

Parachute geckos free fall into synonymy: *Gekko* phylogeny, and a new subgeneric classification, inferred from thousands of ultraconserved elements

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ABSTRACT

Recent phylogenetic studies of gekkonid lizards have revealed unexpected, widespread paraphyly and polyphyly among genera, unclear generic boundaries, and a tendency towards the nesting of taxa exhibiting specialized, apomorphic morphologies within geographically widespread “generalist” clades. This is especially true in Australasia, where monophyly of *Gekko* proper has been questioned with respect to phenotypically ornate flap-legged geckos of the genus *Luperosaurus*, the Philippine false geckos of the genus *Pseudogekko*, and even the elaborately “derived” parachute geckos of the genus *Ptychozoon*. Here we employ sequence capture targeting 5060 ultraconserved elements (UCEs) to infer phylogenomic relationships among 42 representative ingroup gekkonine lizard taxa. We analyze multiple datasets of varying degrees of completeness (10, 50, 75, 95, and 100 percent complete with 4715, 4051, 3376, 2366, and 772 UCEs, respectively) using concatenated maximum likelihood and multispecies coalescent methods. Our sampling scheme addresses four persistent systematic questions in this group: (1) Are *Luperosaurus* and *Ptychozoon* monophyletic, and are any of these named species truly nested within *Gekko*? (2) Are prior phylogenetic estimates of Sulawesi’s *L. iskandari* as the sister taxon to Melanesian *G. vittatus* supported by our genome-scale dataset? (3) Is the high-elevation *L. gulat* of Palawan Island correctly placed within *Gekko*? (4) And, finally, where do the enigmatic taxa *P. rhacophorus* and *L. browni* fall in a higher-level gekkonid phylogeny? We resolve these issues; confirm with strong support some previously inferred findings (placement of *Ptychozoon* taxa within *Gekko*; the sister taxon relationship between *L. iskandari* and *G. vittatus*); resolve the systematic position of unplaced taxa (*L. gulat*, and *L. browni*); and transfer *L. iskandari*, *L. gulat*, *L. browni*, and all members of the genus *Ptychozoon* to the genus *Gekko*. Our unexpected and novel systematic inference of the placement of *Ptychozoon rhacophorus* suggests that this species is not grouped with *Ptychozoon* or even *Luperosaurus* (as previously expected) but may, in fact, be most closely related to several Indochinese species of *Gekko*. With our resolved and strongly supported phylogeny, we present a new classification emphasizing the most inclusive, original generic name (*Gekko*) for these ~60 taxa, arranged into seven subgenera.

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1. Introduction

The family Gekkonidae is the largest gekkotan lizard family comprising ~1200 species and 61 genera (Uetz et al., 2018). Within this family, the genus *Gekko* (Uetz et al., 2018) contains 59 currently recognized species, and the allied but phenotypically distinct species of Flap-legged (*Luperosaurus*) and Parachute (*Ptychozoon*) geckos, each with 13 recognized species (Brown et al., 2012a, b; Grismer et al., 2018, 2019). The results of these studies suggest that the genus *Gekko* is rendered paraphyletic by some species of the other two, highly derived genera (Brown et al., 2012a, b; Heinicke et al., 2012; Pyron et al., 2013). The enigmatic phylogenetic relationships of these peculiar geckos have been the focus of traditional character-based classifications (Boulenger, 1885; Wermuth, 1965), analyses of external and internal anatomical morphological characters (Brown et al., 2001), and more recent multi-locus Sanger sequence datasets with nearly complete taxon sampling, missing only a few key taxa, such as the secretive *Luperosaurus browni* (Brown et al., 2012a, b). To date, analyses of Sanger datasets have inferred fairly consistent topologies for the genus *Gekko*; however, phylogenetic uncertainty increased with the inclusion of closely related genera. For example, lineages of *Luperosaurus* appear to render not only *Gekko*, but also *Lepidodactylus* (not considered here), paraphyletic (Heinicke et al., 2012; Oliver et al., 2018). To date, phylogenetic analyses that include taxa outside *Gekko* have led to unclear taxonomic boundaries, nomenclatural instability, and frequent transfers of taxa between genera (Russell, 1979; Rösler et al., 2012; Brown et al., 2000, 2007, 2012a, b). Thus, a well-resolved phylogeny of *Gekko* and its allies remains outstanding.

To address higher-level relationships of *Gekko sensu stricto* across its wide distribution (Fig. 1), we apply a genomic approach targeting 5060 ultraconserved elements (UCEs) and phylogenomic analyses to address the following questions: (1) Are *Luperosaurus* and *Ptychozoon* each monophyletic, and are they or any of their included taxa nested within *Gekko*? (2) Does our surprising former estimate of the systematic position of Sulawesi's *L. iskandari* (sister species to Melanesian *G. vittatus*), hold up under phylogenomic inference? (3) Is the high-elevation Palawan Island species "*Luperosaurus*" *gulat* correctly placed in *Gekko* (represented by a single specimen and degraded accompanying DNA sample) as suggested by a previous analysis of two Sanger loci? (4) Finally, where do the elusive *P. rhacophorus* and *L. browni* fall within the higher-level gekkonid phylogeny?

2. Materials and methods

2.1. Taxon sampling

Ingroup sampling included 42 individuals representing two species of *Lepidodactylus*, two species of *Pseudogekko*, five *Ptychozoon* species, seven *Luperosaurus* species, and 25 species of *Gekko*, including *G. smithii*, which is the sister species to the genotype, *G. gekko* Linnaeus, 1758 (Table S1). *Cyrtodactylus baluensis*, *C. jellesme*, and *C. redimiculus* were chosen as distant outgroup taxa to root the tree based on a recent phylogenetic study of Southeast Asia geckos (Brown et al., 2012b). Our taxon sampling was selected to resolve a polytomy consisting of several clades assigned to the genera *Gekko*, *Luperosaurus*, and *Ptychozoon* (Brown et al., 2012a).

2.2. Data collection and sequence capture of UCEs

Data collection and sequence capture of UCEs took place in two different batches. The first batch of samples was prepared under the following conditions: high quality genomic DNA was extracted from 26 individuals using the Qiagen DNeasy® kit following the animal tissue protocol. Genomic DNA concentrations were measured using a QUBIT® 2.0 fluorometer and were standardized to 500 ng in 50 µL. We sheared genomic DNA using a Covaris S220 with the following setting: peak

power 175 W, duty factor: 2.0%, cycles per burst: 200, duration: 45 s. We prepared Illumina libraries using NEB/KAPA library preparation kits following Faircloth et al. (2012)—described in detail at <http://ultraconserved.org>. Next, we ligated universal iTru stubs (Glenn et al., 2016) in place of standard-specifics to allow for dual indexing. This was followed by a second 1X volume AMPure XP bead clean up after stub ligation, and by a 17-cycle PCR with NEB Phusion High-Fidelity PCR Master Mix of iTru Dual-indexes (Glenn et al., 2016) with the library fragments.

