HISTORICAL PROCESSES AND GENETIC IMPLICATIONS OF LIMB REDUCTION AND LOSS IN AN ISLAND SKINK LINEAGE

BY

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ABSTRACT

Evolutionary simplification, or loss of complex characters, is a major theme in studies of body form evolution. The apparently infrequent evolutionary reacquisition of complex characters has led to the assertion (Dollo's Law) that once lost, complex characters may be impossible to re-evolve, at least via the exact same evolutionary process. The spectacular, virtually endemic radiation of Philippine semi-fossorial skinks of the genus *Brachymeles* represent one of the few radiations of scincid lizards to possess both fully limbed and limbless species. And yet, nothing is known of the phylogenetic relationships of this exceptional group. Morphologically similar body plans have made it difficult to assess species-level diversity, and the genus has long been recognized as one of the more modest radiations of southeast Asian lizards. However, taxonomic studies indicate that the diversity within the genus *Brachymeles* is grossly underestimated. Here I provide one of the most comprehensive, fine-scale analyses of squamate body-form evolution to date, introducing a new model system of closely related, morphologically variable, lizards. In this study I provide the first robust estimate of phylogenetic relationships within the genus *Brachymeles* using a multi-locus dataset and nearly complete taxonomic sampling. Systematic revisions guided by robust estimates of phylogeny subsequently result in a 125% increase in species diversity. I provide statistical tests of monophyly for all polytypic species and two widespread limb-reduced species and our results indicate wholesale deviations from past summaries and taxonomic evaluations of the genus. A Bayesian reconstruction of ancestral areas indicates strong statistical support for a minimum of five major dispersal events that have given rise to a major component of the observed species diversity across the archipelago. Our phylogenetic results support independent instances of complete limb loss as well as multiple instances of digit and external ear opening loss and re-acquisition. Even more striking, I find strong statistical support for the re-acquisition of a pentadactyl body form from a digit-reduced ancestor. Our findings have broad, general implications for body form evolution in burrowing vertebrates: whatever constraints have shaped trends in morphological evolution among other squamate groups (excluding *Bipes*) have been lost in this one exemplary clade.

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INTRODUCTION

Only four genera of scincid lizards are known to possess both fully limbed and limbless species (*Brachymeles*, *Chalcides*, *Lerista*, and *Scelotes*; Lande, 1978; Wiens and Slingluff, 2001; Brandley et al., 2008). Of these four genera, the genus *Brachymeles* is the least well known, with recent studies indicating the recognized diversity of the group is vastly underestimated (Siler et al., 2009a, 2010a,b, 2011; in press a,b,c,d; Siler and Brown, 2010, 2011). Within the genus, all but two of the 36 recognized species are endemic to the Philippines (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980; Siler et al., 2009a, 2010a,b, 2011; in press a,b,c,d; Siler and Brown, 2010, 2011); the exceptions are *B. apus* from northern Borneo (Hikida, 1982) and *B. miriamae* from Thailand (Siler et al., 2011). Eighteen species are pentadactyl (*B. anim, B. bicolor*, *B. boholensis, B. boulengeri*, *B. gracilis*, *B. kadwa, B. makusog, B. mindorensis, B. orientalis, B. pito, B. schadenbergi*, *B. sampu*, *B. syam*, *B. talinis, B. taylori*, *B. tungaoi, B. vindumi,* and *B. walo*), thirteen are non-pentadactyl, with incompletely developed limbs and reduced numbers of digits (*B. apat*, *B. bonitae*, *B. cebuensis*, *B. elerae*, *B. dalawa*, *B. isa*, *B. lima*, *B. muntingkamay, B. pathfinderi*, *B. samarensis*, *B. tatlo*, *B. tridactylus*, and *B. wrighti*), and five are entirely limbless (*B. apus*, *B. minimus, B. miriamae, B. lukbani,* and *B. vermis*). Within the non-pentadactyl species, there exist a wide range of limb- and digit-reduced states. Some species have minute limbs that lack full digits (*B. apat*, *B. bonitae*, *B. cebuensis*, *B. dalawa*, *B. isa*, *B. lima*, *B. muntingkamay, B. samarensis, B. tatlo*, *B. tridactylus*; Duméril and Bibron, 1839; Brown, 1956; Brown and Rabor, 1967; Siler et al., 2009a, 2010a,b, 2011; in press a,b,c,d; Siler and Brown, 2010, 2011). Other non-pentadactyl species have moderately developed limbs with four digits on the hands and feet (*B. elerae, B. wright*; Siler et al., in press b), or four digits on the feet and five digits on the hands (*B. pathfinderi*: Taylor, 1917, 1925; Siler et al., in press a).

All species are semi-fossorial and typically found in dry, rotting material inside decaying logs or in loose soil, forest floor detritus, and leaf litter.

The genus *Brachymeles* was first described by Duméril and Bibron (1839) for the small, limb-reduced species *Brachymeles bonitae*. As species diversity accumulated, various authors have noted morphological variation among island populations of many of the polytypic and widespread species (Taylor, 1922; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). Historically, the shared body plans and similar external morphological features among populations of *Brachymeles*, and the absence of dense population sampling across the Philippines, proved problematic for diagnosing species (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). Although long considered to be a small clade of Southeast Asian lizards (the last revision enumerated only 15 species; Brown and Alcala, 1980), recent studies have significantly increased the known species diversity and expanded the range of variation in body form (Siler et al., 2009a, 2010a,b, 2011; in press a,b,c,d; Siler and Brown, 2010, 2011). Additionally, several rare, mid-to-high elevation species long represented by only a few specimens, in some cases without knowledge of their exact type locality (e.g., *Brachymeles bicolor, B. elerae, B. wrighti, B. pathfinderi*), have recently been rediscovered (Siler, 2010; Siler et al., in press a,b). These studies, coupled with increased sampling throughout the Philippines, have provided a comprehensive dataset with which to begin evaluating the taxonomic stability of polytypic and widespread species across the Philippines, and address questions concerning the evolution of limb reduction and loss. The availability of tissue samples for all but two known species of *Brachymeles* now allows for robust estimates of phylogenetic relationships among recognized widespread and polytypic species, and evaluation of species boundaries.

In Chapter One (Siler et al., 2011) I investigate the biogeography of *Brachymeles* from a phylogenetic perspective, providing the first estimate of phylogenetic relationships for this unique radiation of Southeast Asian lizards. I strove to estimate the phylogenetic position of *Brachymeles* among scincid lizards in order to provide insight into patterns of body form evolution and polarity of character change and provide the first statistical tests of several hypotheses. I also employ a Bayesian ancestral area reconstruction to gain insight into the biogeographical history of the genus. Finally, I test the following taxonomic hypotheses: (1) *Brachymeles* is monophyletic; (2) All recognized and formerly recognized polytypic species are monophyletic; and (3) All recognized widespread species are monophyletic. My data reveal patterns inconsistent with all of the above predictions and at odds with currently recognized taxonomy; I conclude that species diversity within the genus is vastly underestimated and that cryptic patterns of lineage diversification prevail in this poorly known group of Southeast Asian lizards.

In Chapter Two (Siler and Brown, 2011), I focus on testing hypotheses of body form evolution among squamate reptiles by investigating patterns of body form change in skinks of the genus *Brachymeles* using a phylogenetic comparative approach, derived from morphological data. I explore the data for evidence of threshold values of morphological features after which changes in body form occur. Additionally, I test for patterns of correlated evolution of morphological characters, and provide the first exploration of the impact of various methodological choices used in previous studies of body form evolution, including the impact of choice of morphometric variable as a measurement of body size for non-phylogenetic and phylogenetic size-correction as well as the overall method for multivariate principal component analyses. Finally, using my robust estimate of phylogenetic relationships, I explore the prevalence and directionality of evolutionary changes in limb, digit, and ear character states, and the impact of outgroup sampling and ancestral outgroup character states on ancestral state reconstructions.

The goals of Chapters Three (Siler and Brown, 2010), Four (Siler et al., in press c), and Five (Siler et al., in press d) are to revise the taxonomy of the *B. gracilis*, *B. orientalis, B. samarensis, B. schadenbergi,* and *B. talinis* species complexes such that individual units (species) represent independently evolving, cohesive lineage segments (sensu Simpson, 1961; Wiley 1978; Frost and Hillis, 1990; de Queiroz, 1998, 1999). Comprehensive examination of all recently collected specimens from throughout the known range of these species, and historically collected specimens available in museum collections, results in the complete reorganization of species diversity within the genus, increasing the recognized diversity by more than 125%. I provide a phylogenetic analysis and the first illustrations of many of these taxa, fully describe each species, and clarify taxonomic boundaries. I also provide information on each species' natural history, ecology, and geographic distribution and comment on additional, presently unrecognized putative new species.

