



Short Communication

Testing the phylogenetic affinities of Southeast Asia's rarest geckos: Flap-legged geckos (*Luperosaurus*), Flying geckos (*Ptychozoon*) and their relationship to the pan-Asian genus *Gekko*

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ABSTRACT

Some of Southeast Asia's most poorly known vertebrates include forest lizards that are rarely seen by field biologists. Arguably the most enigmatic of forest lizards from the Indo Australian archipelago are the Flap-legged geckos and the Flying geckos of the genera *Luperosaurus* and *Ptychozoon*. As new species have accumulated, several have been noted for their bizarre combination of morphological characteristics, seemingly intermediate between these genera and the pan-Asian gecko genus *Gekko*. We used the first multilocus phylogeny for these taxa to estimate their relationships, with particular attention to the phylogenetic placement of the morphologically intermediate taxa *Ptychozoon rhacophorus*, *Luperosaurus iskandari*, and *L. gulat*. Surprisingly, our results demonstrate that *Luperosaurus* is more closely related to *Lepidodactylus* and *Pseudogekko* than it is to *Gekko* but that some species currently classified as *Luperosaurus* are nested within *Gekko*. The Flying Gecko genus *Ptychozoon* is also nested within *Gekko*, suggesting that higher-level taxonomic revision of the generic boundaries within Southeast Asian gekkonines will be a priority for the immediate future.

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1. Introduction

The conservation crisis facing Southeast Asian biodiversity (Brooks et al., 2002; Sodhi et al., 2004) is a problem not only of underestimation of species diversity in the face of catastrophic habitat loss and degradation, but also a frustratingly slow accumulation of knowledge concerning the evolutionary process that produced the region's staggering levels of vertebrate diversity (Lomolino et al., 2010; Woodruff, 2010). An understanding of the evolutionary processes that produced the region's land vertebrate diversity has been slow to precipitate for several reasons. These include a lack of comprehensive biodiversity surveys in many inaccessible forests of Southeast Asia (e.g., Lim et al., 2008; Brown and Diesmos, 2009), the slow pace of subsequent taxonomic work, logistical and legal obstacles to field work, and a dearth of well sampled robust phylogenies with which to infer stable evolutionary classifications and determine the content of higher taxonomic entities. At the same time, the pace of Asian forest destruction has been higher than anywhere else on the planet (Bawa et al., 1990; Whitmore and Sayer, 1992; Sodhi et al., 2004).

We initiated this study to understand the evolutionary relationships of some of Southeast Asia's most rare and enigmatic groups of land vertebrates, the "Flap-legged" and "Parachute" geckos (or "Flying" geckos) of the genera *Luperosaurus* and *Ptychozoon*. With a few exceptions, most species are poorly known forest obligates that seldom are encountered by field biologists (Russell, 1979; Brown et al., 1997, 2000; Brown and Diesmos, 2000; Ota et al., 1996; Das et al., 2008). This situation is taken to the extreme in the case of the genus *Luperosaurus*, in which the entire genus (13 or 14 species) is known from fewer than 30 specimens, with roughly half of these species represented only by one or two specimens in research collections (Ota et al., 1996; Brown and Diesmos, 2000; Brown et al., 2000, 2007, 2010, 2011; Das et al., 2008). Collections are made rarely and unpredictably, such as when high canopy species are dislodged from their perches during strong storms (Brown et al., 1997, 2000; Das et al., 2008).

Two fundamental questions of taxonomy and classification have persisted with respect to these rare forest species. First, a variety of authors have debated the systematic affinities and content of these genera, particularly with respect to the remaining, morphologically generalized gekkonines of Southeast Asia: e.g., members of the genera *Gehyra*, *Hemidactylus*, *Hemiphyllodactylus*, *Lepidodactylus*, *Pseudogekko* and *Gekko* (Boulenger, 1885; Taylor, 1922; Wermuth, 1965; Kluge, 1968; Brown and Alcala, 1978; Russell, 1979; Brown et al., 2000). Second, reliable and stable

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character-based diagnostic definitions of the genera *Luperosaurus* and *Ptychozoon* (with respect to *Gekko*) have been elusive. As discussed by Brown et al. (2000, 2007, 2010, 2011), the four or five previously reliable diagnostic character differences between *Luperosaurus* and *Gekko* have broken down with the discovery of several species (*Luperosaurus angliit*, *L. gulat*, *L. iskandari*, and *L. kubli*) that blur the phenotypic distinction between these genera (Brown and Alcalá, 1978; Russell, 1979). Similarly, Ota et al. (1996) and Das et al. (2008) have described small, Bornean species of *Luperosaurus* that bear remarkable character similarity to one member of the genus *Ptychozoon* (*P. rhacophorus*), and Brown et al. (2000) described a *Luperosaurus* from Sulawesi that is very similar to species of *Ptychozoon*.