We then quantified the dual-indexed PCR product and library fragments using a Qubit 2.0 fluorometer, pooled libraries into groups of eight, and enriched each pool for 5060 UCEs. We targeted UCEs with 5472 probes from the Tetrapod 5Kv1 probeset (Arbor Biosciences, formerly MYcroarray). See Faircloth et al. (2012) and <http://ultraconserved.org/#protocols> for details on probe design. Next, we amplified enriched pools using limited-cycle PCR (17 cycles) and sequenced our enriched libraries on a single lane of an Illumina HiSeq 2500 (PE100 reads) at the KU Genome Sequencing Core. The second batch of genomic extractions, for 20 additional individuals, used the Maxwell®RSC Tissue DNA kit on the Promega Maxwell®RSC extraction robot. Genomic DNA was quantified on a Promega Quantus™-fluorometer and standardized to 1000 ng in 50 µL of ultrapure DNA-grade water. Quantified samples were outsourced to MYcroarray (now Arbor Biosciences) for library preparation, following the same sequence-capture protocol outlined above. Libraries were sequenced on a single lane of an Illumina HiSeq 3000 (PE150) at Oklahoma Medical Research Foundation (OMRF).

2.3. Data processing

Data were demultiplexed at the KU sequencing facility for the first batch of samples and at the OMRF for the latter batch. We subjected all samples to a custom bioinformatics pipeline version 1.0 (<https://github.com/chutter/>) to filter and remove adaptor contamination, assemble, and export alignments. We filtered samples and removed adapters using the bbdut.sh script (part of BBMap/BBTools; <http://sourceforge.net/projects/bbmap/>) with the following parameters: `ftm = 5`, `ktrim = r`, `k = 23`, `mink = 8`, `hdist = 1`, `tbo`, `tpe`, and `minlength = 25`. Next we used the bbsplit.sh script to remove other sources of non-focal organism contamination (e.g., *Achromobacter*, *Acidaminococcus*, *Acinetobacter*, *Afiplia*, *Agrobacterium*, *Alcaligenes*, *Aminobacter*, *Aspergillus*, *Bradyrhizobium*, *Brevundimonas*, *Burkholderia*, *Caenorhabditis*, *Corynebacterium*, *Curvibacter*, *Escherichia*, *Flavobacterium*, *Haemophilus*, *Helcococcus*, *Herbaspirillum*, *Legionella*, *Leifsonia*, *Magnaporthe*, *Malassezia*, *Mesorhizobium*, *Methylobacterium*, *Microbacterium*, *Moraxella*, *Mycoplasma*, *Novosphingobium*, *Ochrobactrum*, *Pedobacter*, *Penicillium*, *Phyllobacterium*, *Pseudomonas*, *Pseudonocardia*, *Puccinia*, *Ralstonia*, *Rhodococcus*, *Saccharomyces*, *Salmonella*, *Schizosaccharomyces*, *Sphingomonas*, *Staphylococcus*, *Stenotrophomonas*, and the UniVec database for vector contamination) with a `minid = 0.95`, followed by additional decontamination of singleton reads. Following decontamination, we removed adaptors and error corrected using AfterQC (Chen et al., 2017) with parameters set to: `qualified quality phred = 0`, `number of base limit = 10`, `sequence length requirement = 35`, `unqualified base limit = 60`, `trim front and tail bases set to zero`, and applied to both reads. We merged paired end reads using bbmerge-auto.sh (part of BBMap/BBTools; <http://sourceforge.net/projects/bbmap/>) with the following settings: `verystrict` to decrease the merging rate, `kmer length = 60`, `extend reads by 60` if a failed merge attempt, with error correction (`verystrict = t rem k = 60 extend2 = 60 ecct`).

2.4. UCEs assembly, probe matching, alignment, and trimming

De novo assembly was conducted with SPAdes v3.11.1 (Bankevich et al., 2012) using multiple k-mer sizes (21, 33, 55, 77, 99, and 127),

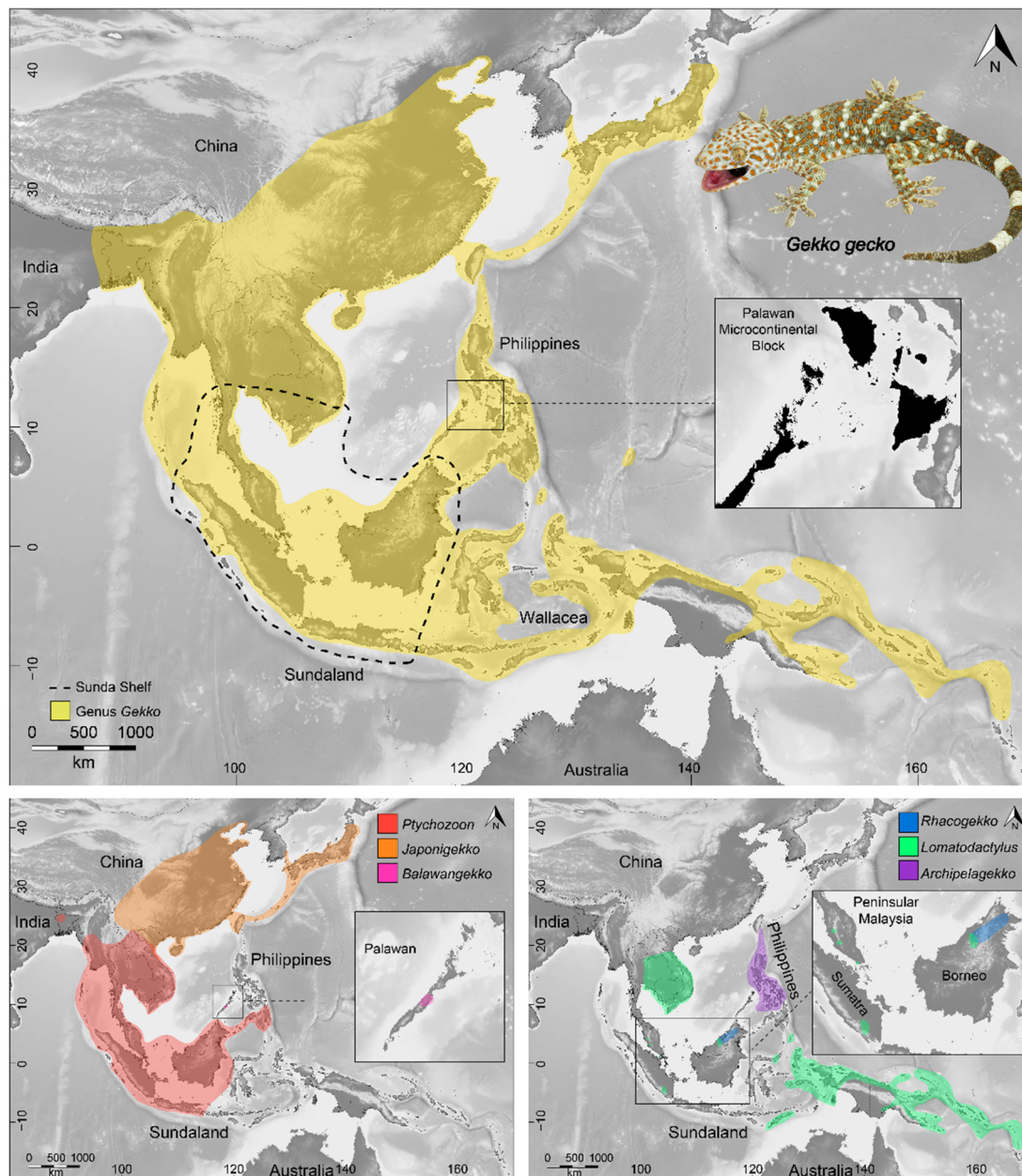


Fig. 1. Hypothesized generic (*Gekko*) and proposed subgeneric distributions based on Rösler et al. (2011) and references therein.