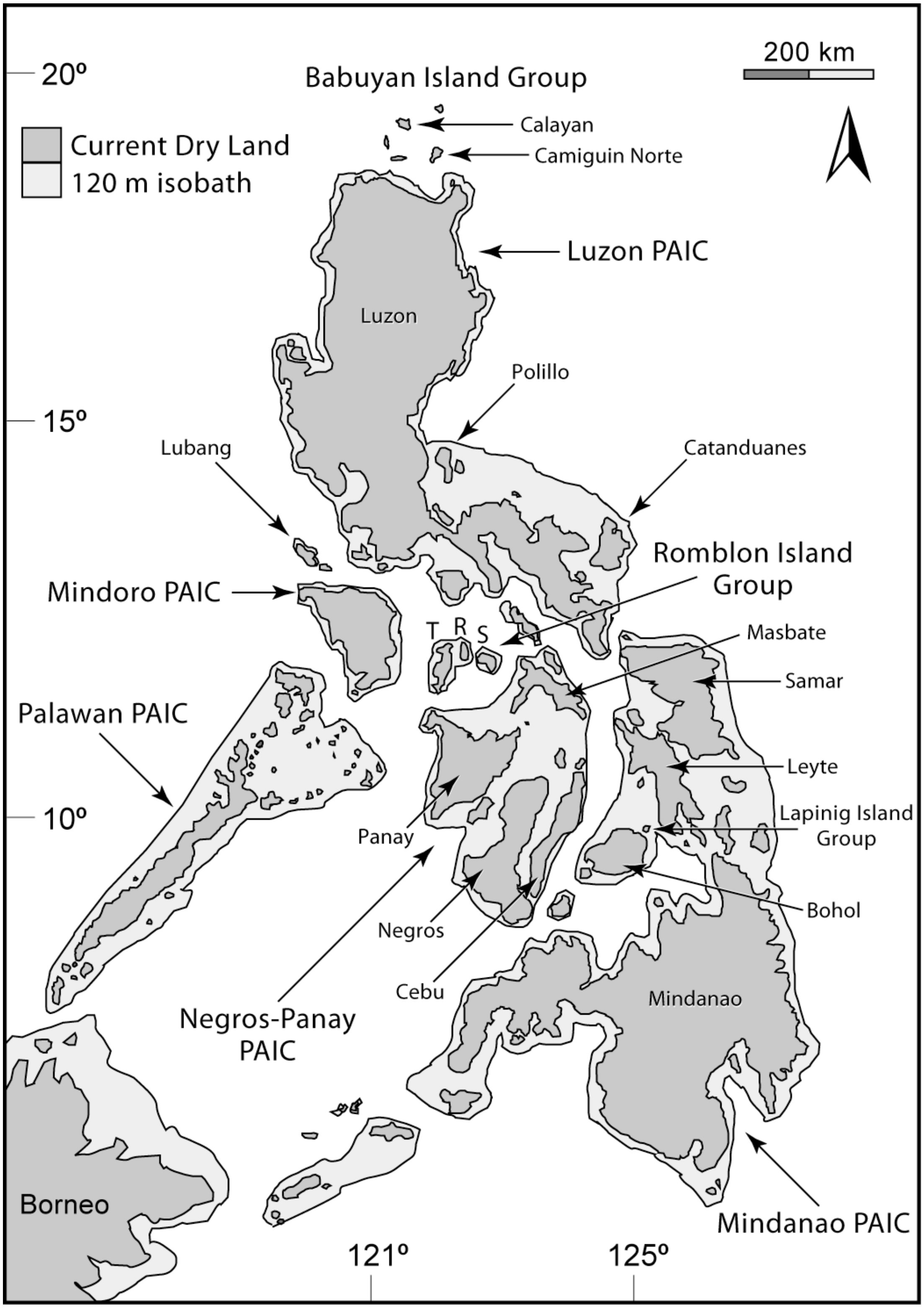
CHAPTER 1

Phylogeny of Philippine slender skinks (Scincidae: *Brachymeles*) reveal underestimated species diversity, complex biogeographical relationships, and cryptic patterns of lineage diversification

Only four genera of scincid lizards are known to possess both fully limbed and limbless species (*Brachymeles*, *Chalcides*, *Lerista*, and *Scelotes*; Lande, 1978; Wiens and Slingluff, 2001; Brandley et al., 2008). Of these four genera, the genus *Brachymeles* is the least well known, with recent studies indicating the recognized diversity of the group is vastly underestimated (Siler, 2010; Siler and Brown, 2010; Siler et al., 2009a, 2010a,b; Siler et al., in press a,b,c,d). Within the genus, all but one of the 25 recognized species are endemic to the Philippines (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980; Siler et al., 2009a, 2010a,b; Siler and Brown, 2010); the exception is *B. apus* from northern Borneo (Hikida, 1982). Thirteen species are pentadactyl (*bicolor*, *boholensis, boulengeri*, *gracilis*, sp. A [Masbate Island; Siler and Brown, 2010], *makusog, mindorensis, orientalis, schadenbergi*, *talinis, taylori,* sp. B [Luzon + Babuyan islands; Siler and Brown, 2010], and sp. C [Jolo Island; Siler and Brown, 2010]), eight are non-pentadactyl, with incompletely developed limbs and reduced numbers of digits (*bonitae*, *cebuensis*, *elerae*, *muntingkamay, pathfinderi*, *samarensis*, *tridactylus*, and *wrighti*), and four are entirely limbless (*apus*, *minimus, lukbani,* and *vermis*). Within the non-pentadactyl species, there exist a wide range of limb- and digit-reduced states. Some species have minute limbs that lack full digits (*bonitae*, *cebuensis*, *muntingkamay, samarensis, tridactylus*; Duméril and Bibron, 1839; Brown, 1956; Brown and Rabor, 1967; Siler et al., 2009a). Other non-pentadactyl species have moderately developed limbs with four digits on the hands and feet (*elerae, wrighti*), or four digits on the feet and five digits on the hands (*pathfinderi*: Taylor, 1917, 1925). All species are semi-fossorial and typically found in dry, rotting material inside decaying logs or in loose soil, forest floor detritus, and leaf litter.

The genus *Brachymeles* was first described by Dumeril and Bibron (1839) for the small, limb-reduced species *Brachymeles bonitae*. As species diversity accumulated, various authors have noted morphological variation among island populations of many of the polytypic and widespread species (Taylor, 1922; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). In *Brachymeles*, several species (*B. Bonitae, B. samarensis, B. tridactylus*) currently span recognized faunal regions within the Philippines, or Pleistocene Aggregate Island Complexes (PAICs; Brown and Guttman, 2002; Brown and Diesmos, 2002, 2009; Fig. 1.1, and defy biogeographic boundaries as traditionally conceived (Brown and Diesmos, 2009). Among skinks and other Philippine land vertebrates, multiple lineages have similar widespread distributions, spanning multiple PAICs. These widespread distributions have been the focus of many recent studies, which have revealed that few endemic Philippine reptiles actually possess broad distributions spanning regional faunistic boundaries (Brown et al., 2000, 2009; Brown and Diesmos, 2002, 2009; Siler et al., 2010a,b; Siler and Brown, 2010; Welton et al., 2009, 2010a,b). Although these recent efforts have shed light on cryptic diversity among Philippine vertebrates, the continued recognition of many widespread species may still compromise our understanding of patterns of regional diversity. Presently, the incredible diversity of endemic vertebrate species in the Philippines is recognized to be distributed among: (1) Pleistocene Aggregate Island Complexes (PAICs; Inger, 1954; Heaney, 1985; Voris, 2000; Brown and Diesmos, 2002), (2) individual islands within PAICs, and (3) upland subcenters of diversity within individual landmasses (review: Brown and Diesmos, 2009).

Figure 1.1. Map of the Philippines showing the five recognized major Pleistocene Aggregate Island Complexes (PAICs) and additional deep-water islands. Current islands in the Philippines are shown in medium grey; light gray areas enclosed in black 120 m bathymetric contours indicate the hypothesized maximum extent of land during the mid- to late Pleistocene.


20º
15º
10º
121º
125º
200 km
Babuyan Island Group
Calayan
Camiguin Norte
Current Dry Land
120 m isobath
Luzon PAIC
Luzon
Polillo
Lubang
Catanduanes
Romblon Island Group
Mindoro PAIC
T
R
S
Masbate
Samar
Palawan PAIC
Leyte
Lapinig Island Group
Panay
Bohol
Negros
Cebu
Mindanao
Negros-Panay PAIC
Borneo
Mindanao PAIC

Historically, the shared body plans and similar external morphological features among populations of *Brachymeles*, and the absence of dense population sampling across the Philippines, proved problematic for diagnosing species (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). Although long considered to be a small clade of Southeast Asian lizards (the last revision enumerated only 15 species; Brown and Alcala, 1980), recent studies have significantly increased the known species diversity and expanded the range of variation in body form (Siler et al., 2009a, 2010a,b; Siler and Brown, 2010). Additionally, several rare, mid-to-high elevation species long represented by only a few specimens, in some cases without knowledge of their exact type locality (e.g., *Brachymeles bicolor, B. elerae, B. wrighti, B. pathfinderi*), have recently been rediscovered (Siler, 2010; Siler et al., in press a,b; Siler and Brown, 2010). These studies, coupled with increased sampling throughout the Philippines, have provided a comprehensive dataset with which to begin evaluating the taxonomic stability of polytypic and widespread species across the Philippines. Additionally, the availability of tissue samples for all but two known species of *Brachymeles* now allows for robust estimates of phylogenetic relationships among recognized widespread and polytypic species, and evaluation of species boundaries. For example, Siler and Brown (2010) recently revised two polytypic species (*B. boulengeri* and *B. schadenbergi*) and one widespread species (*B. talinis*); this work resulted in the recognition of ten genetically and morphologically distinct species. Several other species including *B. samarensis* and *B. bonitae* (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980) are still recognized as having widespread distributions that span multiple historically recognized biogeographic provinces in the Philippines (Dickerson et al., 1925; Kloss, 1929; Inger, 1954; Brown and Diesmos, 2002).

