chinensis* can be easily distinguished by the size of the internasals compared to the nasorostrals (internasals same size or larger than nasorostrals in *G. chinensis* versus always smaller in *G. palmatus*) and statistically significant differences in the number of midbody scales and the number of lamellae on the first, third and fifth fingers as well as the first toe (Ota *et al.* 1995). A key character that allows for proper identification of both aforementioned species is the presence of limb tubercles. These are present in *G. chinensis*, but are completely lacking in *G. palmatus* (our data). Ota *et al.* (1995) indicated shank tubercles for *G. chinensis* and the specimen depicted in Zhao & Adler (1993: pl. 21, fig. G.) has tubercles both on the fore and hind limbs; but the specimen of *G. palmatus* depicted by Nguyen *et al.* (2009: fig. 314) completely lacks such tubercles.

The taxonomic history of *G. similignum* is controversial. The type locality of this taxon is Hainan Island (Smith 1923). Stejneger (1932) synonymized *G. similignum* with *G. chinensis* (see also Zhao *et al.* 1999). However, Ota *et al.* (1995) and Kluge (2001) listed it as valid at the specific rank. *Gekko chinensis* and *G. smilignum* differ in maximum SVL, in the number of scales around midbody and in the number of lamellae on the first and fourth toes (see Table 1).

Gekko liboensis was described by Zhou & Li (1982) based on an adult female specimen collected in 1979. Three further specimens (two females and a juvenile) were collected in 1984 (Zhao *et al.* 1999). Zhao & Adler (1993) synonymized *G. liboensis* with *G. hokouensis* (see also Günther 1994; Kluge 2001; Henkel & Schmidt 2003). In contrast, Kluge (1993), Bauer (1994), Welch (1994), Matsui & Ota (1995), Zhao *et al.* (1999), Rösler (2000), Rösler *et al.* (2005, 2006) treated *G. liboensis* as a valid species. *Gekko liboensis* differs from *G. hokouensis* by a larger SVL (85 versus 70 mm), absence of internasals, more interorbitals (40 versus 30–33), flat dorsal tubercles, fewer dorsal tubercle rows (10 versus 12–18) and by the number of lamellae below the fourth toe (9 versus 15–18). However, as adult males are still lacking for *G. liboensis*, important diagnostic characters and possibly additional distinguishing features such as the number of precloacal pores are still missing. The nares of *G. auriverrucosus* are not in contact with the first supralabial (Zhou & Liu 1982), which seems to represent a derived character of the *Gekko gecko* group (except for *G. verreauxi*).

Zhao & Adler (1993) synonymized *G. scabridus* with *G. chinensis* (see also Kluge 2001), but Matsui & Ota (1995) and Zhao *et al.* (1999) again evaluated the former taxon as valid species. Liu & Zhou (1982) pointed to the phenotypic similarity between *G. scabridus* and *G. japonicus*. According to Liu & Zhou (1982), *G. scabridus* differs from *G. japonicus* by having tubercles on its back and hind limbs and by a higher count of precloacal pores. From Table 1 it is obvious that there exist additional distinguishing features between the two species. Compared with *G.*

japonicus, *G. scabridus* has fewer interorbitals (30 versus 32–35), fewer lamellae below the first toe (6–9 versus 10–12), and fourth toe (7–9 versus 14–16), more dorsal tubercle rows (17–21 versus 9–14) and a higher number of precloacal pores (10–15 versus 6–9). In comparsion to *G. chinensis* it has only slightly developed webbing between the fingers and toes, fewer precloacal pores, and more postcloacal tubercles. We, therefore, accept the specific status of *G. scabridus* and regard it as a valid member of the *Gekko japonicus* group.

Vogt (1922) originally described *G. melli* based on a large series of which now only two specimens still exist (Bauer & Günther 1991). Stejneger (1932) listed *G. melli* as a subspecies of *G. subpalmatus* and Pope (1935) finally synonymized the former species with *G. subpalmatus*. Rösler *et al.* (2005) revalidated *G. melli* as a distinct species (see also Rösler & Tiedemann 2007).

With respect to *G. subpalmatus* it is interesting to note that the back of the holotype is slightly banded and that the vertebral region shows four indistinct light blotches (Rösler *et al.* 2005: figs. 11–12). However, the ground coloration of the live specimen depicted in Zhao & Adler (1993: their Pl. 32, fig. B) is blackish-olive (Black 3U). This specimen, in addition, has a repeatedly interrupted orange (722U) vertebral stripe and tail blotches of the same color; a banded pattern as observable from the holotype is not discernible (see also fig. in Huang & Zong 1998: pl. 29). Whether this reflects intraspecific variation or a persistent confusion over the identity of this species remains to be investigated.

Gekko monarchus group

(Figure 5B–D)

Species. *G. carusadensis* Linkem, Siler, Diesmos, Sy & Brown, 2010; *G. ernstkelleri* Rösler, Siler, Brown, Demegillo & Gaulke, 2006 (Figure 5C); *G. kikuchii* Oshima, 1912; *G. mindorensis* Taylor, 1919 (Figure 5D); *G. monarchus* (Schlegel, 1836) (Figure 5B); *G. palawanensis* Taylor, 1925.

Characters. 63.0–100.0 mm SVL; nares in contact with rostral; nasals 3 (rarely 4 in *G. ernstkelleri*); postmentals relatively large; dorsal tubercle rows 10–24; precloacal pores 32–70; postcloacal tubercles 2–3 (1 in *G. carusadensis* and *G. palawanensis*); no webbing between fingers and toes; tubercles on fore and hind limbs (not on fore limbs of *G. ernstkelleri*); lateral folds without tubercles; subcaudals mostly enlarged, in a longitudinal row; more or less distinct, W-shaped head pattern; light (white to gray), mostly asymmetrically arranged dorsal and lateral flecks.

Distribution. *G. monarchus* is known from the Philippines westwards to Myanmar and to Indonesia (Aru Islands, Kei Islands, New Guinea) in the south (Figure 3A); *G. kikuchii* is endemic to Lanyu Island, Taiwan; remaining group members are endemic to the Philippines.

Remarks. *G. kikuchii* was described by Oshima (1912) from Botel Tobago (Lanyu) near Taiwan. Many subsequently published taxonomic papers refer to Oshima (1912) but do not provide further insights in the form of a redescription of the species or new material (e.g., Horikawa 1927; Wang & Wang 1956; Lue *et al.* 1988); see also relevant comments in Ota (1989b). In describing *G. mindorensis*, Taylor (1919) compared the new species with *G. kikuchii* and *G. monarchus*. According to Taylor (1919), *G. mindorensis* differs from the former species by its longer limbs, more preanofemoral pores and by lacking webbing between toes in both sexes; *G. mindorensis* differs from *G. monarchus* by a relatively larger ear opening, a larger eye diameter, a smaller interorbital distance, more flattened dorsal tubercles, more ventrals and preanofemoral pores, and a distinctly different dorsal pattern (see also Taylor 1922a). However, Wang (1962) pointed to the similarity of *G. kikuchii* with *G. monarchus* and *G. mindorensis*. Brown & Alcala (1978) redescribed *G. mindorensis* based on new specimens, but only provided thorough comparisons with *G. monarchus*, but not with *G. kikuchii*. Based on the new variation in size and scalation reported in the redescription provided by Brown & Alcala (1978), *G. mindorensis* was in fact no longer distinguishable from *G. kikuchii* based on the data on the latter species provided by Taylor (1919), as is also obvious from Table 1. Crombie (in Bauer 1994) thus had doubts on the distinct status of *G. mindorensis* and stated “probably a junior synonym of *Gekko kikuchii*.” Finally, Ferner *et al.* (2001) and Kluge (2001) listed *G. mindorensis* as a synonym of *G. kikuchii*. However, there might be differences in pattern between *G. kikuchii* and *G. mindorensis*. Figures of different specimens of *G. kikuchii* in Ota (1989b, 1991), Lue *et al.* (1999), Shang (2001), and Henkel & Schmidt (2003) show a brown ground coloration with a nearly identical dorsal pattern, consisting of two parallel dark brown pairs of blotches. In contrast, the ground coloration of *G. mindorensis* seems to be gray, with transverse rows (see Gaulke

2003: fig. 8) or rows dissolved into four to six blotches each (see Rösler *et al.* 2006: fig. 13). In addition, the light dorsal blotches in *G. mindorensis* appear to be more distinct than in *G. kikuchii*. We must add that the detailed figures provided by Okada (1936: fig. 4) most probably belong to a *Hemidactylus* species (maybe *H. stejnegeri*), but certainly not *G. kikuchii*. The synonymy of *G. mindorensis* with *G. kikuchii* is also contradicted on zoogeographic grounds. The amphibian and lizard fauna of Lanyu Island shows, according to Okada (1936) and Ota *et al.* (1988), greater affinities to Taiwan than to the Philippines, and *G. mindorensis* does not occur on the northern Philippine Islands (e.g., Luzon, Batanes) that are closest to Taiwan (Brown & Alcala 1970, 1978; Alcala 1986; Gaulke & Altenbach 2006). Kuntz & Ming (1970) listed *G. kikuchii* for Penghu Lieh-tao (Pescador Island), but the species is endemic to Lanyu Island ("Botel Tobago") (see Ota 1989b). Further taxonomic research is required on more specimens, especially of *G. kikuchii*, to clarify whether *G. mindorensis* is a junior synonym of *G. kikuchii*, or whether two closely related cryptic species are involved.

Gekko petricolus group
(Figure 6A–C)

Species. *G. badenii* Nekrasova & Szczerbak, 1993 (Figure 6B); *G. canaensis* Ngo & Gamble, 2011; *G. grossmanni* Günther, 1994 (Figure 6C); *G. lauhachindaei* Panitvong, Sumontha, Konlek & Kunya, 2010; *G. petricolus* Taylor, 1962 (Figure 6A); *G. russelltraini* Ngo, Bauer, Wood & Grismer, 2009; *G. takouensis* Ngo & Gamble, 2010.

Characters. 82.9–108.5 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 8–18; precloacal pores 8–15; postcloacal tubercles 1–3; no webbing between fingers and toes; fore and hind limbs without tubercles (but present on hind limbs of *G. petricolus*); lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; head without pattern or with blotches or short stripes, but not forming a distinctive UU- or W-shaped pattern; back banded (*G. badenii*) or more or less symmetrically blotched (*G. canaensis*, *G. grossmanni*, *G. lauhachindaei*, *G. petricolus*, *G. russelltraini*, *G. takouensis*).

Distribution. Laos, Tailand and Vietnam (Figure 3A).

Remarks. Based on morphological characters, *G. russelltraini* and *G. takouensis* are probable sister species, and both are closely related to *G. canaensis* and *G. lauhachindaei*. Futhermore *G. grossmanni* and *G. petricolus* are likely sister species. *G. grossmanni* has a similar pattern compared with *G. petricolus*, but the latter species is the sole member of the *Gekko petricolus* group that has tubercles on the hind limbs. *G. badenii* differs from the aforementiond taxa from southern Vietnam and Thailand in having a banded dorsal pattern without flecks between bands.

Gekko porosus group
(Figure 6D)

Species. *G. crombota* Brown, Oliveros, Siler & Diesmos, 2008; *G. gigante* Brown & Alcala, 1978; *G. porosus* Taylor, 1922; *G. romblon* Brown & Alcala, 1978 (Figure 6D); *G. rossi* Brown, Oliveros, Siler & Diesmos, 2009.

Characters. 89.2–108.2 mm SVL; nares in contact with rostral; nasals 3; postmentals relatively large; dorsal tubercle rows 12–22; precloacal pores 52–88; postcloacal tubercle single; no webbing between fingers and toes; tubercles present on fore and hind limbs; lateral folds without tubercles; subcaudals enlarged, in a longitudinal row; green to blue coloration of the iris; head pattern without a distinctive (e.g. W-shaped) pattern; dorsum with flecks (*G. gigante* indistinctly banded).

Distribution. Philippines (Figure 3B).

Remarks. *G. porosus* was, for a long time, only known from the juvenile holotype (CAS 60526) (see Taylor 1922b), which was redescribed by Brown & Alcala (1978). The redescription by the latter authors led to slightly smaller measurements, and they did not mention the dark dorsal flecks that were visible in the freshly collected holotype. Brown *et al.* (2009) redescribed *G. porosus* using new material: three adult males with transverse rows of spots.