with the setting to expect significant amounts of gaps, and with haplotype assembly phasing. We used an array of k-mer values to aide in merging orthologous contigs resulting from different k-mer sizes. We further assembled contigs using the DIPSPADES (Safonova et al., 2015) function to assemble exons and orthologous regions by generating a consensus sequence from both orthologous and haplotype regions. The dedupe.sh script (part of BBMap/BBTools; <http://sourceforge.net/projects/bbmap/>) was used to remove near exact duplicates, and pblat (Kent, 2002; Meng, 2018) was used to match samples to targeted reference loci with a tile size set to eight and minimum sequence identity set to 60. All matching loci per species were then merged into a single file for downstream UCE alignments. Prior to UCE alignment, all loci recovered in only one sample were discarded. UCE alignments were constructed using the high-accuracy option in MAFFT v7.130b (Katoh and Standley, 2013) with a max iteration of 1000, automatically adjust the reading direction, gap opening penalty set to three, and an offset “gap extension penalty” set to 0.123. Because large UCE alignments usually contain long stretches of poorly aligned sequence regions, we

internally trimmed all of the alignments using trimAl (Capella-Gutiérrez et al., 2009). We applied the automated1 command, which implements a heuristic search to choose the most appropriate model based on the given characters. Following alignment trimming, we generated five datasets with varying levels of loci completeness (100p, 95p, 75p, 50p, and 10p), where 95p requires 95 percent of the individuals in the alignment for a locus to be included. Summary data for all datasets were produced using scripts available at <https://github.com/dportik/AlignmentAssessment>. Frequency distributions of the genomic data are presented on a per-locus basis for 45 individuals (Fig. S1A–F). All data files are deposited on DRYAD (<https://doi.org/10.5061/dryad.7m0cfxpqk>) and raw sequence data are deposited on GenBank Sequence Read Archive (PRJNA594237).

2.5. Phylogenomic analyses

To reconstruct higher-level phylogenetic relationships of *Gekko*, we analyzed all five datasets (100p–10p) using maximum likelihood for the

concatenated datasets, as well as species-tree analyses. We prepared concatenated PHYLIP files for each dataset with a single partition and estimated maximum likelihood (ML) phylogenies using IQ-TREE v1.6.7 (Nguyen et al., 2015), applying the GTR+ Γ model of molecular evolution. We assessed nodal support using 1000 bootstrap pseudoreplicates via the ultrafast-bootstrap (UFB) approximation algorithm (Minh et al., 2013). Nodes with UFB $\geq$ 95 were considered to be well-supported (Minh et al., 2013; Wilcox et al., 2002).

Under certain conditions, gene-tree/species-tree methods have advantages over the analysis of concatenated datasets (Kubatko and Degnan, 2007; Edwards et al., 2007, 2016), but they may also be sensitive to missing data (Bayzid and Warnow, 2012) and to the resolution of individual gene trees (Castillo-Ramírez et al., 2010). Here we applied two different species-tree methods: ASTRAL-III (Zhang et al., 2017) and SVDQuartets (Chifman and Kubatko, 2014). For ASTRAL, we summarized individual gene trees as input files, whereas we provided a partitioned nexus file for SVDQuartets without estimating individual gene trees, *a priori*. Under both methods we analyzed 100p and 50p complete datasets. Individual gene trees for each locus were estimated in IQ-TREE with implementing ModelFinder (Kalyaanamoorthy et al., 2017) to estimate an accurate model of evolution; these gene trees were used as the input trees for downstream species-tree analyses in ASTRAL-III. We estimated quartet support values implemented in ASTRAL-III, where the quartet support values are the posterior estimate at a given branch where each gene-tree quartet agrees with the respective branch. We interpret posterior probabilities greater than 95 to be strongly supported (Huelsenbeck et al., 2001; Erixon et al., 2003; Huelsenbeck and Rannala, 2004; Wilcox et al., 2002).

Species-tree analyses were inferred using SVDQuartets and implemented in an alpha-test version of PAUP* v4.0a15080 (Swofford, 2003). This algorithm randomly samples quartets using a coalescent model and a quartet amalgamation heuristic to generate a species tree and has proven useful and accurate for estimating species trees from complete alignments of large genomic datasets (Chou et al., 2015). All possible quartet scores were evaluated from the entire alignment using a multispecies coalescent tree model with 100 bootstrap replicates performed to calculate nodal support. The program Quartet MaxCut v2.1.0 (Snir and Rao, 2012) was used to construct a species tree from the sampled quartets. Bootstrap support values for this analysis greater than 95 are considered significantly supported (Felsenstein, 1985).

3. Results

3.1. UCE sequencing, assembly and alignment

Following enrichment and sequencing, we obtained an average of 5462 contigs per sample (range = 2812–8756). An average (per sample) of 4718 of these contigs matched the UCE loci from capture probes (range = 2976–5277). The average length of UCE-matching contigs was 946 bp (range = 550–1413). For the dataset specifying no missing data, we recovered 772 UCE loci across 45 taxa (797,846 bp including indels) with 132,677 informative sites. For the 50p dataset, we recovered 4051 UCE loci across 45 species, with average length of 4,171,817 bp (including indels). For the datasets allowing missing loci for any taxon, we recovered 4715 loci (4,794,263 bp) for 10p, 3376 loci (3,508,564 bp) for 75p, and 2366 loci (2,543,167 bp) for 95p UCE loci across 45 species. We provide summary statistics for sequencing and alignments in Table S1 and in Fig. S1.

3.2. Phylogenomic analyses

For the 100p dataset of 772 UCE loci, the maximum likelihood analysis produced an optimal topology in which all but three nodes received over 95% bootstrap support (Fig. 2). The ML topologies from the four other variably incomplete data matrices (4715, 4051, 3376, and 2366 loci, respectively) reflect the same relationships as the 100p

dataset, with only a few nodes lacking strong support (Fig. 2).

Our phylogenomic estimate provided strong support for novel relationships, placing unequivocally several rare taxa of unknown affinities, while simultaneously resolving several unresolved, problematic relationships. Our UCE data resolved the three-clade polytomy of Brown et al. (2012a: Fig. 1, node 3)—all of the deeper internodes of *Luperosaurus* + *Gekko* + *Ptychozoon*—and most nodes in our concatenated trees were also resolved with strong support in our species-tree analyses.

We inferred strong support for two of the three large clades (Fig. 3, clades 1 and 3), the first of which contains taxa previously referred to *Luperosaurus* (including the genotype, *L. cumingii*, eliminating any doubt that this clade should be considered true *Luperosaurus*), *Lepidodactylus*, and *Pseudogekko*. Surprisingly, a close relationship between *Lepidodactylus lugubris* and members of true *Luperosaurus* (exemplified by *L. cumingii*) was well-supported in the concatenated analyses; however, this group received variable support in the species-tree analyses (Fig. 3 vs. Fig. 2; see also Heinicke et al., 2012). A clade, including *Gekko smithii* (uncontroversial, previously documented as closely related to the genus *Gekko*'s genotype species, *G. gekko*; Rösler et al., 2011), comprises numerous species previously referred to *Gekko*, *Ptychozoon* (including its genotype species *P. kuhli*), and a subset of insular *Luperosaurus* taxa, received low support values (Fig. 3, clade 2).