In this study we investigate the biogeography of *Brachymeles* from a phylogenetic perspective, providing the first estimate of phylogenetic relationships for this unique radiation of Southeast Asian lizards. We strove to estimate the phylogenetic position of *Brachymeles* among scincid lizards in order to provide insight into patterns of body form evolution and polarity of character change and provide the first statistical tests of several hypotheses. We provide the first glimpse into the major body form transitions in *Brachymeles*, particularly with respect to miniaturization, limb reduction, and digit loss. We also employ a Bayesian ancestral area reconstruction to gain insight into the biogeographical history of the genus. Finally we test the following taxonomic hypotheses: (1) *Brachymeles* is monophyletic; (2) All recognized and formerly recognized polytypic species are monophyletic; and (3) All recognized widespread species are monophyletic. Our data reveal patterns inconsistent with all of the above predictions and at odds with currently recognized taxonomy; we conclude that species diversity within the genus is vastly underestimated and that cryptic patterns of lineage diversification prevail in this poorly known group of Southeast Asian lizards.

Methods

Taxon sampling and data collection

Ingroup sampling included 90 individuals collected from 43 localities, with 23 of the 25 currently recognized species of *Brachymeles* represented (Fig. 1.2; Appendix I; Siler and Brown, 2010). The two missing species in our analyses are *Brachymeles vermis* and *B. wrighti*. *Brachymeles wrighti* is known from two damaged specimens from northern Luzon Island, and *B. vermis* occurs in the Sulu archipelago (where biologists are not permitted to work due to logistical and security obstacles). No tissues have ever been collected for either of these species.

To assess the monophyly of the genus as well as investigate appropriate outgroup taxa, a broad sampling of scincid species from the subfamilies Lygosominae and Scincinae were included, as well as a single outgroup sample from the family Lacertidae (Appendix I). For all 108 samples, complete or partial sequences were collected for mitochondrial NADH Dehydrogenase Subunit 1 (ND1), NADH Dehydrogenase Subunit 2 (ND2), ATPase 8 (ATP8), and ATPase 6 (ATP6) genes (Table 1.1). Additionally, three nuclear loci, Brain-derived Neurotrophic Factor (BDNF), R35, and PTGER4, were completely sequenced for nearly all ingroup samples and many of the outgroup samples (Table 1.1, Appendix I). All sequences were deposited in GenBank (Appendix II).

Genomic DNA was extracted from liver tissues stored in 95–100% ethanol following a guanidine thiocyanate protocol (Esselstyn et al., 2008). We used a combination of published and newly developed primers, as well as a variety of thermal profiles (Table 1.1). Amplified products were visualized on 1.5% agarose gels. PCR products were purified with 1 μL of a 20% dilution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ) on the following thermal profile: 31 min at 37°, followed by 15 min at 80°. Cycle sequencing reactions were run using ABI Prism BigDye Terminator chemistry (Ver. 3.1; Applied Biosystems, Foster City, CA), and purified with Sephadex (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). Purified products were analyzed with an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Continuous gene sequences were assembled and edited using Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Figure 1.2. Distribution of pentadactyl and non-pentadactyl *Brachymeles* samples from the Philippines (see species keys within each map). Current islands in the Philippines are shown in medium grey; light gray areas enclosed in black 120 m bathymetric contours indicate the hypothesized maximum extent of land during the mid- to late Pleistocene.

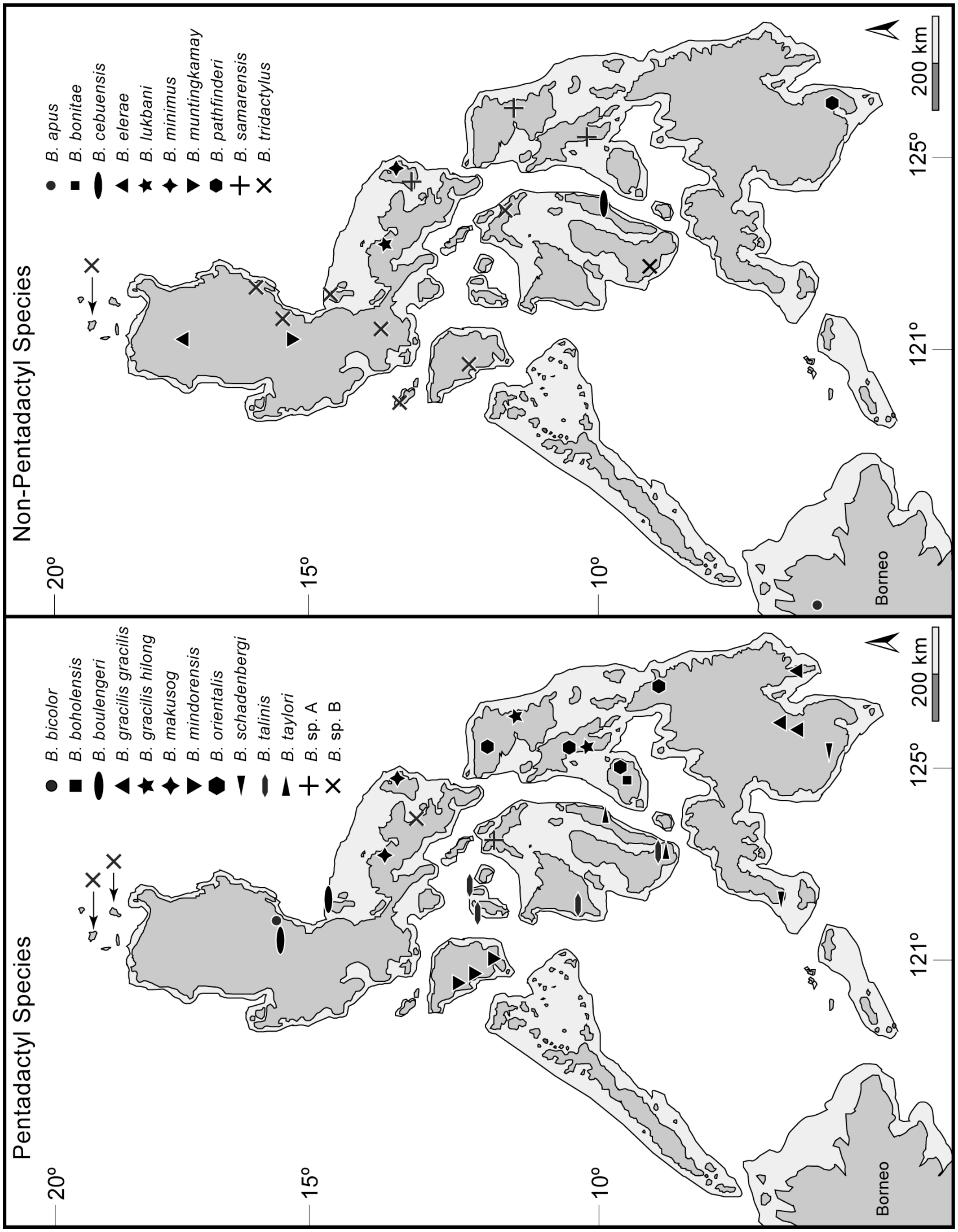

Pentadactyl Species
B. bicolor
B. boholensis
B. boulengeri
B. gracilis gracilis
B. gracilis hilong
B. makusog
B. mindorensis
B. orientalis
B. schadenbergi
B. talinis
B. taylori
B. sp. A
B. sp. B
20°
15°
10°
121°
125°
Borneo
200 km
Non-Pentadactyl Species
B. apus
B. bonitae
B. cebuensis
B. elerae
B. lukbani
B. minimus
B. muntingkamay
B. pathfinderi
B. samarensis
B. tridactylus
20°
15°
10°
121°
125°
Borneo
200 km

Table 1.1. Summary of primers and annealing temperatures employed in this study.