Because persistent questions of generic boundaries exist in these enigmatic species, we undertook this study to (1) estimate the phylogenetic relationships of *Luperosaurus*, *Ptychozoon*, *Lepidodactylus*, *Pseudogekko* and *Gekko* and (2) test the phylogenetic position of three of the most problematic, phenotypically intermediate species, *Luperosaurus gulat*, *L. iskandari*, and *Ptychozoon rhacophorus*.

2. Materials and methods

2.1. Taxon sampling and data collection

Ingroup sampling included eight individuals collected from eight localities, with six of the 13 currently recognized species of *Luperosaurus* represented (Fig. 1; Appendix A). To the best of our knowledge, no tissues have ever been collected for *Luperosaurus brooksii*, *L. browni*, *L. corfieldi*, *L. kubli*, *L. palawanensis*, *L. sorok*, and *L. yasumai*. To assess the monophyly of the genus, test taxonomic hypotheses, and investigate appropriate outgroup taxa, a broad sampling (32 taxa) from the family Gekkonidae were included, as well as a single outgroup sample from the gekkotan family Phyllodactylidae (Appendix A).

Genomic DNA was extracted from liver tissues stored in 95% ethanol. We sequenced a 1247 nucleotide fragment consisting of the mitochondrial gene NADH Dehydrogenase Subunit 2 (ND2) and components of three flanking transfer RNA genes (tRNA^{Trp}, tRNA^{Ala}, tRNA^{Asn}) using the primers and protocols of Brown et al. (2009) in 40 vouchered specimens. For 33 of these samples (Appendix A), we also sequenced a 418 base pair region of the nuclear Phosducin (PDC) gene using the primers and protocols of Gamble et al. (2008). Thermal profiles and PCR and sequencing protocols followed Siler et al. (2012). Amplified products were visualized on 1.5% agarose gels. PCR products were purified with 1 μ L of a 20% dilution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ). Cycle sequencing reactions were run using ABI Prism BigDye Terminator chemistry (Ver. 3.1; Applied Biosystems, Foster City, CA), and purified with Sephadex (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). Purified products were analyzed with an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Continuous gene sequences were assembled and edited using Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI). With one exception, all novel sequences are deposited in GenBank (Appendix A); the short PDC sequence for *Luperosaurus joloensis* is deposited in Dryad (doi:10.5061/dryad.7bn0fr99).

2.2. Sequence alignment and phylogenetic analyses

Initial alignments were produced in Muscle (Edgar, 2004) with minimal manual adjustments. To assess phylogenetic congruence between the mitochondrial and nuclear data, we inferred the phy-

logeny for each gene independently using likelihood and Bayesian analyses and assessed all strongly supported nodes for differences in relationships between mitochondrial and nuclear gene partitions. Following the observation of no statistically significant incongruence between datasets, we felt justified in using the combined, concatenated, data for subsequent analyses. Exploratory analyses of the combined dataset of 41 individuals (including all taxa, some of which were missing data for PDC) and a reduced dataset of individuals with no missing data exhibited identical relationships; we therefore chose to include all available data (41 individuals) for subsequent analyses of the concatenated dataset.

Partitioned Bayesian analyses were conducted in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). Both the mitochondrial and nuclear protein-coding regions were partitioned by codon position; we combined the three tRNAs flanking ND2 into a single partition. The Akaike Information Criterion (AIC), as implemented in jModeltest v0.1.1 (Posada, 2008), was used to select the best model of nucleotide substitution for each partition (Table 1). A rate multiplier model was used to allow substitution rates to vary among subsets, and default priors were used for all model parameters. We ran eight independent MCMC analyses, each with four Metropolis-coupled chains, an incremental heating temperature of 0.02, and an exponential distribution with a rate parameter of 25 as the prior on branch lengths (Marshall, 2010). All analyses were run for 20 million generations, with parameters and topologies sampled every 5000 generations. We assessed stationarity with Tracer v1.4 (Rambaut and Drummond, 2007) and confirmed convergence with AWTY (Wilgenbusch et al., 2004). Stationarity was achieved after 3 million generations (i.e., the first 15%), and we conservatively discarded the first 20% of samples as burn-in.

