Molecular systematics of the Philippine forest skinks (Squamata: Scincidae: *Sphenomorphus*): testing morphological hypotheses of interspecific relationships

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Skinks of the genus *Sphenomorphus* are the most diverse clade of squamates in the Philippine Archipelago. Morphological examination of these species has defined six phenotypic groups that are commonly used in characterizations of taxonomic hypotheses. We used a molecular phylogeny based on four mitochondrial and two nuclear genes to assess the group's biogeographical history in the archipelago and examine the phylogenetic validity of the currently recognized Philippine species groups. We re-examined traditional characters used to define species groups and used multivariate statistics to quantitatively evaluate group structure in morphometric space. Clustering analyses of phenotypic similarity indicate that some (but not all) members of previously defined species groups are phenotypically most similar to other members of the same group. However, when species group membership was mapped on our partitioned Bayesian phylogenetic hypothesis, only one species group corresponds to a clade; all other species group arrangements are strongly rejected by our phylogeny. Our results demonstrate that (1) previously recognized species group relationships were misled by phenotypic convergence; (2) *Sphenomorphus* is widely paraphyletic; and (3) multiple lineages have independently invaded the Philippines. Based on this new perspective on the phylogenetic relationships of Philippine *Sphenomorphus*, we revise the archipelago's diverse assemblage of species at the generic level, and resurrect and/or expand four previously recognized genera, and describe two new genera to accommodate the diversity of Philippine skinks of the *Sphenomorphus* group.

INTRODUCTION

The majority of lizard species in the family Scincidae are found in the subfamily Lygosominae, which is divided into three groups (Greer, 1979). The *Sphenomorphus* group is one of the largest assemblages of squamates on earth, including approximately 30 genera and 500 species defined by the shared presence of several morphological synapomorphies (Greer,

1979). Of these, *Sphenomorphus* Fitzinger is the most species-rich genus (145 species) but the definition of this taxon remains enigmatic because of the lack of clear synapomorphies. Greer & Shea (2003) stated that '*Sphenomorphus* is undiagnosable and is almost certainly not monophyletic' and Myers & Donnelly (1991) referred to *Sphenomorphus* as 'a plesiomorphic taxon not at present definable by derived characters'. Originally named by Fitzinger (1843), *Sphenomorphus* was not recognized by Boulenger (1887) in his catalogue of lizards, but was later designated as a

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section of *Lygosoma* by Smith (1937). Mittleman (1952) redefined *Sphenomorphus* as a genus based on the presence of large prefrontals, paired frontoparietals, enlarged precloacals, exposed auricular openings, and large limbs. Mittleman's definition of the taxon is only slightly improved from Boulenger's (1887) definition of *Lygosoma*, and only includes plesiomorphic characters. Since that time, the genus has been gradually partitioned, as new taxa defined by novel, apomorphic characters have been described (*Ctenotus* Storr, 1969; *Eremiascincus* Greer, 1979; *Lankascincus* Greer, 1991; *Leptoseps* Greer, 1997; *Oligosoma* Girard, 1857; *Parvoscincus* Ferner, Brown & Greer, 1997; *Sigaloseps* Sadlier, 1987). However, other genera (*Otosaurus, Insulasaurus, Ictiscincus, Parotosaurus*) have been combined with *Sphenomorphus* (Loveridge, 1948; Mittleman, 1952; Greer & Parker, 1967). Although the composition of the genus has changed through time, species diversity remains high because of the lack of diagnostic characters, which has resulted in many new species being artificially assigned to *Sphenomorphus*. Currently, *Sphenomorphus* occur in South-East Asia, Asia, Indochina, and Central America.

Two series of taxonomic revisions of Philippine *Sphenomorphus* provided an initial insight into the diversity of this assemblage. Taylor (1922a, b, c, 1923, 1925) recognized 19 species of Philippine forest skinks in the genera *Otosaurus, Insulasaurus*, and *Sphenomorphus*. In their review of Philippine scincids, Brown & Alcala (1980) followed Greer & Parker (1967) in placing *Otosaurus* and *Insulasaurus* in synonymy with *Sphenomorphus*. In addition, they synonymized several species recognized by Taylor and described four new species (reviewed by Brown *et al.*, 2010). Six additional species were described (Brown, 1995; Brown *et al.*, 1999, 2010; Linkem, Diesmos & Brown, 2010a), and one species was moved to the genus *Parvoscincus* (Ferner *et al.*, 1997). Twenty-eight endemic species are recognized as a result of these revisions and descriptions, making *Sphenomorphus* the most diverse squamate genus in the Philippines (Brown *et al.*, 2010).

TAXONOMY AND BIOGEOGRAPHY OF PHILIPPINE *SPHENOMORPHUS*

Species diversity in the Philippines is intrinsically linked to the geological history of the region (Heaney, 1985; Brown & Diesmos, 2001 (2002), 2009). The Philippine archipelago formed during the last 15 Myr as continental plate movement and volcanism caused the emergence of multiple large oceanic islands (Hall, 1998). During low sea-level stands of the Pleistocene, islands separated by shallow channels were connected by land allowing for faunal and floral range expansion through dispersion and dispersal (Fig. 1;

Brown & Guttman, 2002; Roberts, 2006a, b). These connected islands are often referred to as Pleistocene aggregate island complexes (PAICs). Species are commonly endemic to a single PAIC, although some species span multiple PAICs. *Sphenomorphus atrigularis, Sphenomorphus beyeri, Sphenomorphus boyingi, Sphenomorphus diwata, Sphenomorphus hadros, Sphenomorphus igorotorum, Sphenomorphus kitangladensis, Sphenomorphus laterimaculatus, Sphenomorphus lawtoni, Sphenomorphus leucospilos, Sphenomorphus luzonensis, Sphenomorphus tagapayo, Sphenomorphus traanorum, Sphenomorphus wrighti*, and *Sphenomorphus victoria* only occur on one island. *Sphenomorphus acutus, Sphenomorphus arborens, Sphenomorphus bipartalis, Sphenomorphus fasciatus, Sphenomorphus llanosi, Sphenomorphus mindanensis*, and *Sphenomorphus variegatus* are endemic to a single PAIC and can be found on multiple islands within that PAIC. *Sphenomorphus abdictus, Sphenomorphus coxi, Sphenomorphus cumingi, Sphenomorphus decipiens, Sphenomorphus jagori*, and *Sphenomorphus steerei* have widespread distributions occurring on more than one PAIC.

In addition to the 28 endemic species, three species are partitioned into two subspecies: *Sphenomorphus abdictus abdictus, Sphenomorphus abdictus aquilonius, Sphenomorphus coxi coxi, Sphenomorphus coxi divergens, Sphenomorphus jagori grandis* and *Sphenomorphus jagori jagori*. These 31 taxonomic units are organized into six groups in the foundational work of Brown & Alcala (1980); although not created in a phylogenetic framework, these groups have served as convenient phenotypic categories for diagnoses of new species (e.g. Brown, Ferner & Greer, 1995; Ferner *et al.*, 1997; Brown *et al.*, 1999, 2010; Linkem, Diesmos & Brown, 2010a) and as the basis for hypotheses of evolutionary relationships (Linkem *et al.*, 2010b). Each group is diagnosed by a combination of morphological features. Some Philippine groups are similar to *Sphenomorphus* species groups that occur outside of the Philippines (Greer & Parker, 1967). The species in each of the Brown & Alcala (1980) groups are summarized below.

Group 1 *Sphenomorphus* are distinguished by moderate body size, high numbers of paravertebral scales (> 88), and a preference for high elevation, montane habitats (Table 1). Brown & Alcala (1980) placed two species in Group 1, *Sphenomorphus beyeri* and *Sphenomorphus diwata*, but a recent taxonomic revision (Brown *et al.*, 2010) identified three additional species in this group – *Sphenomorphus boyingi, Sphenomorphus hadros*, and *Sphenomorphus igorotorum*. Most species in Group 1 are Luzon endemics, the only exception being *Sphenomorphus diwata*, which is restricted to eastern Mindanao (Fig. 1).
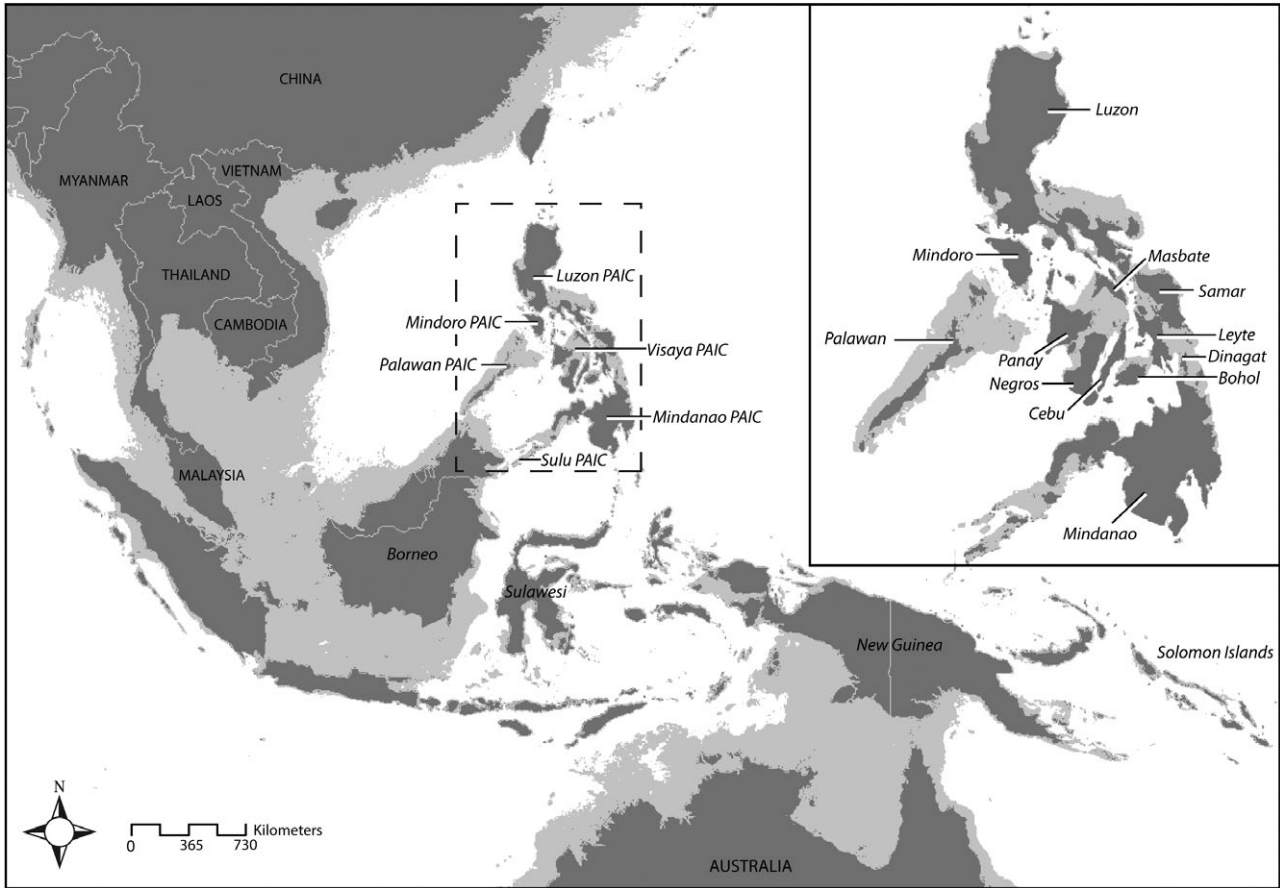
Figure 1. A map of the Philippine Islands with the major landmasses labelled. The light grey areas depict the 120 m bathymetric contour that joined some neighbouring islands into Pleistocene aggregate island complexes (PAICs).

Table 1. Taxonomic groups based on Brown & Alcala (1980) and the characters used to diagnose them

Species group	Species included	Character support for group
Group 1	*Sphenomorphus beyeri*, *Sphenomorphus boyingi*, *Sphenomorphus diwata*, *Sphenomorphus hadros*, *Sphenomorphus igorotorum*	Moderate size, > 88 paravertebral scales
Group 2	*Sphenomorphus atrigularis*, *Sphenomorphus biparietalis*, *Sphenomorphus lawtoni*, *Sphenomorphus luzonensis*, *Sphenomorphus steerei*, *Sphenomorphus tagapayo*, *P. palawanensis*, *P. sisoni*	Small size, with small digits
Group 3	*Sphenomorphus acutus*, *Sphenomorphus laterimaculatus*, *Sphenomorphus leucospilos*, *Sphenomorphus kitangladensis*, *Sphenomorphus mindanensis*, *Sphenomorphus victoria*	Midbody scales 30–40, toe IV lamellae 15–20
Group 4	*Sphenomorphus arborens*, *Sphenomorphus cumingi*, *Sphenomorphus decipiens*, *Sphenomorphus traanorum*, *Sphenomorphus variegatus*, *Sphenomorphus wrighti*	Midbody scales 36–54, toe IV lamellae 20–28
Group 5	*Sphenomorphus abdictus abdictus*, *Sphenomorphus abdictus aquilonius*, *Sphenomorphus coxi coxi*, *Sphenomorphus coxi divergens*, *Sphenomorphus jagori grandis*, *Sphenomorphus jagori jagori*, *Sphenomorphus llanosi*	Large size, midbody scales 32–44, toe IV lamellae > 20
Group 6	*Sphenomorphus fasciatus*	Limbs do not overlap, midbody scales < 36

Group 2 comprises small species with small digits (Table 1). Brown & Alcala (1980) described Group 2 as 'a somewhat artificial assemblage', but specified that *Sphenomorphus atrigularis*, *Sphenomorphus lawtoni*, and *Sphenomorphus steerei* were closely related, and that *Sphenomorphus biparietalis* was most similar to *Sphenomorphus hallieri* from Borneo. The authors also included *Sphenomorphus luzonensis* and *Sphenomorphus palawanensis* in Group 2. The discovery of *Parvoscincus sisoni* led to the transfer of *Sphenomorphus palawanensis* to the genus *Parvoscincus* (Ferner *et al*., 1997). As the two species of *Parvoscincus* resemble Group 2 species morphologically, we conditionally consider them as members of this group for the purpose of this review of phenotypic variation. The most recent species added to Group 2 was *Sphenomorphus tagapayo* (Brown *et al*., 1999); giving a total of eight species in Group 2. Most species in this group have limited distributions, with *Sphenomorphus lawtoni*, *Sphenomorphus luzonensis*, and *Sphenomorphus tagapayo* occurring only in limited regions of Luzon Island; *Sphenomorphus atrigularis* in western Mindanao; *Sphenomorphus biparietalis* in the Sulu Archipelago; *Parvoscincus palawanensis* on Palawan Island; and *Parvoscincus sisoni* on Panay Island. *Sphenomorphus steerei* ranges throughout the archipelago.