The true *Gekko* (+*Ptychozoon*) clade inferred in our phylogenomic analyses was recovered with strong support as most closely related to the Philippine *Gekko* clade (Fig. 3, clade 3), with one surprising result. In contrast to the two-locus analysis of Brown et al. (2012a), the newly-discovered, enigmatic high-elevation Palawan Island endemic *Luperosaurus gulat* was the sister taxon to the Philippine *Gekko* radiation (Figs. 2 and 3).

Similar to previous studies (small multi-locus datasets; Brown et al., 2012a; Heinicke et al., 2012), *Gekko* species are arranged in three major subclades: two *Gekko* clades and one *Gekko* + *Ptychozoon* + *Luperosaurus*. *Gekko* as a whole is non-monophyletic because of the inclusion of *Ptychozoon* and some *Luperosaurus* (Figs. 2 and 3), with the remaining “*Luperosaurus*” taxa (species not recovered in the genotype group) placed with strong support in four different clades (Figs. 2 and 3). The close relationship between the Southeast Asian species pair, *L. browni* + *L. iskandari*, and *Gekko vittatus* is strongly supported, and these are in turn grouped with *G. badenii* and *G. petricolis* (Fig. 3).

Finally, another novel result is the strongly-supported placement of *Ptychozoon rhacophorus* apart from the remaining species of *Ptychozoon*, but as the sister taxon to the (*G. badenii* + *G. petricolis*) (*L. iskandari* + *Gekko vittatus*), *L. browni*) clade of Indochinese, Southeast Asian, and Southwest Pacific island taxa, respectively.

4. Discussion

4.1. Phylogeny, geographic regionalism, and biogeography

Our concatenated ML analyses of 772 (100p), 3376 (75p), and 4715 (10p) loci produced relationships similar, in some ways, to those of earlier analyses of few loci (Brown et al., 2012a; Heinicke et al., 2012). Nevertheless, despite the similarity of these results to the partially resolved earlier study of Brown et al. (2012a), our phylogenomic analysis of UCE-probed loci using both concatenated and species-tree analyses produced novel relationships that allow us to make several strong conclusions. This study establishes the strongly supported placement of the formerly problematic taxon *Luperosaurus gulat* (Brown et al., 2010), provides resolution of a polytomy from an earlier study (Brown et al., 2012a), and confirms the nested placement of taxa with phenotypically apomorphic morphologies within a large clade characterized by a generalized suite of pleisiomorphic traits (Brown et al., 2012b; Heinicke et al., 2012). Aside from confirming the biogeographic regionalism of earlier inferred *Gekko* clades—recognized in our revised classification proposed here as subgenera (see below)—our phylogenomic results

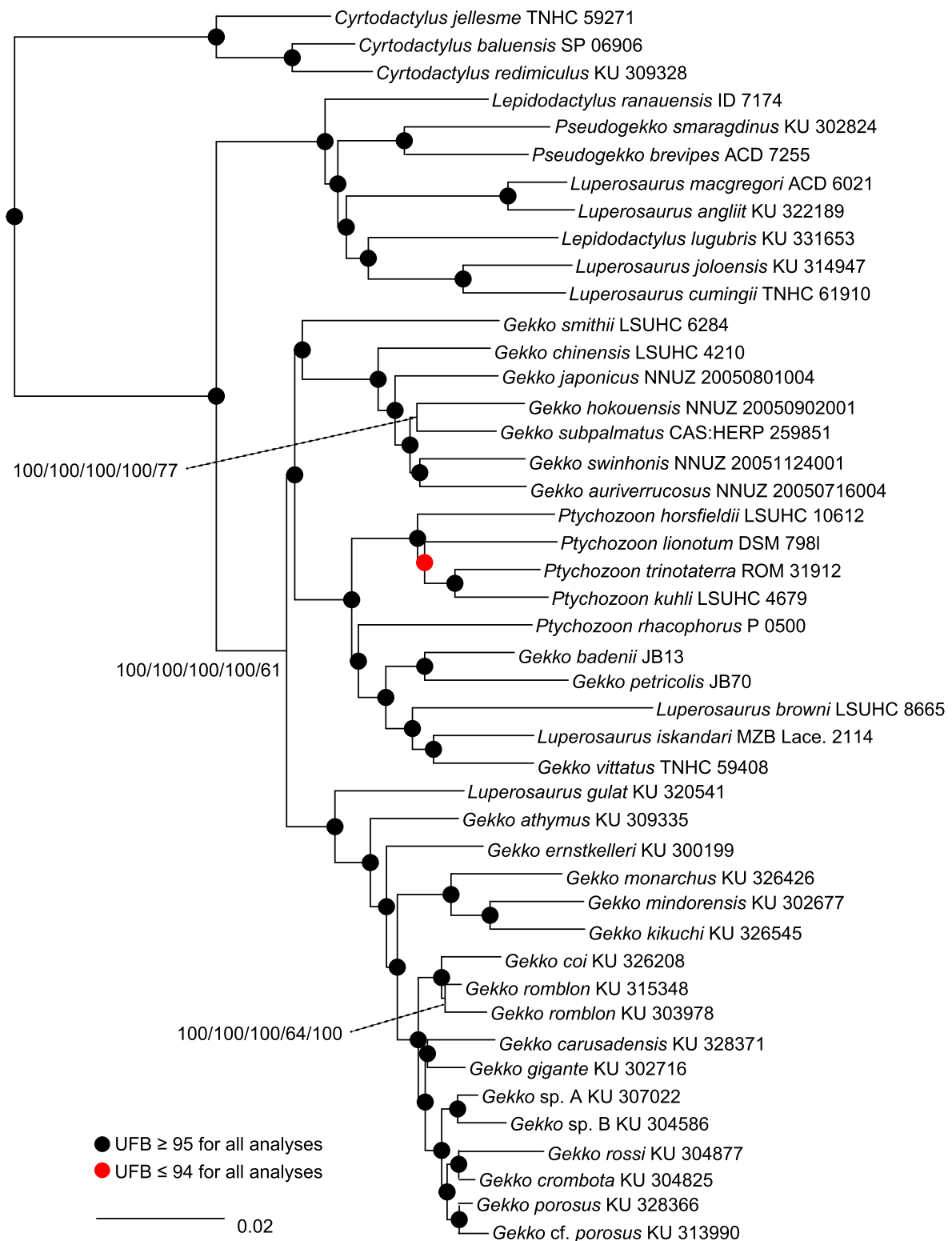


Fig. 2. Maximum likelihood phylogeny based on the 10p dataset (4715 loci, 4,794,263 bp) with UFB for the 10p, 50p, 75p, 95p, and 100p respectively. Black dots represent ultrafast bootstrap support (UFB) values greater than 95, and red dots are support values 94 and below for all datasets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

have additional biogeographic significance. With *L. gulat* (Brown et al., 2010) now recognized as the sister taxon to the remaining Philippine *Gekko*, ancestral range reconstruction of the Palawan Microcontinent Block at the base of the Philippine clade is considerably strengthened (Siler et al., 2012). The first three earliest branching Philippine lineages (*L. gulat*, *G. athymus*, and *G. ernstkelleri*) are all Palawan Microcontinent