Partitioned maximum likelihood (ML) analyses were conducted in RAXMLHPC v7.0 (Stamatakis, 2006) on the concatenated dataset the same partitioning strategy as for Bayesian analysis. The more complex model (GTR + I + Γ) was used for all subsets (Table 1), and 100 replicate ML inferences were performed for each analysis. Each inference was initiated with a random starting tree and nodal support was assessed with 100 bootstrap pseudoreplicates (Stamatakis et al., 2008). Alignments and resulting topologies are deposited in Dryad (doi:10.5061/dryad.7bn0fr99).

2.3. Evaluating the hypothesis of monophyly for *Luperosaurus*

We tested taxonomy-based hypotheses to address questions concerning the generic affinities of three enigmatic species of geckos: *Luperosaurus gulat*, *L. iskandari*, and *Ptychozoon rhacophorus* (Table 2). The focal taxa for our hypothesis testing exhibit conspicuous combinations of morphological characters states (from which their generic classification was based), and yet, are also notably morphologically intermediate between genera, spanning the boundaries of diagnostic character differences traditionally used to define the genera. The recently discovered *Luperosaurus gulat* was acknowledged conceivably to be a member of the genus *Gekko* (Brown et al., 2010). *Luperosaurus iskandari* was also placed in this genus, albeit with the acknowledgement of its similarity to some members of the genus *Ptychozoon* (Brown et al., 2000), suggesting the possibility that it may be a “parachute-less” *Ptychozoon*. Similarly, the morphological similarity of *Ptychozoon rhacophorus* to some members of the genus *Luperosaurus* (particularly *L. yasumai*, *L. sorok*, and *L. joloensis*; Taylor, 1922; Ota et al., 1996; Brown et al., 2000; Das et al., 2008), combined with the fact that it is much smaller and morphologically distinct from the other members of the genus *Ptychozoon* (Russell, 1972; Brown et al., 1997), suggests that it may be a “winged” *Luperosaurus* (Brown and Das, unpublished data).

In this study, we inferred the phylogenetic positions of each focal species using a multilocus phylogenetic estimate, and then