Group 3 consists of small-to-intermediate-sized, slender-bodied species with midbody scale rows 30–40, and lamellae beneath toe IV 15–20 (Table 1). Group 3 was considered most similar to Bornean *Sphenomorphus murudensis* and *Sphenomorphus kinabaluensis*, which are part of the Greer & Parker (1967) *Sphenomorphus variegatus* group. Brown & Alcala (1980) partitioned Philippine species of Greer & Parker's (1967) *Sphenomorphus variegatus* group into Groups 3 and 4 (see below) based on the ratio of midbody scale rows to lamellae beneath toe IV, which were on average fewer in Group 3 species than Group 4 species. Brown & Alcala (1980) placed the following species in Group 3: *Sphenomorphus leucospilos, Sphenomorphus mindanensis*, *Sphenomorphus victoria*, *Sphenomorphus laterimaculatus*, and *Sphenomorphus acutus*. *Sphenomorphus acutus* does not fit into any of Brown & Alcala's (1980) groups, but resembles Groups 3 and 4, and was placed in Group 3 by Brown & Alcala (1980). The Group 3 species occur in disparate parts of the archipelago, with *Sphenomorphus laterimaculatus* and *Sphenomorphus leucospilos* occurring on Luzon Island, *Sphenomorphus victoria* on Palawan Island, and *Sphenomorphus mindanensis* and *Sphenomorphus acutus* broadly distributed on Mindanao, Samar, and Leyte. Since Brown & Alcala's (1980) review, Brown (1995) described another Group 3 species, *Sphenomorphus kitangladensis*, from eastern Mindanao (Brown, 1995).

Brown & Alcala's (1980) Group 4 contains most Philippine members of Greer & Parker's (1967) *Sphenomorphus variegatus* group, defined by midbody scale rows 36–54 and lamellae beneath toe IV 20–28 (Table 1). This group includes the following species: *Sphenomorphus arborens*, *Sphenomorphus cumingi*, *Sphenomorphus decipiens*, *Sphenomorphus variegatus*, and *Sphenomorphus wrighti*. A new species was recently described in Group 4 – *Sphenomorphus traanorum* (Linkem, Diesmos & Brown, 2010a). Two Group 4 species are widespread in the archipelago, *Sphenomorphus cumingi* and *Sphenomorphus decipiens*. The others have more limited distributions, with *Sphenomorphus wrighti* and *Sphenomorphus traanorum* occurring on Palawan Island, *Sphenomorphus arborens* on Negros, Panay, and Masbate, and *Sphenomorphus variegatus* on Mindanao, Samar, Leyte, and Bohol.

Brown & Alcala's (1980) Group 5 was the only group that the authors considered a natural assemblage. It includes large [snout–vent length (SVL) > 53 mm] species with midbody scale rows 32–44, and > 20 toe IV subdigital lamellae (Table 1). Brown & Alcala (1980) placed *Sphenomorphus abdictus abdictus*, *Sphenomorphus abdictus aquilonius*, *Sphenomorphus jagori grandis*, *Sphenomorphus jagori jagori*, *Sphenomorphus coxi coxi*, *Sphenomorphus coxi divergens*, and *Sphenomorphus llanosi* in this group. Linkem *et al*. (2010b) corroborated the monophyly of Group 5, but demonstrated that many of the species and subspecies within the group do not correspond to the clades identified in phylogenetic analysis of mitochondrial DNA sequence data, thereby suggesting the need for a comprehensive review.

Brown & Alcala's (1980) Group 6 was considered a member of Greer & Parker's (1967) *Sphenomorphus fasciatus* group and contains only one species, *Sphenomorphus fasciatus*, found on Mindanao, Bohol, Camiguin Sur, Dinagat, Samar, and Leyte Islands.

Here we test whether Brown & Alcala's cohesive and largely unchallenged phenotypic groupings represent natural assemblages (see also Brown *et al*., 1995, 2010). First, we assess whether there is statistically significant phylogenetic support for the morphological species classifications of Brown & Alcala (1980). We then determine whether these supraspecific assemblages are natural monophyletic groups or whether these apparently cohesive phenotypic clusters of taxa represent instances of morphological convergence. In the context of these broad goals, we address three specific questions. (1) Are the morphologically cohesive, phenotypically defined species groups of Brown & Alcala (1980) natural, monophyletic units or has convergent evolution obscured and confounded our understanding of evolutionary trends in Philippine *Sphenomorphus*? (2) Are Philippine *Sphenomorphus*

species derived from a single common ancestor, or is this diversity the product of multiple invasions from Asian and/or Papuan sources? (3) Is our current understanding of *Sphenomorphus* species diversity accurate (28 species), or is species diversity as grossly underestimated as suggested by recent studies (Brown *et al*., 2010; Linkem *et al*., 2010b)?

MATERIAL AND METHODS
TAXON SAMPLING

To adequately examine the relationships amongst Philippine *Sphenomorphus*, we included 131 samples of lygosomine skinks, representing 64 described species (Appendix). Sampling was predominantly from the *Sphenomorphus* group (53 species), with representatives from the *Eugongylus* (six species) and *Mabuya* groups (five species). We also incorporated representatives from the 'Scincinae' genus *Plestiodon* (*Plestiodon anthracinus*, *Plestiodon fasciatus*, and *Plestiodon quadrilineatus*), and from the families Xantusiidae (*Xantusia vigilis*) and Lacertidae (*Tachydromus sexilineatus*).

We included samples from the following *Sphenomorphus* group genera: *Lipinia*, *Papuascincus*, *Parvoscincus*, *Scincella*, *Glaphyromorphus*, *Eulamprus*, *Eremiascincus*, and *Hemiergis*. The latter four genera are part of the Australian clade of the *Sphenomorphus* group, which is an assemblage of 15 genera previously shown to be well supported (Reeder, 2003; Rabosky *et al*., 2007; Skinner, 2007). We did not include all of the previously published data for this Australian clade because previous studies have found it to have high support, although these analyses lacked adequate outgroup sampling. We ran preliminary analyses (not shown) of our sampling in combination with all the Australian clade genera and found that the Australian clade maintained high support. Thus, we excluded members of the Australian clade to reduce the computational burden associated with this large data set.

We collected 27 of the 28 currently recognized species of Philippine *Sphenomorphus* and included samples of the three subspecies for a total of 30 taxonomic units sampled from the archipelago. We could not sample the species *Sphenomorphus biparietalis* because it occurs in the Sulu Archipelago, a region inaccessible to researchers. Similarly, *Parvoscincus palawanensis* has not been observed by researchers since its original collection and no genetic samples are available. For two widespread species (*Sphenomorphus decipiens* and *Sphenomorphus steerei*), we incorporated samples from multiple populations to maximize geographical coverage across known biogeographical boundaries such as mountain ranges and marine channels (Brown & Diesmos, 2001 (2002), 2009). Sampling comprised each of the 11 clades of the *Sphenomorphus abdictus–Sphenomorphus coxi–Sphenomorphus jagori* complex of Linkem *et al*. (2010b). We included available non-Philippine *Sphenomorphus* from Borneo, Sulawesi, Indochina, China, the Solomon Islands, Central America, and Palau (Appendix). Sampling for *Sphenomorphus* and the *Sphenomorphus* group was far from inclusive, but was sufficient to address the questions that were the focus of this study.

MORPHOLOGICAL DATA AND ANALYSES

Brown & Alcala (1980) based their morphological groupings on a combination of (1) snout–vent length, (2) number of scales around the mid-body, (3) paravertebral scales, and (4) subdigital lamellae of the fourth toe of the right foot (Table 1). As we sought to determine whether Brown & Alcala's classification reflects natural phenotypic variation in the characters that vary amongst Philippine *Sphenomorphus*, we measured and counted the same characters on adults for all species of Philippine *Sphenomorphus* (see Brown *et al*., 2010 for a list of specimens examined). Scale counts, except mid-body scale rows, were taken on the right side of the body and the average value of each species was used for subsequent multivariate analyses (Table 2). Morphological data were analysed in the R statistical package and in JMP8 (SAS Institute Inc.). We used the unweighted pair group method with arithmetic mean (UPGMA: Sokal & Michner, 1958) to create a phenogram of the morphological characters. Principal components analysis (PCA) was conducted using a correlation matrix on the raw scale counts for midbody scale rows and subdigital lamellae and log-transformed paravertebral scale rows and snout–vent length. Log-transformation was needed for the last two variables to achieve a normal distribution. The use of a correlation matrix standardized the variables with a zero mean and unit standard deviation, which is important when variables are not all of the same scale.

GENE CHOICE AND DATA COLLECTION

Tissue samples were extracted using a guanidine thiocyanate protocol modified from the PureGene protocol (Esselstyn, Timm & Brown, 2009, based on a protocol developed by M. Fujita, pers. comm.). Each extraction was amplified for the genes of interest (Table 3) through standard PCR protocols (Palumbi, 1996). PCR products were purified with ExoSAPit (USB corp.) with a 20% dilution of stock ExoSAPit, incubated for 30 min at 37 °C and then 80 °C for 15 min. Cleaned PCR products were dye-labelled

Table 2. Morphological data used for principal components analysis and morphological clustering. Values are averages for each species. See Brown *et al*. (2010) for list of specimens examined

Species	SVL	PV	MBSR	SDL
Parvoscincus palawanensis	31.2	51.0	23.0	11.0
Parvoscincus sisoni	30.1	65.0	25.0	11.5
Sphenomorphus abdictus	86.2	68.5	39.0	23.0
Sphenomorphus abdictus aquionius	87.1	67.5	36.0	22.5
Sphenomorphus acutus	69.6	57.0	28.0	32.0
Sphenomorphus arborens	55.5	69.5	37.5	20.0
Sphenomorphus atrigularis	32.0	56.5	29.0	9.5
Sphenomorphus beyeri	65.4	95.0	40.0	19.5
Sphenomorphus biparietalis	33.7	64.5	32.0	10.0
Sphenomorphus boyingi	56.4	92.0	39.5	20.0
Sphenomorphus coxi coxi	75.0	67.0	35.0	22.5
Sphenomorphus coxi divergens	76.5	69.5	39.0	23.5
Sphenomorphus cumingi	135.8	82.5	51.0	24.5
Sphenomorphus decipiens	38.1	61.5	35.0	16.0
Sphenomorphus diwata	55.0	91.5	40.0	15.0
Sphenomorphus fasciatus	69.9	84.0	30.0	22.0
Sphenomorphus hadros	80.1	109.5	46.0	20.0
Sphenomorphus igorotorum	54.7	102.0	44.5	20.0
Sphenomorphus jagori grandis	90.2	74.0	41.0	25.0
Sphenomorphus jagori jagori	89.9	68.0	38.0	27.0
Sphenomorphus kitangladensis	53.5	74.5	36.0	16.0
Sphenomorphus laterimaculatus	49.6	78.5	36.0	17.5
Sphenomorphus lawtoni	40.1	61.0	28.5	13.5
Sphenomorphus leucospilos	53.5	65.5	31.0	17.0
Sphenomorphus llanosi	80.5	68.5	40.0	22.0
Sphenomorphus luzonensis	43.9	69.0	28.0	10.5
Sphenomorphus mindanensis	49.0	72.0	31.0	18.5
Sphenomorphus steerei	31.2	58.0	30.0	11.5
Sphenomorphus tagapayo	27.6	57.5	29.0	10.0
Sphenomorphus traanorum	50.6	65.5	31.0	16.0
Sphenomorphus variegatus	56.3	71.0	41.0	22.0
Sphenomorphus victoria	46.1	65.0	31.0	19.0
Sphenomorphus wrighti	59.0	74.5	39.0	23.5

MBSR, Midbody scale rows; PV, Paravertebrals; SDL, Subdigital lamellae; SVL, snout–vent length.

using Big-Dye terminator 3.1 (Applied Biosystems), purified using Sephadex (NC9406038, Amersham Biosciences, Piscataway, NJ), and sequenced on an ABI 3730 automated capillary sequencer. Raw sequence data were processed using SEQUENCING ANALYSIS software (Applied Biosystems). Individual sequence chromatograms were examined in SEQUENCHER v. 4.2 and individual single-stranded fragments were assembled into contiguous consensus reads for subsequent analysis. Consensus sequences for each individual for each gene were aligned using MUSCLE v. 3.6 (Edgar, 2004) with default settings. By-eye adjustment of alignments and verification of coding frame was carried out in Se-Al v.2.0a11 (http://tree.bio.ed.ac.uk/software/seal). RNA alignments were adjusted to maintain correct secondary structure based on the structure profile of skinks in Brandley, Schmitz & Reeder (2005).