Block endemics, as are several other species in this clade (*G. palawensis*, *G. romblon*, *G. coi*, and, in part, *G. monarchus*). The phylogenetic placement of *Gekko gulat*, n. comb., thus adds to a suite of recent studies emphasizing the Palawan Microcontinent Block-origins of Philippine archipelago-wide endemic clades, ancient isolation of Eurasian lineages (to the exclusion of Sundaic lineages), a paleotransport-and-dispersal

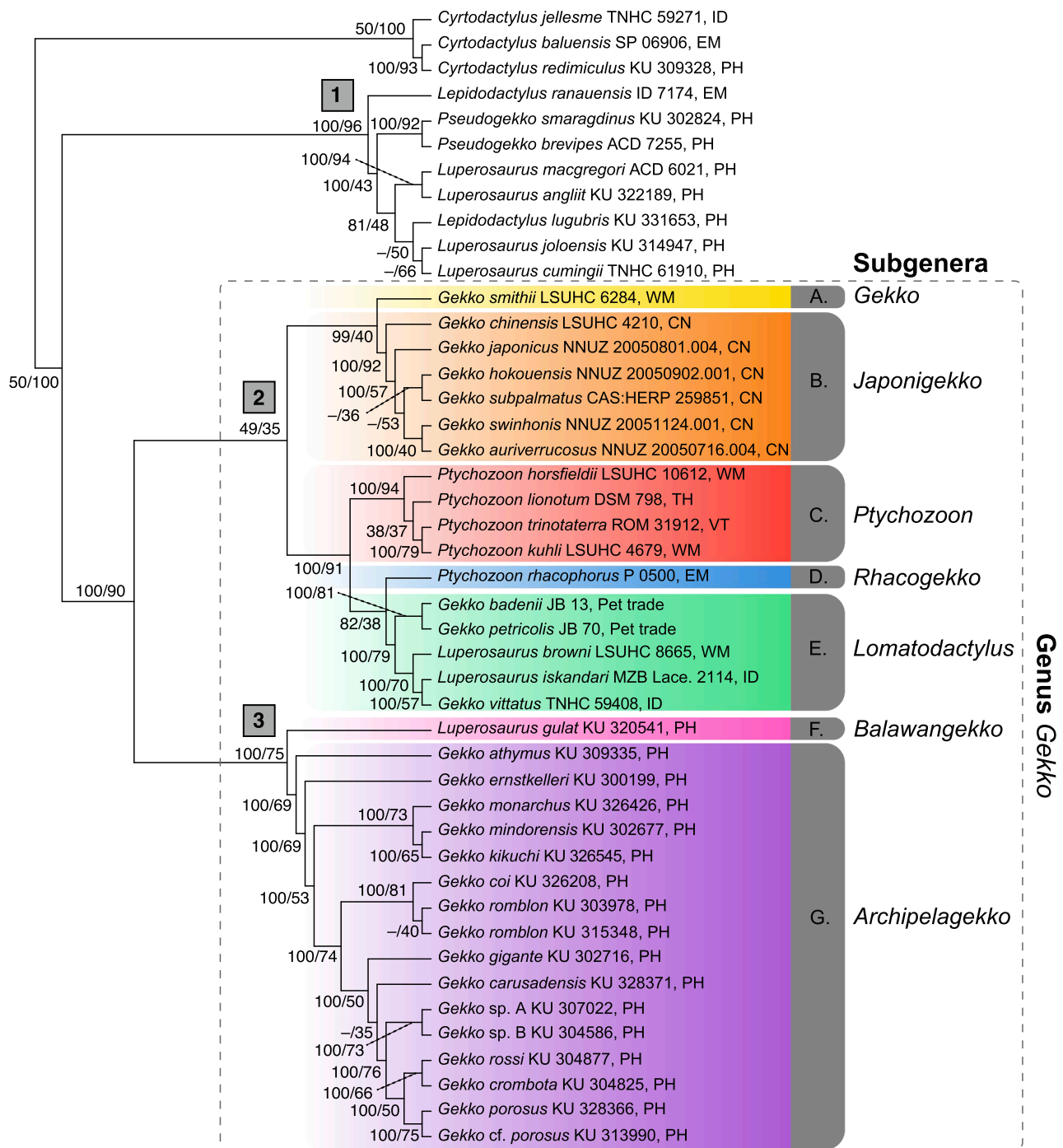


Fig. 3. ASTRAL species tree of gekkonid species included in this study based on the alignment with no missing data 100p (722 loci, 797,846 bp). Node values are SVDQuartet support values and quartet support values inferred from ASTRAL-III, respectively. Quartet support values are the posterior estimate at a given branch where each gene-tree quartet agrees with the respective branch, values greater than 95 are considered well-supported. Bold numbers in grey boxes refer to the three large clades recovered from the phylogenetic analyses. All subgenera groups are labeled A–G and are colored according to the new subgeneric designations. Country codes are as follows: CN, China; EM, East Malaysia; ID, Indonesia; WM, West Malaysia; PH, Philippines; TH, Thailand; VT, Vietnam.

facilitated colonization scenario, and the pivotal role of the Palawan Ark mechanism for biogeographic contributions to accumulation of the archipelago's land vertebrate faunal megadiversity (Blackburn et al., 2010; Siler et al., 2012; Brown et al., 2013, 2016; Grismer et al., 2016; Chan and Brown, 2017).

4.2. Evolution of phenotypic novelty

Our phylogenomic estimate of selected *Gekko* taxa both confirms

previous findings of paraphyly with respect to *Ptychozoon* and some species of *Luperosaurus* (Brown et al., 2012a, b; Heinicke et al., 2012) and provides new insight into the evolution of morphological novelty within gekkonid lizards (Gamble et al., 2012; Oliver et al., 2018). Although *Gekko* is known to be a phenotypically variable, highly diverse clade (Rösler et al., 2011), with some clades more variable than others, none exhibit more structural body-plan novelty than members of the genus *Ptychozoon* (Brown et al., 1997; Russell et al., 2001). Only *Luperosaurus iskandari* (Brown et al., 2000) approaches the degree of

elaboration of dermal structures bordering the limbs, tail, and body—clear adaptations for directed aerial descent (parachuting, gliding; Heyer and Pongsapipatana, 1970; Marcellini and Keefer, 1976; Russell, 1979; Brown et al., 2001; Young et al., 2002; Heinicke et al., 2012) and camouflage (Barbour, 1912; Tho, 1974; Brown et al., 1997; Vetter and Brodie, 1977). Within the family, evolution of similar structures capable of lift generation during aerial locomotion, and breaking up the body's outline when at rest on vertical surfaces have evolved multiple times in the genera *Hemidactylus* and *Luperosaurus* (Dudley et al., 2007; Heinicke et al., 2012).

4.3. Classification

Given our resolution of three major clades of *Gekko*—one comprising almost exclusively Philippine species, another primarily Southeast Asian mainland (plus Sundaland) taxa, and a third consisting of morphologically variable species from Southeast Asia, Wallacea, Melanesia and the Southwest Pacific—we subsume all contained taxa into the oldest, most inclusive generic name, *Gekko* (Laurenti). This solution imparts the fewest alterations of binominal species named pairs, and thus, is the most conservative and preferred option. Accordingly, we place all species of the genus *Ptychozoon*, as well as the Sulawesi endemics *Luperosaurus iskandari* and *L. browni*, and the Palawan species *L. gulat*, into the genus *Gekko*. In consideration of *Gekko* phylogenetic relationships (Rösler et al., 2011; Brown et al., 2012a; Heinicke et al., 2012; this study), distinctly geographically circumscribed regional clades (Japan and adjacent mainland, Indochina, southwest Pacific, the Philippine archipelago), plus associated morphological variability of the contained taxa, we find the recognition of the following six phylogenetically and phenotypically defined subgenera advisable at this time.