Locus	Primer Name	Sequence	Annealing Temperatures	Primer Source
NADH 1	16dr	5'–CTACGTGATCTGAGTTCAGACCGGAG–3'	52–53°	Brandley et al., 2005
	tMet	5'–TCGGGGTATGGGCCCRARAGCTT–3'	52–53°	Brandley et al., 2005
NADH 2	ND2.Brach.F1	5'–TTATCGCAACAAAACACCACCC–3'	52–53°	This study
	ND2.Brach.R1	5'–AGCYCAGAGGTGATTCACGC–3'	52–53°	This study
	ND2.Brach.R2	5'–CCGCTGGATTGGGTGTTTAGC–3'	52–53°	This study
ATP8,6	ATP.F	5'–CTCAGARATCTGCGGGYCAAATCACA–3'	58°	M. Brandley, unpublished data
	ATP.R	5'–GTGCYTTCTCGRRTAATRTCYCGTCAT–3'	58°	M. Brandley, unpublished data
BDNF	BDNF.F	5'–CCCCAATGAAAGAAGTGASCCTC–3'	55°	Crottini et al., 2009
	BDNF.R	5'–TGGGTAGTTCGGCACTGAGAATTCC–3'	55°	Crottini et al., 2009
PTGER4	PTGER4.F1	5'–GACCATCCCGGCCGTMATGTTCATCTT–3'	55°	Townsend et al., 2008
	PTGER4.R5	5'–AGGAAGGARCTGAAGCCCGCATACA–3'	55°	Townsend et al., 2008
R35	R35.F	5'–GACTGTGGAYGAYCTGATCAGTGTGG–3'	55°	Fry et al., 2006
	R35.R	5'–GCCAAAATGAGSGAGAARCGCTTCTG–3'	55°	Fry et al., 2006

Sequence alignment and phylogenetic analyses

Initial alignments were produced in Muscle (Edgar, 2004), and manual adjustments made in MacClade 4.08 (Maddison and Maddison, 2005). To assess phylogenetic congruence between the mitochondrial and nuclear data, we inferred the phylogeny for each gene independently using likelihood and Bayesian analyses, and performed pairwise partition homogeneity tests in PAUP 4.0b 10 (Swofford, 2002) with 100 replicates for each pairwise comparison to assess set congruence. Following the observation of no statistically significant incongruence between datasets, we felt justified in using the combined, concatenated, data for subsequent analyses. Exploratory analyses of the combined dataset of 108 individuals (including outgroup taxa with missing data for several genes) and a reduced dataset of individuals with no missing data exhibited identical relationships; we therefore chose to include all available data (108 individuals) for subsequent analyses of the concatenated dataset. Alignments and resulting topologies were deposited in TreeBase (SN11187).

Parsimony analyses were conducted in PAUP* 4.0b 10 (Swofford, 2002), with gaps treated as missing data and all characters weighted equally. Most parsimonious trees were estimated using heuristic searches with 1000 random addition-sequence replicates and tree bisection and reconnection (TBR) branch swapping. To assess clade support, nonparametric bootstrapping was conducted using 1000 bootstrap replicates, each with 100 random addition-sequence replicates and TBR branch swapping.

Partitioned Bayesian analyses were conducted in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). The mitochondrial dataset was partitioned by codon position for the protein-coding region of ND1 and ND2 and by gene region for the short gene regions ATP8 and ATP6. The Akaike Information Criterion (AIC), as implemented in jModeltest v0.1.1 (Guindon and Gascuel, 2003; Posada, 2008), was used to select the best model of nucleotide substitution for each partition (Table 1.2). The best-fit model for each data partition was implemented in subsequent Bayesian analyses. A rate multiplier model was used to allow substitution rates to vary among subsets, and default priors were used for all model parameters. We ran four independent Metropolis-coupled MCMC analyses, each with four chains and an incremental heating temperature of 0.05. All analyses were run for 18 million generations, sampling every 5000 generations. To assess stationarity, all sampled parameter values and log-likelihood scores from the cold Markov chain were plotted against generation time and compared among independent runs using Tracer v1.4 (Rambaut and Drummond, 2007). Finally, we plotted the cumulative and non-overlapping split frequencies of the 20 most variable nodes, and compared split frequencies among independent runs using Are We There Yet? [AWTY (Wilgenbusch et al., 2004)]. Although all samples showed patterns consistent with stationarity after 2.5 million generations (i.e., the first 12.5%), we conservatively discarded the first 20% of samples as burn-in.

In preliminary Bayesian analyses of the combined dataset, the independent runs failed to converge. We tried (1) lowering the incremental heating temperature to 0.02, (2) using an unconstrained branch length prior with an exponential distribution of 25 (Siler et al. 2010c; Marshall 2006, 2010), and (3) removing outgroup taxa with large amounts of missing data. Although some of the trials of individual permutations of parameters resulted in a failure to converge, the incorporation of the above, plus an unconstrained branch length prior with an exponential distribution and a mean of 25 resulted in convergence. Once complete convergence was achieved, we proceeded with final analyses, presented here.

Table 1.2. Models of evolution selected by AIC and applied for partitioned, phylogenetic analyses.

Partition	AIC Model	Number of Characters
NADH 1, 1st codon position	GTR + Γ	322
NADH 1, 2nd codon position	GTR + Γ	322
NADH 1, 3rd codon position	GTR + Γ	322
NADH 2, 1st codon position	GTR + Γ	287
NADH 2, 2nd codon position	GTR + Γ	287
NADH 2, 3rd codon position	GTR + Γ	287
ATP8	HKY + Γ	157
ATP6	GTR + Γ	682
BDNF	GTR + Γ	715
PTGER4	HKY + Γ	490
R35	GTR + Γ	689

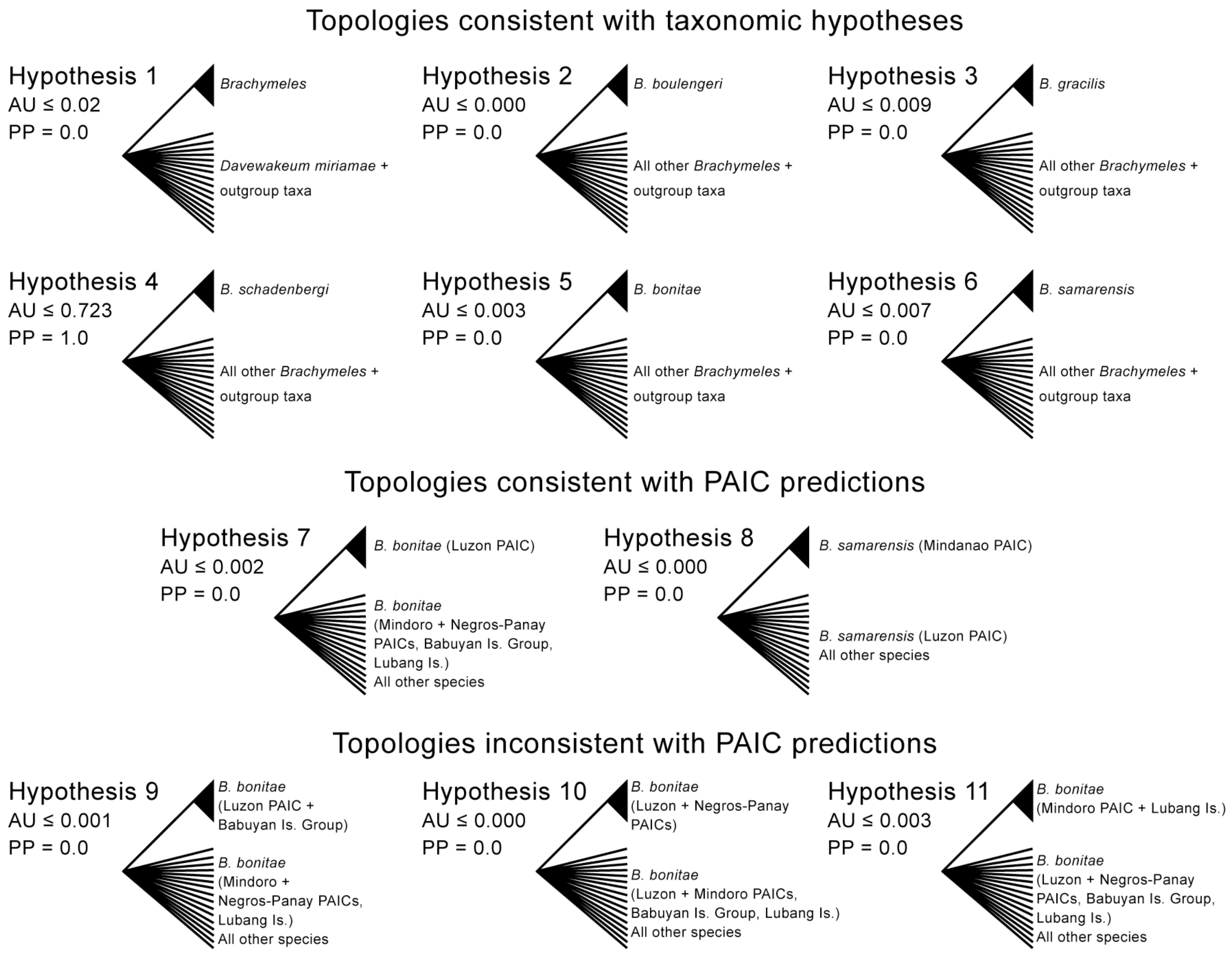
Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.0 (Stamatakis, 2006) on the concatenated dataset the same partitioning strategy as for Bayesian analysis. The more complex model (GTR + Γ) was used for all subsets (Table 1.2), and 100 replicate ML inferences were performed for each analysis. Each inference was initiated with a random starting tree, and employed the rapid hill-climbing algorithm (Stamatakis, 2007). Clade confidence was assessed with 100 bootstrap pseudoreplicates employing the rapid hill climbing algorithm (Stamatakis et al., 2008).