We chose a variety of mitochondrial and nuclear genes to estimate the phylogeny of this group (Table 3). We sequenced the mitochondrial genes Nicotinamide Adenine Dinucleotide (NADH) dehydrogenase subunit 2 (ND2: 1095 bp) and subunit 4 (ND4: 705 bp), and ribosomal 12S (447 bp) and 16S (518 bp) genes as well as two nuclear genes, nerve growth factor beta polypeptide (NGFB: 567 bp) and RNA fingerprint protein 35 (R35: 689 bp). These genes were sequenced for the majority of our novel samples (Appendix), although some sample and gene combinations could not be amplified and were coded as

Table 3. Primer sequences used in this study

Gene	Primer name	Sequence: 5′–3′	Citation
ND2	Metf6	AAGCTTTCGGGCCCATACC	Macey *et al.*, 1997
	SphenoR	TAGGYGGCAGGTTGTAGCCC	Linkem *et al.*, 2010b
	ND2sphR	CTCTTDTTTGTRGCTTTGAAGGC	Linkem *et al.*, 2010b
12S	12S.H1478	GAGGGTGACGGGCGGTGTGT	Kocher *et al.*, 1989
	12S.L1091	AAACTGGGATTAGATACCCCACTAT	Kocher *et al.*, 1989
16S	16SF.SKINK	TGTTTACCAAAAACATAGCCTTTAGC	Whiting, Bauer & Sites, 2003
	16SR.SKINK	TAGATAGAAACCGACCTGGATT	Whiting *et al.*, 2003
ND4	ND4	CACCTATGACTACCAAAAGCTCATGTAGAAGC	Arevalo, Davis & Sites, 1994
	tHis	ATCCTTTAAAAGTGARGRGTCT	T. Reeder (pers. comm.)
NGFB	NGFBF_F2	GATTATAGCGTTTCTGATYGGC	Townsend *et al.*, 2008
	NGFBR_R2	CAAAGGTGTGTGTWGTGGTGC	Townsend *et al.*, 2008
R35	R35F	GACTGTGGAYGAYCTGATCAGTGTGGTGCC	Leaché, 2009
	R35R	GCCAAAATGAGSGAGAARCGCTTCTGAGC	Leaché, 2009

missing data in the matrix. We did not have samples of the Australian group taxa and could therefore only include previously published data, which is limited to 12S, 16S, and ND4. Simulation and empirical studies have suggested that robust estimates of phylogeny can still be obtained despite the presence of missing data, especially when many characters are sampled (Wiens, 2003; Philippe *et al.*, 2004; Wiens & Moen, 2008). As a result, we are not concerned about the missing data in our data set affecting our estimate of phylogeny.

All data are available on GenBank (JF497855–JF498576) and alignments can be downloaded from Dryad (http://datadryad.org/doi:10.5061/dryad.30064)

GENE CONCATENATION, PARTITIONING STRATEGY, MODEL CHOICE, AND PHYLOGENETIC ANALYSES

Our mitochondrial gene sampling is very similar to other studies on skinks, allowing us to make some assumptions in regard to concatenation and partitioning. In addition to two mitochondrial genes (12S, 16S) used in Brandley *et al.* (2005), we sequenced ND2 and ND4, which have been informative in *Sphenomorphus* group skinks (Reeder, 2003; Linkem *et al.*, 2010b). We assumed that these mitochondrial genes share a single evolutionary history as a result of matrilineal inheritance and the lack of recombination of the mitochondrion. Brandley *et al.* (2005) found that the best partitioning strategy for mitochondrial genes was to partition by gene, codon, and ribosomal secondary structure. We therefore concatenated our mitochondrial genes following the partitioning strategy of Brandley *et al.* (2005) for an 11 partition mitochondrial data set. The nuclear genes we sampled have not been used in skink phylogenetics, so we tested whether they should be partitioned by codon or

analysed as a continuous gene. We analysed each gene in MrModelTest v2.2 (Nylander, 2004) to estimate the best-fit nucleotide substitution model, using the Akaike information criterion (AIC) to select the appropriate model. When multiple models had similar scores, we chose the most parameter-rich model within ten AIC units of the best AIC model (Table 4). We assumed that partitions within genes (codons and ribosomal secondary structure) have the same overall model as the entire gene because simulations have shown that choosing the correct model may be difficult with a few hundred characters (Posada & Crandall, 2001).

In order to combine the nuclear and mitochondrial data we tested for statistically significant incongruent phylogenetic relationships amongst the gene trees to ensure that each gene tracks the same evolutionary history. We conducted partitioned Bayesian phylogenetic analyses using MrBayes v. 3.2 (Huelsenbeck & Ronquist, 2001) of each nuclear gene and the mitochondrial data set separately. Each data set was run with four independent analyses for 20 million generations sampling every 1000 generations. Partitioned Bayesian analyses were completed with rates across partitions unlinked and the prior on branch lengths adjusted to exponential base 100 (Marshall, Simon & Buckley, 2006; Marshall, 2010). Chain convergence on the same posterior distribution was assessed using TRACER v. 1.5 (Rambaut & Drummond, 2007) and Are We There Yet (AWTY: Wilgenbusch, Warren & Swofford, 2004; Nylander *et al.*, 2007). The *compare* function in AWTY was used to ensure split frequencies were similar across separate runs, ensuring topological congruence. Majority rule consensus topologies of the posterior distributions from the multiple runs were summarized using the 'sumt' command in MrBayes v. 3.2. We found no statistically significant incongruent

Table 4. Summary of the model of evolution selected using MrModelTest for each partition. Partitions within genes are assumed to share the partition of the whole gene (see text for justification)

Gene partition	Model of substitution based on AIC	Informative characters	Uninformative characters	Constant characters	Total
ND2	GTR + I + G	703	56	270	1029
12S	GTR + I + G	216	29	200	445
16S	GTR + I + G	195	51	266	512
ND4 + tRNA	GTR + I + G	503	56	287	846
NGFB	GTR + I + G	230	55	282	567
R35	GTR + I + G	307	60	322	689
Total		2154	307	1627	4088

AIC, Akaike information criterion; GTR, general time reversible; I, invariant sites; G, gamma.

Table 5. Different partitioning strategies employed for concatenated Bayesian phylogenetic analyses. The last column shows the Bayes factor (BF) difference between the two partitioning strategies

Partitioning strategy	Gene type	Partitions	BF difference to P14
P14	Mitochondrial + nuclear	12Sstems, 12Sloops, 16Sstems, 16Sloops, ND2pos1, ND2pos2, ND2pos3, ND4pos1, ND4pos2, ND4pos3, tRNA, nucDNApos1, nucDNApos2, nucDNApos3	–
P17	Mitochondrial + nuclear	12Sstems, 12Sloops, 16Sstems, 16Sloops, ND2pos1, ND2pos2, ND2pos3, ND4pos1, ND4pos2, ND4pos3, tRNA, NGFBpos1, NGFBpos2, NGFBpos3, R35pos1, R35pos2, R35pos3	53.72

phylogenetic relationships amongst gene trees (Posterior Probability ≥ 0.95; Huelsenbeck & Rannala, 2004) so we combined the nuclear and mitochondrial genes into a single data set for subsequent phylogenetic analysis.

Our combined data set was analysed with two different partitioning schemes, varying the partitioning of the nuclear data: P14, nuclear genes partitioned by codon; P17 nuclear genes partitioned by gene and codon (Table 5). We compared these partitioning strategies using Bayes factors (Nylander *et al.*, 2004; Brandley *et al.*, 2005). Analyses of the combined data used the same protocol as the individual genes mentioned above. All four analyses of the combined data sets for each partitioning strategy converged on the same posterior distribution within two million generations.

TESTING ALTERNATIVE PHYLOGENETIC HYPOTHESES

We used a Bayesian approach to test alternative phylogenetic relationships not represented in our consensus tree. We calculated a 95% credibility set of unique trees in the posterior distribution using the *sumt* command in MrBayes. We rejected the alterna-

tive phylogenetic hypothesis if it was absent from any tree in the 95% credible set.

RESULTS
MORPHOLOGICAL GROUPS

Our statistical analyses of the four morphological variables used by Brown & Alcala (1980) corresponded to most of their phenotypic groupings (Fig. 2). Each of Groups 1, 2, and 5 form morphological clusters in the UPGMA tree, equivalent to the findings of Brown & Alcala (1980). Groups 3 and 4 did not form morphological clusters; however, this seems to reflect the morphological divergence of *Sphenomorphus acutus* and *Sphenomorphus cumingi* (Fig. 2). Morphological clustering places these two species as morphologically divergent from all other Philippine *Sphenomorphus*. The other species that do not fit within morphological clusterings of Group 3 and 4 are *Sphenomorphus traanorum*, which Linkem, Diesmos & Brown (2010a) placed in Group 4, and *Sphenomorphus decipiens*, which Brown & Alcala considered part of Group 4.

Morphological variation of the four variables was summarized with PCA (Table 6). Most of the variation among species is explained by size (69%). Principal
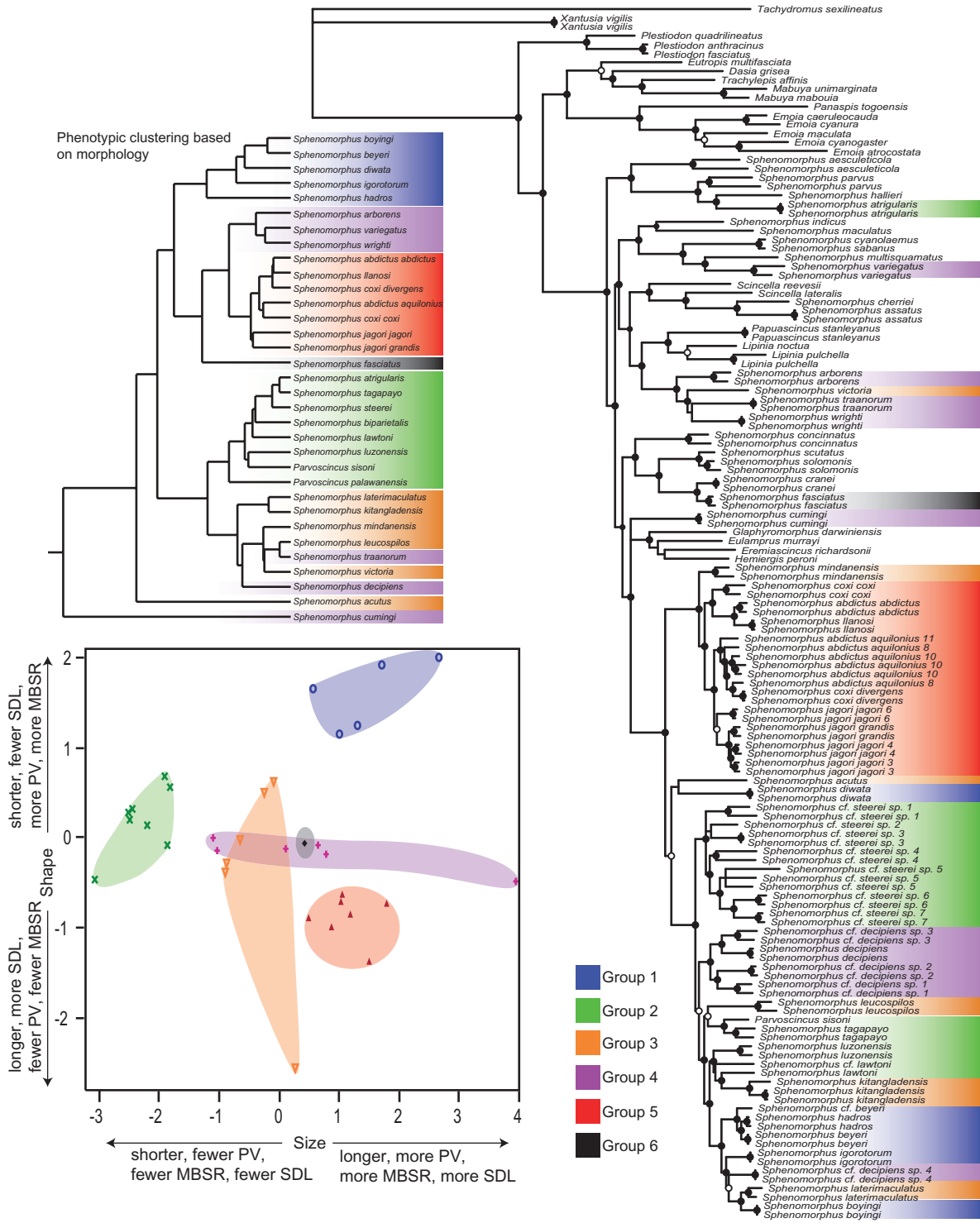
Figure 2. Molecular phylogeny, morphological unweighted pair group method with arithmetic mean (UPGMA) clustering, and principal components analysis (PCA) plot for Philippine *Sphenomorphus*. The molecular phylogeny is the Bayesian maximum consensus tree from the combined 17-partition analysis. Posterior probability values equal or greater than 0.95 are black circles, above 0.75 are white circles, and below 0.75 are not shown. Morphological UPGMA clustering was calculated in JMP using average distances. The PCA plot is for PC1 and PC2 in Table 7. Species groups from Brown & Alcala (1980) are colour-coded. Morphological UPGMA clustering shows species groups are morphologically congruent, but the phylogeny demonstrates that the same morphological types are convergent.

Table 6. Results of principal components analysis (PCA)

Variable	PC1	PC2	PC3	PC4
log(PV)	0.42098	0.70214	0.57273	−0.042
MBSR	0.53437	0.28797	−0.72137	0.33339
SDL	0.48329	−0.56911	0.38239	0.54435
log(SVL)	0.55105	−0.31652	−0.07338	−0.76862
Eigenvalue	2.7976	0.8726	0.2251	0.1047
Percent of variation	69.94	21.81	5.628	2.618

MBSR, Midbody scale rows; PV, Paravertebrals; SDL, Subdigital lamellae; SVL, snout–vent length.

component 2 explains 22% of the morphological variation and is primarily a shape axis of variation in paravertebral scales and midbody scale rows in relation to size. Groups 1, 2, and 5 are separated by PC axis 1 and moderately separate on PC axis 2 (shape). Groups 3 and 4 have a region of broad overlap, with most of the variation for Group 4 being the result of size and that of Group 3 the result of shape. Group 6 falls within Group 4. The range of variation for Group 4 would be smaller if the outlying point at the far right of PC1 was not included. This point is represented by the very large species *Sphenomorphus cumingi*. Similarly, Group 3 would be more compact if the morphologically disparate species *Sphenomorphus acutus* was not included. Comparing the morphological species classifications mapped onto the PCA plot and our best estimate of phylogeny, it is clear that the morphologically cohesive phenotypic classifications of Brown & Alcala (1980) are predominated by evolutionary convergence, with the only exception being Group 5, which is monophyletic.

MOLECULAR PHYLOGENETIC RESULTS

We did not find any incongruent clades above 95% posterior probability between the nuclear and mitochondrial gene trees. Therefore, we concatenated the data into one matrix totalling 4096 nucleotides, in which 155 characters were ambiguous to align and excluded (from 12S and 16S). Each partition was fitted to its best-fit model of evolution and summarized for number of parsimony informative characters, number of invariant characters, and number of uninformative characters (Table 4).

We performed two different partitioning strategy analyses on the full data set, one with the nuclear genes partitioned by gene and codon (P17) and the other with the nuclear genes partitioned by codon position (P14: Table 5). Bayes factor comparisons demonstrated that the more partitioned model is the best model of evolution. Our preferred phylogenetic tree is therefore based on the analysis of the full, 17-partition model (Table 5).

The resulting consensus tree from the Bayesian phylogenetic analyses of the fully partitioned data set has high ($\geq$ 0.95) posterior probability for almost all nodes (Fig. 2). This includes support for Lygosominae and the *Sphenomorphus* group. Other, non-*Sphenomorphus* genera in the *Sphenomorphus* group included in this study render *Sphenomorphus* paraphyletic; these include *Scincella*, *Lipinia*, *Papuascincus*, *Parvoscincus*, and the genera from the diverse radiation of Australian skinks of the *Sphenomorphus* group (*Eremiascincus*, *Eulamprus*, *Glaphyromorphus*, *Hemiergis*).

Philippine *Sphenomorphus* are more diverse phylogenetically than originally expected, with multiple highly divergent and independent clades defined here. One large radiation is represented by 19 of the 28 species found in the Philippines (Fig. 3, clade I). This diverse assemblage is in a polytomy with the Australian *Sphenomorphus* group radiation and with *Sphenomorphus cumingi*. Outside of this large Philippine clade, other Philippine species of *Sphenomorphus* are dispersed throughout the tree, all representing separate invasions of the Philippines. *Sphenomorphus atrigularis*, for example, is nested within a clade of species from Borneo, Sulawesi, and peninsular Malaysia. *Sphenomorphus variegatus* is nested within a clade of Bornean species. *Sphenomorphus arborens*, *Sphenomorphus wrighti*, *Sphenomorphus traanorum*, and *Sphenomorphus victoria* are related to *Lipinia*, which is a widespread genus in South-East Asia, and *Papuascincus*, a genus found on Papua New Guinea. *Sphenomorphus fasciatus* is nested within a clade of species from Papua New Guinea and the Solomon Islands. These separate clades represent six invasions of the Philippines, which occurred primarily via the western island arc of the Philippines.

DISCUSSION

MORPHOLOGICAL VARIATION

Sphenomorphus are often thought of as skinks without morphological novelty (Myers & Donnelly,
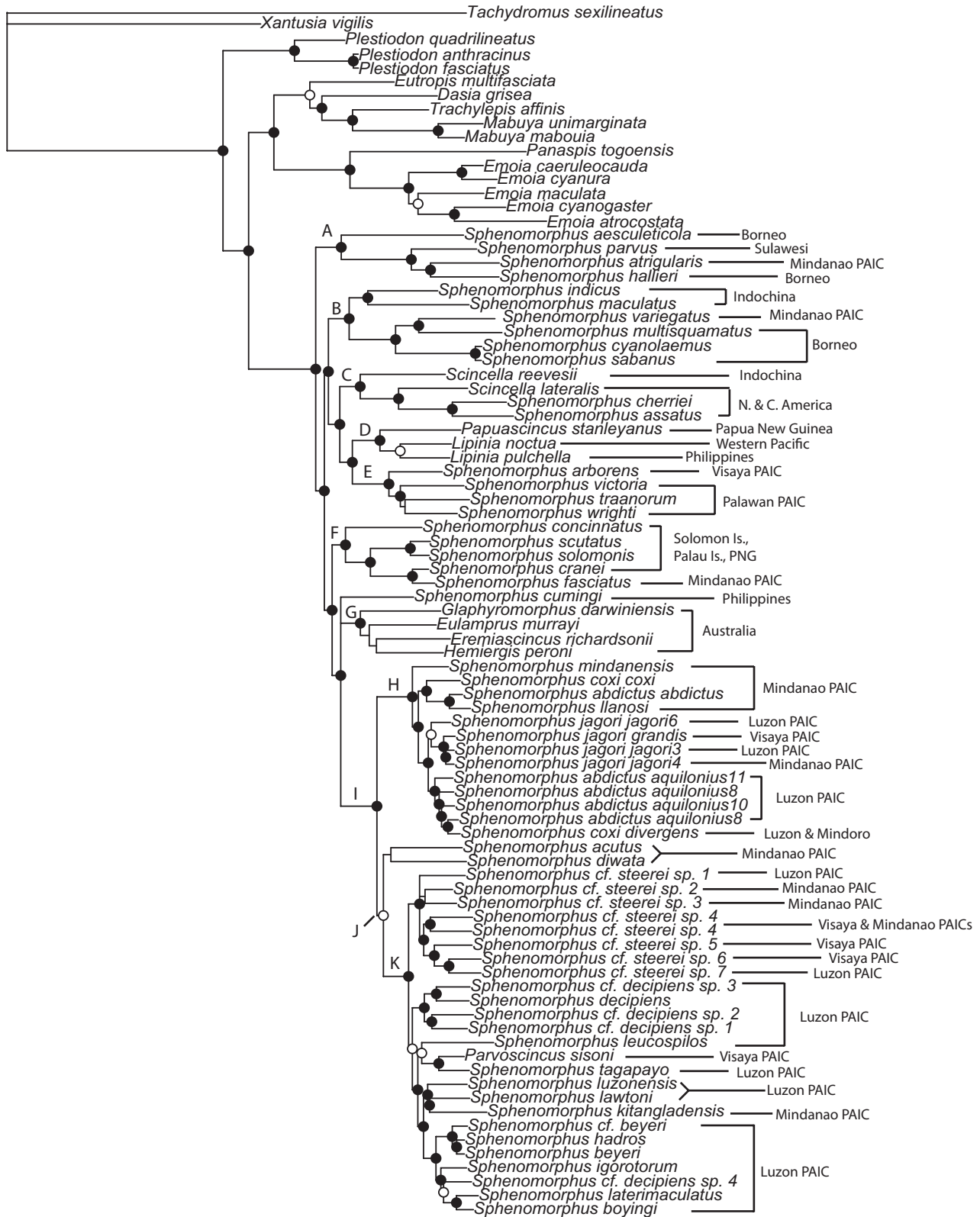
Figure 3. Molecular phylogeny from Figure 2 with sampling reduced to one sample per species. Support is the same as Figure 2. Biogeographical ranges for *Sphenomorphus* species are marked on the phylogeny. Clades discussed in the text are denoted with letters A–K.

1991; Greer & Shea, 2003). When morphological novelties, or derived apomorphic character differences, were found within species assigned to *Sphenomorphus*, the taxa were recognized as different genera (e.g. Greer, 1979, 1991, 1997; Greer & Simon, 1982; Ferner *et al.*, 1997). Our results suggest that these morphological novelties represent multiple evolutionary transitions from a generalized plesiomorphic ancestor, repeated independently throughout the range and evolutionary history of the *Sphenomorphus* group. One such example involves the transition from a scaly lower eyelid to a transparent 'window' in the lower eyelid. Within our sampling the transparent 'window' is found in *Lipinia*, *Scincella*, and *Papuascincus* (clades C and D). It is also found in *Sphenomorphus assatus* and northern populations of *Sphenomorphus cherriei*; however southern populations of *Sp. cheerei* have a scaly eyelid. Clade E is nested within this group of transparent 'window' taxa, but the taxa in clade E have the plesiomorphic state of a scaly eyelid. As *Sphenomorphus cherriei* and clade E both have the plesiomorphic state, there are two equally parsimonious reconstructions of this character within these taxa, one requiring two reversals to the plesiomorphic state and one requiring a convergence of the derived character with one reversal. These convergences and reversals of complex characters have contributed to the complexity of taxonomic and historical evaluations of the *Sphenomorphus* group.

In the case of Brown & Alcala's (1980) taxonomic groups, it seems that the characters employed for most of the groups have evolved convergently, having arisen in multiple clades; therefore, their groupings based on those characters do not reflect phylogenetic history (Fig. 2). The one exception is the *Sphenomorphus abdictus*–*Sphenomorphus coxi*–*Sphenomorphus jagori* complex, Group 5, which corresponds to a clade.

It is not surprising that the phenotypic assemblages of Brown & Alcala (1980) do not correspond to phylogenetic clades as Brown & Alcala (1980) emphasized the doubtful phylogenetic validity of the groups they defined. Nevertheless, their identification of diagnostic characters has proven effective for identifying and describing new species. We have shown that Brown & Alcala's (1980) species groups do form phenotypically defined statistical clusters, but that they are not necessarily the most closely related congeners. Our results therefore suggest that the characters used to define phenotypic assemblages in Philippine *Sphenomorphus* are convergent within the archipelago.

Similarly, our results indicate that changes in body size have occurred repeatedly in Philippine *Sphenomorphus*. Our results suggest that small body size evolved early within clade K (*Sphenomorphus*

steerei, *Sphenomorphus decipiens*, *Parvoscincus sisoni*, *Sphenomorphus lawtoni*, *Sphenomorphus leucospilos*, *Sphenomorphus luzonensis*, *Sphenomorphus tagapayo*) of Philippine species, with a later reversal to increased body size, forming a group of 'giant-dwarfs' (*Sphenomorphus beyeri*, *Sphenomorphus hadros*, *Sphenomorphus igorotorum*, *Sphenomorphus boyingi*, *Sphenomorphus* cf. *decipiens* sp. 4, and *Sphenomorphus laterimaculatus*). All of these 'giant-dwarf' taxa have proportionally more scales than other *Sphenomorphus* in the Philippines – a fact that may be explained by scales being proportionally smaller in miniaturized *Sphenomorphus* (C. W. Linkem, pers. observ.) and an increase in scale number as body size increases (Greer & Parker, 1974). We speculate the increase in body size may have been necessary for the shift to high-elevation, moist cloud forest inhabited by the group of 'giant-dwarfs' on Luzon.

GEOGRAPHICAL PATTERNS OF SPECIES RELATIONSHIPS

Biogeographical relationships found in Philippine *Sphenomorphus* represent novel patterns never before inferred by phylogenetic analyses of other Philippine vertebrate taxa (Brown & Diesmos, 2009; Esselstyn *et al.*, 2009). In particular, our results unequivocally demonstrate that the complex southern and western Philippine communities of forest skinks are assembled from multiple regions of South-East Asia and the Papuan realm (Fig. 3). The finding that these separate invasions primarily have been restricted to clades occupying the south-western portion of the archipelago is expected given the geographically proximate potential sources of dispersal (Inger, 1954; Brown & Alcala, 1970). Invasions seem to have originated from different directions, including two potential invasions from Borneo into Mindanao (*Sphenomorphus atrigularis*, and *Sphenomorphus variegatus*), one potential invasion from an unknown source into Palawan and Panay (*Sphenomorphus arborens*, *Sphenomorphus traanorum*, *Sphenomorphus victoria*, *Sphenomorphus wrighti*), and one potential invasion from the New Guinea faunal region into Mindanao (*Sphenomorphus fasciatus*). *Sphenomorphus variegatus* was conspecific with *Sphenomorphus multisquamatus*, *Sphenomorphus sabanus*, and *Sphenomorphus simus* (Inger, 1958), the first two species, sampled in this study, are from Borneo, the latter is not sampled and is from Papua New Guinea. We infer that *Sphenomorphus variegatus* is derived from Borneo, but future sampling of *Sphenomorphus simus* may show this to be incorrect. The largest clade (Clade I) of Philippine species forms a polytomy with the diverse Australian *Sphenomorphus* group radia-

tion and with another Philippine species, *Sphenomorphus cumingi*. This finding is biogeographically unexpected and may be a result of our missing-taxon sampling from Papua New Guinea and/or Indonesia, or of our phylogenetic misplacement because of our limited gene sampling of the Australian taxa. Outside of the Philippine taxa, clades tend to be geographically restricted, with the caveat that our sampling is taxonomically sparse in these regions (Fig. 3). Additional clades identified in our analysis include: Clade A of Malaysia, Borneo, Sulawesi, and Mindanao species; Clade B of Indochina, Borneo, and Mindanao species; Clade F of Papuan and Mindanao species; Clade G of Australian species; and Clade I of Philippine species.

It is clear that some Philippine *Sphenomorphus* have evolved from multiple independent origins. Only two clades (E, I) show signs of within-archipelago speciation, with Clade I diversifying to a much greater extent than Clade E. The species in Clade E are located on the Visayan PAIC (Panay, Negros, Masbate, Guimaras) and on Palawan Island. The islands of the Visayan PAIC and Palawan are geographically distant, with more than 150 km of intervening open water.

In a recent paper Blackburn *et al*. (2010) presented the 'Palawan Ark Hypothesis' and the supposition that the portion of the island arc now consisting of Palawan, southern Mindoro, and northern Panay was potentially emergent for the last 30 million years as it drifted south-east from continental Asia. Clade E *Sphenomorphus* on Panay and Palawan present a possible extension of this hypothesis, although lack of fossil calibrations prevents reliable divergence time estimation. Our current taxon sampling makes it difficult to infer if clade E is closely related to the species in Asia, Borneo, or elsewhere in South-East Asia. Clade I shows some biogeographical patterns similar to those seen in other Philippine animals (Heaney, 1985; Kennedy *et al*., 2000; Brown & Diesmos, 2001 (2002), 2009), with speciation events occurring across PAIC boundaries, although there are many speciation events within PAICs. The biogeography of Clade H is discussed in detail by Linkem *et al*. (2010b). Generally, widespread species in Clade H do not conform to PAIC predictions and there are multiple instances of divergent clades within a species occurring sympatrically. On Luzon Island, there are multiple instances of speciation on the island within Clade K – cases of potential allopatry across mountain ranges. The most obvious example of this is the clade of *Sphenomorphus beyeri*, *Sphenomorphus boyingi*, *Sphenomorphus* cf. *decipiens* sp. 4, *Sphenomorphus hadros*, *Sphenomorphus igorotorum*, and *Sphenomorphus laterimaculatus*. All of these species are high-elevation endemics found on different moun-

tain ranges on Luzon (Brown *et al*., 2010). The *Sphenomorphus decipiens* complex may be another example, but the putative new species have not yet been described.

SPECIES RELATIONSHIPS

This study confirms a long-held suspicion of researchers interested in the relationships of skinks of the *Sphenomorphus* group – viz., that the genus *Sphenomorphus* is widely paraphyletic with respect to a number of lygosomine taxa (Greer & Shea, 2003; Honda *et al*., 2003; Reeder, 2003). Nevertheless, the degree of paraphyly is surprising given that every genus of the *Sphenomorphus* group sampled is nested within *Sphenomorphus sensu lato*. One explanation for this problem is that *Sphenomorphus* was never properly defined with diagnostic characters (Myers & Donnelly, 1991; Greer & Shea, 2003). Thus, species were placed in the genus if they possessed generalized plesiomorphic character states or if their phylogenetic affinities were unclear (Grismer, Ahmad & Onn, 2009).

Clade A is a group of small skinks represented here by *Sphenomorphus aesculeticola*, *Sphenomorphus parvus*, *Sphenomorphus hallieri*, and *Sphenomorphus atrigularis*. These leaf-litter specialists occur in Borneo, Sulawesi, Borneo, and Mindanao, respectively. When describing *Sphenomorphus aesculeticola*, Inger *et al*. (2001) hypothesized that it was most closely related to the Philippine species *Sphenomorphus atrigularis*, *Sphenomorphus biparietalis*, and *Sphenomorphus luzonensis*, the Bornean species *Sphenomorphus buettikoferi* and *Sphenomorphus hallieri*, and the Malaysian species *Sphenomorphus malayanus* and *Sphenomorphus butleri*. As we lack samples of *Sphenomorphus buettikoferi*, *Sphenomorphus malayanus*, and *Sphenomorphus butleri*, we cannot comment on the relationships of those species, but the others are closely related, except *Sphenomorphus luzonensis*. Recently, numerous small, diminutive species have been described from Malaysia (Grismer, 2006, 2007a, b; Grismer, Ahmad & Onn, 2009; Grismer, Wood & Grismer, 2009). In the recent description of *Sphenomorphus temengorensis*, Grismer, Ahmad & Onn (2009) summarized the eight species of diminutive skinks in Peninsular Malaysia, all of which are morphologically and ecologically similar to the species in Clade A. We also expect that diminutive species in Indonesia: *Sphenomorphus temmincki*, *Sphenomorphus schlegeli*, *Sphenomorphus sanana*, *Sphenomorphus textus*, *Sphenomorphus necopinatus*, and *Sphenomorphus vanheurni* to be part of this clade based on morphological similarity. Expanded taxon sampling to include these other diminutive species will hopefully resolve their

relationships to Clade A, or elucidate part of another convergent lineage.

The genera *Lipinia*, *Scincella*, and *Papuascincus* are all nested within a clade of *Sphenomorphus* species from Indochina, Borneo, and the Philippines (Clades B, C, D, E). The Central American *Sphenomorphus* species *Sphenomorphus cherriei* and *Sphenomorphus assatus* are nested within *Scincella* and closely related to *Scincella lateralis*. *Lipinia* is monophyletic and sister to *Papuascincus*. There is low support for the monophyly of *Lipinia* (posterior probability = 0.83), but we note that we only included *Lipinia noctua* and *Lipinia pulchella*. More sampling may increase support for this genus. Pustulated structures on the surface of the eggshells in three species of *Lobulia* skinks led Allison & Greer (1986) to describe *Papuascincus*. These structures are unique amongst skinks and may represent a reliable synapomorphy for this clade. Additionally, Greer (1974) hypothesized that *Lipinia*, *Lobulia*, and *Prasinohaema* were related. Given the hypothesis of Greer (1974) and that *Papuascincus* was previously included in *Lobulia*, we expect that *Lobulia* and *Prasinohaema* will be related to Clade D of *Lipinia* and *Papuascincus*.

Clade B consists of one Philippine species, *Sphenomorphus variegatus*, which is closely related to a clade of the Bornean species *Sphenomorphus multisquamatus, Sphenomorphus sabanus*, and *Sphenomorphus cyanolaemus*. Both *Sphenomorphus multisquamatus* and *Sphenomorphus sabanus* were considered *Sphenomorphus variegatus* until Inger (1958) distinguished them. The species in Clade B are part of Greer & Parker's (1967) *Sphenomorphus variegatus* group, which was defined based on external morphology. These skinks are considered surface dwellers and Greer & Parker (1967) included a diverse array of species in the group. The *Sphenomorphus variegatus* group is not monophyletic in our phylogeny, with representatives in Clade B, E, G, and K. We speculate that with increased sampling, we will find that most of the species in the *Sphenomorphus variegatus* group belong to Clade B. However, given the placement of some species in the *Sphenomorphus variegatus* group in other clades, it would be premature to assign unsampled species to clades identified here on the basis of overall morphological gestalt.

We do not have a sample of *Sphenomorphus melanopogon*, the type species of the genus *Sphenomorphus*. There are few samples of this species in museums and the type series contains multiple species, raising the question of the true identity of *Sphenomorphus melanopogon* (C. W. Linkem, pers. observ.). The type series for *Sphenomorphus melanopogon* contains species that are morphologically similar to species in Clades B and F. There is one sample of *Sphenomorphus melanopogon* sequenced and available through GenBank from the work of Schmitz (2003), which is related to species in Clade F (not shown). A revision of *Sphenomorphus melanopogon* is in progress (G. Shea, pers. comm.), which will resolve the placement of the type species of *Sphenomorphus*. Until then, it is unclear whether *Sphenomorphus sensu stricto* is our Clade B or Clade F.

Papua New Guinea and the islands of the West Pacific are the most diverse regions for *Sphenomorphus*. Our sampling from these regions is limited in this phylogeny, but all species sampled are closely related in Clade F. Thus, we suspect that most of the Papuan and West Pacific diversity of *Sphenomorphus* will be related to Clade F. Greer & Parker (1967) divided Papuan *Sphenomorphus* into the *Sphenomorphus variegatus* and the *Sphenomorphus fasciatus* groups. Part of the *Sphenomorphus fasciatus* group was later put in the *Sphenomorphus maindroni* group based on a synapomorphic scale character (Greer & Shea, 2003). We have shown that the *Sphenomorphus variegatus* group is nonmonophyletic, and the one species (*Sphenomorphus concinnatus*) from the Papuan region that we sampled appears in Clade F. However, other species in the *Sphenomorphus variegatus* group fall into different clades. Members of the *Sphenomorphus maindroni* group (*Sphenomorphus cranei*, *Sphenomorphus fasciatus*, *Sphenomorphus solomonis*, and *Sphenomorphus scutatus*) form a clade based on the four species sampled (of the 22 species in the group). Our results suggest that the *Sphenomorphus maindroni* group may be a monophyletic assemblage, whereas the *Sphenomorphus variegatus* group should be revised.

The *Sphenomorphus* group is most diverse in Australia, where it is represented by 15 genera (Reeder, 2003; Skinner, 2007). In these studies of the Australian genera, outgroup sampling for the *Sphenomorphus* group included only limited sampling of Papuan *Sphenomorphus* species. We have found that the Australian group forms a polytomy with Philippine species in Clade I + *Sphenomorphus cumingi*, and is not closely related to Papuan species. The Australia + Philippines polytomy has a posterior probability of 1.0, rejecting all possibilities for alternative Australian clade relationships given our current sampling and analyses. We cannot reject the hypothesis that the Australia group is sister to clade I + *Sphenomorphus cumingi*, as these groups collapse to a polytomy (Table 7). Increased gene sampling from the Australian clade and inclusion of more taxa from Papua and Indonesia may help to resolve this set of relationships.

Most of the Philippine species are found in Clade I, which can be subdivided into Clades H and J. If *Sphenomorphus mindanensis* is removed from Clade

Table 7. Tests of multiple phylogenetic hypotheses using the most partitioned (P17) analysis. The presence of any trees within the 95% confidence set of unique trees that are congruent with the hypothesized relationship specifies that the hypothesis cannot be rejected by the data

Phylogenetic hypothesis	Number of congruent trees
Total no. of trees in 95% CI	14426
Sphenomorphus cumingi + Clade I – Clade G	4619
Group 1	0
Group 2	0
Group 3	0
Group 4	0
Monophyly of Philippine taxa	0

CI, confidence interval.

H, the lineage is the same as Brown & Alcala's (1980) Group 5 and the same group examined in Linkem *et al*. (2010b). The relationships amongst the *Sphenomorphus abdictus*–*Sphenomorphus coxi*–*Sphenomorphus jagori* group are similar to those found in Linkem *et al*. (2010b), but one of the clades identified in that study (*Sphenomorphus abdictus aquilonius* 8) is not monophyletic with the increased gene sampling in this study. *Sphenomorphus abdictus aquilonius* 8 is a large clade with a disjunct geographical distribution in the south-west of Luzon and the islands north of Luzon. Finding that the populations in these geographical regions differ with the analysis of more data is not surprising, showing that even the division of widespread taxa in Linkem *et al*. (2010b) may still be insufficient to explain the diversity in the *Sphenomorphus abdictus*–*Sphenomorphus coxi*–*Sphenomorphus jagori* group. *Sphenomorphus mindanensis* was not included in the Linkem *et al*. (2010b) analysis of Group 5. It is interesting that we uncovered *Sphenomorphus mindanensis* as sister to Group 5 because it has nearly identical coloration to *Sphenomorphus coxi coxi*, but is smaller. *Sphenomorphus mindanensis* is part of Brown & Alcala's (1980) Group 3, and based on our morphological analyses of scale counts does not resemble members of the morphologically cohesive Group 5.

The placement of *Sphenomorphus acutus* and *Sphenomorphus diwata* is tenuous. Clade J, supporting these species as sister to Clade K, has low support (posterior probability = 0.77). Morphologically, it is also difficult to ascertain where these species might fit best within the Philippine taxa. *Sphenomorphus acutus* is morphologically unique, with a body shape most similar to *Emoia*, a distantly related genus. It does not resemble *Sphenomorphus diwata*, or any of the other species in the Philippines. Based on its unique appearance, we expected that it would be related to species outside the Philippines, but clearly our assumptions were incorrect. *Sphenomorphus diwata* has been considered part of Group 1, and morphologically similar to the Luzon high-elevation species *Sphenomorphus beyeri*, *Sphenomorphus boyingi*, *Sphenomorphus hadros*, and *Sphenomorphus igorotorum*; however, *Sphenomorphus diwata* clearly is not related to these taxa. Increased gene sampling will probably help to resolve the relationship of these two Mindanao species with respect to the rest of Clade I in the Philippines.

We sampled multiple populations for two widespread species that we suspected contained cryptic genetic lineages. *Sphenomorphus steerei* is abundant on all the major Philippine islands except Palawan, where it is absent, and our analyses infer two highly divergent clades on Luzon, four divergent clades on Mindanao, and four clades on the Visayan PAIC. In some cases, these divergent clades occur in sympatry (*Sphenomorphus* cf. *steerei* sp. 5 & 6 on Panay; *Sphenomorphus* cf. *steerei* sp. 4 & 5 on Negros; *Sphenomorphus* cf. *steerei* sp. 1 & 7 on Mt. Banahao on Luzon), thereby suggesting that these may be exclusive lineages in need of species recognition. As *Sphenomorphus steerei* is a diminutive skink it is difficult to find externally diagnosable characters for these separate lineages. Populations of *Sphenomorphus decipiens* also show significant levels of genetic divergence; unlike *Sphenomorphus steerei*, there are pronounced morphological differences amongst clades. The most divergent population (*Sphenomorphus* cf. *decipiens* sp. 4) occurs at high elevations on Mt. Banahao and Mt. Palali on Luzon Island. Genetically, this population is most similar to the other high-elevation species – *Sphenomorphus beyeri*, *Sphenomorphus boyingi*, *Sphenomorphus hadros*, *Sphenomorphus igorotorum*, and *Sphenomorphus laterimaculatus*. Scale counts and the size of *Sphenomorphus* cf. *decipiens* sp. 4 diagnose it as *Sphenomorphus decipiens*; however, these resemblances clearly are convergences because these populations of skinks are genetically so distinct from other *Sphenomorphus decipiens*. *Sphenomorphus decipiens* and *Sphenomorphus* cf. *decipiens* species 1, 2, and 3 form a clade, but there are morphological differences amongst these subclades. Additionally, *Sphenomorphus* cf. *decipiens* sp. 1, 2, and 4 all occur on Mt. Banahao on Luzon, with *Sphenomorphus* cf. *decipiens* sp. 1 and 2 occurring in sympatry and *Sphenomorphus* cf. *decipiens* sp. 4 occurring at a higher elevation on the mountain.

We were surprised to find that the diminutive, high-elevation *Parvoscincus sisoni* on Panay Island is sister to the small, high-elevation *Sphenomorphus tagapayo* on Luzon Island. These miniaturized

species seem to have limited ranges on the mountains on which they occur; thus, it is difficult to ascertain relationships between these distant populations, especially given the suspected low probability of detection in intervening forested regions.

TAXONOMIC REVISION

Our analyses reveal that *Sphenomorphus* is not monophyletic, and that a large portion of its diversity is more closely related to a variety of other skink genera. Paraphyly has been shown in other studies of lygosomine skinks (Honda *et al*., 2003), but far less severe than that characterizing our results. Although most of our sampling was from species in the genus *Sphenomorphus*, and primarily from the Philippines, every other genus of the *Sphenomorphus* group included in this study renders *Sphenomorphus* paraphyletic.

Given the apparent wholesale paraphyly characterizing the *Sphenomorphus* group, we will avoid some taxonomic changes until future analyses incorporate more taxon sampling (C. W. Linkem, unpubl. data). However we agree with Graybeal & Cannatella (1995) that phylogenetic definitions of taxon names are often best viewed as works in progress, allowing for some well-substantiated changes to be made as evidence justifying such changes becomes available. To that end, we have implemented a few taxonomic changes that are clearly warranted on the basis of our current results. These changes are an initial step toward a generic revision for the *Sphenomorphus* group and primarily affect the species from the Philippines, where our sampling is robust (Fig. 4).

Our fully partitioned Bayesian tree presents six separate invasions of the Philippines, each of which is a monophyletic, historical unit. Future taxonomic work will benefit from the recognition of these units as independent from *Sphenomorphus sensu stricto*. Previously defined names are available for most of the lineages defined herein. *Insulasaurus* and *Otosaurus* are revalidated and *Scincella* and *Parvoscincus* are expanded to include clades defined here. We define two new genera based on phylogenetic results and apply stem-based names to these groups.

NEW GENERA

Tytthoscincus gen. nov.
Type species: Tytthoscincus hallieri (Lidth de Jeude, 1905).