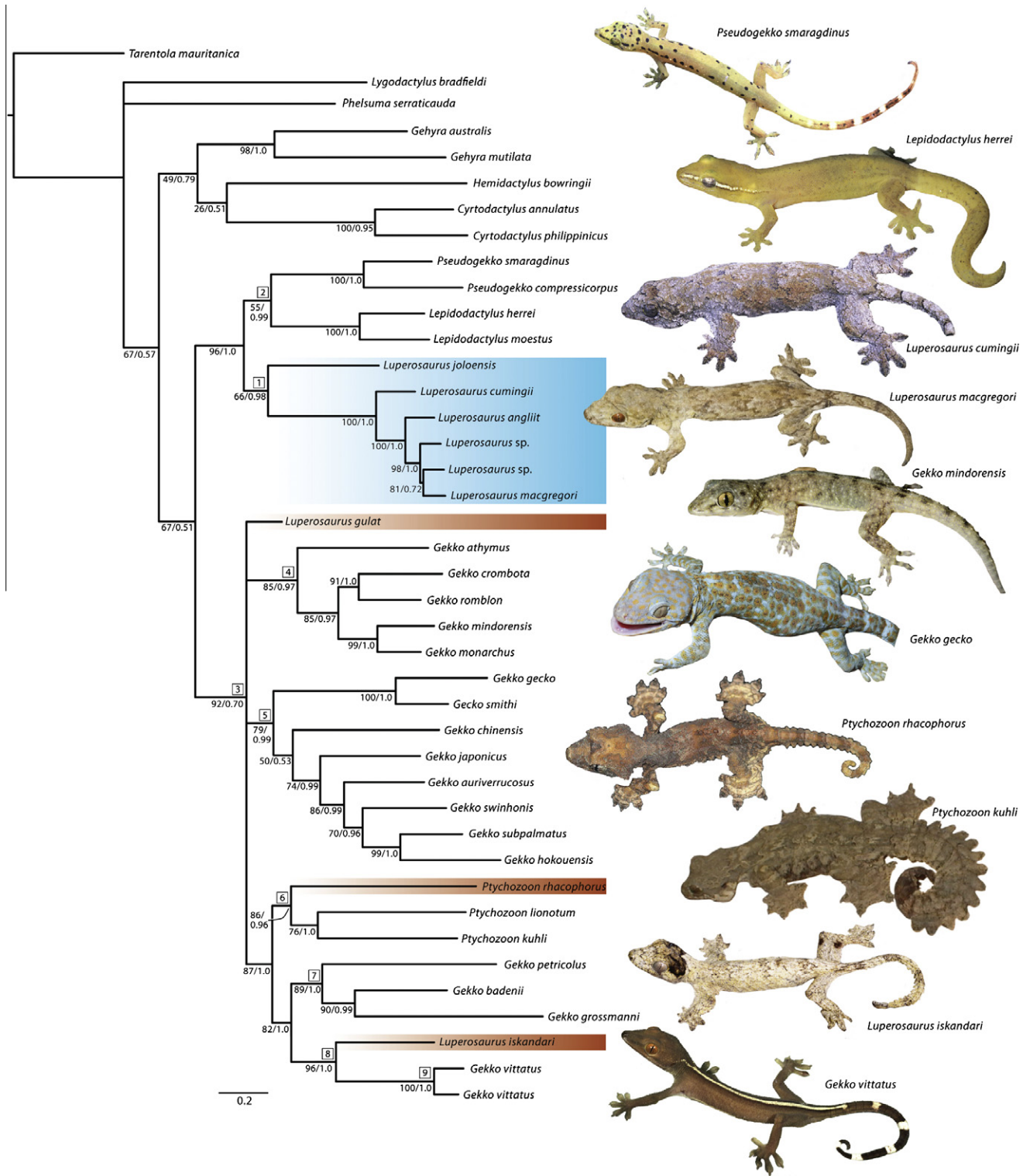


Fig. 1. Hypothesized relationships of gekkonid species included in this study, illustrated by the maximum clade credibility tree resulting from Bayesian analyses. Nodes supported by ≥ 0.95 Bayesian PP and $\geq 70\%$ MLBP were considered highly supported. Terminals are labeled with taxonomic names, with representative photographs showing the diversity of morphologies across the phylogeny. Numerical labels correspond to clades referred to in the Results and Discussion.

used Bayesian topology tests to evaluate alternate phylogenetic relationships to the genus *Luperosaurus*. We also used this approach to test the monophyly of *Gekko*, *Luperosaurus*, and *Ptychozoon*. In order to statistically evaluate the probability of each

experimentally constrained topology, we estimated the probability of each hypothesis within a Bayesian framework using proportion of 16,004 post burn-in trees consistent with each topology as an estimate of the posterior probability of that hypothesis.

Table 1
Models of evolution selected by AIC and applied for partitioned, model-based phylogenetic analyses.

Partition	AIC model	Number of characters
NADH 2, 1st codon position	HKY + I + Γ	346
NADH 2, 2nd codon position	HKY + Γ	346
NADH 2, 3rd codon position	GTR + Γ	346
All tRNAs (Trp, Ala, Asn)	HKY + Γ	223
Phosducin, 1st codon position	HKY + I	137
Phosducin, 2nd codon position	HKY + I	136
Phosducin, 3rd codon position	GTR + I	136

3. Results

3.1. Taxon sampling, data collection, and sequence alignment

The complete, aligned matrix contains eight samples of *Luperosaurus*, representing six of the 13 currently recognized species. Thirty-five additional samples are included from the families Gekkonidae and Phyllodactylidae, including representative taxa of the following genera: *Cyrtodactylus*, *Gehyra*, *Gekko*, *Hemidactylus*, *Lepidodactylus*, *Lygodactylus*, *Phelsuma*, *Pseudogekko*, *Ptychozoon*, and *Tarentola*. Following initial unrooted analyses, and gekkonid phylogenetic analyses (Gamble et al., 2011) we rooted the tree using the representative sample of *Tarentola mauritanica* (Phyllodactylidae). Variable and parsimony-informative characters are: 950 and 844 of 1247 (ND2); 78 and 48 of 418 (PDC).

3.2. Phylogenetic analyses

Analyses of the combined data result in topologies with high ML bootstrap support and posterior probabilities among species within major clades in the inferred phylogeny. Although analyses resulted in poor to moderate support for many higher-level relationships, general topological patterns are congruent across these analyses.

As mentioned, we found no strongly supported topological incongruence between preliminary single gene tree analyses. Additionally, the major phylogenetic findings discussed below (i.e., the position of *P. rhacophorus*, occurrence of *P. iskandari* as part of well supported clade with *P. vittatus* and three other species of *Gekko*) was observed in separate analyses of mitochondrial and nuclear DNA sequences.

In combined analyses, the focal taxa from the genus *Luperosaurus* were not supported to be monophyletic (Fig. 1). In fact, only four of the six recognized species, and two possible undescribed species of *Luperosaurus*, were supported as a monophyletic group (Fig. 1, Clade 1). All species of *Luperosaurus* recovered in this clade are endemic to the Philippines, and are sister to a clade consisting of species of *Lepidodactylus* and *Pseudogekko* (Fig. 1, Clade 2). Both *Luperosaurus gulat* and *L. iskandari* are recovered as part of a four-clade polytomy, to the exclusion of all other sampled *Luperosaurus* (Fig. 1, Clade 3). In ML analyses, *Luperosaurus gulat* is part of a clade

of Philippine geckos in the genus *Gekko* (Fig. 1, Clade 4; results not shown), albeit with weak support. All analyses result in strong support for the sister relationship between the Southwest Pacific species pair, *Luperosaurus iskandari* and *Gekko vittatus* (Fig. 1, Clade 8). This pair of species is included in a strongly supported clade also containing samples of *G. petricolus*, *G. badenii*, and *G. grossmanni* (all from Indochina). (Fig. 1).

The genus *Ptychozoon* is recovered as monophyletic (Fig. 1, Clade 6), with *P. rhacophorus* strongly supported as sister to *P. lionotum* + *P. kuhli*. No analyses support the monophyly of *Gekko*, with species in four major clades (Fig. 1, Clades 4, 5, 7, 9). Our results clearly suggest that *Ptychozoon*, and some species of *Luperosaurus* are nested within *Gekko* (Fig. 1, Clade 3).

3.3. The non-monophyly of *Luperosaurus*

Among the taxonomy-based hypotheses we set out to evaluate, our Bayesian approach provided no support (posterior probability approaching 0) for the monophyly of the genus *Luperosaurus* or the genus *Gekko*, as currently understood (Fig. 1). Furthermore, analyses did not support the species *L. gulat*, *L. iskandari*, or *Ptychozoon rhacophorus* to be members of *Luperosaurus* (Table 2). Contrary to our expectations, the genus *Ptychozoon* was supported to be monophyletic (Table 2), including the *Luperosaurus*-like taxon, *P. rhacophorus*.

4. Discussion

4.1. Phylogeny and evaluation of alternate taxonomic hypotheses

Phylogenetic analysis of our multilocus dataset demonstrates that true *Luperosaurus* (the clade containing the type species *L. cumingii* Gray 1845) is more closely related to *Lepidodactylus* and *Pseudogekko* than it is to the genus *Gekko* (Fig. 1). However, at least two species currently assigned to *Luperosaurus* (*L. gulat* and *L. iskandari*) appear to be members of a large, partially-resolved clade, otherwise consisting of species of the genera *Gekko* and *Ptychozoon* (Fig. 1).

Our findings of well-supported relationships between *Luperosaurus iskandari* and *Gekko vittatus*, and the strongly supported relationship between *Ptychozoon rhacophorus* and *P. kuhli* + *P. lionotum*, are quite surprising. The striking phenotypic differences between *L. iskandari* and *G. vittatus* (i.e., extensive cutaneous expansions bordering the limbs and tail of *L. iskandari*; absence of interdigital webbing in *G. vittatus*; Fig. 1) body and has led no previous gekkonid systematists to suggest a close relationship between these two lineages. *Ptychozoon rhacophorus* is not only morphologically dissimilar from the remaining species of *Ptychozoon* (e.g., small body size, absence of a terminal tail flap, absence of imbricate support scales on the dorsal surface of the parachute; Russell, 1972; Brown et al., 1997), and recent discoveries of *Luperosaurus* from the same island (Borneo) have revealed several strikingly similar species (e.g., small body size, pronounced

Table 2
Description of topology tests conducted using Bayesian methods.

Hypothesis	Description of constraint	Posterior probability	
<i>Taxonomy-based hypotheses</i>			
H ₁	Monophyly of genus <i>Gekko</i>	All samples of <i>Gekko</i>	0.0
H ₂	Monophyly of genus <i>Luperosaurus</i>	All samples of <i>Luperosaurus</i>	0.0
H ₃	Monophyly of genus <i>Ptychozoon</i>	All samples of <i>Ptychozoon</i>	0.96
H ₄	Generic affinity of <i>Luperosaurus gulat</i>	<i>L. angliit</i> , <i>L. cumingii</i> , <i>L. gulat</i> , <i>L. joloensis</i> , <i>L. macgregori</i> , and <i>L. sp.</i>	0.0
H ₅	Generic affinity of <i>Luperosaurus iskandari</i>	<i>L. angliit</i> , <i>L. cumingii</i> , <i>L. iskandari</i> , <i>L. joloensis</i> , <i>L. macgregori</i> , and <i>L. sp.</i>	0.0
H ₅	Generic affinity of <i>Ptychozoon rhacophorus</i>	<i>L. angliit</i> , <i>L. cumingii</i> , <i>L. joloensis</i> , <i>L. macgregori</i> , <i>L. sp. nov.</i> , and <i>P. rhacophorus</i>	0.0

ornamental tuberculation, denticulate tail lobes present; *L. yasumai* and *L. sorok*; Ota et al., 1996; Das et al., 2008). Although these discoveries suggest a close relationship between *P. rhacophorus* and some *Luperosaurus* taxa, our results clearly support *P. rhacophorus* as sister to the remaining species of *Ptychozoon* (Fig. 1).

Given the rarity of *Luperosaurus* species and the low probability of obtaining genetic sampling for all members of the genus, we feel justified in providing some speculative discussion of possible phylogenetic affinities of lineages unsampled by us. In a phylogenetic analysis of morphological data Brown et al. (2000) found that the robust bodied species of the Philippines and Borneo (*L. macgregori*, *L. palawanensis*, *L. cumingii*, *L. joloensis*, and *L. yasumai*) formed a clade, sister to a monophyletic group containing the slender bodied forms of Malaysia, Indonesia, and Sulawesi (*L. iskandari*, *L. brooksi*, and *L. browni*). Thus we find it likely that the unsampled species *L. palawanensis*, *L. corfieldi* (Gaulke et al., 2007) and *L. kubli* (Brown et al., 2007) may be related to the clade we identify here as true *Luperosaurus* (the clade containing the generotype *L. cumingii*; Clade 1, Fig. 1) and that *L. brooksi* and *L. browni* may turn out to be more closely related to the *L. iskandari*–*G. vittatus* (Clade 8, Fig. 1).

Despite our expectations based on phenotypic similarities and a past phylogenetic analysis of morphological character data (Brown et al., 2000), our Bayesian evaluation of alternate topologies strongly reject the hypotheses that *L. gulat*, *L. iskandari*, and *P. rhacophorus* are true *Luperosaurus* (Fig. 1; Table 2). Similarly, we found no support for the monophyly of *Gekko* and *Luperosaurus*. The lack of resolution within the large clade corresponding to *Gekko* (Clade 3; Fig. 1) prevents us, at present, from undertaking taxonomic reorganization of this group.

4.2. Generic boundaries and taxonomy of Southeast Asian geckos

Additional studies, with greater taxon and gene sampling, will be necessary to resolve the classification of this diverse group. With that said, it is clear that the genus *Gekko* is paraphyletic with respect to *Ptychozoon* and some species of *Luperosaurus*, and that future taxonomic arrangements will need to consider two alternatives to resolve the classification of this clade. The first of these could involve subdividing the genus *Gekko* and elevating older names currently in the synonymy of this widely distributed, pan-Asian group, and if no names are in existence, establishing new generic names. This option might lead to the retention of *Ptychozoon* as a valid genus. Alternatively, the genus *Ptychozoon* could be sunk into the genus *Gekko*. If the second alternative is taken (submerging all these taxa into *Gekko*), *L. gulat*, *L. iskandari*, and all species currently assigned to the genus *Ptychozoon* will be transferred to the genus *Gekko*.

4.3. Conservation significance of phylogenetic studies of Asian land vertebrates

An understanding of the phylogenetic relationships of biodiverse clades is key to understanding their evolutionary history as it relates to patterns of endemism and concentration of biodiversity across the geographical template (Rosenzweig, 1995; Wiens and Donoghue, 2004). Without some kind of historical context, inferring patterns of the concentration of Southeast Asia's biodiversity will amount solely to enumeration of numbers of species in space. There can be no doubt of the value of this approach for identifying geographical concentration of species diversity for conservation planning (Brooks et al., 2002). However, this method tells us nothing of the processes that have produced and maintained biodiversity, with all species treated as equivalent entities for priority setting exercises. An alternative might be to emphasize phylogenetic distribution of taxa, and prioritize the use of conser-

vation resources for equitably conserving divergent evolutionary lineages.