Genus *Gekko* Laurenti, 1768 (Fig. 3, clades A–G)

Subgenus *Gekko* (Fig. 3A)

Type species: *Lacerta gekko* Linnaeus, 1758, designated by tautonymy fide Stejneger (1936).

Definition: Subgenus *Gekko* is a maximum crown-clade name referring to the clade originating with the most recent common ancestor of *Gekko* (*Gekko*) *gekko*, and *G. (G.) smithii*, and including all extant species that share a more recent common ancestor with these taxa than with any of the type species of other subgenera recognized here. Although unambiguous synapomorphies for this group have not been identified, members of the subgenus *Gekko* are larger than most conspecifics (adults SVL > 110 mm), with tubercles present on ventrolateral folds, more than 18 subdigital Toe IV scansors, femoral pores absent, and with a relatively low number of precloacal pores (Bauer et al., 2008).

Content: *Gekko* (*Gekko*) *G. albofasciolatus* Günther, 1867; *G. (G.) gekko* (Linnaeus, 1758); *G. (G.) nutaphandi* Bauer, Sumontha, and Pauwels (2008); *G. (G.) reevesii* (Gray, 1831); *G. (G.) siamensis* Grossmann and Ulber, 1990; *G. (G.) smithii* Gray, 1842; *G. (G.) verreauxi* Tytler, 1864.

Comment: The subgenus comprises taxa from Rösler et al. (2011) *G. gekko* Group. In recognizing this assemblage, Rösler et al. (2011) resurrected *G. reevesii* and provided data on two subspecies of *G. (G.) gekko*. Undescribed species in this subgenus have been reported from Sulawesi, the Togian Islands of Indonesia, and possibly the islands of Tioman and Tulai of Malaysia (Grismer, 2006; Rösler et al., 2011).

Subgenus *Japonigekko* subgen. nov. (Fig. 3B)

Type species: *Platydictylus japonicus* Schlegel in Duméril and Bibron, 1836, the oldest name available for a taxon included in the new subgenus, here designated.

Definition: *Gekko* (Subgenus *Japonigekko*) is a maximum crown-

clade name referring to the clade originating with the most recent common ancestor of *Gekko* (*Japonigekko*) *chinensis*, *G. (J.) swinhonis*, and including all extant species (including the type species *G. (J.) japonicus*) that share a more recent common ancestor with these species than with any of the type species of the other subgenera recognized here. Members of the subgenus *Japonigekko* are usually relatively small to moderate-sized (59–99 mm SVL); possess or lack dorsal tubercle rows (a few species possess up to 21 rows); possess up to 32 precloacal pores (most lack pores altogether); and lack tubercles on ventrolateral folds. All contained taxa possess some degree of interdigital webbing (minimally to extensively webbed). Other than the presence of interdigital webbing, unambiguous synapomorphies for the new subgenus have not been identified; nevertheless, our phylogeny strongly corroborates this phenotypically variable clade.

Content: *Gekko* (*Japonigekko*) *adleri* Nguyen, Wang, Yang, Lehmann, Le, Ziegler and Bonkowski, 2013; *G. (J.) aaronbaueri* Tri, Thai, Phimvohan, David, and Teynié, 2015; *G. (J.) auriverrucosus* Zhou & Liu, 1982; *G. (J.) bonkowskii* Luu, Calme, Nguyen, Le, and Ziegler, 2015; *G. (J.) canhi* Rösler, Nguyen, Doan, Ho and Ziegler, 2010; *G. (J.) chinensis* Gray, 1842; *G. (J.) guishanicus* Lin and Yao, 2016; *G. (J.) hokouensis* Pope, 1928; *G. (J.) japonicus* (Schlegel, 1836); *G. (J.) kwangsiensis* Yang, 2015; *G. (J.) lauhachindaei* Panitvong, Sumontha, Konlek and Kunya, 2010; *G. (J.) liboensis* Zaho and Li, 1982; *G. (J.) melli* Vogt, 1922; *G. (J.) nadenensis* Luu, Nguyen, Le, Bonkowski, and Ziegler, 2017; *G. (J.) palmatus* Boulenger, 1907; *G. (J.) scabridus* Liu and Zhou, 1982; *G. (J.) scientiadventura* Rösler, Ziegler, Vu, Herrmann and Böhme, 2004; *G. (J.) sengchanthavongi* Luu, Calme, Nguyen, Le, and Ziegler 2015; *G. (J.) shibatai* Toda, Sengoku, Hikida and Ota, 2008; *G. (J.) similignum* Smith, 1923; *G. (J.) subpalmatus* Günther, 1864; *G. (J.) swinhonis* Günther, 1864; *G. (J.) taibaiensis* Song, 1985; *G. (J.) tawaensis* Okada, 1956; *G. (J.) thakhekensis* Luu, Calme, Nguyen, Le, Bonkowski, and Ziegler, 2014; *G. (J.) truongi* Phung and Ziegler, 2011; *G. (J.) vertebralis* Toda, Sengoku, Hikida and Ota, 2008; *G. (J.) vietnamensis* Sang, 2010; *G. (J.) wexianensis* Zhou and Wang, 2008; *G. (J.) yakuensi* Matsui and Okada, 1968.

Comment: The subgenus is equivalent in content to the *G. japonicus* Group of Rösler et al. (2011). See Rösler et al. (2011) for discussions of the considerable interspecific morphological variability and lengthy taxonomic controversy that characterizes this assemblage (Boulenger, 1885, 1907; Smith, 1935; Bourret, 1937; Bauer, 1994; Ota et al., 1995; Nguyen et al., 2009).

Etymology: *Japonigekko* is a masculine noun, referring to geographic origin (Japan) of the type species (*G. japonicus*). We use the spelling “Japon” following Schlegel (1836) who used this French spelling in the construction of the name *Platydictylus japonicus*.

Subgenus *Ptychozoon* Kuhl and van Hasselt, 1822 (Fig. 3C)

Type species: *Lacerta homalocephala* Creveldt, 1809 (preoccupied [as *Lacerta homalocephala*]; nomen novum *P. kuhli* proposed by Stejneger, 1902), the oldest name available for a taxon included in this subgenus.

Definition: *Gekko* (Subgenus *Ptychozoon*) is a maximum crown-clade name referring to the clade originating with the most recent common ancestor of *Ptychozoon horsfieldii* (Gray, 1827) and *Gekko* (*Ptychozoon*) *kuhli*, and including all extant species that share a more recent common ancestor with these taxa than with any of the type species of other subgenera recognized here. Unambiguous synapomorphies for the subgenus *Ptychozoon* include the presence of a midbody axilla–groin patagial membrane (“parachute”), denticulate dermal lobes along lateral margins of the tail, expanded dermal flaps on anterior and posterior margins of the limbs, and the presence of extensive interdigital webbing of the hands and feet. Additionally, all taxa possess enlarged, imbricate parachute support scales, an infraauricular cutaneous flap (“canard wing”), and a variably enlarged terminal tail flap.