Definition: The clade comprising *Tytthoscincus hallieri* (Lidth de Juede, 1905) and all species that share a more recent common ancestor with *Tytthoscincus hallieri* than with *Anomalopus verreauxii, Calyptotis*

scutirostrum, Coeranoscincus frontalis, Coggeria naufragus, Ctenotus taeniolatus, Eremiascincus richardsonii, Eulamprus quoyiii, Glaphyromorphus isolepis, Gnypetoscincus queenslandiae, Hemiergis decresiensis, Insulasaurus wrighti, Lerista lineata, Lipinia pulchella, Nangura spinosa, Notoscincus ornatus, Ophioscincus australis, Otosaurus cumingi, Papuascincus stanleyanus, Parvoscincus sisoni, Pinoyscincus jagori, Prasinohaema flavipes, Saiphos equalis, Scincella lateralis, and *Sphenomorphus melanopogon.*

Etymology: From the Greek *tytthos*, meaning 'small' and the Latin *scincus* for lizard; the combination refers to the small sizes of the species in this genus. Suggested common name: diminutive Asian skink.

Description: Tytthoscincus can be identified by the following characters: (1) body size diminutive, usually less than 45 mm SVL; (2) temporal scales small, same size and shape as lateral body scales (Fig. 5); and (3) digits small, toe IV slightly longer than, or equal to, toe III.

Included species: Tytthoscincus aesculeticolus (Inger *et al*., 2001), *Tytthoscincus atrigularis* (Stejneger, 1905), *Tytthoscincus biparietalis* (Taylor, 1918), *Tytthoscincus hallieri* (Lidth de Juede, 1905), and *Tytthoscincus parvus* (Boulenger, 1897).

Comment: This clade of diminutive species has unique features that diagnoses it from all other skinks of the *Sphenomorphus* group. Although we lack genetic data for *Tytthoscincus biparentialis*, we nonetheless include it in this genus because it shares the unique presence of divided parietal scales with *Tytthoscincus hallieri*. The diminutive skinks of Malaysia (Grismer, Ahmad & Onn, 2009) should probably also be placed in this new genus, although we prefer to leave that decision in abeyance until a morphological and genetic examination of those taxa are complete. *Tytthoscincus parvus* (Boulenger, 1897) is one of three species of diminutive skinks described from Sulawesi Island. It is likely that the other diminutive species on Sulawesi, *Sphenomorphus temmincki* and *Sphenomorphus textus* are also part of *Tytthoscincus*. Future examination of temporal scales on small skinks in South-East Asia should reveal the species composition of *Tytthoscincus*.

Pinoyscincus gen. nov.
Type species: Pinoyscincus jagori (Peters, 1864).

Definition: The clade comprising *Pinoyscincus jagori* (Peters, 1864) and all species that share a more recent common ancestor with *Pinoyscincus jagori*
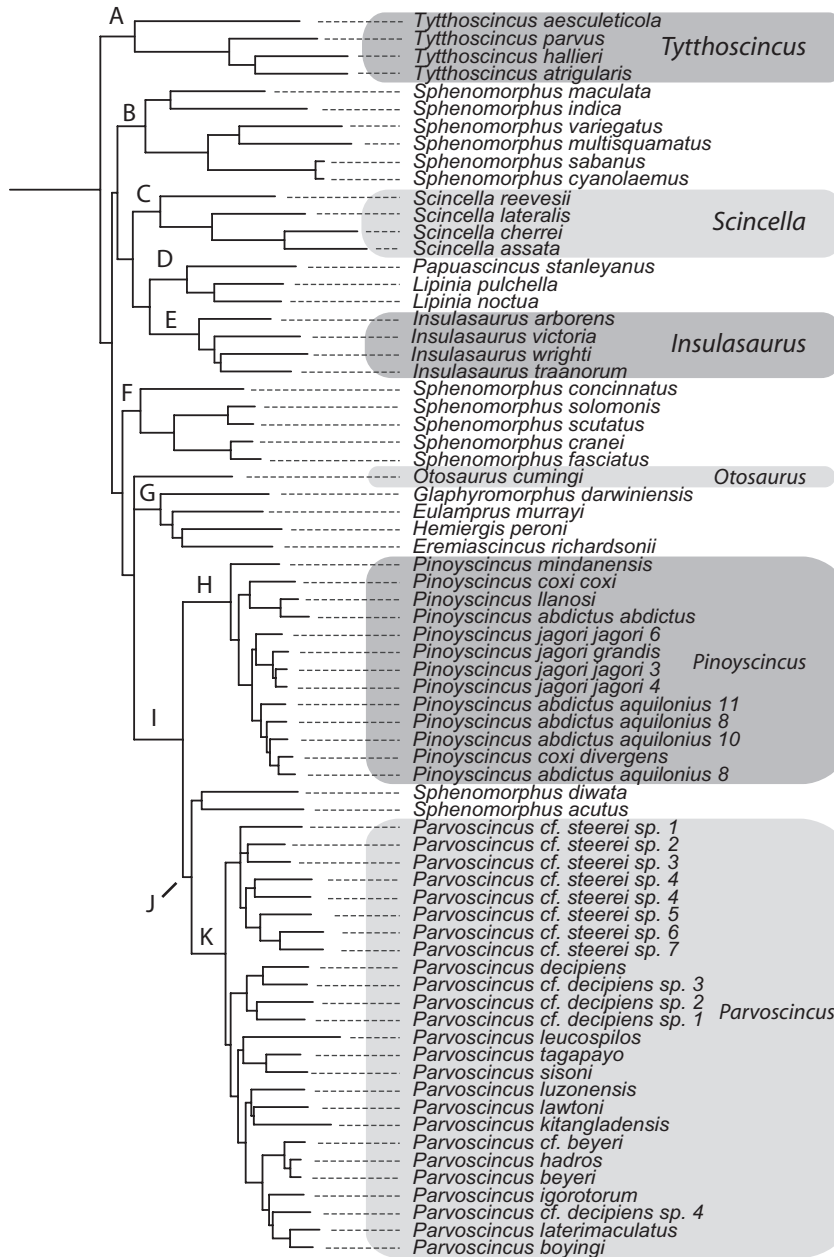
Figure 4. Molecular phylogeny from Figure 3 with the species names changed to reflect our new generic taxonomy.

than with *Anomalopus verreauxii*, *Calyptotis scutirostrum*, *Coeranoscincus frontalis*, *Coggeria naufragus*, *Ctenotus taeniolatus*, *Eremiascincus richardsonii*, *Eulamprus quoyii*, *Glaphyromorphus isolepis*, *Gnypetoscincus queenslandiae*, *Hemiergis decresiencsis*, *Insulasaurus wrighti*, *Lerista lineata*, *Lipinia pulchella*, *Lobulia elegans*, *Nangura spinosa*, *Notoscincus ornatus*, *Ophioscincus australis*, *Otosaurus cumingi*, *Papuascincus stanleyanus*, *Parvoscincus sisoni*, *Prasinohaema flavipes*, *Saiphos equalis*, *Scincella*

lateralis, *Sphenomorphus melanopogon*, and *Tytthoscincus hallieri*.

Etymology: The word *pinoy* is a commonly used Tagalog term of endearment amongst Filipinos, referring to an individual Filipino or the nation as a whole. We use it here in conjunction with the Latin *scincus*, meaning lizard, to name a clade of skinks found on the Philippine Archipelago. Suggested common name: Filipino skinks.
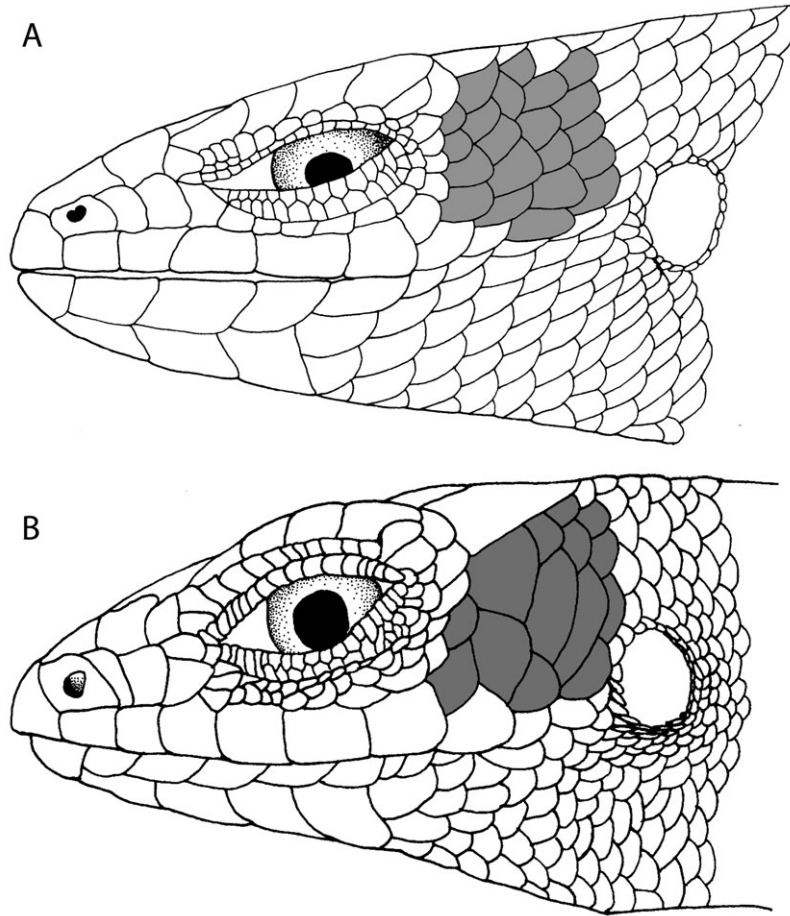
Figure 5. Lateral view of the heads of *Tytthoscincus hallieri* (A, redrawn from Inger *et al*., 2001: fig. 4) and of *Parvoscincus* cf. *decipiens* 1 (B). The temporal scales (highlighted in grey) of the new genus *Tytthoscincus* are small and blend in with the body scales, which is different from the typical shield-like temporal scales (B).

Description: Pinoyscincus can be identified by the following combination of characters: (1) body size medium to large (> 42 mm SVL); (2) paravertebral scale rows 56–80; (3) midbody scale rows 30–44; and (4) subdigital lamellae 17–26. In addition to these scale characters, species in this genus share a unique morphology of the hemipenis. The main shaft of the hemipenis, before the bifurcation, is wide with a large bulbous lobe on each lateral side of the shaft (Fig. 6).

Included species: Pinoyscincus abdictus (Brown & Alcala, 1980), *Pinoyscincus coxi* (Taylor, 1915), *Pinoyscincus jagori* (Peters, 1864), *Pinoyscincus llanosi* (Taylor, 1919), and *Pinoyscincus mindanensis* (Taylor, 1922).

Comment: This morphologically cohesive genus includes Brown & Alcala's (1980) Group 5 and *Pinoyscincus mindanensis*. All of these species are easily diagnosable among the Philippine skink fauna. The

morphology of the hemipenis in this genus has been observed in *Pinoyscincus mindanensis*, *Pinoyscincus abdictus*, *Pinoyscincus jagori*, and *Pinoyscincus llanosi* and has not been observed in any other Philippine skink examined (*Otosaurus cumingi*, *Insulasaurus arborens*, *Insulasaurus traanorum*, *Parvoscincus beyeri*, *Parvoscincus decipiens*, *Sphenomorphus fasciatus*, *Sphenomorphus variegatus*). We have not examined the hemipenis of *Sphenomorphus acutus* or *Sphenomorphus diwata* yet to see if they share the *Pinoyscincus* character so we prefer to leave them *incertae sedis* until a more thorough examination can be performed.

GENERIC RESURRECTION

Insulasaurus Taylor, 1922
Type species: Insulasaurus wrighti Taylor, 1922.

Definition: The clade comprising *Insulasaurus wrighti* Taylor, 1922 and all species that share a more recent

Figure 6. Sulcate, lateral, and asulcate views of *Pinoyscincus abdictus abdictus* hemipenis showing (arrows) the unique bulbous lobe structures on the lateral region of the main shaft before the bifurcation. Scale bar = 5 mm.

common ancestor with *Insulasaurus wrighti* than with *Anomalopus verreauxii*, *Calyptotis scutirostrum*, *Coeranoscincus frontalis*, *Coggeria naufragus*, *Ctenotus taeniolatus*, *Eremiascincus richardsonii*, *Eulamprus quoyii*, *Glaphyromorphus isolepis*, *Gnypetoscincus queenslandiae*, *Hemiergis decresiencsis*, *Lerista lineata*, *Lipinia pulchella*, *Lobulia elegans*, *Nangura spinosa*, *Notoscincus ornatus*, *Ophioscincus australis*, *Otosaurus cumingi*, *Papuascincus stanleyanus*, *Parvoscincus sisoni*, *Pinoyscincus jagori*, *Prasinohaema flavipes*, *Saiphos equalis*, *Scincella lateralis*, *Sphenomorphus melanopogon*, and *Tytthoscincus hallieri*.

Description: Insulasaurus is diagnosed by the following combination of characters: (1) medium body size, 45–64 mm SVL; (2) paravertebral scale rows 62–78; (3) midbody scale rows 29–41; and (4) subdigital lamellae 15–25.

Included species: Insulasaurus arborens (Taylor, 1917), *Insulasaurus traanorum* (Linkem, Diesmos & Brown, 2010a), *Insulasaurus wrighti* Taylor, 1925, and *Insulasaurus victoria* (Brown & Alcala, 1980).

Comment: The monotypic genus *Insulasaurus* was described by Taylor (1925) based on the presence of a divided frontonasal scale. Greer & Parker (1967) found this character to be variable within *Insulasaurus wrighti*, and subsequently placed *Insulasaurus wrighti* in the *Sphenomorphus variegatus* group and synonymized *Insulasaurus* with *Sphenomorphus*. We found that *Insulasaurus wrighti*, *Insulasaurus victoria*, *Insulasaurus traanorum* (all from Palawan Island), and *Insulasaurus arborens* (Panay Island) are monophyletic, and distinct from other Philippine skinks. Our phylogeny suggests that this small, unique, and biogeographically circumscribed clade is more closely related to the genera *Lipinia* and *Papuascincus*, but separate from both, and therefore worthy of designation as a unique genus.

At this time, we have no data suggesting that other *Sphenomorphus* species would be properly placed in the genus *Insulasaurus*, although species in Borneo (e.g. *Sphenomorphus kinabaluensis* and *Sphenomorphus murudensis*) are potential candidates should future phylogenetic studies determine that they are more closely related to *Insulasaurus* than they are to *Sphenomorphus s.s.*

Otosaurus Gray, 1845
Type species: Otosaurus cumingi Gray, 1845.