With respect to our analysis, it is clear that a common, most likely pleisiomorphic morphology has led taxonomists to refer to the majority of taxa in Clade 3 as members of the genus *Gekko*, but that some morphologically divergent lineages nested within this clade have been recognized as members of the genera *Luperosaurus* and *Ptychozoon*. These taxa are among the most poorly known and seldom encountered gekkonid lizards in Southeast Asia, and their apparent rarity has encouraged speculation and debate over their preferred microhabitats (Brown and Diesmos, 2000; Brown et al., 2000, 2007, 2010; Ota et al., 1996; Das et al., 2008). With many species of gekkonids continually being discovered and described in Southeast Asia, it is clear that molecular phylogenies will continue to play an important role in species delimitation, clarification of higher taxonomic boundaries, and provision of an enhanced understanding of evolutionary processes of differentiation in this diverse assemblage of land vertebrates (Rösler et al., 2011; Gamble et al., 2008, 2011; Siler et al., 2012).

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Appendix A

Summary of specimens corresponding to genetic samples included in the study. ACD = Arvin Diesmos field series, specimen deposited at the National Museum of the Philippines; AMB = Aaron M. Bauer field series; AMS = Australian Museum, Sydney, Australia; CAS = California Academy of Sciences Herpetological Collections; DSM = David McLeod field series, specimen deposited in the University of Kansas Natural History Museum; HOFH = Hidetoshi Ota genetic samples deposited in the Museum of Nature and Human Activities, University of Hyogo, Japan; JAM = Jim McGuire field series, specimen deposited in the Museum Zoologicum Bogoriense (National Museum of Indonesia, Cibinong, Java); JB = Jon Boone captive collection; JFBM = James Ford Bell Museum of Natural History; KU = University of Kansas Natural History Museum; LSUHC = La Sierra University Herpetological Collections; MZB = Museum Zoologicum Bogoriense (National Museum of Indonesia, Cibinong, Java); NNU Z = Nanjing Normal University; P = Pui Yong Min field series, deposited at UNIMAS; RMB = Rafe Brown field number, uncataloged specimen deposited at the National Museum of the Philippines; TG = Tony Gamble field series; TNHC = Texas Natural History Collections, University of Texas at Austin; USNM = United States National Museum; * = No voucher/locality information provided by source publication.

Species	Voucher	Locality	Genbank accession numbers	
			ND2	PDC
<i>Cyrtodactylus annulatus</i>	KU 314944	Barangay Kaimpugan, Municipality of San Francisco, Agusan del Sur Province, Mindanao Island, Philippines	GU366088	–
<i>Cyrtodactylus philippinicus</i>	KU 304784	Barangay Babuyan Claro, Municipality of Calayan, Cagayan Province, Babuyan Claro Island, Philippines	GU550900	–
<i>Gehyra australis</i>	AMS 139934	El Questro Station, Jackeroos Waterhole, Western Australia, Australia	JN019081	JN019113
<i>Gehyra mutilata</i>	AMB 7515	Nimalawa, Sri Lanka	JN019082	JN019114
<i>Gekko athymus</i>	KU 309335	Barangay Mainit, Municipality of Brooke's Point, Palawan Province, Palawan Island, Philippines	JQ173403	JQ173559
<i>Gekko auriverrucosus</i>	NNU Z 20050716.004	China, Shanxi, Yuncheng	JN019062	JN019096
<i>Gekko badenii</i>	JB 13	Captive	JN019065	JN019099
<i>Gekko chinensis</i>	LSUHC 4210	China, Hainan Island, Wuzhi Shan	JQ173409	JQ173547
<i>Gekko crombota</i>	KU 304825	Barangay Babuyan Claro, Municipality of Calayan, Cagayan Province, Babuyan Claro Island, Philippines	JQ173410	JQ173549
<i>Gekko gekko</i>	LSUHC 7364	Cambodia, Kampong Speu Province, 1.5 km E. of Aural Village	JQ173416	–
<i>Gekko grossmanni</i>	JFBM 9	Captive	JN019064	JN019098
<i>Gekko hokouensis</i>	HOFH 89053103	Republic of China, Orchid Island, Lanyu Township	JQ173422	JQ173556
<i>Gekko japonicus</i>	HOFH 10061402	Ryukyu Islands	JQ173424	JQ173558
<i>Gekko mindorensis</i>	KU 302668	Barangay Formon, Municipality of Bongabong, Oriental Mindoro Province, Mindoro Island, Philippines	JN710490	JN710501
<i>Gekko monarchus</i>	ACD 1278	Philippines, Palawan Island, Palawan Province, Municipality of Brooke's Point, Mt. Mantalingajan	JQ173501	JQ173594
<i>Gekko petricolis</i>	JB 70	Captive	JN019066	JN019100
<i>Gekko romblon</i>	KU 315348	Barangay Balogo, Municipality of Calatrava, Romblon Province, Tablas Island, Philippines	JN710497	JN710506
<i>Gekko smithii</i>	LSUHC 6095	West Malaysia, Pahang, Pekan	JQ173534	JQ173616
<i>Gekko subpalmaris</i>	AMB 5567	Chengdu, Szechuan, China	JN019063	JN019097
<i>Gekko swinhonis</i>	NNU Z 20050902.001	China, Henan, Boai	JN019061	JN019095
<i>Gekko vittatus</i>	JAM 2171	Pet trade, reportedly from eastern Indonesia	JQ437899	JQ437942
<i>Gekko vittatus</i>	USNM 533255	Solomon Islands, Temotu, Santa Cruz Island, Luesalo	JN019073	JN019106
<i>Hemidactylus bowringii</i>	CAS 206649	Myanmar: Sagaing Division: Alaungdaw Kathapa National Park	EU268373	–
<i>Lepidodactylus herrei</i>	RMB 4330	Philippines, Leyte Island, Leyte Province, Municipality of Baybay	JQ173539	–
<i>Lepidodactylus moestus</i>	USNM 521730	Ngerur Island, Palau	JN019079	JN019111
<i>Luperosaurus angliit</i>	KU 322189	Barangay Zabali, Municipality of Baler, Aurora Province, Luzon Island, Philippines	JQ437903	JQ439744
<i>Luperosaurus cumingii</i>	TNHC 61910	Philippines, Luzon Island, Albay Province, Municipality of Tiwi, Mt. Malinao	JQ437902	–
<i>Luperosaurus gulat</i>	KU 320541	Barangay Ransang, Municipality of Rizal, Palawan Province, Palawan Island, Philippines	–	JQ437947
<i>Luperosaurus iskandari</i>	MZB 2114	Indonesia, Sulawesi Is., Central Sulawesi Province, Kabupaten Banggai, Kecamatan Pagimana, Desa Siuna, Mt. Tompotika	JQ437906	JQ437948
<i>Luperosaurus joloensis</i>	KU 314947	Barangay Pasanonca, Zamboanga City, Mindanao Island, Philippines	JQ437900	See Dryad Submission
<i>Luperosaurus sp.</i>	KU 304797	Barangay Babuyan Claro, Municipality of Calayan, Cagayan Province, Babuyan Claro Island, Philippines	JQ437904	JQ437945
<i>Luperosaurus macgregori</i>	ACD 6021	Philippines, Calayan Island, Cagayan Province, Municipality of Calayan	JQ437905	JQ437946
<i>Luperosaurus sp.</i>	KU 314021	Barangay San Antonio, Municipality of Basco, Batanes Province, Batanes Island, Philippines	JQ437901	JQ437945
<i>Lygodactylus bradfieldi</i>	AMB 7628	63.5 km W Kamanjab, Kunene Region, Namibia	EU423279	–
<i>Phelsuma serraticauda</i>	*	*	EU423296	–
<i>Pseudogekko compressicorpus</i>	KU 324426	Barangay Danicop, Municipality of Sierra Bullones, Bohol Province, Bohol Island, Philippines	JQ437898	JQ437941
<i>Pseudogekko smaragdinus</i>	KU 302819	Barangay Pinaglubayan, Municipality of Polillo, Quezon Province, Polillo Island, Philippines	JQ437897	JQ437940
<i>Ptychozoon kuhli</i>	LSUHC 4679	West Malaysia, Pahang, Pulau Tioman, Tekek-Juara Trail	JQ437918	JQ437960
<i>Ptychozoon lionotum</i>	DSM 798	Thailand, Khao Luang National Park, Nakhon Si Thammarat	JQ437914	JQ437956
<i>Ptychozoon rhacophorus</i>	P 0501	East Malaysia, Sarawak, Gunung Penrissen	JQ437913	JQ437955
<i>Tarentola mauritanica</i>	TG 00129	Egypt	EU443255	–

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