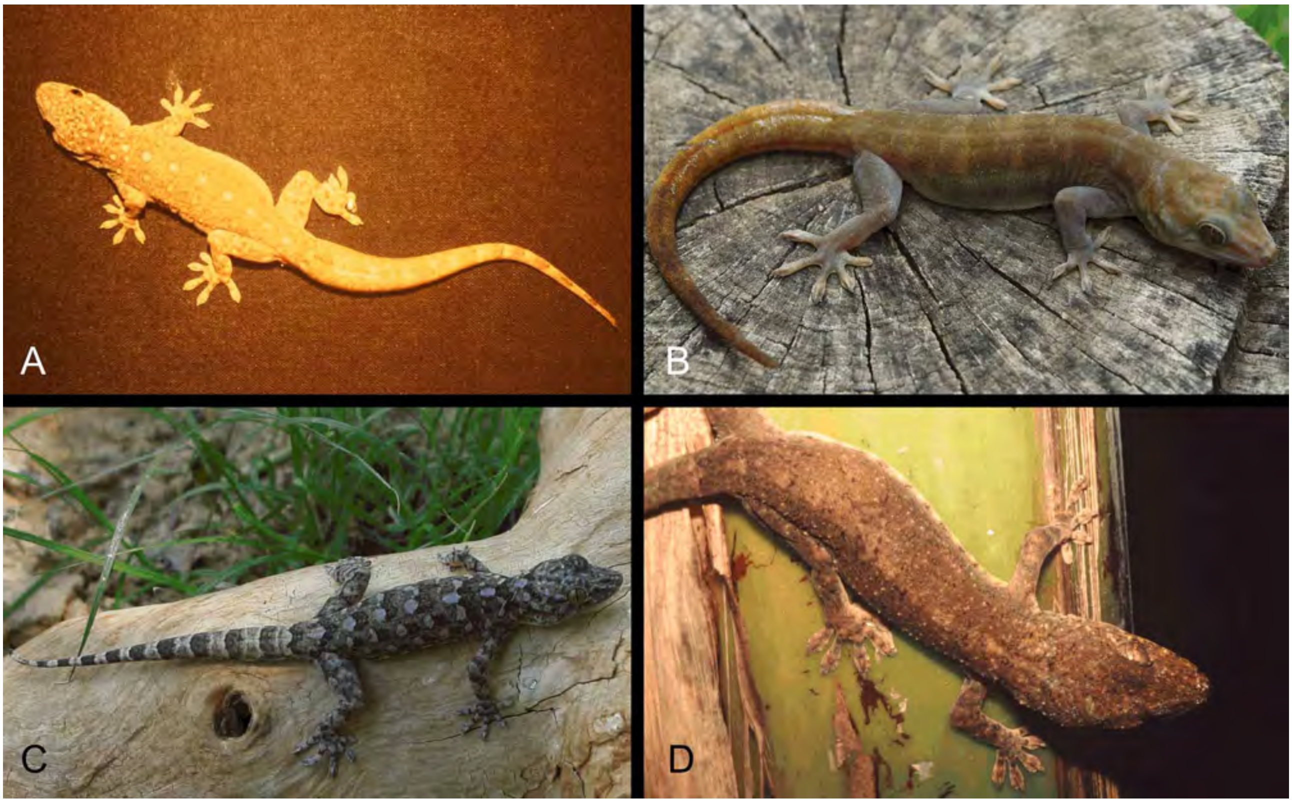

FIGURE 6. A. Male *Gekko petricolus* (*G. petricolus* group), photo by H. Rösler; B. Male *G. badenii* (*G. petricolus* group), photo by J. Boone; C. *G. grossmanni* (*G. petricolus* group), photo by J. Boone; D. *G. romblon* (*G. porosus* group), Sibuyan Island, Philippines, photo by M. Gaulke.

Gekko vittatus group
(Figure 7)

Species. *G. vittatus* Houttuyn, 1782 (Figure 7A–B); *Gekko* sp. "Belau"; *Gekko* sp. "Malaupaina."

Characters. Maximum SVL 140.0 mm; nares in contact with rostral; nasals 3–4; postmentals relatively small; dorsal tubercle rows 12–14; precloacal pores 14–58; postcloacal tubercles 1–3; no webbing between fingers and toes; fore and hind limbs with tubercles; lateral folds with tubercles; subcaudals not enlarged; head unicolored, without pattern; nominate form with white, anteriorly bifurcated dorsal stripe.

Distribution. *G. vittatus* is known from Indonesia (from Java to New Guinea), Papua New Guinea, the Solomon Islands and northern Vanuatu (Torres and Banks Islands, Malakula Island); *Gekko* sp."Belau" is currently recorded from the Republic of Palau; *Gekko* sp. "Malaupaina" is currently reported from Malaupaina Island (Olu Malau Islands), Solomons (Crombie & Pregill 1999; McCoy 2006).

Remarks. *Gekko vittatus* was described by Houttuyn (1782) with the locality data "zekerlyk uit de India." Fitzinger (1826) referred the species to the genus *Platydactylus* Goldfuss, 1820 (see also Schlegel 1827; Wagler 1830; Duméril & Bibron 1836), which was subsequently split into three subgenera by Fitzinger (1843), of which *vittatus* belonged to his new subgenus *Scelotretus*. *Lacerta unistriata*, which was described by Shaw (1792), proved to be a synonym of *G. vittatus* (e.g., Daudin 1802; Gray 1845; Boulenger 1885; Wermuth 1965; Bauer 1994; Kluge 2001). Likewise *Platydactylus bivittatus*, which was described by Duméril & Bibron (1836) from New Guinea and Waigeo Island, Indonesia, was synonymized with *G. vittatus* (Loveridge 1948). Fitzinger's (1843) *Platydactylus* (*Scelotretus*) *bivittatus* and Boulenger's (1885) *Gecko vittatus* var. *bivittatus* referred to the same taxon. *Gecko trachylaemus*, described by Peters (1873), was also synonymized with *G. vittatus* (Peters & Doria 1878).

The number of preanofemoral pores recorded in *G. vittatus* varies considerably according to different authors (Boulenger 1885: 50–59, De Rooij 1915: 14–58, Loveridge 1948: 21–57). Such variation of preanofemoral pores has not been described for any other *Gekko* species and likely points to the existence of cryptic species. However,

FIGURE 7. *Gekko vitattus* (*G. vittatus* group): A. Duabo, Pini Range, SW of Alotau, Milne Bay Province, Papua New Guinea, photo by F. Kraus; B. Sudest Island, Milne Bay Province, Papua New Guinea, photo by F. Kraus.

in the series of *G. vittatus* from New Guinea and Ambon Island which was studied by us, we could not find any significant differences (see Table 1). With respect to pattern, we observed only slight variation in the number of light tail bands (4–6) and in the shape of the vertebral stripe on the tail and its bifurcation in the shoulder region (bifurcated branches may reach only as far as the back of head or may reach the eyes).

Gekko sp. ”Malaupaina“ is known from the eastern Solomons (e.g., Malaupaina Island). This form differs from *G. vittatus* s. str. in the coloration of the iris (gray versus light brown), ground coloration (black olive versus brown olive) and in pattern (light vertebral stripe that bifurcates on the neck lacking in *G. vittatus* s. str.), see McCoy (1980: Pl.2, fig. D, Pl. 6, fg. A) and McCoy (2006: Pl. 15). Mertens (1934: plate 2, fig. 7) pointed to a similarly patternless *G. vittatus* s. lat. from Nissan Atoll (Green Island Group, Papua New Guinea). The taxonomy of the southern Malaupaina form clearly deserves further research.

Gekko vittatus from the Belau Islands (Republic of Palau) was mentioned as a distinct species by Crombie & Pregill (1999), however, it remains undescribed. The obscurely striped *Gekko* sp. ”Belau” was occasionally referred to *Gecko vittatus bivittatus* (e.g., Boulenger 1885; Dryden & Taylor 1969), but Crombie & Pregill (1999) refer to significant differences between *Gekko* sp. ”Belau” and the unstriped *Gekko vittatus* from New Guinea and the Solomons. The Belau form of *G. vittatus* shows some genetic divergence from *G. vittatus* across the remainder of the range (see above). The *G. vittatus* of Vanuatu shares its greatest molecular affinity with the form from the southern Solomons (see Figure 1).

Status uncertain

Gekko athymus Brown & Alcala, 1962 is distributed in the Philippines (Figure 3A). This species is phenetically similar to members of the *Gekko japonicus* group (e.g., *G. melli*, *G. scientiadventura*, *G. subpalmatus*) in having broad webbing between finges and toes, but *G. athymus* differs from these species in having a relatively large SVL (> 100 mm), a higher number of lamellae below the fourth toe and more precloacal pores. The molecular data (Figure 1) strongly suggest that *G. athymus* is part of a larger Philippine clade that also incorporates the *G. porosus* and *G. monarchus* groups, but it is nonetheless highly distinctive from these forms.

Most *Gekko* species possess precloacal or preanofemoral pores. In *G. vertebralis* the number of pores varies between 0 and 3, and 0 and 1 in *G. shibatai*, whereas they are completely lacking in *G. tawaensis*. Most recently, Nguyen (2010) described another poreless *Gekko* from southern Vietnam (Figure 3B), *G. vietnamensis*. This species differs from *G. tawaensis* by having a greater size (SVL 100 mm versus 71 mm) and lacking characteristic pale blotches in the vertebral region. *Gekko vietnamensis* is also distinguished from remaining Vietnamese congeners by its coloration, which consists of four diffuse bands. Thus, and due to the scarce scalation data currently available for this species, its group status must remain open at time.

On the gamma taxonomy of *Gekko gecko* (Linnaeus, 1758) with the revalidation and redescription of *G. reevesii* (Gray, 1831)

Gekko gecko has the widest distribution of all currently known congeners. In east-west extent the species is reported from China to India and Nepal, and it stretches southwards to the Aru Islands. The type locality of *Gekko g. gecko* was restricted to Java, Indonesia, by Mertens (1955). *G. gecko* is polytypic. Besides the nominate form, *G. gecko azhari* Mertens, 1955 is currently recognized as a second valid subspecies. However, additional geographic morphotypes differ in scalation, measurements, coloration and pattern, but most of them are represented by only a few specimens from scattered regions (e.g., Zhang *et al.* 1997; Rösler 2001, 2005a). Of these morphotypes, the most distinctive to us is the dark, blackish-gray northeastern form from parts of Vietnam and southern China. In southern China, two forms of *G. gecko*, “red” and “black” have long been recognized on morphological grounds (Zhang *et al.* 1997; Chan *et al.* 2006), and are even distinguished as having different medicinal value (Zhang *et al.* 2006). Liu *et al.* (2000), Zhang *et al.* (2006), and Qin *et al.* (2007) examined relationships between these two putative taxa using mitochondrial genes and recognized that there are relatively deep divergences between the two, as much as 8.6–9.5% in cytochrome *b* between Guangxi “black” geckos and “red” tokays from Vietnam, Laos, and Nanning, Guangxi. Of these various authors, only Qin *et al.* (2007) concluded that “red” and “black” tokays were taxonomically distinct. However, they did not suggest a resurrected or new name for the latter form.

Thus, we investigated synonyms of *G. g. gecko* to determine whether any were available for the "black" tokay of China and adjacent northern Vietnam. It must be noted that the name *Gekko Ceilonicus* Seba, 1734, which was subsequently cited and depicted by Herz von Herzberg & Riedel (1788), but without description (see Niekisch 2008), is pre-Linnean and thus not available (Kraus 2000). Of the available synonyms of *G. g. gecko* (*G. aculeatus* Houttuyn, 1782; *G. annulatus* Kuhl, 1820; *G. guttatus* Daudin, 1802; *G. indicus* Girard, 1858; *G. perlatus* Houttuyn, 1782; *G. reevesii* Gray, 1831; *G. tenuis* Hallowell, 1857; *G. teres* Laurenti, 1768; *G. verticillatus* Laurenti, 1768; *G. verus* Merrem, 1820; see also Rösler *et al.* 2005), the range of *G. reevesii* (type locality: China) corresponded best with the northeastern form. *G. reevesii* was synonymized with *G. gecko* by Boulenger (1885), and this action has been followed in all subsequent taxonomic lists (Wermuth 1965; Kluge 1991, 1993; Rösler 2000; Kluge 2001). As the original description of *G. reevesii* (Gray 1831) is short and relatively unspecific ("Black, with cross band of white spots, and some obscure rather larger tubercular scales") we reinvestigated Gray's holotype of this taxon. The holotype corresponded well with the series of specimens we had available of this northeastern form and all were unambiguously morphologically distinguishable from the nominate form from Java. As the name *reevesii* fulfills the nomenclatural requirements for availability (International Commission on Zoological Nomenclature 1999, Article 10.6) we herein redescribe the taxon *reevesii* and revalidate it at specific rank, for morphological, molecular and zoogeographical reasons given below.

***Gekko reevesii* Gray, 1831**

1831 *Gecko reevesii* Gray in Griffith & Pidgeon, Anim. Kingdom Cuvier., 9 Synops. Spec.: 48.

Diagnosis. A large species of *Gekko*, with SVL > 150 mm; head distinct from body; body somewhat flattened; tail round in section, not thickened at base; supralabials 10–14; sublabials 9–13; nares in contact with rostral; nasals 3–6; internasal 0–1; interorbitals 17–29; dorsal tubercle rows 12–18; scales between mental and cloacal slit 133–141; midbody scales 82–103; subdigital lamellae below first toe 13–19; subdigital lamellae below fourth toe 18–24; no extensive webbing between fingers and toes; forearm and hind limbs with tubercles; precloacal pores 13–20; postcloacal tubercles 1–4; tail tubercles present; subcaudals not enlarged; grayish brown to grayish green ground coloration, with reddish brown dorsal blotches; dorsal pattern tends to consist of transverse bands and short stripes.

Holotype: BMNH 1946.8.2598—male, ad., China, collector unknown (Figures 8, 9).

SVL 130.0 mm; TL 110.0 mm; LT 28.5 mm; HL 36.4 mm; HW 26.2 mm; HH 14.0 mm; SE 11.5 mm; EE 12.4 mm. SVL/TL 1.18; SVL/LT 4.56; SVL/HL 3.57; HL/HW 1.39; HL/HH 2.60; SE/EE 0.93.