Definition: The clade comprising *Otosaurus cumingi* (Gray, 1845) and all species that share a more recent common ancestor with *Otosaurus cumingi* than with *Anomalopus verreauxii, Calyptotis scutirostrum, Coeranoscincus frontalis, Coggeria naufragus, Ctenotus taeniolatus, Eremiascincus richardsonii, Eulamprus quoyii, Glaphyromorphus isolepis, Gnypetoscincus queenslandiae, Hemiergis decresiencsis, Insulasaurus wrighti, Lerista lineata, Lipinia pulchella, Lobulia elegans, Nangura spinosa, Notoscincus ornatus, Ophioscincus australis, Papuascincus stanleyanus, Parvoscincus sisoni, Pinoyscincus jagori, Prasinohaema flavipes, Saiphos equalis, Scincella lateralis, Sphenomorphus melanopogon,* and *Tytthoscincus hallieri.*

Description: Otosaurus is diagnosed by the following combination of characters: (1) body large and robust, with adults being longer than 115 mm SVL; (2) large supranasal scales in contact medially, occluding frontonasal contact with the rostral; and (3) supraoculars seven or eight.

Included species: Otosaurus cumingi Gray, 1845.

Comments: The species *Otosaurus cumingi* Gray, 1845 has always been a morphological outlier to the other Philippine skinks. Being the only *Sphenomorphus* group skink in the region to have large supranasal scales and having an average body size double that of other species (Gray, 1845; Taylor, 1922a, Brown & Alcala, 1980), it has been recognized as phenotypically distinct and unique amongst Philippine skinks. Our genetic and morphological results confirm its uniqueness amongst other lineages. Historically, this species was placed in the genus *Otosaurus* Gray, 1845 because of its distinctive morphology. As *Otosaurus cumingi* is the type species for the genus *Otosaurus* and is found to be both morphologically and genetically distinct, and our phylogenetic analyses place it in a polytomy with the Australian genera of the *Sphenomorphus* group and with the clade of *Parvoscincus* and *Pinoyscincus,* we re-establish *Otosaurus* as a monotypic genus, moving *cumingi* from *Sphenomorphus* to *Otosaurus.*

GENERIC REVISION

Parvoscincus Ferner, Brown & Greer, 1997
Type species: Parvoscincus sisoni Ferner, Brown & Greer, 1997.

Definition: The clade comprising *Parvoscincus sisoni* (Ferner, Brown & Greer, 1997) and all species that share a more recent common ancestor with *Parvoscincus sisoni* than with *Anomalopus verreauxii, Calyptotis scutirostrum, Coeranoscincus frontalis, Coggeria naufragus, Ctenotus taeniolatus, Eremiascincus richardsonii, Eulamprus quoyii, Glaphyromorphus isolepis, Gnypetoscincus queenslandiae, Hemiergis decresiencsis, Insulasaurus wrigthi, Lerista lineata, Lipinia pulchella, Lobulia elegans, Nangura spinosa, Notoscincus ornatus, Ophioscincus australis, Otosaurus cumingii, Papuascincus stanleyanus, Pinoyscincus jagori, Prasinohaema flavipes, Saiphos equalis, Scincella lateralis, Sphenomorphus melanopogon,* and *Tytthoscincus hallieri.*

Description: Parvoscincus is diagnosed by the following combination of characters: (1) body size usually small (< 55 mm SVL) but larger in high-elevation species (46 mm < SVL < 86 mm); (2) four enlarged supraoculars; (3) paravertebral scales 51–110; (4) midbody scale rows 23–46; and (5) subdigital lamellae 10–20.

Included species: Parvoscincus beyeri (Taylor, 1922), *Parvoscincus boyingi* (Brown *et al.,* 2010), *Parvoscincus decipiens* (Boulenger, 1894), *Parvoscincus hadros* (Brown *et al.,* 2010), *Parvoscincus igorotorum* (Brown *et al.,* 2010), *Parvoscincus laterimaculatus* (Brown & Alcala, 1980), *Parvoscincus leucospilos* (Peters, 1872), *Parvoscincus lawtoni* (Brown & Alcala, 1980), *Parvoscincus luzonensis* (Boulenger, 1894), *Parvoscincus kitangladensis* (Brown, 1995), *Parvoscincus palawanensis* (Brown & Alcala, 1961), *Parvoscincus sisoni* (Ferner, Brown & Greer, 1997), *Parvoscincus steerei* (Stejneger, 1908), and *Parvoscincus tagapayo* (Brown *et al.,* 1999).

Comments: The recently described genus *Parvoscincus* (Ferner, Brown & Greer, 1997) is nested within a large clade of Philippine *Sphenomorphus* (Clade K). Represented in our phylogeny by the type species, *Parvoscincus sisoni,* it is clear that this genus is not phylogenetically distinct from other Philippine *Sphenomorphus* as originally proposed (Ferner, Brown & Greer, 1997). The other species in this genus, *Parvoscincus palawanensis,* was not sampled; therefore, it is uncertain if it would be related to *Parvoscincus sisoni,* but we assume that it is until contrary evidence is presented. Clade K is clearly a unique and supported group of mostly small species of Philippine *Sphenomorphus.* As *Parvoscincus* is placed within this clade, we recommend that the name *Parvoscincus* be expanded to include the other small-bodied species in this Philippine clade (*Parvoscincus leucospilos, Parvoscincus tagapayao, Parvoscincus luzonensis,*

Parvoscincus lawtoni, *Parvoscincus kitangladensis*, *Parvoscincus laterimaculatus*, *Parvoscincus steerei*, *Parvoscincus decipiens*) in addition to the secondarily enlarged, montane forest species (*Parvoscincus beyeri*, *Parvoscincus boyingi*, *Parvoscincus igorotorum*, and *Parvoscincus hadros*). Two species (*Sphenomorphus acutus* and *Sphenomorphus diwata*) in the Philippines are not diagnosable to either *Parvoscincus* or *Pinoyscincus*. These morphologically distinct species are genetically most similar to *Parvoscincus*, but this relationship has low phylogenetic support. We prefer to leave these species *incertae sedis* until a more thorough examination can be performed.

Scincella Mittleman, 1950
Type species: Scincella lateralis (Say, 1823).

Definition: The clade comprising *Scincella lateralis* (Say, 1823) and all species that share a more recent common ancestor with *Scincella lateralis* than with *Anomalopus verreauxii*, *Calyptotis scutirostrum*, *Coeranoscincus frontalis*, *Coggeria naufragus*, *Ctenotus taeniolatus*, *Eremiascincus richardsonii*, *Eulamprus quoyii*, *Glaphyromorphus isolepis*, *Gnypetoscincus queenslandiae*, *Hemiergis decresiencsis*, *Insulasaurus wrighti*, *Lerista lineata*, *Lipinia pulchella*, *Lissonota maculata*, *Lobulia elegans*, *Nangura spinosa*, *Notoscincus ornatus*, *Ophioscincus australis*, *Otosaurus cumingii*, *Papuascincus stanleyanus*, *Parvoscincus sisoni*, *Pinoyscincus jagori*, *Prasinohaema flavipes*, *Saiphos equalis*, *Sphenomorphus melanopogon*, *Tytthoscincus hallieri*.

Description: Scincella can be diagnosed by the following combination of characters: (1) body size medium (SVL usually < 65 mm); (2) alpha palate (Greer, 1974) with nine premaxillary teeth; (3) long, thin postorbital bone usually present; and (4) with a transparent window in a movable lower eyelid. Transparent window may be lacking in southern populations of *Sp. cheerei*.

Included species: Scincella apraefrontalis Nguyen, Nguyen, Bohme & Ziegler, 2010, *Scincella assata* (Cope, 1864), *Scincella barbouri* (Stejneger, 1925), *Scincella boettgeri* (Van Denburgh, 1912), *Scincella capitanea* Oubeter, 1986, *Scincella caudaequinae* (Smith, 1951), *Scincella cherriei* (Cope, 1893), *Scincella doriae* (Boulenger, 1887), *Scincella forbesora* (Taylor, 1937), *Scincella formosensis* (Van Denburgh, 1912), *Scincella gemmingeri* (Cope, 1864), *Scincella inconspicua* (Müller, 1894), *Scincella incerta* (Stuart, 1940), *Scincella kikaapoa* Garcia-Vazquez, Canseco-Marquez & Nieto-Montes de Oca, 2010, *Scincella lateralis* (Say, 1823), *Scincella macrotis* (Steindachner, 1867), *Scincella melanosticta* (Boulenger, 1887), *Scincella modesta* (Günther, 1864), *Scincella monticola* (Schmidt, 1927), *Scincella ochracea* (Bourret, 1937), *Scincella potanini* (Günther, 1896), *Scincella przewalskii* (Bedriaga, 1912), *Scincella punctatolineata* (Boulenger, 1893), *Scincella rarus* (Myers & Donnelly), 1991, *Scincella reevesi* (Gray, 1838), *Scincella rufocaudatus* Darevsky & Nguyen, 1983, *Scincella rupicola* (Smith, 1927), *Scincella schmidti* (Barbour, 1927), *Scincella silvicola* (Taylor, 1937), *Scincella tsinglingensis* (Hu & Djao, 1966), *Scincella vandenburghi* (Schmidt, 1927), and *Scincella victoriana* (Shreve, 1940).

Comment: The New World species *Scincella cherriei* and *Scincella assata* are nested within the genus *Scincella*, sister to the North American species *Scincella lateralis*. We predict that *Scincella rarus*, and *Scincella incertus* also will be members of this clade. When Greer (1974: 33) revised the genus *Leiolepisma*, he provided detailed comments about the potential relationships of these Central American skinks. Morphologically, these species are a mix of *Sphenomorphus* and *Scincella*, with *Scincella assatus* and *Scincella incertus* lacking a postorbital bone but possessing a window in the lower eye (characters of *Scincella*) and *Scincella cherriei* possessing a postorbital bone but having population variation in the presence of the lower eyelid window. Greer (1974) inferred that *Scincella cherriei* was the primitive form of the Central American radiation owing to the possession of the postorbital bone and placed these species in *Sphenomorphus*. He noted that this did not make sense biogeographically because it inferred a separate migration across the Bering Bridge, but he argued it was more plausible than the re-evolution of the postorbital bone in *Scincella cherriei*. Our molecular evidence shows that the Central American species are part of the same radiation as North American *Scincella*, following the biogeographical expectation. It is therefore reasonable to move these Central American skinks to the genus *Scincella*.

CONCLUSIONS

This study, along with several other recent works, demonstrates the need for thorough systematic revision of Scincidae, the largest monophyletic family of squamates. We have shown that the largest genus of skinks in Scincidae is highly paraphyletic. Based on our phylogeny, morphological convergence in scale characters and body size are common within Philippine *Sphenomorphus*; these phenomena clearly have confounded past supraspecific taxonomic treatments. Taxonomic revisions based on robust molecular phylogenies may avoid misdiagnosing phylogenetic relationships resulting from high levels of homoplasy in

some morphological characters. However, it is clear that many of these same morphological characters are useful for identifying new species. We have shown that species composition varies on different islands, with Luzon and Palawan being composed of closely related species, and the Mindanao faunal region being composed of an assembled fauna, derived from multiple separate invasions of the archipelago. Widespread species in the Philippines continue to show divergent relationships both within and between islands, and divergent clades often occur in sympatry. It is likely that morphological examination of subclades of these widespread species may reveal greater species diversity than currently recognized. If so, a more comprehensive understanding of Philippine *Sphenomorphus* group skinks will require a deeper knowledge of the diversity of the skinks in this unique archipelago.

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APPENDIX

Taxonomic identification	Voucher number	GenBank numbers					
		ND2	12S	16S	ND4	NGFB	R35
Lacertidae							
Tachydromus sexilineatus	KU 311512	HQ907420	–	JF498098	–	JF498325	HQ907624
Xantusiidae							
Xantusia vigilis	KU 220088	JF498215	JF497976	JF498107	–	JF498334	JF498458
Xantusia vigilis	KU 220090	JF498216	JF497977	JF498108	–	JF498335	JF498459
Scincidae							
Scincinae							
Plestiodon quadrilinectus	KU 311490	HQ907422	JF497945	JF498073	JF498547	JF498301	HQ907628
Plestiodon fasciatus	KU 289462	HQ907423	JF497944	JF498072	JF498546	JF498300	HQ907629
Plestiodon anthracinus	KU 290718	HQ907424	JF497943	JF498071	JF498545	JF498299	HQ907630
Lygosominae							
Dasia grisea	KU 305573	HQ907425	JF497855	JF497978	JF498460	JF498217	HQ907631
Emoia caeruleocauda	KU 307154	JF498109	JF497857	JF497980	JF498462	JF498219	JF498336
Emoia cyanogaster	KU 307235	JF498111	JF497859	JF497982	JF498464	JF498221	JF498338
Emoia cyanura	TNHC 58932	JF498110	JF497858	JF497981	JF498463	JF498220	JF498337
Emoia schmidti	KU 307133	–	JF497860	JF497983	JF498465	JF498222	JF498339
Emoia atrocostata	KU 304896	HQ907421	JF497856	JF497979	JF498461	JF498218	HQ907627
Eremiascincus richardsonii	–	–	AY169582	AY169619	AY169657	–	–
Eulamprus murrayi	–	–	AY169584	AY169621	AY169659	–	–
Eutropis multifasciata	KU 302890	JF498112	JF497861	JF497984	JF498466	JF498223	JF498340
Glaphyromorphus darwiniensis	–	–	DQ915286	DQ915310	DQ915334	–	–
Hemiergis peroni	–	–	AY169590	AY169627	AY169665	–	–
Insulasaurus arborens	KU 306712	JF498114	JF497863	JF497986	JF498468	JF498225	JF498342
Insulasaurus arborens	KU 306805	JF498113	JF497862	JF497985	JF498467	JF498224	JF498341
Insulasaurus traanorum	KU 311442	JF498115	JF497864	JF497987	JF498469	–	JF498343
Insulasaurus traanorum	KU 311443	JF498116	JF497865	JF497988	JF498470	JF498226	JF498344
Insulasaurus victoria	KU 309443	JF498117	–	JF497989	–	–	JF498345
Insulasaurus wrighti	KU 311422	JF498118	JF497866	JF497990	JF498471	JF498227	JF498346
Insulasaurus wrighti	KU 311438	JF498119	JF497867	JF497991	JF498472	JF498226	JF498347
Lipinia noctua	CAS 236454	JF498120	JF497868	JF497992	JF498473	–	JF498348
Lipinia pulchella	TNHC 56378	JF498121	JF497869	JF497993	JF498474	JF498228	JF498349
Lipinia pulchella	TNHC 56379	JF498122	JF497870	JF497994	JF498475	JF498229	HQ907625
Mabuya mabouia	KU 214970	JF498123	JF497871	JF497995	–	JF498230	JF498350
Mabuya unimarginata	KU 291283	JF498124	JF497943	JF497996	JF498476	JF498231	JF498351
Otosaurus cumingi	RMB 808	JF498125	JF497873	JF497997	JF498477	JF498232	JF498352
Otosaurus cumingi	RMB 985	JF498126	JF497874	JF497998	JF498478	–	JF498353
Panaspis togoensis	KU 290440	JF498127	JF497875	JF497999	–	JF498233	JF498354
Papuascincus stanleyanus	RNF 0065	JF498128	JF497876	–	JF498479	JF498234	JF498355
Papuascincus stanleyanus	RNF 0067	JF498129	JF497877	JF498000	JF498480	JF498235	JF498356
Parvoscincus beyeri	FMNH 266118	JF498130	–	JF498001	JF498481	JF498236	JF498357
Parvoscincus beyeri	TNHC 06267	JF498131	JF497878	JF498002	JF498482	JF498237	JF498358
Parvoscincus boyingi	FMNH 267561	JF498133	JF497880	JF498004	JF498484	JF498239	JF498360
Parvoscincus boyingi	FMNH 267664	JF498132	JF497879	JF498003	JF498483	JF498238	JF498359
Parvoscincus cf. *beyeri*	KU 308666	JF498134	JF497881	JF498005	JF498485	JF498240	JF498361
Parvoscincus cf. *decipiens* sp. 1	KU 306558	JF498135	JF497882	JF498006	JF498486	JF498241	JF498362

APPENDIX *Continued*

Taxonomic identification	Voucher number	GenBank numbers					
		ND2	12S	16S	ND4	NGFB	R35
Parvoscincus cf. *decipiens* sp. 1	TNHC 62889	JF498136	JF497883	–	JF498487	–	–
Parvoscincus cf. *decipiens* sp. 2	KU 306560	JF498137	JF497884	JF498007	JF498488	JF498242	JF498363
Parvoscincus cf. *decipiens* sp. 2	TNHC 62679	JF498138	JF497885	JF498008	JF498489	–	JF498364
Parvoscincus cf. *decipiens* sp. 3	TNHC 62883	JF498139	JF497886	JF498009	JF498490	JF498243	JF498365
Parvoscincus cf. *decipiens* sp. 3	TNHC 62897	JF498140	JF497887	JF498010	JF498491	JF498244	JF498366
Parvoscincus cf. *decipiens* sp. 4	TNHC 62893	JF498142	JF497888	JF498012	JF498493	JF498246	JF498368
Parvoscincus cf. *decipiens* sp. 4	ACD 1020	JF498141	–	JF498011	JF498492	JF498245	JF498367
Parvoscincus cf. *lawtoni*	FMNH 266278	JF498143	JF497889	JF498013	JF498494	JF498247	JF498369
Parvoscincus decipiens	ACD 2233	JF498144	–	JF498014	JF498495	JF498248	JF498370
Parvoscincus decipiens	ACD 2423	JF498145	JF497890	JF498015	JF498496	JF498249	JF498371
Parvoscincus hadros	PNM 9618	–	–	JF498016	–	–	JF498372
Parvoscincus hadros	PNM 9620	–	–	JF498017	–	–	JF498373
Parvoscincus igorotorum	FMNH 259448	JF498146	JF497891	JF498018	JF498497	JF498250	JF498374
Parvoscincus igorotorum	PNM 9623	JF498147	JF497892	JF498019	JF498498	–	JF498375
Parvoscincus kitangladensis	KU 326618	JF498148	JF497893	JF498020	JF498499	JF498251	JF498376
Parvoscincus kitangladensis	KU 326619	JF498149	JF497894	JF498021	JF498500	JF498252	JF498377
Parvoscincus kitangladensis	KU 326627	JF498150	JF497895	JF498022	JF498501	JF498253	JF498378
Parvoscincus laterimaculatus	TNHC 62675	JF498151	JF497896	JF498023	JF498502	JF498254	JF498379
Parvoscincus laterimaculatus	TNHC 62676	JF498152	JF497897	JF498024	JF498503	JF498255	JF498380
Parvoscincus lawtoni	KU 308668	JF498153	JF497898	JF498025	JF498504	JF498256	JF498381
Parvoscincus leucospilos	KU 320522	JF498154	JF497899	JF498026	JF498505	JF498257	JF498382
Parvoscincus leucospilos	TNHC 62682	JF498155	JF497900	JF498027	JF498506	JF498258	JF498383
Parvoscincus luzonensis	FMNH 258990	JF498156	JF497901	JF498028	JF498507	JF498259	JF498384
Parvoscincus luzonensis	FMNH 263506	JF498157	–	JF498029	JF498508	JF498260	JF498385
Parvoscincus sisoni	RMB 700	JF498158	JF497902	JF498030	JF498509	JF498261	JF498386
Parvoscincus steerei 1	RMB 3944	JF498160	JF497904	JF498032	JF498511	–	JF498388
Parvoscincus steerei 1	TNHC 63091	JF498159	JF497903	JF498031	JF498510	–	JF498387
Parvoscincus steerei 2	ACD 1203	JF498161	JF497905	JF498033	JF498512	JF498262	JF498389
Parvoscincus steerei 3	ACD 2696	JF498162	JF497906	JF498034	–	JF498263	JF498390
Parvoscincus steerei 3	ACD 2709	JF498163	–	JF498035	–	JF498264	JF498391
Parvoscincus steerei 4	EMD 429	JF498164	JF497908	JF498036	–	JF498265	JF498392
Parvoscincus steerei 5	KU 306736	JF498165	JF497909	JF498037	–	JF498266	JF498393
Parvoscincus steerei4	TNHC 56356	JF498166	JF497910	JF498038	JF498513	JF498267	JF498394
Parvoscincus steerei5	KU 302937	JF498167	JF497911	JF498039	JF498514	JF498268	JF498395
Parvoscincus steerei5	KU 302938	JF498168	JF497912	JF498040	JF498515	JF498269	JF498396
Parvoscincus steerei6	KU 306840	JF498169	JF497913	JF498041	JF498516	JF498270	JF498397
Parvoscincus steerei6	GVAG 273	JF498170	JF497914	JF498042	JF498517	JF498271	JF498398
Parvoscincus steerei7	TNHC 63086	JF498171	JF497915	JF498043	JF498518	JF498272	JF498399
Parvoscincus steerei7	TNHC 63093	JF498172	JF497916	JF498044	JF498519	JF498273	JF498400
Parvoscincus tagapayo	KU 308926	JF498173	JF497917	JF498045	JF498520	JF498274	JF498401
Parvoscincus tagapayo	KU 326400	JF498174	JF497918	JF498046	JF498521	JF498275	JF498402
Pinoyscincus abdictus abdictus	ACD 2687	JF498175	JF497920	JF498048	JF498523	JF498277	JF498404
Pinoyscincus abdictus abdictus	KU 306538	GU573559	JF497919	JF498047	JF498522	JF498276	JF498403
Pinoyscincus abdictus aquilonius10	FMNH 266115	JF498176	JF497921	JF498049	JF498524	JF498278	JF498405
Pinoyscincus abdictus aquilonius10	KU 302920	GU573666	JF497922	JF498050	JF498525	JF498279	JF498406
Pinoyscincus abdictus aquilonius10	TNHC 62758	GU573648	JF497923	JF498051	JF498526	JF498280	JF498407
Pinoyscincus abdictus aquilonius11	RMB 953	JF498177	JF497924	JF498052	JF498527	JF498281	JF498408
Pinoyscincus abdictus aquilonius8	KU 307018	JF498178	JF497925	JF498053	JF498528	JF498282	JF498409
Pinoyscincus abdictus aquilonius8	TNHC 63108	JF498179	JF497926	JF498054	JF498529	JF498283	JF498410
Pinoyscincus coxi coxi	KU 309908	GU573562	JF497927	JF498055	JF498530	JF498284	JF498411

APPENDIX *Continued*

Taxonomic identification	Voucher number	GenBank numbers					
		ND2	12S	16S	ND4	NGFB	R35
Pinoyscincus coxi coxi	ACD 2685	GU573564	JF497928	JF498056	JF498531	JF498285	JF498412
Pinoyscincus coxi divergens	KU 308380	GU573561	JF497929	JF498057	JF498532	–	JF498413
Pinoyscincus coxi divergens	ACD 925	GU573640	JF497930	JF498058	JF498533	JF498286	JF498414
Pinoyscincus jagori grandis	GVAG 266	GU573597	JF497931	JF498059	JF498534	JF498287	JF498415
Pinoyscincus jagori grandis	TNHC 62860	JF498180	JF497932	JF498060	JF498535	JF498288	JF498416
Pinoyscincus jagori jagori 3	TNHC 63095	JF498181	JF497933	JF498061	JF498536	JF498289	JF498417
Pinoyscincus jagori jagori 3	TNHC 63102	GU573571	JF497934	JF498062	JF498537	JF498290	JF498418
Pinoyscincus jagori jagori 4	KU 306546	GU573587	JF497935	JF498063	JF498538	JF498291	JF498419
Pinoyscincus jagori jagori 4	TNHC 56380	JF498182	JF497936	JF498064	JF498539	JF498292	JF498420
Pinoyscincus jagori jagori 6	KU 302929	GU573610	JF497937	JF498065	JF498540	JF498293	JF498421
Pinoyscincus jagori jagori 6	KU 307684	JF498183	JF497938	JF498066	–	JF498294	JF498422
Pinoyscincus llanosi	KU 306556	GU573557	JF497939	JF498067	JF498541	JF498295	JF498423
Pinoyscincus llanosi	KU 306557	GU573558	JF497940	JF498068	JF498542	JF498296	JF498424
Pinoyscincus mindanensis	KU 310135	JF498184	JF497941	JF498069	JF498543	JF498297	JF498425
Pinoyscincus mindanensis	TNHC 56351	JF498185	JF497942	JF498070	JF498544	JF498298	JF498426
Scincella assatus	KU 289795	–	JF497946	JF498074	JF498548	JF498302	JF498427
Scincella assatus	KU 291286	JF498186	–	JF498075	JF498549	JF498303	JF498428
Scincella cherrei	–	–	JF497947	JF498076	JF498550	JF498304	JF498429
Scincella lateralis	KU 289460	JF498187	JF497948	JF498077	–	JF498305	JF498430
Scincella reevesii	FMNH 255540	HQ907428	JF497949	JF498078	JF498551	–	HQ907634
Sphenomorphus acutus	KU 319962	JF498188	JF497950	JF498079	JF498552	JF498306	JF498431
Sphenomorphus concinnatus	KU 307213	JF498189	–	JF498080	JF498553	JF498307	JF498432
Sphenomorphus concinnatus	KU 307348	JF498190	JF497951	JF498081	JF498554	JF498308	JF498433
Sphenomorphus cranei	KU 307167	JF498191	JF497952	JF498082	JF498555	JF498309	JF498434
Sphenomorphus cranei	KU 307168	JF498192	JF497953	JF498083	JF498556	JF498310	JF498435
Sphenomorphus cyanolaemus	FMNH 239867	JF498193	JF497954	JF498084	JF498557	JF498311	JF498436
Sphenomorphus diwata	EMD 368	JF498194	JF497955	JF498085	JF498558	JF498312	JF498437
Sphenomorphus diwata	EMD 428	JF498195	JF497956	JF498086	JF498559	JF498313	JF498438
Sphenomorphus fasciatus	KU 310807	JF498196	JF497957	JF498087	JF498560	JF498314	JF498439
Sphenomorphus fasciatus	KU 315061	JF498197	JF497958	JF498088	JF498561	JF498315	JF498440
Sphenomorphus indicus	CAS 214892	JF498198	JF497959	JF498089	JF498562	JF498316	JF498441
Sphenomorphus maculatus	FMNH 261863	JF498199	JF497960	JF498090	JF498563	JF498317	JF498442
Sphenomorphus multisquamatus	FMNH 243828	JF498200	JF497961	JF498091	JF498564	JF498318	JF498443
Sphenomorphus sabanus	FMNH 239881	JF498201	JF497962	JF498092	JF498565	JF498319	JF498444
Sphenomorphus scutatus	CAS 236398	JF498202	JF497963	JF498093	JF498566	JF498320	JF498445
Sphenomorphus solomonis	KU 307173	JF498203	JF497964	JF498094	JF498567	JF498321	JF498446
Sphenomorphus solomonis	KU 307349	JF498204	JF497965	JF498095	JF498568	JF498322	JF498447
Sphenomorphus variegatus	KU 309900	JF498205	JF497966	JF498096	–	JF498323	JF498448
Sphenomorphus variegatus	KU 315087	JF498206	JF497967	JF498097	JF498569	JF498324	JF498449
Trachylepis perroteti	KU 291923	JF498207	JF497968	JF498099	–	JF498326	JF498450
Tytthoscincus aesculeticola	SP 06913	JF498208	JF497969	JF498100	JF498570	JF498327	JF498451
Tytthoscincus aesculeticola	FMNH 239839	JF498209	JF497970	JF498101	JF498571	JF498328	JF498452
Tytthoscincus atrigularis	KU 315055	JF498210	JF497971	JF498102	JF498572	JF498329	JF498453
Tytthoscincus atrigularis	KU 315060	JF498211	JF497972	JF498103	JF498573	JF498330	JF498454
Tytthoscincus hallieri	FMNH 230184	JF498212	JF497973	JF498104	JF498574	JF498331	JF498455
Tytthoscincus parvus	RMB 4707	JF498213	JF497974	JF498105	JF498575	JF498332	JF498456
Tytthoscincus parvus	JAM6275	JF498214	JF497975	JF498106	JF498576	JF498333	JF498457