Topology tests

We tested taxonomy- and phylogeography-based hypotheses to address questions concerning the patterns of *Brachymeles* diversification (Fig. 1.3): (1) Is the genus *Brachymeles* monophyletic? (2) Are the currently and formerly recognized polytypic species (*B. boulengeri, B. gracilis, B. schadenebergi*) monophyletic? (3) Are the two "widespread" species (*B. bonitae, B. samarensis*) monophyletic? (4) Does the PAIC model of diversification explain the patterns of genetic diversity found in widespread species of Philippine *Brachymeles*? And, (5) Are the patterns of genetic diversity in widespread species of Philippine *Brachymeles* similar to those noted in other lineages (Siler et al., 2010c; Jones & Kennedy, 2008; McGuire & Kiew, 2001; Steppan et al., 2003; Alfaro et al., 2004)?

We evaluated each question using Bayesian methods, and the approximately unbiased (AU) test (Shimodaira and Hasegawa, 2001; Shimodaira, 2002) as implemented in Siler et al. (2010c). The topological constraints for these questions are illustrated in Figure 1.3, with hypotheses 1–6 derived from taxonomic questions, and hypotheses 7 and 8 derived from the PAIC predictions; the remaining hypotheses (9–11) have been observed in other taxa and are, in part, derived from

Figure 1.3. Six taxonomy-based hypotheses tested in the study. Each hypothesis is illustrated by constraint trees used in AU and Bayesian tests. The highest P-values recovered from each AU test (AU), and the posterior probabilities (PP) of the constraint topology, are shown.


Topologies consistent with taxonomic hypotheses
Hypothesis 1
AU ≤ 0.02
PP = 0.0
Brachymeles
Davewakeum miriamae + outgroup taxa
Hypothesis 2
AU ≤ 0.000
PP = 0.0
B. boulengeri
All other Brachymeles + outgroup taxa
Hypothesis 3
AU ≤ 0.009
PP = 0.0
B. gracilis
All other Brachymeles + outgroup taxa
Hypothesis 4
AU ≤ 0.723
PP = 1.0
B. schadenbergi
All other Brachymeles + outgroup taxa
Hypothesis 5
AU ≤ 0.003
PP = 0.0
B. bonitae
All other Brachymeles + outgroup taxa
Hypothesis 6
AU ≤ 0.007
PP = 0.0
B. samarensis
All other Brachymeles + outgroup taxa
Topologies consistent with PAIC predictions
Hypothesis 7
AU ≤ 0.002
PP = 0.0
B. bonitae (Luzon PAIC)
B. bonitae (Mindoro + Negros-Panay PAICs, Babuyan Is. Group, Lubang Is.)
All other species
Hypothesis 8
AU ≤ 0.000
PP = 0.0
B. samarensis (Mindanao PAIC)
B. samarensis (Luzon PAIC)
All other species
Topologies inconsistent with PAIC predictions
Hypothesis 9
AU ≤ 0.001
PP = 0.0
B. bonitae (Luzon PAIC + Babuyan Is. Group)
B. bonitae (Mindoro + Negros-Panay PAICs, Lubang Is.)
All other species
Hypothesis 10
AU ≤ 0.000
PP = 0.0
B. bonitae (Luzon + Negros-Panay PAICs)
B. bonitae (Luzon + Mindoro PAICs, Babuyan Is. Group, Lubang Is.)
All other species
Hypothesis 11
AU ≤ 0.003
PP = 0.0
B. bonitae (Mindoro PAIC + Lubang Is.)
B. bonitae (Luzon + Negros-Panay PAICs, Babuyan Is. Group, Lubang Is.)
All other species

expectations based on geological history and/or island proximity. Using the full, combined dataset, and the same settings as the RAxML analyses described above, 100 ML searches were performed under each of the 13 constraints. All 1,200 trees produced by RAxML (100 from the unconstrained analysis and 100 from each of the 11 constrained analyses), were filtered in PAUP to remove identical topologies. A modified version of RAxML (provided by Alexandros Stamatakis) allowed the per-site likelihoods to be estimated for each of the 116 unique topologies under a partitioned model. An AU test was then performed on the per-site likelihoods from all 116 using CONSEL v0.1i (Shimodaira and Hasegawa, 2001). The p-value reported for a given hypothesis is the largest p-value of all the trees inferred under that constraint. To automate various steps in the process, perl and python scripts were written by J. Oaks and CDS (available by request). For the Bayesian approach, we took the percentage of 11520 post burn-in trees consistent with each hypothesis to represent the posterior probability that the hypothesis is true.

Relative time analyses

To test the combined dataset for deviations from a molecular clock, we optimized likelihood scores in PAUP* 4.0b10 with a molecular clock enforced and not enforced on the maximum-likelihood topology. A likelihood ratio test ([LRT] Arbogast et al., 2002; Felsenstein, 2004) significantly rejected a molecular clock ($p \leq 0.00$), and subsequent analyses were conducted within a relaxed clock framework. The chronogram used for ancestral state reconstructions in this study was inferred in a Bayesian framework using BEAST v1.5.3 (Drummond and Rambaut, 2007). A starting tree was designated for each run by manually adjusting the xml BEAUti v1.5.2 (Drummond and Rambaut 2007) output file. The consensus tree file from Bayesian analyses was imported into R (R Development Team, 2008), and using the ape (Paradis et al., 2004), the phylogeny was paired down into individual lineages per species or morphologically distinct, non-monophyletic populations (*B. bonitae* and *B. samarensis*). The 47-taxon phylogeny was then converted to a chronogram using the nonparametric rate smoothing method of Sanderson (1997) implemented in the ape (Paradis et al. 2004) package of R, and was exported in Newick format for use as the starting tree for BEAST analyses. Four independent BEAST runs of 50 million generations were completed under the same partitioning strategy as for Bayesian analyses, imposing an uncorrelated lognormal relaxed clock prior on substitution rate (Drummond et al., 2006) and Yule speciation prior. Parameters were sampled every 5000 generations and the initial 50% of each run was discarded as burn-in, leaving a combined 20,000 trees in the posterior distribution. To evaluate convergence among MCMC analyses, trends and distributions of parameters, including the likelihood score, were examined in Tracer (Rambaut and Drummond 2007).

Biogeographical reconstructions

To explore whether there is statistical support for historical biogeographic patterns within Philippine species of the genus *Brachymeles*, we compared empirically observed (extant) species distributions to estimates of ancestral distributions using the program BayesTraits version 1.0 (Pagel, 1994; Pagel and Lutzoni, 2002). For all analyses we examined a model of character evolution that assumed equal rates of distributional transitions. For all analyses we seeded the mean and variance of the gamma prior from uniform distributions on the interval 0 to 20 by enforcing the “Hyperpriorall” command of BayesTraits. The LogCombiner v1.5.4 program of the BEAST v1.5.3 (Drummond and Rambaut 2007) package was used to combine trees from the posterior distributions of the four independent Beast runs, producing a file with 2,000 trees from the posterior distribution. All 2,000 chronograms were then used in analyses of distribution data in BayesTraits in an effort to account for phylogenetic uncertainty. In the program BayesTraits, we ran MCMC chains for 25 million generations, sampling every 5000th generation, and discarded the first 50% of samples as burn-in. The remaining 2,500 samples were used to summarize the posterior probabilities of ancestral character states for all nodes of the tree. The "AddNode" command of BayesTraits was used to specify all nodes in the chronograms for visualization of the posterior probabilities of character states at each node.

We ran a series of additional analyses on nodes with ambiguous estimated ancestral character states. The "fossil" command of BayesTraits was used to sequentially enforce the character states making up 95% of the posterior probability at a single node, prioritizing character states with the highest posterior probability. Bayes factors were again applied, and the state supported at each ambiguous node was summarized with the Bayes factors measure of support for that ancestral state (Kass and Raftery 1995; Nylander et al. 2004). We enforced the ancestral states for all nodes sister to Philippine *Brachymeles* to be considered non-Philippine in distribution.