Rostral concave above, wider than high (RW 4.80 mm, RH 2.70 mm, RW/RH 1.78), wider than mental (RW/MW 1.71); 13/13 supralabials; 22/18 snout scales adjacent to supralabials; nares not in contact with rostral (Figure 9A); 5/4 nasals; nasorostrals ca. double the size of supranasals and five times larger than postnasals; internasal single, large (Figure 9B); snout medially with flat, elongate depression; lateral snout scales round to oval, curved, next to each other; ca. 12–13 large scales between postnasals and orbital cavity; 61 scales between seventh supralabials; medial snout scales barely smaller than lateral snout scales; dorsal ciliary scales 1.5 times higher than medial snout scales; temporal scales larger than lateral snout scales; ear opening vertical, oval; 20 interorbitals, granular, in orbital region twice as large as medially; back of head and neck granular; granular scales slightly larger than medial interorbitals; neck tubercles round, concial; mental pentagonal, longer than wide (MW 2.8 mm, ML 3.0 mm, MW/ML 0.93), not distinctly larger than first sublabials (Figure 9C); 11/11 sublabials; 17/15 gular scales adjacent to sublabials; 2 small postmentals, hexagonal, 1.5 times longer than wide, anteriorly in contact with mental and first sublabials; 5 gular scales adjacent to postmentals; outer gular scales ca. 1.5 times larger than inner ones; gular scales as large as medial snout scales, round, slightly curved, smooth, next to each other, arranged in more or less regular transverse rows; dorsals as large as medial snout scales, round flat, next to each other, arranged in more or less regular transversal rows; dorsal tubercles 2–3 times as large as adjacent dorsals (DTL 2.1 mm, DTW 1.5 mm, DTL/DTW 1.40, DTLx100/SVL 1.62, DTWx100/SVL 1.15), oval, asymmetrically conical (Figure 9D), arranged in 14 more or less regular longitudinal rows, encircled by 9 dorsals; lateral tubercles smaller than dorsal ones (LTL 1.8 mm, LTW 1.2 mm, LTL/LTW 1.50, LTLx100/SVL 1.39, LTWx100/SVL 0.92); lateral folds slightly developed;

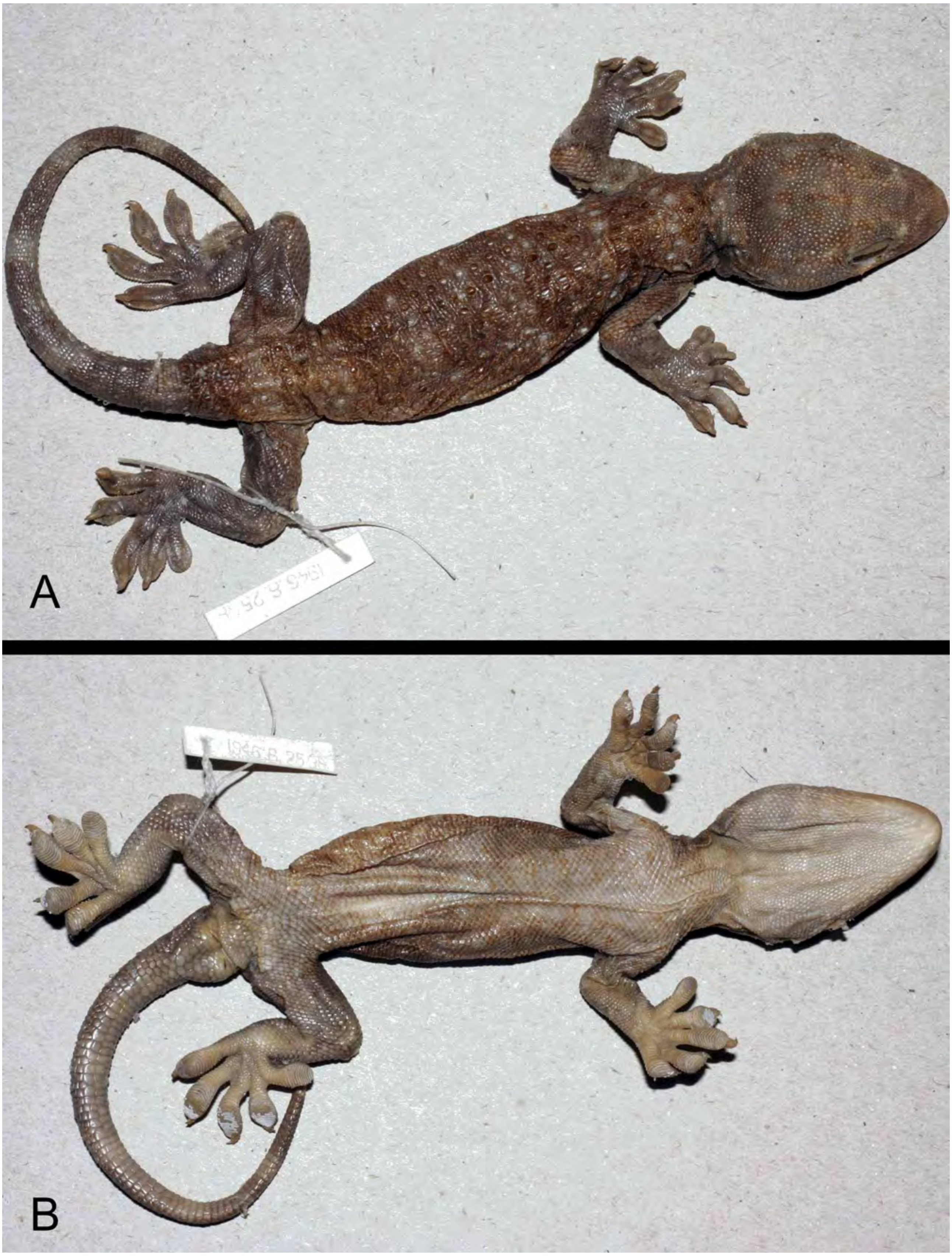

FIGURE 8. Dorsal (A) and ventral (B) view of *Gekko reevesii* Gray, 1831 (holotype, BMNH 1946.8.2598), photo by T. Ziegler.

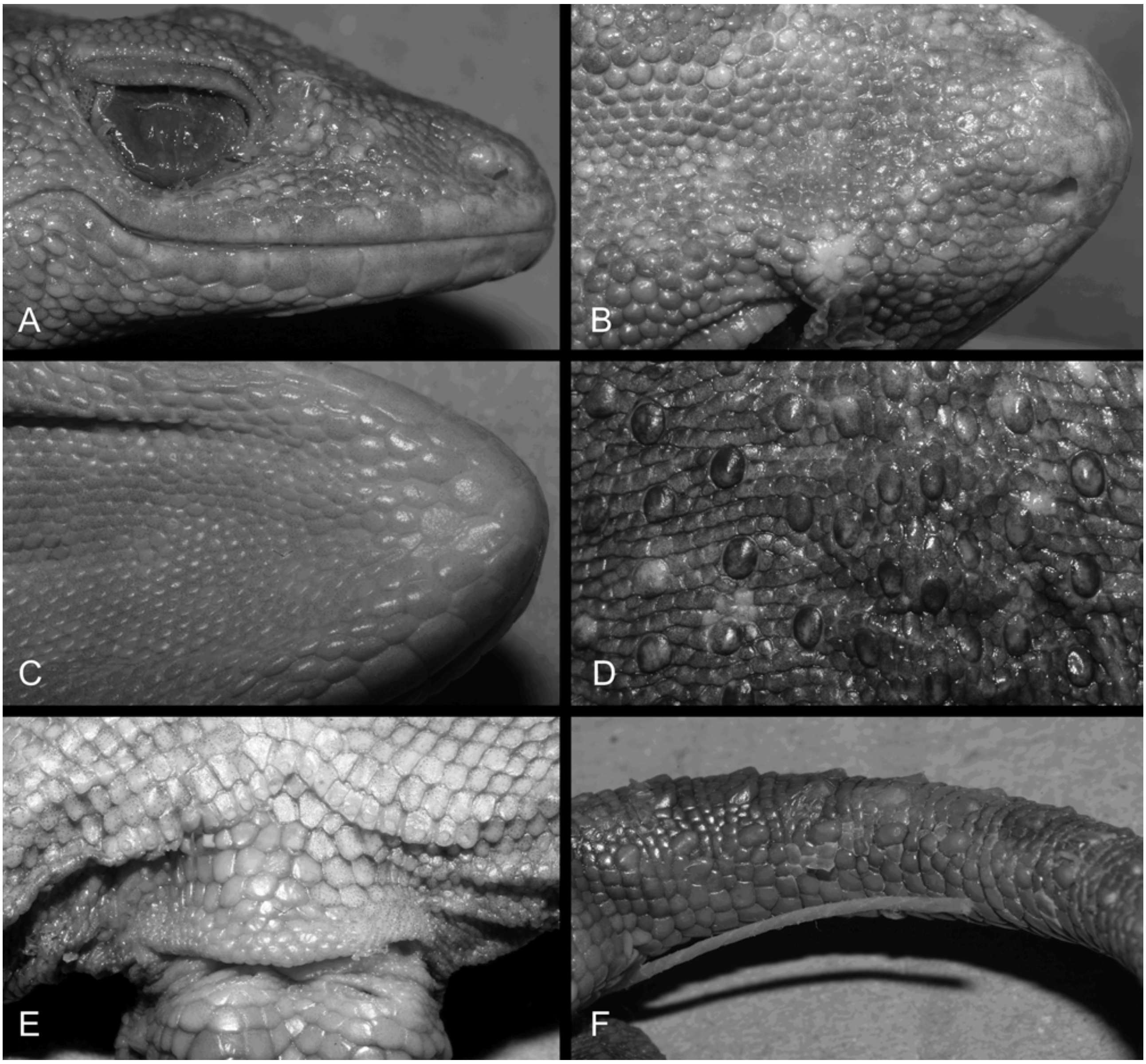

FIGURE 9. *Gekko reevesii* Gray, 1831 (holotype, BMNH 1946.8.2598): A. Lateral view of head; B. Nasal region; C. Gular region; D. Dorsum; E. Precloacal region; F. Tail, photos by T. Ziegler.

ventrals flat, smooth, subimbricate, and larger than dorsals; 102 scales around midbody; limbs without tubercles; arm and forearm scales flat, smooth, subimbricate; shank with curved tubercles; dorsal and ventral thigh scales anteriorly flat, imbricate, posteriorly smaller, curved; enlarged femoral scales lacking; 9/10 tubercles on thigh; fingers and toes 1–4 basally with narrow webbing; 19/19 subdigital lamellae below first finger and 21/23 below fourth finger; 18/18 subdigital lamellae below first toe and 23/24 below fourth toe; 19 precloacal pores in a continuous, angular-shaped row (Figure 9E); ca. five rows of enlarged scales behind precloacal pores; 1/1 blunt, conical postcloacal tubercles; tail not thickened at base, with whorls; dorsal tail scales larger than scales of body dorsum, more or less squarish, slightly curved, subimbricate, arranged in relatively regular transverse rows; six dorsal, medial scale rows in the third tail whorl; anterior tail tubercles asymmetrically conical, posterior ones curved; six tubercles in the third and fifth tail whorl, in a transverse row in posterior whorl region; four scale rows between tubercle rows 2–3 and 3 scale rows between tubercle rows 3–4; subcaudals larger than dorsal tail scales, flat, smooth, subimbricate, arranged in two parallel rows, 2–3 rows per whorl (Figure 9F).

Dorsum olive brown (4655U); head with indistinct brown (478U) stripes and blotches; back with dark brown bands (469U); back tubercles light gray (Cool Gray 1U) as well as encircling dorsals, resulting in a light flecked dorsal pattern; those light flecks displaced, in ca. 8 transverse rows; limbs marbled, with scattered light tubercles;

six dark and six light tail bands, of which the dark ones are broader (Figure 8A); venter gray (400U); throat light gray, with indistinct pattern; medially stronger pigmented belly, with few brown (4635U) blotches (Figure 8B); anterior tail slightly banded, posterior parts with more distinct bands; tail tip dark.

Further specimens: We list the characters of 42 additional specimens from China and Vietnam that proved to be morphologically assignable to *G. reevesii* (see Appendix 1): 70.0–173.0 mm SVL; 58.0–138.0 mm TL; 15.4–35.2 mm LT; 20.8–46.5 mm HL; 16.0–37.5 mm HW; 9.6–22.5 mm HH; 9.6–16.4 mm SE; 8.9–17.7 mm EE.

Body proportions: SVL/TL 1.03–1.26; SVL/LT 4.25–5.34; SVL/HL 3.02–3.75; HL/HW 1.25–1.60; HL/HH 1.91–2.85; SE/EE 0.73–1.12.

Scalation: RW 3.8–6.3 mm; RH 1.90–3.70 mm (RW/RH 1.41–2.20); MW 2.10–4.60 mm; ML 1.80–4.00 mm (MW/ML 0.85–1.50); RW/MW 1.20–2.14; 10–14 SPL; 9–13 SBL; 3–6 N; 0–1 IN; 17–29 IO; 2 PM; 3–6 GP; 12–18 DTR; 5–10 GSDT; 133–141 SMC; 86–102 SR; 28–32 V; 15–19 LF1; 18–24 LF4; 13–19 LT1; 18–24 LT4; 2–24 TT; 13–20 PP; 0–18 PS; 1–4 PAT; 6 T1W; 6 T5W; 3–5 scales between second and third and third and fourth caudal tubercle rows.

TABLE 3. Measurements and proportions of the subspecies of *Gekko gecko* (data for *G. g. gecko* from Java only) and *G. reevesii*; for abbreviations see Material and methods.

	G. g. gecko	*G. g. azhari*	*G. reevesii*
SVL	37.0–161.0 105.25±38.02 n = 23	148.0–148.0 n = 2	70.0–173.0 125.10±23.66 n = 41
TL	32.0–105.5 79.47±34.39 n = 6	135,5 n = 1	58.0–138.0 102.58±17.06 n = 25
LT	7.5–34.2 22.73±8.70 n = 23	30.5–31.0 n = 2	15.4–35.2 26.51±4.92 n = 36
HL	13.2–42.4 30.91±0.24 n = 23	44.0–46.0 n = 2	20.8–46.5 36.16±5.98 n = 39
HW	9.0–33.6 23.33±8.40 n = 23	31.7–33.8 n = 2	16.0–37.5 26.62±5.12 n = 38
HH	6.45–21.8 14.49±5.17 n = 23	18.0–20.2 n = 2	9.6–22.5 15.34±3.41 n = 37
SE	4.6–13.6 10.33±3.22 n = 22	15.2–16.3 n = 2	9.6–16.4 12.33±1.66 n = 36
EE	4.1–16.5 11.07±4.01 n = 22	15.7–17.0 n = 2	8.9–17.7 12.55±2.36 n = 35
RW	1.90–5.60 4.15±1.25 n = 22	6.50–6.70 n = 2	3.80–6.30 4,.6±0.–67 n = 36
RH	0.90–3.30 2.30±0.72 n = 22	3.50 n = 2	1.90–3.70 2.75±0.48 n = 36
MW	1.40–4.00 2.87±0.78 n = 23	4.70 n = 2	2.10–4.60 3.06±0.54 n = 36
ML	1.20–3.50 2.49±0.69 n = 23	3.10–3.80 n = 2	1.80–4.00 2.83±0.51 n = 36

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TABLE 3. (continued)

	G. g. gecko	*G. g. azhari*	*G. reevesii*
DTL	0.50–1.90 1.27±0.49 n = 25	1.60 n = 2	0.80–2.10 1.50±0.31 n = 36
DTW	0.40–1.80 1.09±0.45 n = 25	1.60 n = 2	0.60–1.90 1.13±0.32 n = 36
LTL	0.50–2.10 1.41±0.51 n = 24	2.00 n = 2	0.80–2.50 1.63±0.36 n = 36
LTW	0.30–1.70 1.25±0.47 n = 24	1.70 n = 2	0.70–2.70 1.39±0.44 n = 36
SVL/TL	1.04–1.27 1.15±0.09 n = 6	1.09 n = 1	1.03–1.26 1.12±0.06 n = 19
SVL/LT	4.22–5.20 4.69±0.27 n = 23	4.77–5.08 n = 2	4.25–5.34 4.71±0.27 n = 30
SVL/HL	2.80–3.82 3.36±0.23 n = 23	3.36–3.61 n = 2	3.02–3.75 3.44±0.17 n = 33
HL/HW	1.23–1.50 1.35±0.09 n = 23	1.36–1.39 n = 2	1.25–1.60 1.38±0.09 n = 32
HL/HH	1.90–2.58 2.15±0.17 n = 23	2.28–2.44 n = 2	1.91–2.85 2.38±0.25 n = 31
SE/EE	0.85–1.26 1.00±0.11 n = 21	0.96–0.97 n = 2	0.73–1.12 0.99±0.10 n = 30
RW/MW	1.22–1.72 1.45±0.16 n = 22	1.38–1.43 n = 2	1.20–2.14 1.62±0.18 n = 30
RW/RH	1.52–2.33 1.83±0.20 n = 22	1.86–1.91 n = 2	1.41–2.20 1.80±0.19 n = 31
MW/ML	0.97–1.38 1.17±0.13 n = 22	1.24–1.52 n = 2	1.20–2.14 1.62±0.18 n = 30
DTL/DTW	0.89–1.50 1.18±0.14 n = 25	1.00 n = 2	1.00–2.14 1.37±0.25 n = 30
LTL/LTW	0.65–1.42 1.10±0.19 n = 22	1.18 n = 2	0.67–1.89 1.25±0.26 n = 30

Comparisons: Comparisons with subspecies of *G. gecko*: Characters of different geographic populations of *G. gecko* are in part overlapping. Mean values of supralabials, sublabials, dorsal tubercle rows, lamellae below fingers and toes change clinally from north to south (Rösler 2005a). *Gekko reevesii* significantly differs ($p < 0.001$) from *G. g. gecko* sensu stricto from Java, by having a smaller SVL, a proportionally smaller head height, fewer supralabials, interorbitals, femoral tubercles, and postcloacal tubercles, as well as by having greater number of tubercles rows, precloacal pores, lamellae below first finger, lamellae below first toe, and lamellae below fourth toe (see Tables 3–

4). The ground coloration of *G. reevesii* is grayish brown to grayish green (Figure 10) versus ultramarine gray to bluish gray in *G. g. gecko*. The dorsal blotches of *G. reevesii* are reddish brown to dark brown versus cinnober red in the nominate form. Furthermore, the dorsal pattern of *G. reevesii* tends to comprise transverse bands and short stripes versus relatively irregularly arranged, distinct single blotches (see figures in Zhao & Adler 1993; Rösler 1995; Ziegler 2002; Grossmann 2004a; Nguyen *et al.* 2009). *Gekko reevesii* does not co-occur with *G. g. azhari*. Because the latter was described based on two females only (Mertens 1955), and because no further specimens have been collected since then, comparisons and relations with adjoining Indian populations of *G. gecko* (e.g., West Bengal, Dhaka) are barely known and require further investigation (Peterson 1980; Ahmed & Dasgupta 1992; Tikader & Sharma 1992). Based on current knowledge, *G. reevesii* can be morphologically distinguished from *G. g. azhari* by its larger SVL and domed versus flat dorsal tubercles (see Tables 3–4).

TABLE 4. Scalation of the subspecies of *Gekko gecko* (data for *G. g. gecko* from Java only) and *G. reevesii*; for abbreviations see Material and methods, except for T3W = tubercles in the third tail whorl; SB2/3 = scales between second and third tail tubercle rows; SB3/4 = scales between third and fourth tail tubercle rows.

	G. g. gecko	*G. g. azhari*	*G. reevesii*
SPL	11–15 13.28±0.91 n = 46	12–15 13.00±1.41 n = 4	10–14 12.27±0.92 n = 85
SBL	9–14 11.17±0.99 n = 47	10–11 10.50±0.58 n = 4	9–13 10.80±0.89 n = 81
N	3–6 4.41±0.98 n = 46	4 0.00±0.00 n = 4	3–6 4.23±0.69 n = 83
I	0–3 1.04±0.47 n = 23	1 n = 2	0–1 0.95±0.22 n = 42
IO	16–28 23.00±2.28 n = 24	20–23 n = 2	17–29 20.49±2.00 n = 43
PM	2–3 2.04±0.21 n = 23	2 n = 2	2 0.00±0.00 n = 42
GP	3–7 4.87±0.76 n = 23	5 n = 2	3–6 4.71±0.64 n = 41
DTR	11–13 11.96±0.36 n = 24	15 n = 2	12–18 13.89±1.32 n = 44
GSDT	8–9 8.17±0.38 n = 24	7–8 n = 2	5–10 7.98±0.88 n = 44
SMC	135–153 143.00±7.44 n = 23	—	133–141 136.25±3.59 n = 39
SR	81–105 93.74±6.40 n = 23	90–97 n = 2	82–103 92.56±4.56 n = 39
V	30–34 32.50±1.73 n = 23	—	28–32 30.75±1.89 n = 39

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TABLE 4. (continued)

	G. g. gecko	*G. g. azhari*	*G. reevesii*
TT	6–22 13.40±4.30 n = 40	2–5 3.50±1.29 n = 4	2–24 9.05±3.61 n = 82
LF1	12–18 15.83±1.26 n = 40	15–19 16.50±1.91 n = 4	15–19 16.70±0.90 n = 82
LF4	17–21 19.19±0.86 n = 42	19–21 20.25±0.96 n = 4	18–24 21.04±1.10 n = 80
LZ1	14–19 16.26±1,08 n = 38	17–18 17.25±0.50 n = 4	13–19 16.79±1.12 n = 84
LZ4	19–23 20.55±0.90 n = 40	22–24 23.00±1.00 n = 3	18–24 21.98±1.14 n = 81
PP	12–16 14.13±1.25 n = 15	—	13–20 18.00±1.78 n = 25
PS	0–13 5.78±4.71 n = 9	12 n = 2	0–18 1.74±5.23 n = 19
PAT	1–3 1.93±0.50 n = 45	2–3 2.50±0.58 n = 4	1–4 1.48±0.74 n = 82
T3W	5–7 6.00±0.33 n = 19	6 n = 2	6 0.00±0.00 n = 37
ST2/3	4–5 4.05±0.23 n = 19	4–5 n = 2	3–5 3.65±0.68 n = 37
ST3/4	4–5 4.17±0,.8 n = 18	4 n = 2	3–5 3.61±0.73 n = 36

Our genetic samples did not include representatives of *G. reevesii*. However, Qin *et al.* (2007) found significant differences between geckos from as close as 85 km in Guangxi (red tokay from Nanning versus black tokays from Chongzuo and Qinzhou). Such differences (> 8%) among probably parapatric, if not sympatric, taxa are certainly taxonomically noteworthy. In addition, further taxonomic subdivisions may also be present in *Gekko gecko*. Our molecular phylogeny revealed two relatively deeply divergent evolutionary lineages: a western clade (Myanmar, Thailand) and an eastern clade (China, Cambodia, Indonesia, Malaysia), within which close relationships of Chinese and Indonesian *G. gecko* exist (Figure 1). As extensive human-mediated movement of *G. gecko* occurs in association with the traditional medicine trade throughout the range of the species (Bauer 2009), and *G. gecko* is common around human habitations, it is possible that the observed relationships may be confounded by translocations. Certainly, much deeper sampling of *G. gecko* across its entire range is needed. Comparisons of the western *G. gecko* with *G. g. azhari* are particularly crucial, as is, of course, the evaluation of *G. reevesii*. Possible further evidence of multiple species in *G. gecko* comes from chromosomal studies. All *G. gecko* karyotyped to date have a diploid number of 38 and a fundamental number of 48 (Cohen *et al.* 1967; Wu & Zhao 1984; Solleder & Schmid 1984; Sharma & Kasid 1992; Du *et al.* 2002), however, Solleder & Schmid (1984) found heteromorphic sex chromosomes in males, while these were not reported by other workers, and some researchers have reported acrocentric pairs (Cohen *et al.* 1967), whereas others explicitly state that none are present (Sharma & Kasid 1992).

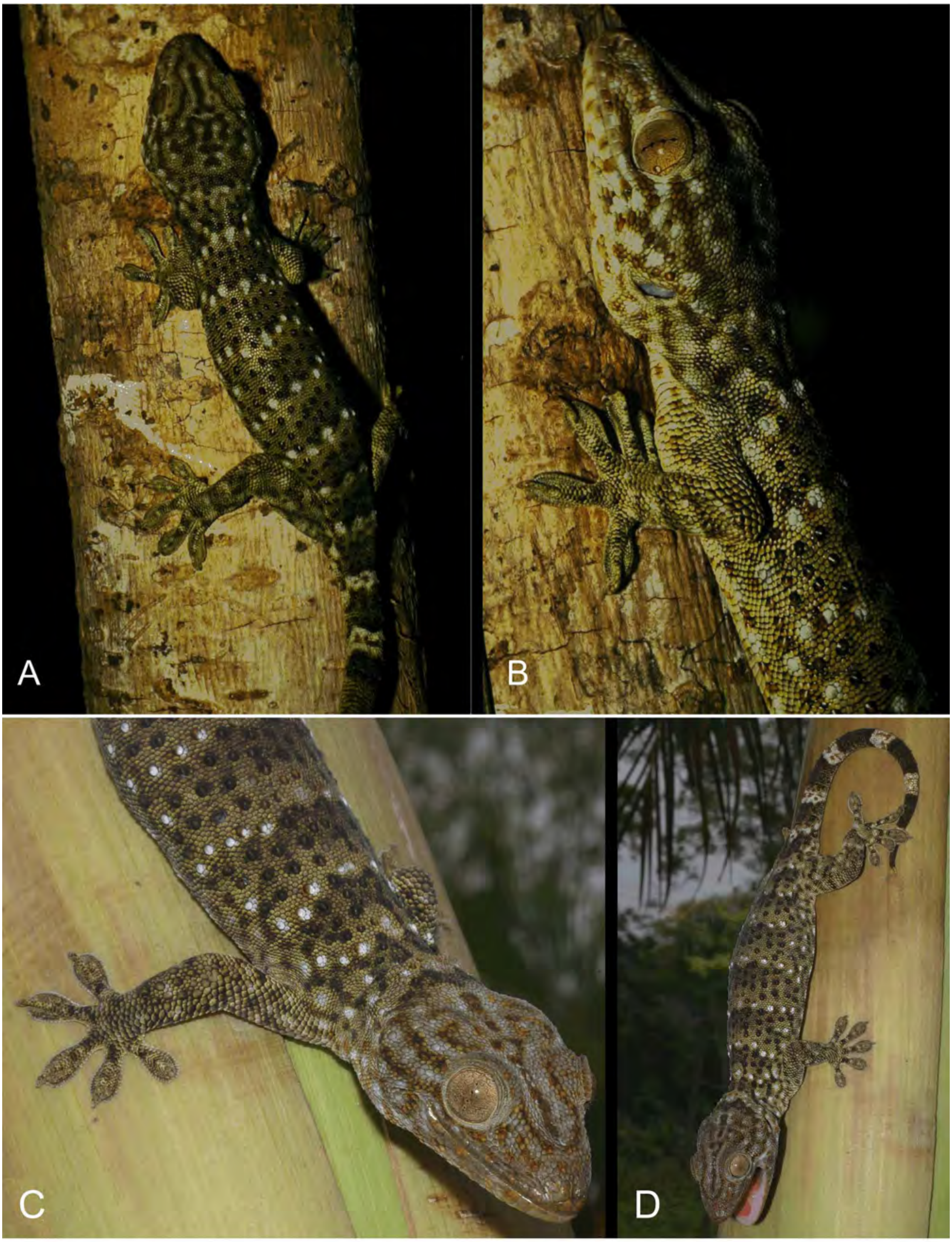


FIGURE 10. *Gekko reevesii*: A, B. Male specimen, ZFMK 76232, from surroundings of Ky Thuong, Ha Tinh Province, Vietnam; C, D. Released specimen from Cat Ba Island, Hai Phong Province, Vietnam, photos by T. Ziegler.

Comparisons with remaining *Gekko* species: *G. reevesii* differs from all other *Gekko* species by its large SVL (> 170 mm), in combination with narial contact with rostral only, more than ten lamellae below fourth toe, subcaudals not enlarged, and a variable gray ground coloration (see identification key below).

Distribution. *Gekko reevesii* is currently known from southern China (provinces of Fujian, Guangdong, Guangxi, and Yunnan) and northern Vietnam (southwards to Quang Binh Province). According Lue *et al.* (1999) and Shang (2001), several early 20th century records of *G. reevesii* from Taiwan represent individuals artificially transported from the Chinese mainland. At least within Guangxi both red and black tokays occur in close proximity. Indeed, based on the sampling of Qin *et al.* (2007), red tokay (*G. gecko gecko*) populations from Nanning, Ningming County are virtually surrounded by black tokay (*G. reevesii*) sites. Both forms also occur in northern Vietnam. The exact boundaries of *G. reevesii* thus remain uncertain.

Discussion

Intrageneric grouping based on overall morphology. The highly derived toe structure of the genus *Gekko*, which makes it a clearly definable monophyletic group, can be regarded as among the most elaborate of all geckos. Underwood (1954) and Kluge (1967) provided gecko classifications at the family level and more recently Han *et al.* (2004), Feng *et al.* (2007), and Gamble *et al.* (2008a, b) have investigated relationships among gekkotans using molecular data, verifying the taxa included along with *Gekko* in the Gekkonidae sensu stricto. Within his morphologically-defined *Gekko* group, Russell (1972) included the genera *Gehyra* Gray, 1834, *Gekko* Laurenti, 1768, *Hemiphyllodactylus* Bleeker, 1860, *Lepidodactylus* Fitzinger, 1843, *Luperosaurus* Gray, 1845, *Perochirus* Boulenger, 1885, *Pseudogekko* Taylor, 1922, and *Ptychozoon* Kuhl, 1822. Among these taxa *Ptychozoon* is likely the most closely related to *Gekko*. Toe structures in both genera are similar, including the lack of claws on the inner fingers and toes, which may be a common derived character. According to Russell (1979b), the structure of the lateral body muscles of *Gekko* and *Ptychozoon* are also similar. Derived characters of *Ptychozoon* are skin folds that enable gliding and which can be found on head, body and tail except for *P. rhacophorus*, where they are only poorly developed (Scheiba 1990; Russell *et al*. 2001; Young *et al.* 2002).

The genus *Gekko* was subdivided by Russell (1972) into three major sections, which are characterized below (species that are still allocated to the genus *Gekko* are shown in parentheses): Russell's section 1, with broad digits with numerous scansors; penultimate phalanx moderately arcuate; dorsal interrossei muscles fleshy; large SVL; tubercles developed markedly to mildly (*G. gecko*, *G. smithii*, *G. vittatus*). Russell's section 2, characterized by narrower digits than the first section; penultimate phalanx more arcuate; dorsal interrossei muscles fleshy only for half of their length; large to moderate SVL; tubercles developed markedly to mildly (*G. kikuchii*, *G. mindorensis*, *G. monarchus*, *G. palawanensis*). Russell's section 3, with moderately wide digits; penultimate phalanx very much arched; dorsal interrossei muscles not fleshy; tubercles weakly developed or lacking (*G. athymus*, *G. chinensis*, *G. japonicus*, *G. subpalmatus*, *G. petricolus*, *G. palmatus*, *G. porosus*, *G. swinhonis*, *G. tawaensis*, *G. yakuensis*). Based on Russell's (1972) data and the combination of scalation characters with ground coloration (light versus dark), two major evolutionary lineages, i.e., a northern versus a southern lineage, are obvious, exclusive of our *Gekko gecko* and *Gekko vittatus* groups, which occupy special positions.

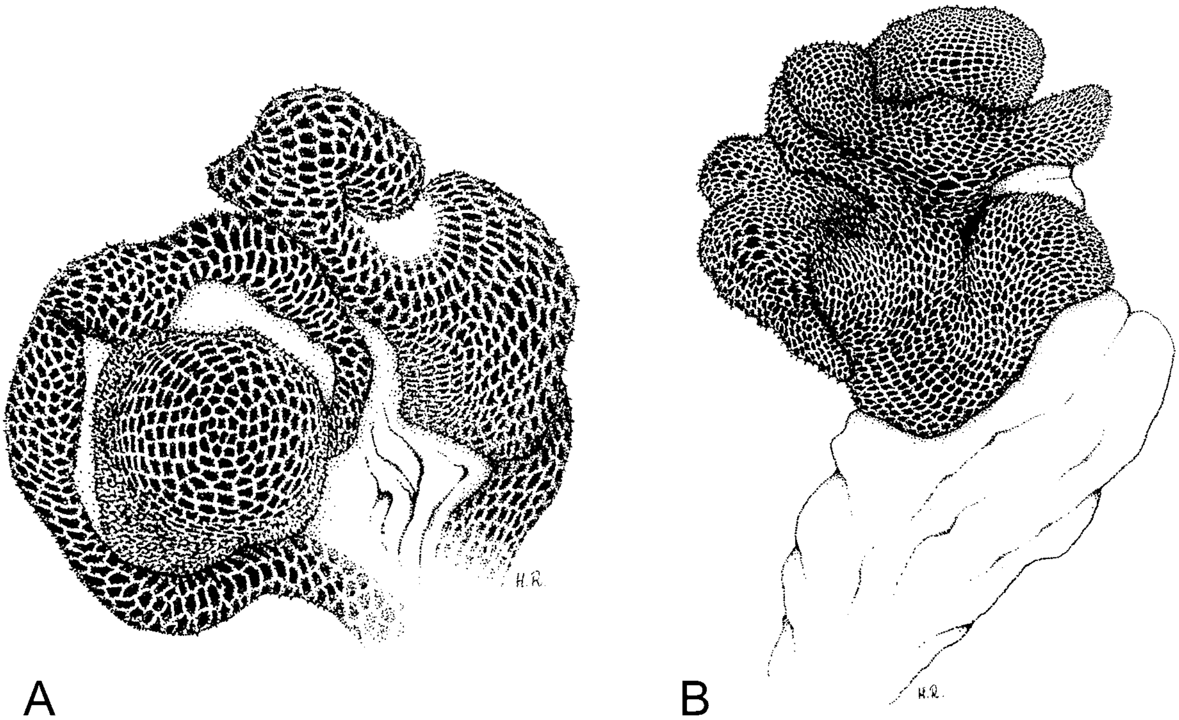
The southern lineage consists of the *Gekko petricolus*, *Gekko porosus*, and *Gekko monarchus* groups. Members of the *Gekko petricolus* group occur only on the mainland and are characterized by a low midbody scale count (83–137), 26–35 ventrals and 8–18 precloacal pores, whereas the *Gekko porosus* group is endemic to the Philippines and has a higher midbody scale count (145–211), more ventrals (33–50) and precloacal pores (52–88). The *Gekko monarchus* group is geographically isolated from the *Gekko petricolus* group, and significantly differs from the latter, e.g., by a higher number of precloacal pores (32–70 versus 8–15). The species composition of the *Gekko monarchus* group is nearly identical with Russell's (1972) section 2, except for the more recently described *G. carusadensis*and *G. ernstkelleri*. Karyological studies have also revealed the same karyotype (2n = 44) for investigated members of this group (*G. monarchus*, *G. kikuchii*, see Ota *et al.* 1990). From Table 2 it is obvious, that the *Gekko monarchus* and *Gekko porosus* group share similarities in several character states, such as midbody scales, ventrals, and precloacal pores, although members of the former group lack the prominent light dorsal blotches of the latter.

The northern lineage comprises the *Gekko japonicus* group. This group shares a relatively small SVL (< 100 mm) and enlarged subcaudals. This corresponds with Russell's (1972) section 3, except for *G. petricolus*. Within the *Gekko japonicus* group *G. chinensis*, *G. palmatus*, and *G. similignum* are differentiated by their high number of precloacal pores (17–32 versus a maximum of 15 in the other species of this group). Tubercles on fore and hind limbs are present in the *G. auriverrucosus*, *G. chinensis*, *G. scabridus*, *G. swinhonis*, and modestly developed in *G. japonicus*, whereas in the remainder of this species group limb tubercles are lacking. Some members of the *Gekko japonicus* group are characterized by and distinguished from all other *Gekko* groups by the complete lack of tubercles on the back, tail dorsum and limbs (*G. melli*, *G. scientiadventura*, *G. subpalmatus*, and *G. tawaensis*). However, some members of the *Gekko japonicus* group tend to have more rows of dorsal tubercles and a higher number of postcloacal tubercles (*G. auriverrucosus*, *G. canhi*, *G. japonicus*, and *G. scabridus*). A shared character state of *G. auriverrucosus*, *G. hokouensis*, *G. japonicus*, *G. liboensis*, *G. scabridus*, *G. shibatai*, *G. swinhonis*, *G. taibaiensis*, *G. tawaensis*, *G. vertebralis*, and *G. yakuensis* is the nearly linearly arranged precloacal pores. The species *G. chinensis*, *G. palmatus*, *G. scientiadventura*, *G. similignum*, and *G. subpalmatus* possess extensive webbing between the fingers and toes and differ from each other in different morphological features (scales along underside of body from mental to the front of cloacal slit, scales around the middle of the body, precloacal pores, etc.). *Gekko athymus*, another species with extensive webbing between the fingers and toes, differs in having a greater snout-vent length (119 mm versus 99.2 mm in *Gekko japonicus* group). Whereas the northern *Gekko* lineages share a number of character states, *G. athymus* deserves a special position. Due to the presence of extensive toe webbing (1/4 to 1/3 webbed, see Brown & Alcala 1962) and a lack of dorsal tubercles, the latter species is distinct from all other Philippine *Gekko* species (Brown & Alcala 1978, Brown *et al.* 2008, 2009, Linkem *et al.* 2010) although it shares a close relationship to the other Philippine *Gekko* groups. *Gekko athymus* is also distinct in its low precloacal pore counts (20–24 versus 32–88 in remaining Philippine group species). It is an endemic species of Palawan Island, with the largest snout-vent length of the endemic Philippine *Gekko* species.

Members of the *Gekko gecko* and *Gekko vittatus* groups share many character states, such as the distinctly reduced subcaudals and the high number of nasals (see Table 1). However, with respect to size and body mass, the groups differ significantly, with *G. gecko* reaching up to 365 mm total length and a weight of 200 g (Grossmann 2004a, 2008b). Another peculiar feature of the *Gekko gecko* group is nostril contact with the rostral (except in *G. verreauxi*). This has been considered as the primitive state in other gecko genera such as *Phelsuma* (Loveridge 1942; Mertens 1962). However, this condition seems to have been derived and lost multiple times within the Gekkota. The members of the *Gekko vittatus* group are further distinguished by their thinner habitus, lateral folds with tubercles, and the possession of throat tubercles. Their isolated phylogenetic position (Fig. 1) also demonstrates that similarities to the *G. gecko* group are superficial.

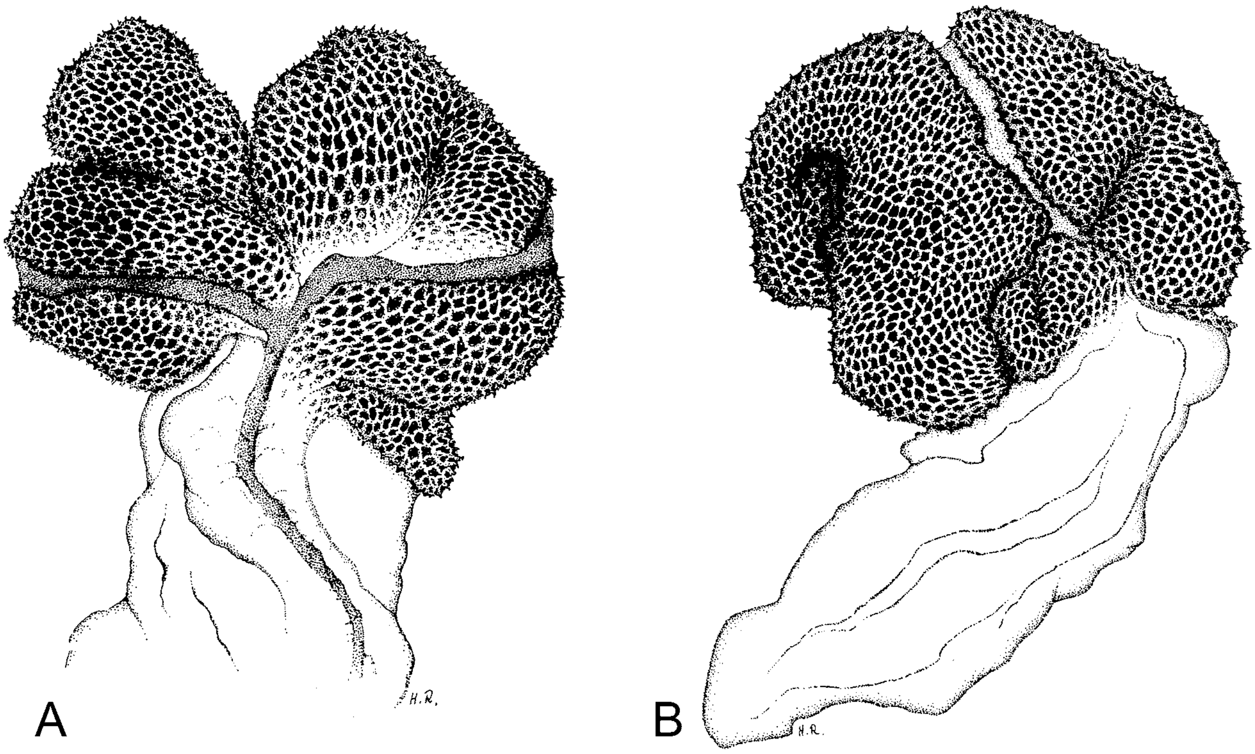
Genital morphology in the genus *Gekko*. Whereas the structure of hemipenes is already well known in some lizard groups, such as chameleons, lacertids, and platynotan lizards (e.g., Böhme 1971, 1988; Klaver & Böhme 1986; Ziegler & Böhme 1997), hemipenis morphology in *Gekko* is poorly known (see Böhme 1988). Thus, neither taxonomic nor phylogenetic conclusions have been published based on genital morphology in *Gekko*. We here provide an initial cursory overview of hemipenis morphology and related taxonomy in *Gekko*.

Zhang (1986: fig. A) described the hemipenis of *G. japonicus*. The massive, sightly bifurcated (medially only) apex and the upper truncus region show distinct transverse folds, but without discernible calyces. This corresponds to the only slightly bifurcated hemipenis of *G. tawaensis* (see Utsunomiya *et al.* 1996) and the hemipenis of *G. scientiadventura*, which also is only slightly bifurcated, but shows less distinct folds both on the sulcal and asulcal sides. However, the hemipenis description of *G. scientiadventura* was based on an incompletely everted organ (see Rösler *et al.* 2005: fig. 3). We can add that at maximum turgidity the sulcal lips are distinctly protruded in the hemipenis of *G. scientiadventura*. Both the lobes and the upper part of the truncus are covered with tiny calyces in the aforementioned species (Fig. 11). The hemipenis of *G. kikuchii*, as depicted in Shang (2001), is only incompletely everted. The hemipenes of *G. palmatus* have bulging, apical lobes with folds, with many relatively deep calyces with spinose borders, both on the sulcal as well as on the asulcal side (Fig. 12). The sulcus shape of the hemipenis of *G. smithii* is similar to the condition in *G. gecko* (see Unterhössel 1902: Fig. 7). In both species, bulging sulcal lips encompass a thin sperm groove in the region of the truncus, the bifurcation of which extends to the outer region of the barely differentiated apical lobes. *Gekko smithii* has large, deep hemipenial calyces on the asulcal side and tiny ones on the sulcal side of the lobes (Fig. 13). *Gekko badenii* has a slightly bifurcated hemipenis. The relatively flat calyces are bordered by seams and reach from the truncus to the pedicel on both the sulcal and asulcal sides (Fig. 14). Of the genital organs studied within the framework of the current study, only the hemipenis of *G. badenii* showed fine, black pigmented dots on the sulcal side.



A B

FIGURE 11. Hemipenis of *Gekko scientiadventura* (CPHR uncatalogued) from Vietnam, (A) sulcal view, (B) asulcal view. Drawings by H. Rösler.



A B

FIGURE 12. Hemipenis of *Gekko palmatus* from Vietnam, (A) sulcal view (IEBR A.0738), (B) asulcal view (IEBR 0737). Drawings by H. Rösler.

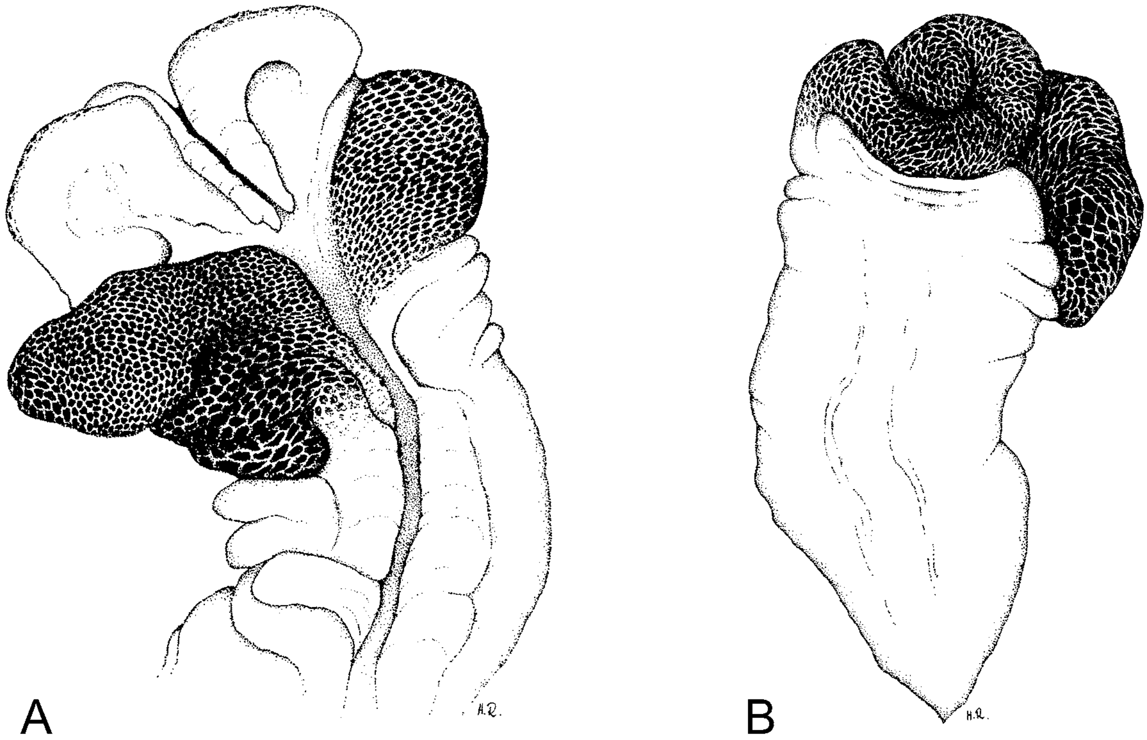


FIGURE 13. Hemipenis of *Gekko smithii* (CPHR 293) from Malaysia, (A) sulcal view, (B) asulcal view. Drawings by H. Rösler.

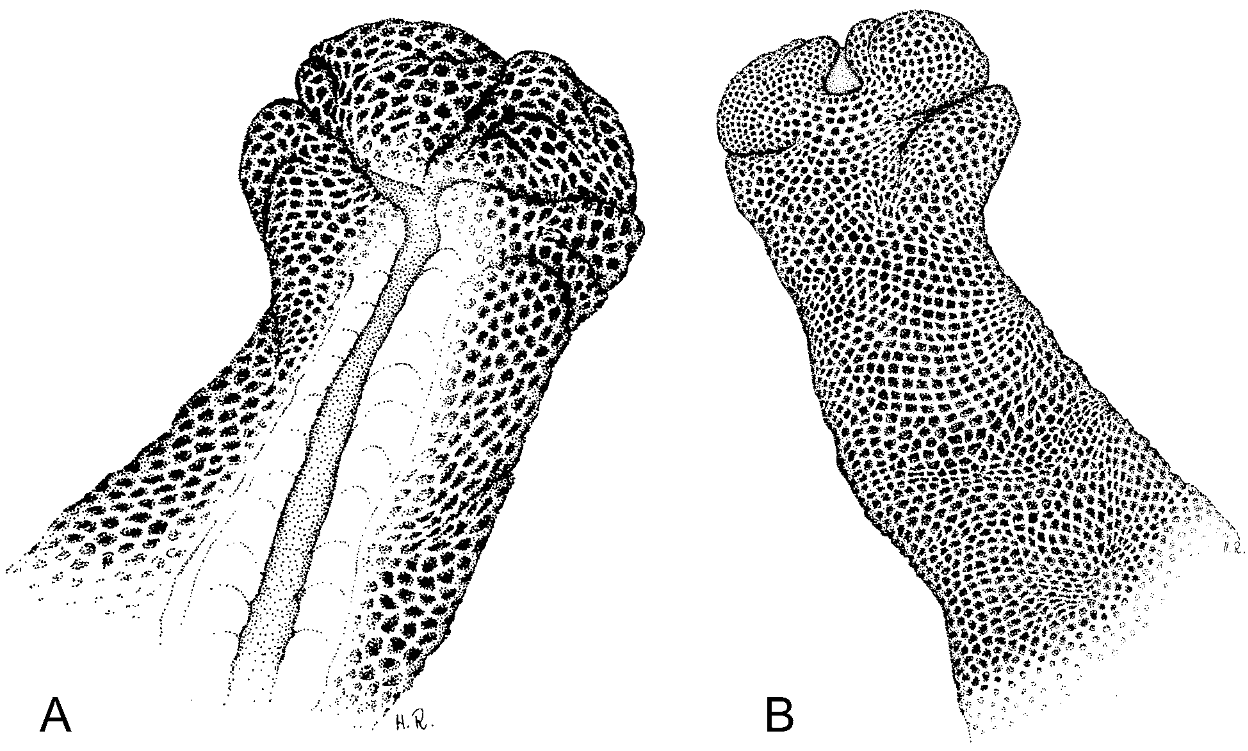


FIGURE 14. Hemipenis of *Gekko badenii* (IEBR A.0944) from Vietnam, (A) sulcal view, (B) asulcal view. Drawings by H. Rösler.

From this preliminary genital morphological overview it can already be stated with respect to our morphological groupings, that 1) hemipenes of two investigated *Gekko gecko* group members correspond in morphology and suggest group specific character constancy, 2) investigated *Gekko japonicus* group members share calyces with spinose borders, and 3) the hemipenis of *G. badenii* has less differentiated lobes than *G. carusadensis* (see Linkem *et al.* 2010: fig. 4).

Preliminary identification key to the currently recognized species and subspecies of the genus *Gekko*

Species of uncertain taxonomic status are indicated with an asterisk.

1	Nares in contact with rostral only	2
1'	Nares in contact with rostral and first supralabial	9
2	SVL > 100 mm; more than 10 lamellae below fourth toe; subcaudals not enlarged	3
2'	SVL < 100 mm; 6–8 lamellae below fourth toe; subcaudals enlarged	*G. auriverrucosus*
3	SVL up to 173 mm; ground coloration variable gray; iris yellow	4
3'	SVL up to 191 mm; ground coloration green; iris green or blue or reddish	6
4	SVL > 160 mm; dorsal tubercles curved; back with brick red to blood red pattern	5
4'	SVL < 160 mm; dorsal tubercles flat; back with brown pattern; Bangladesh	*G. gecko azhari*
5	SVL < 170 mm; 30–34 ventrals; Nepal/India to South Vietnam, Indo-Australian Archipelago	*G. gecko gecko*
5'	SVL > 170 mm; 28–32 ventrals; South China and North Vietnam	*G. reevesii*
6	SVL > 150 mm; 13 or fewer dorsal tubercle rows	7
6'	SVL up to 150 mm; 14–19 dorsal tubercle rows	8
7	8-13 dorsal tubercle rows; 29–39 ventrals	*G. smithii*
7'	10 dorsal tubercle rows; 26 ventrals	*G. albofasciolatus**
8	SVL up to 150 mm; 28–34 interorbitals, 33–37 ventrals	*G. siamensis*
8'	SVL up to 117 mm; 24 interorbitals, 30–31 ventrals	*G. nutaphandi*
9	Throat and lateral folds without tubercles	10
9'	Throat and lateral folds with tubercles	*G. vittatus*
10	SVL < 110 mm; iris not green	11
10'	SVL > 110 mm; iris green; Andaman Islands	*G. verreauxi*
11	Webbing between fingers and toes present	12
11'	Webbing between fingers and toes absent	18
12	SVL < 100 mm; 7–17 lamellae below fourth toe	13
12'	SVL > 100 mm; 19–21 lamellae below fourth toe	*G. athymus*
13	Dorsal tubercles present	14
13'	Dorsal tubercles absent	16
14	Limb tubercles absent; 139–156 midbody scales	15
14'	Limb tubercles present; 118–140 midbody scales	*G. chinensis*
15	Postmentals large; 24–32 preanofemoral pores	*G. palmatus*
15'	Postmentals small; 17 precloacal pores	*G. similignum**
16	32–39 interorbitals; 7–14 lamellae below fourth toe; 1 postcloacal tubercle	17
16'	41–51 interorbitals; 14–17 lamellae below fourth toe; 2–3 postcloacal tubercles	*G. scientiadventura*
17	SVL > 80 mm; 35–39 interorbitals, 12–14 lamellae below fourth toe	*G. melli*
17'	SVL< 80 mm; 32 interorbitals; 7–10 lamellae below fourth toe	*G. subpalmatus*
18	More than 20 preanofemoral pores	19
18'	18 or fewer precloacal pores (or condition unknown)	29
19	SVL up to 100 mm	20
19'	SVL > 100 mm	27
20	SVL > 80 mm; more than 10 dorsal tubercle rows	21
20'	SVL up to 63 mm; 10 dorsal tubercle rows	*G. palawanensis*
21	32–50 preanofemoral pores	22
21'	47–84 preanofemoral pores	25
22	10–13 lamellae below first toe; 14–17 lamellae below fourth toe	23
22'	14–17 lamellae below first toe; 17–20 lamellae below fourth toe	24
23	SVL 100 mm; 32–40 preanofemoral pores; W-shaped head pattern	*G. monarchus*
23'	SVL 80 mm; 48 preanofemoral pores; no head pattern; Lanyu Island	*G. kikuchii*
24	SVL 97.2 mm; 14 lamellae below first toe; 46–50 preanofemoral pores; Philippines (Luzon Island)	*G. carusadensis*
24'	SVL 84 mm; 15–17 lamellae below first toe; 38–48 preanofemoral pores; Philippines (Panay Island)	*G. ernstkelleri*
25	12–17 dorsal tubercle rows; 70–84 preanofemoral pores	26
25'	16–19 dorsal tubercle rows; 47–61 preanofemoral pores	*G. mindorensis*
26	155–160 scales around the middle of the body; 15–17 dorsal tubercle rows	*G. porosus*
26'	145–150 scales around the middle of the body; 12–15 dorsal tubercle rows	*G. romblon*

27 Fewer than 75 preanofemoral pores; back not banded ... 28
27’ 77–88 preanofemoral pores; back banded ... *G. rossi*
28 145–164 scales around midbody; 18–22 dorsal tubercle rows ... *G. crombota*
28’ 180–190 scales around midbody; 12–18 dorsal tubercle rows ... *G. gigante*
29 0–3 precloacal pores ... 30
29’ More than 3 precloacal pores (or unknown) ... 33
30 SVL < 100; 9–17 lamellae below fourth toe ... 31
30’ SVL up to 100; 18–20 lamellae below fourth toe ... *G. vietnamensis*
31 2–12 dorsal tubercle rows ... 32
31’ No dorsal tubercles ... *G. tawaensis*
32 0–3 precloacal pores; upper surface of tail with tubercles; Kojima and Takarajima Islands (Japan) ... *G. shibatai*
32’ 0–1 precloacal pore; upper surface of tail without tubercles; Kodakarajima, Amamioshima, Kakeromajima, Ukejima, Yarojima, and Tokunoshima (Japan) ... *G. vertebralis*
33 9 or fewer lamellae below first and fourth toe; China ... 34
33’ 9 or more lamellae below first and fourth toe ... 38
34 SVL > 75 mm; 30–40 interorbitals ... 35
34’ SVL < 75 mm; fewer than 30 interorbitals (or unknown) ... 36
35 SVL up to 85 mm; 40 interorbitals; 10 dorsal tubercle rows; limb tubercles absent ... *G. liboensis**
35’ SVL up to 77 mm; 30 interorbitals; 17–21 dorsal tubercle rows; limb tubercles present ... *G. scabridus**
36 SVL > 60 mm; 4–9 precloacal pores ... 37
36’ SVL 59 mm; 6–8 precloacal pores ... *G. wenxianensis*
37 23–24 interorbitals; 7–9 precloacal pores ... *G. swinhonis*
37’ 28 interorbitals; 4–6 precloacal pores ... *G. taibaiensis*
38 Less than 200 scales around midbody ... 39
38’ 205–227 scales around midbody ... *G. canhi*
39 83–107 scales around midbody ... 40
39’ 112–144 scales around midbody ... 42
40 SVL < 85 mm; 8–11 precloacal pores ... *G. russelltraini*
40’ SVL > 90 mm; 11–18 precloacal pores ... 41
41 10–14 dorsal tubercle rows; 14–18 precloacal pores ... *G. canaensis*
41’ 14–17 dorsal tubercle rows; 11–14 precloacal pores ... *G. takouensis*
42 SVL < 80 mm ... 43
42’ SVL > 100 mm ... 45
43 119–130 scales around midbody; hind limbs without tubercles; 1 postcloacal tubercle ... 44
43’ 130–144 scales around midbody; hind limbs with tubercles; 2–4 postcloacal tubercles ... *G. japonicus*
44 internasal distinctly larger than more posterior snout scales; paired dorsal tubercles along entire length of original tail ... *G. yakuensis*
44’ internasal scale not enlarged; paired dorsal tubercles absent from tail or restricted to basal portion of original tail ... *G. hokouensis*
45 1 postcloacal tubercle ... 46
45’ 2 postcloacal tubercles ... 47
46 14 dorsal tubercle rows; 12–14 lamellae below fourth toe; 12–13 precloacal pores ... *G. lauhachindaei*
46’ 15–18 dorsal tubercle rows; 16–18 lamellae below fourth toe; 9–11 precloacal pores ... *G. petricolus*
47 SVL 89 mm; 8–12 dorsal tubercle rows; no tubercles on dorsal surface of tail ... *G. grossmanni*
47’ SVL 108 mm; 12–17 dorsal tubercle rows; tubercles on dorsal surface of tail ... *G. badenii*

Zoogeography of the genus *Gekko*

The distribution of the genus *Gekko* extends from India in the west to Korea in the east, and southwards to the Solomons (Santa Cruz Islands) and Vanuatu (Figure 3).

The northern lineage occupies large parts of southeastern China (e.g., Vogt 1922; Mell 1929; Pope 1935). Seven species from four groups (*G. gecko*, *G. hokouensis*, *G. japonicus*, and *G. subpalmatus* groups) are reported in the adjoining provinces of Zhejiang (sympatric species *G. hokouensis*, *G. japonicus*, *G. subpalmatus*, and *G. swinhonis*), Fujian (sympatric species *G. chinensis*, *G. gekko*, *G. hokouensis*, and *G. japonicus*), Guangdong (sympatric species *G. chinensis*, *G. gekko*, *G. melli*, and *G. subpalmatus*), and Guangxi (sympatric species *G. chinensis*, *G. gekko*, *G. japonicus*, and *G. subpalmatus*). According to Zhao & Adler (1993), these four provinces are located within two zoological divisions of China: Zhejiang and Fujian in the Central China region and Guangdong and Guangxi in the South China region. Further species that occur in southern China are *G. auriverrucosus*, *G. liboensis*, *G. scabridus*, *G. swinhonis*, and *G. taibaiensis*. The distribution pattern of Chinese *Gekko* coincides in large part with the Sinopacific arboreal (Lattin 1967). The overall distribution of the genus *Gekko* in China highlights, in contrast to other faunal elements (see Sedlag & Weinert 1987), a relatively distinct faunistic border between the Palaearctic and Indo-Malayan regions.

The species of the *Gekko japonicus* group are distributed in China, Korea, and Vietnam as well as on the islands of Japan. Temporary land connections between China, Taiwan and the Ryukyu Islands on the one hand (southern route) and between China, Korea, and Japan on the other (northern route) discontinuously existed from late Tertiary to the Pleistocene (Mertens 1934; Kizaki & Oshiro 1977; Kuramoto 1979; Thenius 1980). Japan may have been reached by *Gekko* via both routes. The Ryukyu Islands probably were colonized by *Gekko* representatives by mainland ancestors that migrated via Taiwan, as is known for other amphibians and reptiles (see Hikida *et al.* 1989; Ota 1991). The occurrence of endemic species (*G. shibatai*, *G. tawaensis*, *G. vertebralis*, *G. yakuensis*) on southern Japanese islands may be due to subsequent isolation and speciation.

Gekko japonicus is known from Honshū, Kyūshu and Shikoku, as well as the Tanegashima island group, and is sympatric with *G. hokouensis* in Kyushu and Yaku-shima (Okada 1936; Goris & Maeda 2004). However, it is unclear when these species reached the Japanese islands. These islands evolved due to strong tectonic pressure and vulcanism in the Tertiary (Hartsch 1978). In this context, Mertens (1934) also referred to the close relations between Japanese reptiles and continental representatives. Glacial periods probably also played a crucial role in the establishment of species distributions in the Holarctic (Bănărescu & Boşcaiu 1978; Sedlag 1995). Thus, if the recent distribution of *G. hokouensis* and *G. japonicus* in the Japanese islands is not based upon human agency, it could be due to immigration via the northern or southern route in the Pleistocene, when the East China Sea was reduced to its narrowest. *Gekko japonicus* is also known from southern Korea. Its occurrence in Korea may be anthropogenic, but may also be explainable as a glacial refuge (arboreal Sino-Korean subcenter, see Lattin 1957). Records of *G. japonicus* from Vietnam remain perplexing. Records from northern Vietnam (Tonkin) are based on descriptions of Bourret (1927, 1937a, b, 1940b), however, there is no relevant material from Bourret’s collection in the Muséum national d’Histoire naturelle, Paris (David & Ineich 2009). However, *Gekko japonicus* agrees in some morphological aspects with the recently described *G. canhi* (see Rösler *et al.* 2010). Taylor (1962) described *Luperosaurus amissus* from Tablas Island (Philippines). Brown & Alcala (1978) questioned the locality information given and synonymized *L. amissus* with *G. japonicus*. However, at the time *G. hokouensis* was not considered a valid species (see Wermuth 1965). Zhou *et al.* (1982) subsequently revalidated *G. hokouensis* at the specific rank and Ota *et al.* (1989c) transferred *L. amissus* to the synonymy of this species.

South Vietnam, the border region between Laos and Cambodia, and Thailand support a second, geographically limited lineage, with seven mostly allopatric species: *G. badenii*, *G. gecko*, *G. grossmanni*, *G. lauhachindaei*, *G. petricolus*, *G. russelltraini*, *G. takouensis*, and *G. vietnamensis* (e.g., Bobrov 1992, 1995b; Teynié *et al.* 2004; Nguyen *et al.* 2005; Harbig 2006; Bobrov & Semenov 2008; Ngo *et al.* 2009; Nguyen *et al.* 2009; Ngo & Gamble 2010; Nguyen 2010; Panitvong *et al.* 2010). The southern lineage also includes the *Gekko vittatus* group.

Towards the western edge of the range, the number of *Gekko* species decreases rapidly. *Gekko monarchus* only reaches the south of Thailand (Taylor 1963; Pauwels & Sumontha 2007), and only *members of the G. gecko* group are recorded from more northerly regions (Theobald 1868; Smith 1940). The presence of *G. smithii* in Myanmar is uncertain according to Smith (1935), but Ota *et al.* (1991) list at least one specimen from Myanmar (Burma: Rangoon, see also Grossmann 2004b). Eastern India and northern Nepal, with *G. gecko* as the sole occurring species, marks the westernmost border of the distribution of the genus *Gekko* (e.g., Smith 1935; Tikader & Sharma 1992; Kästle 2002).

Likewise, only a few species of *Gekko* have expanded southward. Only two species, *G. monarchus* and *G. vittatus*, occur as far east as New Guinea. Of these, *Gekko vittatus* reaches furthest to the southeast (Santa Cruz Islands and northern Vanuatu) and is mainly restricted to the Indo-Australian Archipelago (De Rooij 1915; Brongersma 1934; Bauer 1994). The record of *G. vittatus* from Fiji by Vogt (1912) has been disproven (see Zug 1991) whereas that from Vanuatu (see Baker 1928) has been confirmed by Ineich (2009) and Hamilton (2010). The migration of the *Gekko vittatus* group is an example of the successful settlement of Wallacea by Indo-Malayan versus Australian faunal elements, as is known from other animal groups (Mertens 1934; Sedlag 1995). Gekkonid dispersal must have been mainly by island hopping, because even during Pleistocene glacial maxima continuous land connections between New Guinea and Australia on the one hand and the western mainland on the other did not exist.

The third lineage is predominantly endemic to the Philippines. Its high species richness, with almost exclusively autochthonous species (*G. athymus*, *G. carusadensis*, *G. crombota*, *G. ernstkelleri*, *G. gigante*, *G. mindorensis*, *G. palawanensis*, *G. porosus*, *G. romblon*, and *G. rossi*; see Brown & Alcala 1978; Brown *et al.* 2008, 2009;

Linkem *et al.* 2010), is somewhat surprising, because endemic *Gekko* species are lacking on more southerly islands, such as on Borneo, the Sunda Islands, and Halmahera, except for some forms related to *G. smithii*, the taxonomic status of which is currently being reassessed (see Das 1996, 2004; Rösler *et al.* 2005; Koch *et al.* 2009). However, at least on Borneo, other gekkonid genera (e.g., *Cyrtodactylus*, *Lepidodactylus, Luperosaurus*) are represented by endemic species (see Barbour 1912; De Rooij 1915; Mertens 1934; Bauer 1994; Manthey & Grossmann 1997; Das 2004).

Of the eleven endemic *Gekko* species that occur on the Philippines, the *Gekko porosus* group is most closely related to the *Gekko monarchus* group. A potential common ancestor may have reached the Philippines via a land connection in the Sunda region connecting Borneo with the southern Malay Peninsula, which is partially supported by the basal position of the Palawan endemic *G. athymus* as compared to other Philippine *Gekko* species. Conversely, *G. monarchus* may have reached the mainland in relatively recent times via Palawan, Borneo and the Greater Sundas.

From zoogeographical point of view, *G. kikuchii* is generally considered as a Philippine faunal element of the mainly continentally (Chinese) influenced herpetofauna of Taiwan (e.g., Okada 1932; Ota 1991). However, the question of whether the records from Lanyu Island represent an old relict occurrence, or are due to passive dispersal, only can be answered after clarification of its taxonomic status. A distinct (specific) status would argue for a relatively early separation from Philippine ancestors and thus a longer isolation.

Gekko athymus is a very old part of the Philippine *Gekko* radiation. This receives unambiguous support from the phylogeny (Fig. 1). Despite any similarities to other groups, it is clear that our molecular data support an old split of Palawan from the more northerly Philippines.

In the *Gekko gecko* group, *G. gecko* has an extensive distribution. The wide distribution range is chiefly due to its broad ecological tolerances, which are advantageous in disturbed or human-mediated environments, especially when compared with species that are more ecologically restricted (compare Aowphol *et al*. 2006).

Finally it can be stated concerning the general distribiution of the genus *Gekko* that arboreal species (e.g., *G. monarchus*, *G. smithii*, see Schäfer 1992; Grossmann 2004b) typically have wider distributional ranges than rupicolous species (e.g., *G. scientiadventura*, *G. ernstkelleri*, *G. siamensis*, see Grossmann 2006; Rösler *et al.* 2006; Heidrich 2007). This suggests that a closed forest cover would have facilitated expansion of such species. Subsequent forest contraction in a more structured landscape may have promoted niche diversification and speciation (e.g., Bănărescu & Boşcaiu 1978; Sedlag 1995).

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APPENDIX 1

Specimens used for phylogenetic analyses in this study. Voucher abbreviations are as follows: Australian Museum, Sydney (AMS), Bernice P. Bishop Museum (BPBM), California Academy of Sciences (CAS), Jon Boone captive collection (JB), James Ford Bell Museum (JFBM), Jay Sommers captive collection (JS), Kansas University Natural History Museum (KU), Museum Zoologicum Bogoriense (MZB), Nanjing Normal University (NNU Z), Port Elizabeth Museum (PEM R), United States National Museum (USNM), Aaron M. Bauer field series (AMB), Hinrich Kaiser field series (CMD), Indraneil Das field series (ID), L. Lee Grismer field series (LLG). Sequences generated for this study have Genbank accession numbers JN019048-JN019146.

			Genbank Accession Number		
Species	Voucher Number	Locality	ND2	RAG-1	PDC
Gekko gecko	MZB Lace 6628	Gunung Raja Basa, Lampung, Sumatra, Indonesia.	JN019048	JN019115	JN019083
Gekko gecko	CMD 425	Timor Village Hotel, Wailakurini Aldea, Loihunu Suco, Ossu Subdistrict, Viqueque District, East Timor.	JN019049	—	JN019084
Gekko gecko	LLG 7364	1.5 km E Aural Village, Pursat Province, Cambodia.	JN019050	JN019116	JN019085
Gekko gecko	LLG 6813	Lubuk Sembilang, Pulau Langkawi, Kedah, West Malaysia.	JN019051	JN019117	JN019086
Gekko gecko	—	Nanning, Guangxi Zhuang AR, China.	NC007627	—	—
Gekko gecko	CAS 204952	vic Mwe Hauk Village, Myaungmya District, Ayeyarwady Division, Myanmar.	JN019052	EU054272	EU054256
Gekko gecko	—	Phuket Island, Phuket Province, Thailand.	AF114249	—	—

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APPENDIX 1. (continued)