Content: *Gekko* (*Ptychozoon*) *banannensis* Wang, Wang, and Liu,

2016, *G. (P.) cicakterbang* Grismer, Wood, Grismer, Quah, Thy, Phimmachak, Sivongxay, Seateun, Stuart, Siler, Mulcahy, and Brown, 2019, *G. (P.) horsfieldii* (Gray, 1827), *G. (P.) intermedium* Taylor 1915, *G. (P.) kabkaebii* Grismer, Wood, Grismer, Quah, Thy, Phimmachak, Sivongxay, Seateun, Stuart, Siler, Mulcahy, and Brown, 2019, *G. (P.) kaengkrachanense* Sumontha, Pauwels, Kunya, Limlikhitaksorn, Ruksue, Taokratok, Ansermet, and Chanhom, 2012, *G. (P.) kuhli* (Stejneger, 1902), *G. (P.) lionotum* Annandale, 1905, *G. (P.) nicobarensis* Das and Vijayakumar 2009, *G. (P.) popaense* Grismer, Wood, Thura, Grismer, Brown, and Stuart, 2018, *G. (P.) tokehos* Grismer, Wood, Grismer, Quah, Thy, Phimmachak, Sivongxay, Seateun, Stuart, Siler, Mulcahy, and Brown, 2019; *G. (P.) trinitaterra* Brown, 1999.

Comment: In revising species “group” classification of *Gekko*, Rösler et al. (2011) did not comment on the inclusion of *Ptychozoon* species (unsampled in that study), which were later found to be imbedded within *Gekko* (Brown et al., 2012a, b; Heinicke et al., 2012).

Subgenus *Rhacogekko* subgen. nov. (Fig. 3D)

Type species: *Gekko rhacophorus* Boulenger, 1899, the oldest (and only) name available for a taxon included in the new subgenus, here designated.

Definition: *Rhacogekko* (new subgenus) is a maximum crown-lineage name referring to *Gekko (R.) rhacophorus* the sister lineage to *Lomatodactylus*. Although unambiguous synapomorphies for the new subgenus have not been identified, *Gekko (R.) rhacophorus* differs from other subgenera by lacking lateral skin folds on head (infra-auricular cutaneous flaps), lacking imbricate dorsal parachute support scales and an enlarged terminal tail flap (Brown et al., 1997), and by having fully half-webbed fingers and toes (Boulenger, 1899; Malkmus et al., 2002).

Content: *Gekko (R.) rhacophorus* (Boulenger, 1899) and *Gekko (R.) sorok* (Das et al., 2008).

Etymology: *Rhacogekko* is derived from the Greek noun *rhakos*, meaning “rag” or “wrinkle” in relation to the rounded lobe-like fringes or wrinkles on the lateral folds of the body.

Subgenus *Lomatodactylus* van der Hoeven, 1833 (Fig. 3E)

Type species: *Lomatodactylus vittatus* (Houttuyn, 1782) (type species by subsequent designation [Stejneger’s, 1907]). This genus-group name was originally applied by van der Hoeven (1833) to representatives of what are now considered multiple gekkotan genera. Stejneger’s (1907) action was made without comment.

Definition: *Lomatodactylus*, is a maximum crown-clade name referring to the clade originating with the most recent common ancestor of *Gekko (Lomatodactylus) vittatus*, *G. (L.) browni*, and *G. (L.) iskandari* (new combination) and including all extant species that share a more recent common ancestor with these taxa than with any of the type species of other subgenera recognized here. Unambiguous synapomorphies for the new subgenus have not been identified, but three known (and two inferred) members of *Lomatodactylus* are gracile and slender (*G. [L.] iskandari*, *G. [L.] vittatus*, *G. [L.] browni*, presumably *G. [L.] brooksi* and *G. [L.] remotus*) with thin, elongate bodies and ornate tubercles present on ventrolateral folds (Brown et al., 2000; McCoy, 2006; Rösler et al., 2012).

Content: *Gekko (Lomatodactylus) brooksi*, Boulenger, 1920 (new combination), *Gekko (L.) browni*, (Russell, 1979), *Gekko (L.) flavimaritus* Rujirawana, Fong, Ampai, Yodthong, Termprayoon, and Aowphol, 2019; *Gekko (L.) iskandari*, (Brown, Supriatna, and Ota, 2000) (new combination), *G. (L.) remotus* Rösler, Ineich, Wilms, and Böhme, 2012; *(L.) vittatus* Houttuyn, 1782; *Gekko (L.) badenii* Nekrasova and Szczerbak, 1993; *G. (L.) boehmei* Luu, Calme, Nguyen, Le, and Ziegler, 2015; *G. (L.) canaensis* Ngo and Gamble, 2011; *G. (L.) grossmanni* Günther, 1994; *G. (L.) petricolus* Taylor, 1962; *G. (L.) russelltrani* Ngo, Bauer, Wood and Grismer, 2009; *G. (L.) takouensis* Ngo and Gamble, 2010.

Comment: Our phylogenomic approach confirms the phenotypically dissimilar pairing of the taxa *Gekko (L.) vittatus* (plus the closely-related *G. remotus*) and *G. (L.) iskandari* (inferred previously with two genes (Brown et al., 2012a). Despite their morphological differences (Crombie and Pregill, 1999; Brown et al., 2000; McCoy, 2006), we note that the proximate geographic ranges in the islands of Melanesia, Palau, and the southwest Pacific lend geographical support to the recognition of this subgenus (Brown et al., 2000; McCoy, 2006).

Subgenus *Balawangekko* subgen. nov. (Fig. 3F)

Type species: *Luperosaurus gulat* Brown, Diesmos, Duya, Garcia, and Rico, 2010, here designated.

Definition: *Balawangekko* is the sister lineage to a crown clade of Philippine endemics described below. At present containing a single species (*G. [B.] gulat*), the new subgenus is intended to include any species discovered in the future to share a more recent common ancestor with *G. (B.) gulat* than with any of the type species of other subgenera recognized here.

Content: *Gekko (B.) gulat* (Brown, Diesmos, Duya, Garcia, and Rico, 2010).

Etymology: *Balawangekko* is derived from the ancient Chinese word “*Bālāwāng*” from the Song Dynasty state Ma-I, which consisted of three islands, presumably Palawan, Busunaga-Calamianes, and Mai (Mindoro). “Balawan” derived from “*Bālāwāng*” meaning Palawan and “gekko,” for gekkonid lizards; this name is chosen in reference to recent changes in understanding biogeographical relationships and evolutionary history of many iconic vertebrate lineages endemic to Palawan Island (Blackburn et al., 2010; Esselstyn et al., 2010; Siler et al., 2012; Brown et al., 2016), erroneously and over simplistically assumed previously to be a simple faunal extension of the Sunda Shelf island of Borneo.

Subgenus *Archipelagekko* subgen. nov. (Fig. 3G)

Type species: *Gekko mindorensis* Taylor, 1919, the oldest name available for a taxon included in the new subgenus.

Definition: *Archipelagekko* is a maximum crown-clade name referring to the clade originating with the most recent common ancestor of *Gekko (Archipelagekko) athymus* and including all extant species that share a more recent common ancestor with these taxa than with any of the type species of other subgenera recognized here.