Results

Taxon sampling, data collection, and sequence alignment

The complete, aligned matrix contains 82 samples of *Brachymeles*, representing 23 of the 25 recognized taxa, for the mitochondrial genes and nuclear loci. Seventeen additional samples are included as outgroups, consisting of representatives from the subfamilies Lygosominae and Scincinae within the family Scincidae as well as a single representative from the lizard family Lacertidae. Following initial unrooted analyses, and the results of recent squamate evolution studies (Whiting et al., 2003; Townsend et al., 2004; Wiens et al., 2006; Brandley et al., 2005; Brandley et al., 2008), we rooted the tree using samples of *Takydromus sexilineatus* from China. Within each gene, variable and parsimony-informative characters are observed as follows: 118 and 107 out of 158 (ATP8); 357 and 339 out of 683 (ATP6); 504 and 464 out of 966 (ND1); 575 and 531 out of 861 (ND2); 115 and 69 out of 715 (BDNF); 127 and 95 out of 490 (PTGER); 304 and 220 out of 689 (R35). The number of most parsimonious trees and consistency indices resulting from MP analyses of the combined dataset is 78 trees/CI = 0.318.

Phylogenetic analyses

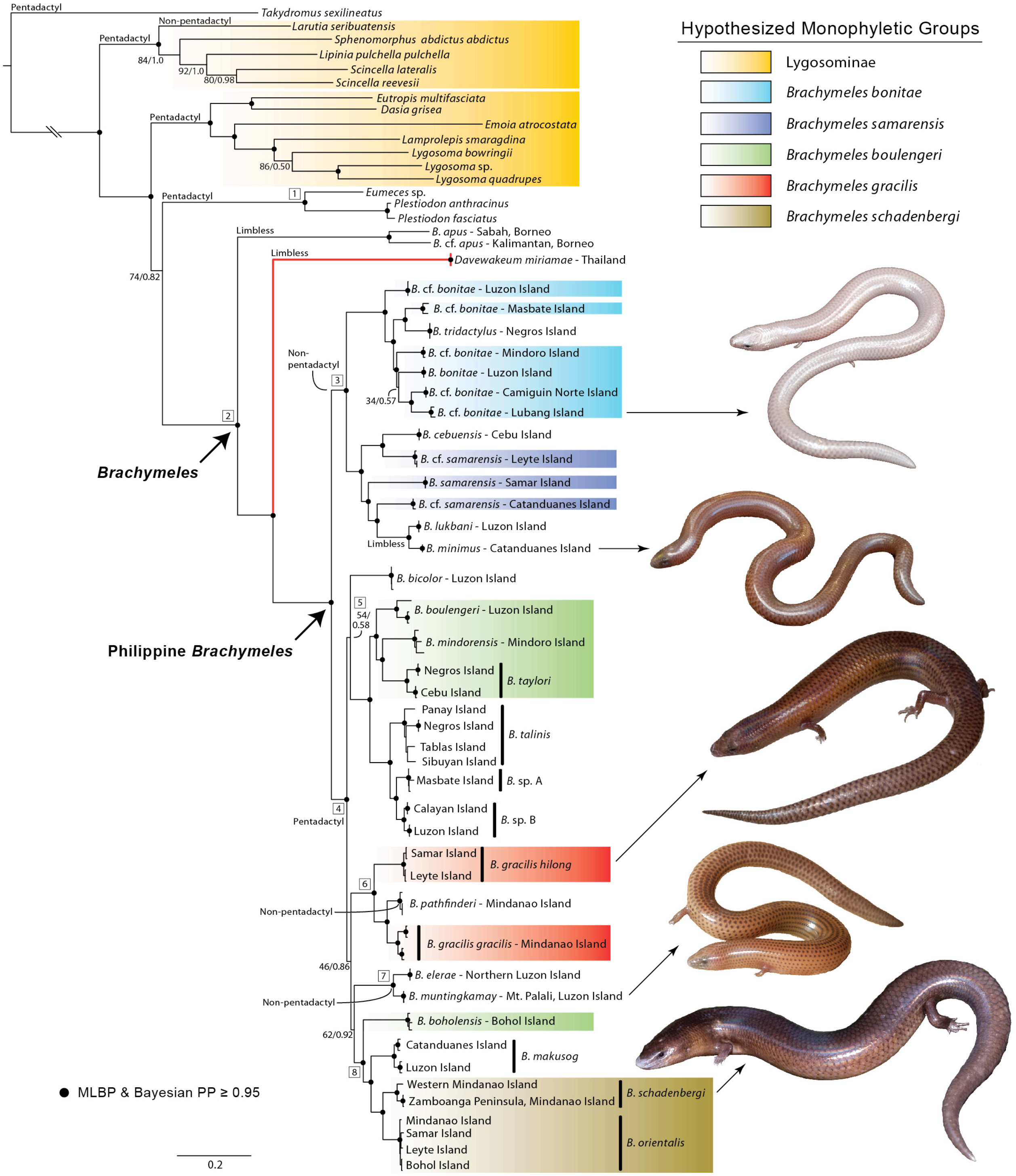
Analyses of the combined data (ND1, ND2, ATP8, ATP6, BDNF, PTGER4, R35) result in topologies with high Maximum Likelihood bootstrap support and posterior probabilities (Fig. 1.4). Topologies are congruent across these analyses (Fig. 1.4). All analyses support three clades of outgroup scincid taxa (Fig. 1.4). Outgroup samples from the subfamily Lygosominae are never recovered as part of a single clade (Fig. 1.4); however, given the possibility that the chosen root for analyses and the outgroup sampling strategy likely influence outgroup relationships, additional taxa should be obtained for a more exhaustive analysis of scincid relationships before definitive conclusions may be drawn.

The genera *Eumeces* and *Plestiodon* are recovered as a single, strongly supported clade in all analyses (Fig. 1.4, Clade 1). Although this clade is often supported as the closest group of outgroup species to *Brachymeles* + *Davewakeum* (ML; Fig. 1.4), support for its placement was always low, and in Bayesian analyses, the clade is regularly recovered as part of a three clade polytomy of outgroup samples (results not shown). The species *Davewakeum miriamae* is always recovered nested within *Brachymeles* samples, between the clade *B. apus* + *B.* cf. *apus* from Borneo and all Philippine *Brachymeles* (Fig. 1.4).

Although the genus *Brachymeles* (as currently recognized) is never recovered as a monophyletic group, all analyses strongly support the monophyly of *Brachymeles* + *Davewakeum* (Fig. 1.4, Clade 2). The two limbless species *Brachymeles apus* (Borneo) and *Davewakeum miriamae* (Thailand) are always recovered as the two lineages most closely related to all Philippine *Brachymeles* (Fig. 1.4). Within the Philippines, all limbless species and the majority of limb-reduced species are recovered as part of two reciprocally monophyletic sub-clades, and together are sister to all pentadactyl species and the remaining non-pentadactyl taxa (Fig. 1.4, Clade 3). Sampled populations of the currently recognized widespread, limb-reduced species *Brachymeles bonitae* and *B. samarensis* are never recovered as monophyletic (Fig. 1.4, Clade 3). *Brachymeles cebuensis*, one of only two species of *Brachymeles* with unequal numbers of fingers and toes (three fingers/two toes) is recovered as sister to *B. samarensis* from Leyte Island (Fig. 1.4, Clade 3). Within Clade 1, all analyses recover a population of *Brachymeles bonitae* with one fore-limb digit and one hind limb digit as sister to the tridactyl species *B. tridactylus,* and the five other populations of *B. bonitae* (Fig. 1.4). Additionally, a morphologically distinct population of *B.* cf. *bonitae* with limbs but no digits is supported to be the sister species to *B. tridactylus* (Fig. 1.4, Clade 3).

All pentadactyl species and three non-pentadactyl species of *Brachymeles* are always recovered as part of a clade, sister to Clade 3 (Fig. 1.4, Clade 4). Although the two species formerly part of the *Brachymeles schadenbergi* species complex (*B. orientalis* and *B. schadenbergi*) are always recovered as reciprocally monophyletic lineages (Fig. 1.4, Clade 8), the polytypic species *B. gracilis*, and the four species formerly part of the *B. boulengeri* species

Figure 1.4. Hypothesized relationships of *Brachymeles*, illustrated by ML estimates (-ln L 54137.110363). Nodes supported by ≥95% Bayesian PP and ML bootstrap support were considered significantly supported and are indicated by black circles. Terminals are labeled with abbreviated taxonomic names, followed by general geographic distribution (Appendix I). The placement of the genus *Davewakeum* is indicated by red braches. Colored boxes highlight hypothesized monophyletic groups. Colored clade bars highlight general body plans observed for species within designated clades. Alpha and numerical labels correspond to clades referred to in the Results and Discussion. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.