Species	Voucher Number	Locality	Genbank Accession Number ND2	RAG-1	PDC
Gekko gecko	CAS 213628	Mimbu (Sagu) Township, Shwesettaw Wildlife Sanctuary, Magway Division, Myanmar.	JN019053	JN019118	JN019087
Gekko smithi	ID 8774	Gunung Mulu National Park, Sarawak, Malaysia.	JN019054	JN019119	JN019088
Gekko smithi	LLG 6890	Tekek-Juara Trail, Pulau Tioman, Pahang, West Malaysia.	JN019055	JN019120	JN019089
Gekko smithi	LLG 7648	Peta, Endau-Rompin, Johor, West Malaysia.	JN019056	JN019121	JN019090
Gekko smithi	none	captive	JN019057	JN019122	JN019091
Gekko smithi	—	Ulu Gombak Field Studies Center, Selangor, West Malaysia.	FJ487868	—	—
Gekko chinensis	LLG 4209	Wuzhi Shan, Hainan Island, China.	JN019058	JN019123	JN019092
Gekko japonicus	NNU Z 20050801.004	Zhoushan, Zhejiang, China.	JN019059	JN019124	JN019093
Gekko hokouensis	NNU Z 20050902.001	Jinzhai, Anhui, China.	JN019060	JN019125	JN019094
Gekko swinhonis	NNU Z 20051124.001	Boai, Henan, China.	JN019061	JN019126	JN019095
Gekko auriverrucosus	NNU Z 20050716.004	Yuncheng, Shanxi, China.	JN019062	JN019127	JN019096
Gekko subpalmatus	AMB 6567	Chengdu, Szechuan, China.	JN019063	JN019128	JN019097
Gekko grossmanni	JFBM 9	captive	JN019064	JN019129	JN019098
Gekko badenii	JB 13	captive	JN019065	JN019130	JN019099
Gekko petricolus	JB 70	captive	JN019066	JN019131	JN019100
Gekko petricolus	JS 5	captive	JN019067	JN019132	JN019101
Gekko vittatus	USNM 514063	Ngetkib village, Babeldaob Island, Palau.	JN019068	JN019133	—
Gekko vittatus	—	captive	NC008772	—	—
Gekko vittatus	BPBM 19780	Rossel Island, Louisiade Island, Milne Bay Province, Papua New Guinea.	JN019069	JN019134	JN019102
Gekko vittatus	AMS 134913	Karikari Island, Solomon Islands.	JN019070	JN019135	JN019103
Gekko vittatus	AMS 138873	Valuwa Village, Mota Lava Island, Vanuatu.	JN019071	JN019136	JN019104
Gekko vittatus	AMS 138865	Gaua Island, Vanuatu.	JN019072	JN019137	JN019105
Gekko vittatus	USNM 533255	Luesalo, Santa Cruz Island, Temotu, Solomon Islands.	JN019073	JN019138	JN019106
Gekko vittatus	AMS 127288	Makira Island, San Cristobal Island, Solomon Islands.	JN019074	—	—
Gekko athymus	KU 309335	Barangay Mainit, Palawan, Philippines.	JN019075	JN019139	JN019107
Gekko sp. 1	—	Dalupiri Island, Babuyan Group, Cagayan Province, Philippines.	FJ487884	—	—
Gekko sp. 1	—	Dalupiri Island, Babuyan Group, Cagayan Province, Philippines.	FJ487882	—	—
Gekko sp. 2	—	Camiguin Norte Island, Babuyan Group, Cagayan Province, Philippines.	FJ487877	—	—
Gekko crombota	—	Babuyan Claro Island, Babuyan Group, Cagayan Province, Philippines.	FJ487874	—	—
Gekko porosus	—	Batan Island, Batanes Group, Philippines.	FJ487880	—	—

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APPENDIX 1. (continued)

Species	Voucher Number	Locality	Genbank Accession Number ND2	RAG-1	PDC
Gekko rossi	—	Calayan Island, Babuyan Group, Cagayan Province, Philippines.	FJ487871	—	—
Gekko mindorensis	KU 303912	Barangay Formon, Sitio Balogbob, Cueba Simbahan, Mindoro Oriental Province, Philippines.	JN019076	JN019140	JN019108
Gekko mindorensis	—	Mindoro Island, Mindoro Oriental Province, Philippines.	FJ 487887	—	—
Gekko mindorensis	—	Mindoro Island, Mindoro Oriental Province, Philippines.	FJ 487885	—	—
Gekko monarchus	PEM R 5412	South Africa.	JN019077	JN019141	JN019109
Gekko monarchus	LLG 4824	FRIM, Kepong, Selangor, West Malaysia.	JN019078	JN019142	JN019110
Gekko monarchus	—	Bogani Nani Wartabone NP, Desa Lombongo, Kabupaten Bone Bolango, Gorontolo Province, Sulawesi, Indonesia.	FJ487870	—	—
Gekko monarchus	—	Tangkoko Nature Reserve, Kabupaten Minihasa, Sulawesi Utara Province, Sulawesi, Indonesia.	FJ487869	—	—
Lepidodactylus moestus	USNM 521730	Ngerur Island, Palau.	JN019079	JN019143	JN019111
Lepidodactylus orientalis	BPBM 19794	Sudest Island, Louisiade Archipelago, Milne Bay Province, Papua New Guinea.	JN019080	JN019144	JN019112
Gehyra australis	AMS 139934	El Questro Station, Jackeroos Waterhole, Western Australia, Australia.	JN019081	JN019145	JN019113
Gehyra mutilata	AMB 7515	Nimalawa, Sri Lanka.	JN019082	JN019146	JN019114

APPENDIX 2

Specimens examined. Collection abbreviations as in Material and methods.

Gekko badenii
CPHR 1888—male, South Vietnam; IEBR A.0944–A.0945—male, Tay Ninh, South Vietnam.

Gekko canhi
IEBR A.0910—male, Huu Lien (21º40'N, 106º20'E), Huu Lung, Lang Son Province, North Vietnam (holotype); ZFMK 88879—female, Sa Pa, Lao Cai Province, North Vietnam (paratype); VNMN 1001–1002—adult females from Huu Lien, Lang Son Province, North Vietnam (paratypes).

Gekko ernstkelleri
CPHR 2170—male, ad., Panay, Antique Province, Municipality of Pandan, Barangay Santo Rosario, entrance of a limestone cave, 80 m a.s.l., Philippines; CPHR 2389–2390—2 females, limestone outcrop, Bulanao Trail, NW-Panay, Philippines.

Gekko gecko gecko
CPHR 160—male, Java, Indonesia; CPHR 162—male, Java, Indonesia; CPHR 164—male, Java, Indonesia; CPHR 482—juvenile, Java, Indonesia; MTD 35316—male, Jakarta, Java, Indonesia; ZFMK 20626—male, Java, Indonesia; ZMB 354—male, Java, Indonesia; ZMB 13969—female, Batavia (= Jakarta), Java, Indonesia; ZMB 14303—male, Gombong, Java, Indonesia; ZMB 14437—female, Java, Indonesia; ZMB 14457—male, southern Java, Indonesia; ZMB 29681—female, Java, Indonesia; ZMB 31295—male, Residentie Bezoekie, Java, Indonesia; ZMB 65986–65891—3 males, 2 females, 1 juvenile, Batavia (= Jakarta), Java, Indonesia; ZMB 66001–66003—3 females, southern Java, Indonesia; ZSM 2642/0—male, Java, Indonesia; ZSM 140/1926/1 and ZSM 140/1926/2—1 male, 1 female, west Java, Indonesia.

Gekko gecko azhari
SMF 46788 (holotype) and SMF46789 (paratype)—2 females, Barkal, Chittagong Hill Tracts, Bangladesh.

Gekko grossmanni
CPHR 1182—male, South Vietnam; ZMB 52580–52583 (paratypes)—3 males, 1 female, Khanh Hoa Province, South Vietnam; ZMB 52586–52587 (paratypes)—2 females.

Gekko hokouensis
ZSM 174/1987/1 and ZSM 174/1987/2—1 male, 1 female, Chihnankuang, Taipei, Taiwan; ZSM 443/2002 to ZSM 445/2002—1 male, 2 females, Shaowo, Fujien (= Fujian), China.

Gekko japonicus
ZSM 210/1907/1 to ZSM 210/1907/5—1 male, 4 females, Pingshiang, Kiangsi (= Jiangxi Sheng) Province, China; ZSM 8/1959—male, Tonnbabashi, Fushimiku, Kyoto, Japan.

Gekko monarchus
CPHR 161—male, Indonesia; CPHR 416—male, Indonesia; CPHR 518—male, Indonesia.

Gekko mindorensis
CPHR without number—2 males, 1 female, SE Panay, Philippines.

Gekko nutaphandi
CUMZ.R. 2003.12 (holotype), IRSNB 2647 (paratype)—females, IRSNB 2648–2649 (paratypes)—males, Sai Yok Noi waterfall, Kanchanaburi Province, Thailand.

Gekko palmatus
CPHR 701—female, Tam Dao, Vinh Phuc, North Vietnam; CPHR 939–940—1 male, 1 female, Tam Dao, Vinh Phuc, North Vietnam; CPHR 2380–2381—2 males, Cat Hai, Cat Ba Island, northeastern Vietnam; IEBR A.0731–A.0732—2 males, Hai Phong, Cat Hai, Cat Ba Island, northeastern Vietnam; IEBR A.0734–A.0736—2 males, 1 female, Hai Phong, Cat Hai, Cat Ba Island, northeastern Vietnam; IEBR A.0738—male, Cat Hai, Cat Ba Island, northeastern Vietnam; IEBR 3700–3702—1 male, 2 females, Hai Phong, Cat Ba Island, Trung Trang Cave and Eo Bua, 20°47.233’N, 106°59.974’E, elev. 80 m a.s.l., Vietnam; IEBR A.0812—male, Vietnam; Hai Phong, Cat Ba Island, northeastern Vietnam; IEBR 3223–3224—1 male, 1 female, Tam Dao, Vinh Phuc, North Vietnam; IEBR 3619–3623—1 male, 2 females, 2 juveniles, Loc Binh District, Mau Son Commune, Khuoi Cap Village, 21º49.617’N, 106º55.549’E, elev. ~ 850 m a.s.l., Lang Son Province, Vietnam; IEBR 3638—female, Son Dong District, Thanh Luan Commune, Dong Ri, 21º09.961’N, 106º48.709’E, elev. 300 m a.s.l., Bac Giang Province, Vietnam; IEBR 3672—female, Son Dong District, Thanh Son Commune, Dong Thong, 21º11.131’N, 106º43.411’E, elev. ~ 250 m a.s.l., Bac Giang Province, Vietnam; IEBR A.0807—female, Uong Bi, Thuong Yen Cong Commune, Yen Tu, 21º08.282’N, 106º43.403’E, elev. 240 m a.s.l., Quang Ninh Province, Vietnam; IEBR FN 29174—female, Sa Pa, Lao Cai, North Vietnam; IEBR A.0948—female, Na Hang, Sinh Long, Tuyen Quang, North Vietnam; IEBR A.0950—female, Ba Be, Bac Kan, North Vietnam; IEBR A.0951—female, Ba Be, Bac Kan, North Vietnam; IEBR A.0949—male, Huu Lien, Huu Lung, Lang Son, North Vietnam; IEBR A.0952—female, Huu Lien, Huu Lung, Lang Son, North Vietnam; IEBR A.0954—female, Quy Hop, Chau Thanh, Nghe An, North Vietnam; IEBR A.0953—male, Quy Hop, Chau Quang , Nghe An, North Vietnam; IEBR A.0955—male, Quy Hop, Chau Quang , Nghe An, North Vietnam; IEBR A.0956—female, Cao Bang, North Vietnam.

Gekko petricolus
CPHR 148—male, Thailand; CPHR 319–320—females, Thailand.

Gekko reevesii
BMNH 1946.8.2598 (holotype)—male, China; CPHR 192–194—3 males, Ka-sha-toii, Kuangtung (= Guangdong) Province, China; CPHR 196—female, Ka-sha-toii Kuangtung (= Guangdong) Province, China; MTD D 42805—male, Vietnam; ZFMK 76234—male, NW Ky Thuong, Ha Tinh Province, Vietnam; ZFMK 76232—male, NW Ky Thuong, Ha Tinh Province, Vietnam; ZFMK 76233—female, NW Ky Thuong, Ha Tinh Province, Vietnam; ZFMK 59233– 59234—2 males, Vietnam; ZFMK 76227–76231—1 male, 4 females, Vietnam; ZMB 4074—male, China; VNUH uncatalogued—male, Quang Binh Province, Vietnam; ZMB 14182—male, Canton (= Guangdong), China; ZMB 14422—male, Funnei, China; ZMB 23527—female, China (label: coll. R. Mell); ZMB 23539—female, China (label: coll. R. Mell); ZMB 24222—male, China (label: coll. R. Mell); ZMB 24138—male, China (label: coll. R. Mell); ZMB 24237—female, China (label: coll. R. Mell); ZMB 24249—female, China (label: coll. R. Mell); ZMB 65974–65977—1 male, 3 females, China (label: coll. R. Mell); ZMB 65983–65985—1 male, 2 females, Funnei, China; ZMB 65992–65993—1 male, 1 female, Canton (= Guangdong), China; ZMB 65994–65995—1 male, 1 female, China (label: coll. R. Mell); ZMB 65996–65600—4 males, 1 female, China (label: coll. R. Mell).

Gekko russelltraini

CPHR 2575—male, Xuan Loc, Dong Nai Province, South Vietnam; IEBR A.0831 and IEBR A.0835—1 male and 1 female, Xuan Loc, Dong Nai Province, South Vietnam.

Gekko siamensis

CPHR 249—male, Tharon Khao Yai, Thailand.

Gekko smithii

CPHR 171–173—3 juveniles, Malaysia; CPHR 262–263—males, Malaysia; CPHR 398—female, Malaysia.

Gekko scientiadventura

CPHR 2071—female, Phong Nha Ke Bang, Quang Binh Province, Vietnam; CPHR 2263—male, Phong Nha Ke Bang, Quang Binh Province, Vietnam; ZFMK 76198 (holotype)—male, Phong Nha Ke Bang, 17°32'N 106°16'E, 50-150 m a.s.l., Quang Binh Province, Vietnam; ZFMK 76174–76179 (paratypes)—1 female, 5 juveniles, Phong Nha Ke Bang, 17°32'N 106°16'E, 50-150 m a.s.l., Quang Binh Province, Vietnam; ZFMK 80651–80652—2 females, Phong Nha - Ke Bang, 17°32'N 106°16'E, 50–150 m a.s.l., Quang Binh Province, Vietnam.

Gekko subpalmatus

BMNH 1946.82592 (holotype)—female, Chkiang (= Zhejiang) Province, China.

Gekko vittatus

CPHR 124—female, New Guinea; CPHR 392–393—2 females, New Guinea;

ZSM 285/0/1–285/0/3—1 male, 2 juveniles, Amboina (= Pulau Ambon), New Guinea, Indonesia; ZSM 30/1972/1–301972/9—4 males, 5 females, Asmat near Agats, New Guinea, Indonesia; ZSM 105/1979—female, Mt. Bosavi, Didessa, Southern Highlands, Papua New Guinea; ZSM 106/1979—female, Airdhills, Papua New Guinea; ZSM 507/1998—male 54 km south from Nabire, New Guinea, Indonesia.