Content: *Gekko (Archipelagekko) athymus* Brown and Alcala, 1962; *G. (A.) carusadensis* Linkem, Siler, Diesmos, Sy, and Brown, 2010; *G. (A.) coi* Brown, Siler, Oliveros, and Alcala, 2011; *G. (A.) crombota* Brown, Oliveros, Siler, and Diesmos, 2006; *G. (A.) ernstkeileri* Rösler, Siler, Brown, Demeglio, and Gaulke, 2006; *G. (A.) gigante* Brown and Alcala 1978; *G. (A.) kikuchii* (Oshima, 1912); *G. (A.) monarchus* (Schlegel, 1836); *G. (A.) mindorensis* Taylor, 1919; *G. (A.) palawanensis* Taylor, 1925; *G. (A.) romblon* Brown and Alcala 1978; *G. (A.) rossi* Brown, Oliveros, Siler, and Diesmos, 2009.

Comment: The new subgenus contains *G. athymus* (not previously placed in a species group due to its morphological distinctiveness; Rösler et al., 2011), the *G. porosus* Group, and the *G. monarchus* Group (Rösler et al., 2011). We are aware of at least two additional unrecognized species in this clade (*G. sp. A.* [Dalupiri Isl.] and *G. sp. B.* [Camiguin Norte Isl.]; Brown et al., 2009); all are restricted to the Philippines, with the exception of *G. monarchus* (a widespread taxon that is known from Palawan [Philippines], parts of Indonesia, Malaysia, and Thailand [Rösler et al., 2011; Grismer, 2011; Siler et al., 2012], and *G. kikuchii*, a northern Philippine species with a distribution extending to Lanyu Island, Taiwan [Oshima, 1912; Siler et al., 2014]). An additional 4–7 species likely currently reside within the synonymy of *G. (A.) mindorensis* (Siler et al., 2014).

Etymology: *Archipelagekko* is a masculine noun, derived from the English noun Archipelago, in recognition of the observation that nearly

all contained taxa are restricted to the Philippine Archipelago. Suggested common name: Philippine Geckos.

4.4. Taxonomic vandalism

Taxonomic vandalism is the deliberate disabling or unnecessary atomization of scientific classification, through professional misconduct, based solely on secondary information, gleaned unscientifically from others' publications (e.g., results of other scientists; not the work of the vandal her/his-self); further lacking, (1) adequate genus and species-level documentation information on a uniquely-designated type series/species in the form of voucher specimens deposited in an internationally-accessible biodiversity repository or museum, (2) accompanying data, and rigorous analyses, unique to that publication and justifying the nomenclatural change, and (3) publication in peer-reviewed scientific journals. Changes committed as acts of taxonomic vandalism via nomenclatural change, without accompanying data, original analyses, and peer review do not receive naming priority over proper, scientific, peer-reviewed taxonomic or revisionary classification, published with accompanying data.

While this manuscript was in preparation, a series of three papers appeared (Hoser, 2018a, b, c), in which revised taxonomies were presented for *Gekko*, *Luperosaurus*, *Ptychozoon*, *Lepidodactylus*, and *Pseudogekko*. The contained unjustified taxonomic changes were based solely on the various publications cited herein (e.g., Rösler et al., 2011; Brown et al., 2012a, b; Heinicke et al., 2012; Oliver et al., 2018) in which phylogenetic hypotheses based on Sanger sequencing results were presented, without concomitant taxonomic rearrangements, pending the presentation of data that would permit more advanced analyses, and well-supported topologies (this work). Hoser (2018a, b, c) proposed 10 new generic and six subgeneric names to deal with cases of paraphyly and polyphyly as they were understood and misunderstood by him. Additionally, he proposed 10 new species names, based on unsubstantiated (i.e., presented without accompanying data from voucher specimens) and operationally non-diagnostic "diagnoses" based, apparently with "character states" gleaned from figures/photographs included in Brown et al. (2012a, b), Heinicke et al. (2012), and Oliver et al. (2018). Aside from his disregarding of conventions for species descriptions, some of his higher taxonomic proposals are partly, though not entirely, congruent with the units recognized herein, and also include some generic proposals that our current data suggest are non-monophyletic. Despite the temporal precedence, we follow Kaiser et al. (2013) and Kaiser (2014) and reject Hoser's taxonomic vandalism, and we regard these names as unavailable for nomenclatural purposes. We echo the belief that the extraordinary chaos and rampant ethical violations resulting from Hoser's actions require urgent use of the plenary powers by the ICZN. Without such action, scientists must knowingly violate the principle of priority, defensively and prematurely name supraspecific taxa in order to protect their discoveries (novel clades, etc.), or risk that their own original research be used to fuel the ongoing deluge of taxonomic vandalism (Inger, 1996; Borrell, 2007; Pauly et al., 2009; Moore et al., 2014; Jones, 2017).

We provide a novel phylogenetic hypothesis, based on the most data-intensive analysis of the group ever conducted, and we endorse the most conservative/inclusive generic arrangement (*Gekko*), and provide a subgeneric classification that has the desirable properties of (1) being based on the most robust phylogeny available, (2) involves minimal numbers of genus-species couplet changes (stabilizing taxonomy), (3) the subgeneric classification allows for continued use of names associated with iconic species and celebrated apomorphies (e.g., *Ptychozoon*, *Rhacogekko*), and (4) now protects *Gekko* classification from future vandalism.

If widely adopted during the standard process of phylogeny-based revisionary classification, the practice of formally proposing and, thus, making formally available subgeneric names to recognize phylogenetically identified and defined clades and lineages has an added

practical benefit of potentially alleviating the motivation behind taxonomic vandalism. Whether defined by standard Linnaean system, character-based diagnoses (Glaw and Vences, 2006), phylogenetically-defined and rank free (Hillis and Wilcox, 2005; Leaché et al., 2009; Wallach et al., 2009; Yuan et al., 2016), or with parallel classifications that embrace both systems (Brown et al., 2013), the existence of a node-based subgenus name (defined with reference to a phylogeny) in synonymy with a more inclusive genus name, and satisfying the qualifying conditions of The Code (including a character-based diagnosis and designation of a type species), alleviates the threat of taxonomic vandalism via the simple requirement that the subgenus name be used, should future systematists effectively argue for a more atomized classification. Although this simple practice may involve additional behind-the-scenes steps (defining and naming supraspecific taxa that will not be used in today's binomial classification), it effectively eliminates the motivation behind taxonomic vandalism, while ensuring that supraspecific names are created only when accompanied by phylogenetic data, and that they explicitly involve appropriate specifiers in the form of type species and, ultimately, type specimens.

CRediT authorship contribution statement

Perry L. Wood: Writing - original draft, Writing - review & editing, Formal analysis, Methodology. **Xianguang Guo:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Scott L. Travers:** Methodology, Writing - original draft, Writing - review & editing. **Yong-Chao Su:** Methodology, Writing - original draft, Writing - review & editing. **Karen V. Olson:** Methodology, Writing - original draft, Writing - review & editing. **Aaron M. Bauer:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **L. Lee Grismer:** Writing - review & editing. **Cameron D. Siler:** Methodology, Writing - original draft, Writing - review & editing. **Robert G. Moyle:** Methodology, Writing - original draft, Writing - review & editing. **Michael J. Andersen:** Methodology, Writing - original draft, Writing - review & editing. **Rafe M. Brown:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://>

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