Hypothesized Monophyletic Groups
Lygosominae
Brachymeles bonitae
Brachymeles samarensis
Brachymeles boulengeri
Brachymeles gracilis
Brachymeles schadenbergi
Pentadactyl
Takydromus sexilineatus
Non-pentadactyl
Larutia seribuatensis
Pentadactyl
Sphenomorphus abdictus abdictus
Lipinia pulchella pulchella
84/1.0
92/1.0
Scincella lateralis
80/0.98
Scincella reevesii
Eutropis multifasciata
Dasia grisea
Pentadactyl
Emoia atrocostata
Lamprolepis smaragdina
Lygosoma bowringii
86/0.50
Lygosoma sp.
Lygosoma quadrupes
Pentadactyl
1
Eumeces sp.
Plestiodon anthracinus
Plestiodon fasciatus
Limbless
B. apus - Sabah, Borneo
B. cf. apus - Kalimantan, Borneo
74/0.82
Limbless
Davewakeum miriamae - Thailand
B. cf. bonitae - Luzon Island
B. cf. bonitae - Masbate Island
B. tridactylus - Negros Island
Non-pentadactyl
B. cf. bonitae - Mindoro Island
3
B. bonitae - Luzon Island
B. cf. bonitae - Camiguin Norte Island
34/0.57
B. cf. bonitae - Lubang Island
2
Brachymeles
B. cebuensis - Cebu Island
B. cf. samarensis - Leyte Island
B. samarensis - Samar Island
B. cf. samarensis - Catanduanes Island
B. lukbani - Luzon Island
Limbless
B. minimus - Catanduanes Island
B. bicolor - Luzon Island
5
54/0.58
B. boulengeri - Luzon Island
Philippine Brachymeles
B. mindorensis - Mindoro Island
Negros Island
Cebu Island
B. taylori
Panay Island
Negros Island
Tablas Island
Sibuyan Island
B. talinis
Masbate Island
B. sp. A
4
Calayan Island
Pentadactyl
Luzon Island
B. sp. B
Samar Island
Leyte Island
B. gracilis hilong
6
B. pathfinderi - Mindanao Island
Non-pentadactyl
B. gracilis gracilis - Mindanao Island
46/0.86
7
B. elerae - Northern Luzon Island
Non-pentadactyl
B. muntingkamay - Mt. Palali, Luzon Island
B. boholensis - Bohol Island
62/0.92
Catanduanes Island
B. makusog
Luzon Island
8
● MLBP & Bayesian PP ≥ 0.95
Western Mindanao Island
Zamboanga Peninsula, Mindanao Island
B. schadenbergi
Mindanao Island
Samar Island
Leyte Island
Bohol Island
B. orientalis
0.2

complex, are strongly supported to be paraphyletic (Fig. 1.4, Clades 5, 6, 8). All analyses recover four well-supported clades within Clade 4 (Fig. 1.4). Although Bayesian analyses provided high support for the relationships between these clades, likelihood analyses provide less support (Fig. 1.4, Clade 4).

Three non-pentadactyl species are recovered as part of Clade 4 in all analyses (Fig. 1.4). The tetradactyl species *Brachymeles elerae* and the tridactyl species *B. muntingkamay* are always recovered as sister taxa (Fig. 1.4, Clade 7); however, the relationship of Clade 7 to the other major clades in Clade 4 is less well supported. *Brachymeles pathfinderi*, the only other species with unequal digit numbers (five fingers/four toes), is recovered with strong support to be nested within the polytypic species *B. gracilis* (Fig. 1.4, Clade 6).

Brachymeles bicolor, the longest species, is recovered as sister to a subclade of three medium-sized species (*B. boulengeri* + *B. mindorensis* + *B. taylori*) and three large species (*B. talinis* + two undescribed species [Siler and Brown, 2010]). *Brachymeles boholensis*, formerly recognized as a subspecies of the *B. boulengeri* species complex, is consistently supported as part of Clade 8, sister to *B. orientalis, B. schadenbergi*, and *B. makusog* (Fig. 1.4).

Topology tests

Results from the Bayesian methods and the approximately unbiased (AU) test were highly consistent. Among the taxonomy-based hypotheses, both methods rejected hypotheses of monophyly for the genus *Brachymeles*, the widespread species *B. bonitae, B. gracilis*, and *B. samarensis*, and the former polytypic species *B. boulengeri* (Fig. 1.3). Additionally, both methods failed to reject the monophyly of the former polytypic species *B. schadenbergi*, now recognized as two distinct sister species (Siler and Brown, 2010; Fig. 1.3). All biogeography-based hypotheses were rejected by both methods (Fig. 1.3).

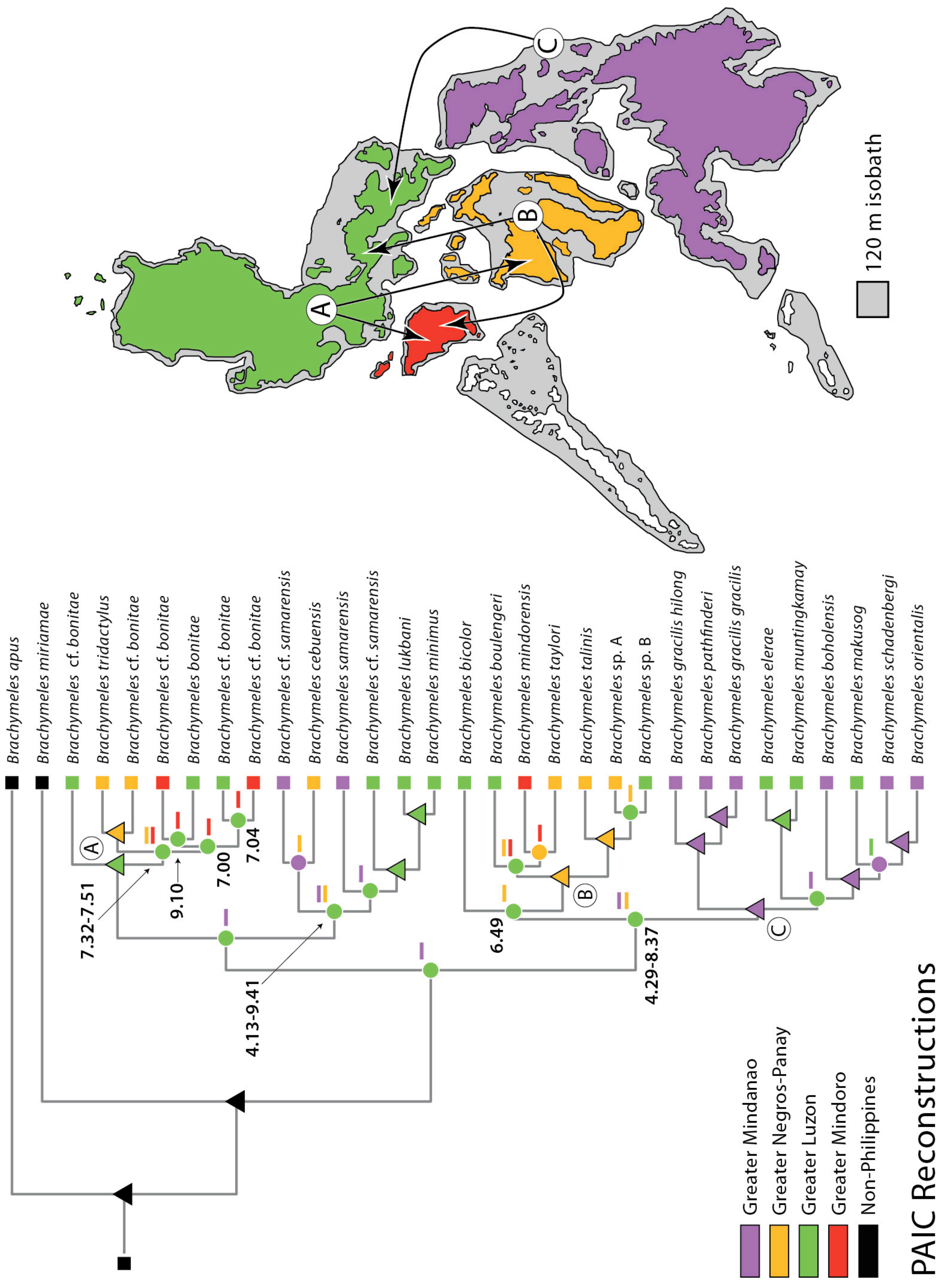
Body form evolution

Our simplified mapping of major body plan variation onto the preferred phylogenetic tree (Fig. 1.4) makes it clear that the evolutionary history of *Brachymeles* involves multiple instances of evolutionary shifts in body size, limb reduction, and digit loss. Although a full understanding of these trends will require a comprehensive analysis of both external (body size, limb proportions, digital states) and internal (vertebral numbers and elongation) morphology, preliminary trends can be ascertained on the basis of results presented here. If it is assumed, for example, that the ancestors of *Brachymeles* possessed similar body plans as the genus' putative closest relatives (*Eumeces, Plestiodon, Lygosoma, Emoia Dasia* and *Eutropis*), then limb reduction and loss may have occurred along the lineages leading to *B. apus* and *B.* cf. *apus,* in the lineage leading to *Davewakeium miriamae,* in the lineage leading to the *B. bonitae* and *B. samarensis* complexes, and independently in the lineages leading to *B. pathfinderi* and *B. muntingkamay* + *B. elerae*. It is interesting to note that the known diversity of pentadactyl species in the genus is endemic to the Philippine.

Historical biogeography

Although the placement of *Brachymeles* within the family Scincidae remains somewhat ambiguous, the impact of ancestral range for all *Brachymeles* does not appear to heavily impact ancestral reconstructions within the genus (not shown). The results of analyses of ancestral areas are never significantly impacted by placing restrictions on the ancestral character states among outgroup taxa and the node giving rise to all *Brachymeles* (not shown). Without *a priori*

Figure 1.5. Maximum clade credibility chronograms and estimated ancestral states of geographic range in *Brachymeles* skinks. Ancestral area reconstructions are indicated at each node. Triangles indicate unambiguous reconstructions of an ancestral area (posterior probability ≥ 0.95), colored according to the hypothesized state. Circles represent ambiguous character reconstructions, with colors representing the preferred area. Colored blocks at each ambiguous node represent alternate states supported in analyses. Bayes factors are provided as an indication of the strength of support for preferred states at ambiguous nodes receiving moderate to strong statistical. For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.


Brachymeles apus
Brachymeles miriamae
Brachymeles cf. bonitae
Brachymeles tridactylus
Brachymeles cf. bonitae
Brachymeles cf. bonitae
Brachymeles bonitae
Brachymeles cf. bonitae
Brachymeles cf. bonitae
Brachymeles cf. samarensis
Brachymeles cebuensis
Brachymeles samarensis
Brachymeles cf. samarensis
Brachymeles lukbani
Brachymeles minimus
Brachymeles bicolor
Brachymeles boulengeri
Brachymeles mindorensis
Brachymeles taylori
Brachymeles talinis
Brachymeles sp. A
Brachymeles sp. B
Brachymeles gracilis hilong
Brachymeles pathfinderi
Brachymeles gracilis gracilis
Brachymeles elerae
Brachymeles muntingkamay
Brachymeles boholensis
Brachymeles makusog
Brachymeles schadenbergi
Brachymeles orientalis
A
B
C
7.32-7.51
9.10
7.00
7.04
4.13-9.41
6.49
4.29-8.37
0
25
50
Greater Mindanao
Greater Negros-Panay
Greater Luzon
Greater Mindoro
Non-Philippines
PAIC Reconstructions
120 m isobath

knowledge of the true patterns of diversification within the Philippines, we conservatively chose a model allowing for equal rates of transition among major faunal regions of the Philippines. Ancestral state reconstruction analyses resulted in many nodes where the reconstructed ancestral range is ambiguous (Fig. 1.5). The Luzon PAIC is the preferred ancestral range in most cases with varying degrees of support (Fig. 1.5). Importantly, all analyses resulted in unambiguous support for ancestral ranges at eleven nodes in the phylogeny, supporting the Luzon, Negros-Panay, and Mindanao PAICs as the ancestral ranges for several clades of Philippine *Brachymeles* (Fig. 1.5A–C). Given strong statistical support for ancestral areas at eleven nodes, we are confident in hypothesizing five dispersal events (Fig. 1.5), including clear dispersal from Luzon to Mindoro, Luzon to the central Visayan islands, dispersal from the Visayas to Mindoro and Luzon, and a clear instance of dispersal from the Mindanao island group to southern Luzon. Considering the moderate to strong statistical support for a specific reconstruction at seven ambiguous nodes (indicated by Bayes factors of 4.13–9.10; Kass and Raftery 1995; Nylander et al. 2004), we infer the possibility of five additional dispersal events (Fig. 1.5).

Discussion

Taxon sampling

Our widespread sampling of individuals across the range of most Philippines *Brachymeles* species allows for fine-scale resolution of phylogenetic relationships and an unprecedented and comprehensive taxonomic review (Siler, 2010; Siler et al., 2009a, 2010a,b; Siler and Brown, 2010; Siler et al., in press c,d). The two species missing in our analyses are *Brachymeles wrighti* from northern Luzon Island and *B. vermis* from the Sulu Archipelago in the southern Philippines. Both species are represented by only a few museum specimens worldwide, and no genetic samples have ever been collected. Previous studies that have included samples of *Brachymeles* have not been able to confidently place the genus *Brachymeles* within the family Scincidae (Brandley et al., 2005, 2008). Although our attempt to sample widely from outgroup taxa results in some well-supported relationships, the most closely related species to the genus *Brachymeles* remains unclear (see also Brandley et al., 2005). We are unable to collect full sequence data for all included outgroup taxa (Appendix I), and missing data may have contributed to weaker support for outgroup relationships. It is anticipated that additional outgroup and gene sampling will aid resolution of these relationships.

Phylogeny and cryptic genetic diversity

Cryptic diversity has been documented as a global phenomenon (Pfenninger and Schwenk, 2007; Bickford et al., 2007), and we now suspect the phenomenon to also characterize Philippine slender skinks (Siler et al., 2009a, 2010a,b; Siler and Brown, 2010; Siler et al., in press c,d). Although we focus on diversity of skinks of the genus *Brachymeles*, our results support the taxonomic issues identified in numerous studies for the family Scincidae (e.g., the non-monophyly of Lygosominae), and phylogenetic studies across the family are needed to provide sweeping taxonomic revisions. Although we did not expect to find that *Davewakeum miriamae* is nested within the genus *Brachymeles*, this result, in retrospect, is not surprising when comparing morphology of this genus to species of *Brachymeles*. *Davewakeum* shares several unique morphological features with *B. apus, B. bonitae*, and *B. samarensis*, including the fusion of the mental and first infralabial scales, the presence of a moderate-sized interparietal scale, nasal scales, two loreal scales, a frontal scale, frontoparietal scales, the presence of a single scale row on the lower eyelid (Siler et al., 2010b; Siler, pers. obs.), and a general elongated, limb-reduced body plan.

With the results of this study, and the fact that the genus *Brachymeles* (Duméril and Bibron, 1839) was described well before *Davewakeum* (Heyer, 1972), we consider *Davewakeum* to be a junior synonym of *Brachymeles* and, consequently, *Brachymeles miriamae*, new combination, to be the fifth limbless species of *Brachymeles*. We note that at least one additional known limbless species (*B.* cf. *apus*, from Kalimantan, south Borneo) awaits description (Iskandar and Bickford, unpublished data).

The conservative body plans within the genus *Brachymeles* have led to confusion over species boundaries, the long accepted recognition of polytypic species, and the recognition of "widespread" species with distributions across accepted faunal boundaries (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). With the exception of *Brachymeles schadenbergi*, the results of this study do not support the monophyly of the currently and previously recognized polytypic species in the genus (Fig. 1.3, 1.4). Furthermore, all currently recognized subspecies within the genus are both strongly supported divergent lineages in the phylogeny and represent unique morphologies, most likely worthy of specific rank (Fig. 1.4; Siler and Brown, 2010; Siler et al., in press d).

The degree to which convergent morphology has led to the underestimation of diversity within the genus can further be exemplified by examining the "widespread" species densely sampled in this study. Populations of the previously-recognized widespread pentadactyl species, *B. talinis*, have recently been revised to represent five unique pentadactyl species in the genus, each with non-overlapping geographic distributions (Fig. 1.4): *B. makusog* (Siler et al., 2010a), *B. talinis*, *B.* sp. A (Siler and Brown, 2010), *B.* sp. B (Siler and Brown, 2010), and *B.* sp. C (Siler and Brown, 2010). Additionally, populations of the two former polytypic species, *B. boulengeri* and *B. schadenbergi*, have recently been revised, with all subspecies being elevated to full, morphologically distinct species (Siler and Brown, 2010; Fig. 1.4, Clade 5, 8).

Currently, *Brachymeles bonitae* and *B. samarensis* are recognized to have atypical distributions that span multiple PAICs (Fig. 1.4, Clade 3). *Brachymeles samarensis* is known to occur on two islands in the Greater Luzon PAIC (Catanduanes, Luzon), as well as two islands and one small island group in the Mindanao PAIC (Leyte, Samar, Lapinig Island Group; Fig. 1.1, 1.2). In comparison, *B. bonitae* has the widest recognized distribution of any species in the genus. Populations referable to this species occur in three distinct PAICs (Greater Luzon, Greater Mindoro, Greater Negros-Panay) and two small deep-water island groups (Babuyan, Romblon). However, our results indicate that both *B. bonitae* and *B. samarensis* are complexes of numerous, morphologically similar species (Fig. 1.4, Clade 3). Although populations within both species complexes share similar body plans, unique sets of characters do exist, including differences in the numbers of fore- and hind limb digits (Siler et al., in press c; Siler, unpublished data). These inter-population differences have historically been recognized as morphological variation within widespread species (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980); however, upon our observation that character differences coincide with deep genetic divergences and biogeographic breaks in lineage distributions, we suspect that many inter-populational variants in *B. samarensis* and *B. bonitae* will prove to be full species in accordance with any modern lineage-based species concept (see Siler et al., in press c), as they have in the *B. boulengeri* and *B. shadenbergi* complexes (Siler and Brown, 2010).

Recent studies have revealed numerous other “widespread” Philippine endemic reptiles to actually represent complexes of cryptic diversity, with few species actually possessing distributions that span recognized faunistic boundaries (Brown et al., 2000; Brown and Diesmos, 2002, 2009; Siler et al., 2010a,b; Siler and Brown, 2010; Welton et al., 2009, 2010a,b). