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.

ADDITIONAL KEYWORDS: Australia – Lipinia – new genera – Papuascincus – Parvoscincus – Scincella – Sphenomorphus group – South-East Asia – taxonomy.

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
section of *Lygosoma* by Smith (1937). Mittleman (1952) redefined *Sphenomorphus* as a genus based on the presence of large prefrontals, paired frontoparietals, enlarged preoculars, 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; Parvoscinicus Ferner, Brown & Greer, 1997; Sigaloseps Sadlier, 1987). However, other genera (*Otosaurus, Insulasaurus, Ictiscincus, Parotosaurs*) 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 *Parvoscinicus* (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 lautom*, *Sphenomorphus leucopilos*, *Sphenomorphus luzonensis*, *Sphenomorphus tagapayo*, *Sphenomorphus trauorum*, *Sphenomorphus wrighti*, and *Sphenomorphus victoria* only occur on one island. *Sphenomorphus acutus*, *Sphenomorphus arborens*, *Sphenomorphus bipartalis*, *Sphenomorphus fasciatus*, *Sphenomorphus llanos*, *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 aquiloinius*, *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).
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          |
|               | *Sphenomorphus atrigularis*, *Sphenomorphus biparietalis*, *Sphenomorphus lautoni*, *Sphenomorphus luzonensis*, *Sphenomorphus steerei*, *Sphenomorphus tagapayo*, *P. palawanensis*, *P. sisoni* | Small size, with small digits                     |
| Group 2       | *Sphenomorphus acutus*, *Sphenomorphus laterimaculatus*, *Sphenomorphus leucospilos*, *Sphenomorphus kitangladensis*, *Sphenomorphus mindanensis*, *Sphenomorphus victoria* | Midbody scales 30–40, toe IV lamellae 15–20       |
| Group 3       | *Sphenomorphus arbores*, *Sphenomorphus cumingi*, *Sphenomorphus decipiens*, *Sphenomorphus tranorum*, *Sphenomorphus variegatus*, *Sphenomorphus wright* | Midbody scales 36–54, toe IV lamellae 20–28       |
| Group 4       | *Sphenomorphus abdictus abdictus*, *Sphenomorphus abdictus aquilonius*, *Sphenomorphus caxi caxi*, *Sphenomorphus caxi divergens*, *Sphenomorphus jagori grandis*, *Sphenomorphus jagori jagori*, *Sphenomorphus ilanoni* | Large size, midbody scales 32–44, toe IV lamellae > 20 |
| Group 5       | *Sphenomorphus fasciatus*                                                         | Limbs do not overlap, midbody scales < 36         |

**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).
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 Parvoscinus sisoni led to the transfer of Sphenomorphus palawanensis to the genus Parvoscinus (Fern & al., 1997). As the two species of Parvoscinus 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; Parvoscinus palawanensis on Palawan Island; and Parvoscinus 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’s (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 leucosiplos, 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 leucosiplos 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 arbores, 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 arbores 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 addicts addicts, Sphenomorphus addicts aquilonius, Sphenomorphus jagori grandis, Sphenomorphus jagori jagori, Sphenomorphus coxi coxi, Sphenomorphus coxi diversens, and Sphenomorphus ilanos 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 superspecific 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 sexlineatus).

We included samples from the following Sphenomorphus group genera: Lipinia, Papuascincus, Parvoscinus, Scincella, Glaphyromorphus, Eulamprus, Eremitascincus, 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 bipartitalis because it occurs in the Sulu Archipelago, a region inaccessible to researchers. Similarly, Parvoscinus 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
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

| 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 abdicus       | 86.2| 68.5| 39.0 | 23.0|
| Sphenomorphus abdicus 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 cuningi       | 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| 108.5| 46.0 | 20.0|
| Sphenomorphus igerorotum    | 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 taqapayo      | 27.6| 57.5| 29.0 | 10.0|
| Sphenomorphus tranororum    | 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.
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 & Swoford, 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

| Gene | Primer name | Sequence: 5′–3′ | Citation |
|------|-------------|-----------------|----------|
| ND2  | Metf6       | AAGCTTTCCGGGCCTACCC | Macey et al., 1997 |
| Sphenor |           | TAGGYYGCGAAGGGTGAGCC | Linkem et al., 2010b |
| ND2sphR |           | CTCTTTTTGTGCTTTTGGACC | Linkem et al., 2010b |
| 12S  | 12S.H1478   | GAGGGTGACGGCGGTGTG | Kocher et al., 1989 |
| 12S.L1091 |         | AAACTGGGATAGAACCCACTC | Kocher et al., 1989 |
| 16S  | 16SF.SKINK  | TGTTAACCACAACTACGCTTACGC | Whiting, Bauer & Sites, 2003 |
| 16SR.SKINK |         | TAGATGAAACCCACTCCGATT | Whiting et al., 2003 |
| ND4  | ND4         | CACCTATGACTACAAACGGCTATGAGAC | Arevalo, Davis & Sites, 1994 |
|      | tHis        | ATCTTTTTAAAGTGARGRCTTCT | T. Reeder (pers. comm.) |
| NGFB | NGFBF_F2    | GATATACGCTTTCTGATGGGC | Townsend et al., 2008 |
|      | NGFBR_R2    | AAAAGTGTGTGTGTGTTGGTG | Townsend et al., 2008 |
| R35  | R35F        | GACTGTGGAGYCTGATCATGTGGGTTGCC | Leaché, 2009 |
|      | R35R        | GCCAAAATGAGSGAGAARCCTTCTGAGC | Leaché, 2009 |
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.

**PHYLLOGENETIC RELATIONSHIPS**

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 alternative 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
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.
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 (≥ 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 arboreus*, *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.
When morphological novelties, or derived apomorphic character differences, were found within species assigned to \textit{Sphenomorphus}, the taxa were recognized as different genera (e.g. Greer, 1979, 1991, 1997; Greer & Simon, 1982; Ferner \textit{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 \textit{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 \textit{Lipinia}, \textit{Scincella}, and \textit{Papuascincus} (clades C and D). It is also found in \textit{Sphenomorphus assatus} and northern populations of \textit{Sphenomorphus cherriei}; however southern populations of \textit{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 \textit{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 \textit{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 \textit{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 \textit{Sphenomorphus} are convergent within the archipelago.

Similarly, our results indicate that changes in body size have occurred repeatedly in Philippine \textit{Sphenomorphus}. Our results suggest that small body size evolved early within clade K (\textit{Sphenomorphus steerei}, \textit{Sphenomorphus decipiens}, \textit{Parvoscinicus sisoni}, \textit{Sphenomorphus lautom}, \textit{Sphenomorphus leucopilos}, \textit{Sphenomorphus luzonensis}, \textit{Sphenomorphus tagapayo}) of Philippine species, with a later reversal to increased body size, forming a group of ‘giant-dwarfs’ (\textit{Sphenomorphus beyeri}, \textit{Sphenomorphus hadros}, \textit{Sphenomorphus igorotorum}, \textit{Sphenomorphus boyangi}, \textit{Sphenomorphus cf. decipiens} sp. 4, and \textit{Sphenomorphus laterimaculatus}). All of these ‘giant-dwarf’ taxa have proportionally more scales than other \textit{Sphenomorphus} in the Philippines — a fact that may be explained by scales being proportionally smaller in miniaturized \textit{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.

\section*{Biogeographical relationships}

Biogeographical relationships found in Philippine \textit{Sphenomorphus} represent novel patterns never before inferred by phylogenetic analyses of other Philippine vertebrate taxa (Brown & Diesmos, 2009; Esselstyn \textit{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 (\textit{Sphenomorphus atrigularis}, and \textit{Sphenomorphus variegatus}), one potential invasion from an unknown source into Palawan and Panay (\textit{Sphenomorphus arbores}, \textit{Sphenomorphus traanorum}, \textit{Sphenomorphus victoria}, \textit{Sphenomorphus wrighti}), and one potential invasion from the New Guinea faunal region into Mindanao (\textit{Sphenomorphus fasciatus}). \textit{Sphenomorphus variegatus} was conspecific with \textit{Sphenomorphus multisquamatus}, \textit{Sphenomorphus sabanus}, and \textit{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 \textit{Sphenomorphus variegatus} is derived from Borneo, but future sampling of \textit{Sphenomorphus simus} may show this to be incorrect. The largest clade (Clade I) of Philippine species forms a polytomy with the diverse Australian \textit{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 are 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 aesculetica*, *Sphenomorphus parvus*, *Sphenomorphus hallieri*, and *Sphenomorphus atrigularis*. These leaf-litter specialists occur in Borneo, Sulawesi, Borneo, and Mindanao, respectively. When describing *Sphenomorphus aesculetica*, 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 cheriei 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 – | 4619 |
| Clade G | 0 |
| 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 igororum; 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 sympathy (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 igororum, 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 sympathy 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 clades 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 Juede, 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*, *Calyptrodes scutirostrum*, *Coeranoscincus frontalii*, *Coggeria naufragus*, *Ctenotus taeniolatus*, *Eremiascincus richardsonii*, *Eulamprus quoyii*, *Glaphyromorphus isolepis*, *Gnypetosaurus queenslandiae*, *Hemiergis decresiensis*, *Insulasaurus wrighti*, *Lerista lineata*, *Lipinia pulchella*, *Nangura spinosa*, *Notoscincus ornatus*, *Ophioscincus australis*, *Otostaurus cumingi*, *Papuascincus stanleyanus*, *Parvoscincus sisoni*, *Pinoyscincus jagori*, *Prasinohaema flavipes*, *Saiphos equalis*, *Scincella lateralis*, and *Sphenomorphus melanocephalus*.

*Etymology:* From the Greek *tythos*, 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 biparietalis*, 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 (Grismes, 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, Gephyrotoscinus queenslandiae, Hemiergis peroni, Insulasaurus arborens, Insulasaurus victoria, Insulasaurus wrighti, Insulasaurus traanorum, Sphenomorphus concinnatus, Sphenomorphus solomonis, Sphenomorphus scutatus, Sphenomorphus cranei, Sphenomorphus fasciatus, Otosaurus cumingi, Sphenomorphus darwiniensis, Eulanthus murrayi, Eremiascincus richardsonii, Pinoscyincus mindanensis, Pinoscyincus coxi coxi, Pinoscyincus llianos, Pinoscyincus abdictus abdictus, Pinoscyincus jagor jagor 6, Pinoscyincus jagor jagor 4, Pinoscyincus jagor jagor 3, Pinoscyincus jagor jagor 4, Pinoscyincus abdictus aquilonius 11, Pinoscyincus abdictus aquilonius 8, Pinoscyincus abdictus aquilonius 8, Pinoscyincus abdictus aquilonius 10, Pinoscyincus coxi diversius, Pinoscyincus abdictus aquilonius 8, Sphenomorphus diwata, Sphenomorphus acutus, Parvoscyincus cf. steerei sp. 1, Parvoscyincus cf. steerei sp. 2, Parvoscyincus cf. steerei sp. 3, Parvoscyincus cf. steerei sp. 4, Parvoscyincus cf. steerei sp. 4, Parvoscyincus cf. steerei sp. 5, Parvoscyincus cf. steerei sp. 6, Parvoscyincus cf. steerei sp. 7, Parvoscyincus decipiens, Parvoscyincus decipiens sp. 3, Parvoscyincus cf. decipiens sp. 2, Parvoscyincus cf. decipiens sp. 1, Parvoscyincus leucospilos, Parvoscyincus tagapayo, Parvoscyincus sisoni, Parvoscyincus luzonis, Parvoscyincus lawtoni, Parvoscyincus kitagladensis, Parvoscyincus cf. beyeri, Parvoscyincus hadros, Parvoscyincus beyeri, Parvoscyincus igororum, Parvoscyincus cf. decipiens sp. 4, Parvoscyincus laterimaculatus, Parvoscyincus boyingi.

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.
**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 arborvens, 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
common ancestor with Insulasaurus wrighti than with Anomalopus verreauxii, Calyptotis scutirostrum, Coeranoscincus frontalis, Coggeria naufragus, Ctenotus taeniolatus, Eremiascincus richardsonii, Eulamprus quoyii, Glaphyromorphus isolepis, Gnyptoscincus queenslandiae, Hemiergis decresiensis, Lerista lineata, Lipinia pulchella, Lobulia elegans, Nangura spinosa, Notoscincus ornatus, Ophioscincus australis, Otosaurus cumingi, Papuascincus stanleyanus, Parvoscincus sisoni, Pinoyscincus jagori, Prasinothaema flavipes, Saiphos equalis, Scincella lateralis, Sphenomorphus melanopogon, and Tythoscincus 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 naufrae*, *Ctenotus taeliolatus*, *Eremiascincus richardsonii*, *Eulamprus quoyii*, *Gephyromorphus isolepis*, *Gnypetoscinqueenslandiae*, *Hemiergis decresiencsis*, *Insulasaurus wrighti*, *Lerista lineata*, *Lipinia pulchella*, *Lobulia elegans*, *Nangura spinosa*, *Notoscincus ornatus*, *Ophioscincus australis*, *Otosaurus cumingi*, *Papuascincus stanleyanus*, *Pinoyscincus jagori*, *Prasinohaema flavipes*, *Saiphos equalis*, *Scincella lateralis*, *Sphenomorphus melanopogon*, and *Tythoscincus 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 frontal 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 *Parvoscinus* and *Pinoyscincus*, we re-establish *Otosaurus* as a monotypic genus, moving *cumingi* from *Sphenomorphus* to *Otosaurus*.

**Generic revision**

*Parvoscinus* Ferner, Brown & Greer, 1997  
*Type species:* *Parvoscinus sisoni* Ferner, Brown & Greer, 1997.

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

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

**Comments:** The recently described genus *Parvoscinus* (Ferner, Brown & Greer, 1997) is nested within a large clade of Philippine *Sphenomorphus* (Clade K). Represented in our phylogeny by the type species, *Parvoscinus 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, *Parvoscinus palawanensis*, was not sampled; therefore, it is uncertain if it would be related to *Parvoscinus 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 *Parvoscinus* is placed within this clade, we recommend that the name *Parvoscinus* be expanded to include the other small-bodied species in this Philippine clade (*Parvoscinus leucospilos*, *Parvoscinus tagapayo*, *Parvoscinus luzonensis*, *Parvoscinus beyeri*, *Parvoscinus boyingi*, *Parvoscinus decipiens*, *Parvoscinus hadros*, *Parvoscinus igerorum*, *Parvoscinus laterimaculatus*, *Parvoscinus leucospilos*, *Parvoscinus lawtoni*, *Parvoscinus luzonensis*, *Parvoscinus kitangladensis*, *Parvoscinus palawanensis*, *Parvoscinus sisoni*, *Parvoscinus steerei*, and *Parvoscinus tagapayo*).
Parvoscinus lawtoni, Parvoscinus kitangladensis, Parvoscinus laterimaculatus, Parvoscinus steerei, Parvoscinus decipiens) in addition to the secondarily enlarged, montane forest species (Parvoscinus bayeri, Parvoscinus boyangi, Parvoscinus igororum, and Parvoscinus hadros). Two species (Sphenomorphus acutus and Sphenomorphus diwata) in the Philippines are not diagnosable to either Parvoscinus or Pinoscinus. These morphologically distinct species are genetically most similar to Parvoscinus, 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 Anomalopus verreauxii, Calyptotis scutirostrum, Coeranoscinus frontalis, Coggeria naufragus, Ctenotus taeniolatus, Eremiascincus richardsonii, Eulamprus quoyii, Glyphyromorphus isolepis, Gnypeutoscincus queenslandiae, Hemiergis decresienscis, Insulasaurus wrighti, Lerista lineata, Lipinia pulchella, Lissotornata maculata, Lobulia elegans, Nangura spinosa, Notoscincus ornatus, Ophiosciocinus australis, Otosaurus cunningii, Papuascincus stanleyanus, Parvoscinus sisoni, Pinoscinus jagori, Prasinohaema flavipes, Saiphos equalis, Sphenomorphus melanopogon, Tythoscincus 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. cherriei.

Included species: Scincella apraefrontalis Nguyen, Nguyen, Bohme & Ziegler, 2010, Scincella assata (Cope, 1864), Scincella barbouri (Stejneger, 1925), Scincella boettgeri (Van Denburgh, 1912), Scincella capitanae Oubeter, 1986, Scincella caudaequinae (Smith, 1951), Scincella cherriei (Cope, 1893), Scincella doriae (Bouleguer, 1887), Scincella forbesora (Taylor, 1937), Scincella formosensis (Van Denburgh, 1912), Scincella gemmingeri (Cope, 1864), Scincella inconspicua (Müller, 1894), Scincella incerta (Stuart, 1940), Scincella kikaapo Garcia-Vazquez, Cansec-Marquez & Nieto-Montes de Oca, 2010, Scincella lateralis (Say, 1823), Scincella macrotis (Steindachner, 1867), Scincella melanosticta (Bouleguer, 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 schmidtii (Barbour, 1927), Scincella silvicola (Taylor, 1937), Scincella tsinglingensis (Hu & Diao, 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 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 sympathy. 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 | 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 |
| **Scincidae**             |                |      |      |      |      |      |      |
| **Scincinae**             |                |      |      |      |      |      |      |
| *Plestiodon quadrilineatus* | KU 311490      | HQ907420 | JF497945 | JF498073 | JF498547 | JF498301 | HQ907628 |
| *Plestiodon fasciatus*    | KU 289462      | HQ907423 | JF497944 | JF498072 | JF498546 | JF498300 | HQ907629 |
| *Plestiodon anthracinus*  | KU 307133      | JF497786 | JF497893 | JF498465 | JF498222 | JF498339 |
| **Lygosominae**           |                |      |      |      |      |      |      |
| *Dasia grisea*            | KU 305573      | HQ907425 | JF497855 | JF497978 | JF498460 | JF498217 | HQ907631 |
| *Emoia caeruleocauda*     | KU 307154      | JF498109 | JF497857 | JF497980 | JF498462 | JF498219 | JF498336 |
| *Emoia cyanogaster*       | KU 311442      | JF498110 | JF497858 | JF497981 | JF498463 | JF498220 | JF498337 |
| *Emoia anthracinus*       | KU 307133      | JF497786 | JF497893 | JF498465 | JF498222 | JF498339 |
| **Emoia atrocostata**     | KU 304896      | JF497856 | JF497983 | JF498461 | JF498218 | JF498339 |
| **Emoia schmidti**        | –              | –     | –    | –    | –    | –    | –    |
| **Insulasaurus victoria** | KU 309443      | JF498117 | –    | JF497989 | –    | JF498345 |
| **Insulasaurus wrighti**  | KU 311422      | JF498118 | JF497866 | JF497990 | JF498471 | JF498227 | JF498346 |
| **Insulasaurus unimarginata** | TNHC 56379   | JF498119 | JF497867 | JF497991 | JF498472 | JF498269 | JF498347 |
| **Insulasaurus boyingi**  | FMNH 266118    | JF498120 | JF497868 | JF497992 | JF498473 | –    | JF498348 |
| **Insulasaurus cf. beyeri** | TNHC 60267   | JF498130 | –    | JF498001 | JF498481 | JF498236 | JF498357 |
| **Insulasaurus cf. boyingi** | TNHC 267561  | JF498131 | JF497878 | JF498002 | JF498482 | JF498237 | JF498358 |
| **Insulasaurus cf. boyingi** | TNHC 267664  | JF498132 | JF497879 | JF498003 | JF498483 | JF498238 | JF498359 |
| **Insulasaurus cf. beyeri** | TNHC 08666   | JF498133 | JF497880 | JF498004 | JF498484 | JF498239 | JF498360 |
| **Insulasaurus cf. decipiens** | TNHC 086558 | JF498135 | JF497882 | JF498006 | JF498485 | JF498240 | JF498361 |

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| Taxonomic identification                        | Voucher number               | GenBank numbers                          |
|-----------------------------------------------|------------------------------|------------------------------------------|
| Parvoscincus cf. decipiens sp. 1              | TNHC 62889                    | JF498136 – JF497883 – JF498487 – JF498363 |
| Parvoscincus cf. decipiens sp. 2              | KU 306560                     | JF498137 – JF497884 – JF498007 – JF498364 |
| Parvoscincus cf. decipiens sp. 2              | TNHC 62679                    | JF498138 – JF497885 – JF498008 – JF498365 |
| Parvoscincus cf. decipiens sp. 3              | TNHC 62883                    | JF498139 – JF497886 – JF498009 – JF498366 |
| Parvoscincus cf. decipiens sp. 3              | TNHC 62897                    | JF498140 – JF497887 – JF498010 – JF498367 |
| Parvoscincus cf. decipiens sp. 4              | TNHC 62893                    | JF498142 – JF497888 – JF498012 – JF498368 |
| Parvoscincus cf. decipiens sp. 4              | ACD 1020                      | JF498141 – JF498011 – JF498492 – JF498370 |
| Parvoscincus cf. lautoni                     | FMNH 266278                   | JF498143 – JF497889 – JF498013 – JF498371 |
| Parvoscincus decipiens                       | ACD 2233                      | JF498144 – JF498014 – JF498495 – JF498372 |
| Parvoscincus decipiens                       | ACD 2423                      | JF498145 – JF497890 – JF498015 – JF498373 |
| Parvoscincus hadros                          | PNM 9618                      | JF498016 – JF498017 – JF498374           |
| Parvoscincus igororum                       | FMNH 259448                   | JF498146 – JF497891 – JF498018 – JF498375 |
| Parvoscincus kitangladensis                 | KU 326618                     | JF498148 – JF497892 – JF498019 – JF498376 |
| Parvoscincus kitangladensis                 | KU 326619                     | JF498149 – JF497894 – JF498021 – JF498377 |
| Parvoscincus kitangladensis                 | KU 326627                     | JF498150 – JF497895 – JF498022 – JF498378 |
| Parvoscincus laterimaculatus                | TNHC 62675                    | JF498151 – JF497896 – JF498023 – JF498379 |
| Parvoscincus laterimaculatus                | TNHC 62676                    | JF498152 – JF497897 – JF498024 – JF498380 |
| Parvoscincus lautoni                        | KU 308668                     | JF498153 – JF497898 – JF498025 – JF498381 |
| Parvoscincus leucospilos                    | KU 320522                     | JF498154 – JF497899 – JF498026 – JF498382 |
| Parvoscincus luzonensis                      | TNHC 62682                    | JF498155 – JF497900 – JF498027 – JF498383 |
| Parvoscincus sisoni                         | RMB 700                       | JF498158 – JF497902 – JF498030 – JF498384 |
| Parvoscincus steerei 1                      | RMB 3944                      | JF498160 – JF497904 – JF498032 – JF498385 |
| Parvoscincus steerei 1                      | TNHC 63091                    | JF498159 – JF497903 – JF498031 – JF498386 |
| Parvoscincus steerei 2                      | ACD 1203                      | JF498161 – JF497905 – JF498033 – JF498387 |
| Parvoscincus steerei 3                      | ACD 2696                      | JF498162 – JF497906 – JF498034 – JF498388 |
| Parvoscincus steerei 3                      | ACD 2709                      | JF498163 – JF498035 – JF498389           |
| Parvoscincus steerei 4                      | EMD 429                       | JF498164 – JF497908 – JF498036 – JF498390 |
| Parvoscincus steerei 5                      | KU 306736                     | JF498165 – JF497909 – JF498037 – JF498391 |
| Parvoscincus steerei 6                      | TNHC 56356                    | JF498166 – JF497910 – JF498038 – JF498392 |
| Parvoscincus steerei 6                      | TNHC 56356                    | JF498166 – JF497910 – JF498038 – JF498393 |
| Parvoscincus steerei 7                      | TNHC 63093                    | JF498171 – JF497915 – JF498043 – JF498394 |
| Parvoscincus steerei 7                      | TNHC 63093                    | JF498172 – JF497916 – JF498044 – JF498395 |
| Parvoscincus tagapayo                       | KU 308926                     | JF498173 – JF497917 – JF498045 – JF498396 |
| Parvoscincus tagapayo                       | KU 326400                     | JF498174 – JF497918 – JF498046 – JF498397 |
| Pinoscyincus abdictus abdictus              | ACD 2687                      | JF498175 – JF497920 – JF498048 – JF498398 |
| Pinoscyincus abdictus abdictus              | KU 306538                     | GU573559 – JF497919 – JF498047 – JF498399 |
| Pinoscyincus abdictus abdictus              | FMNH 266115                   | JF498176 – JF497921 – JF498049 – JF498400 |
| Pinoscyincus abdictus abdictus              | KU 302920                     | GU573666 – JF497922 – JF498050 – JF498401 |
| Pinoscyincus abdictus abdictus              | TNHC 62758                    | JF497923 – JF498051 – JF498526 – JF498402 |
| Pinoscyincus abdictus abdictus              | RMB 953                       | JF498177 – JF497924 – JF498052 – JF498403 |
| Pinoscyincus abdictus abdictus              | KU 307018                     | JF498178 – JF497925 – JF498053 – JF498404 |
| Pinoscyincus abdictus abdictus              | TNHC 63108                    | JF498179 – JF497926 – JF498054 – JF498405 |
| Pinoscyincus coxi coxi                      | KU 309908                     | GU573562 – JF497927 – JF498055 – JF498406 |

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## APPENDIX Continued

| Taxonomic identification | Voucher number | 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 jagori diversis* | ACD 925 | GU573640 | JF497930 | JF498058 | JF498533 | JF498286 | JF498414 |
| *Sphenomorphus acutus* | FMNH 239881 | JF498201 | JF497962 | JF498092 | JF498565 | JF498319 | JF498444 |
| *Sphenomorphus scutatus* | CAS 236398 | JF498202 | JF497963 | JF498093 | JF498566 | JF498320 | JF498445 |
| *Trachylepis perroteti* | FMNH 239839 | JF498209 | JF497970 | JF498101 | JF498571 | JF498328 | JF498452 |
| *Tythoscincus aesculetico* | SP 06913 | JF498213 | JF497974 | JF498105 | JF498575 | JF498332 | JF498454 |
| *Tythoscincus parvus* | FMNH 230184 | JF498212 | JF497973 | JF498104 | JF498574 | JF498331 | JF498455 |
| *Tythoscincus parvus* | RMB 4707 | JF498213 | JF497974 | JF498105 | JF498575 | JF498332 | JF498456 |
| *Tythoscincus parvus* | JAM6275 | JF498214 | JF497975 | JF498106 | JF498576 | JF498333 | JF498457 |

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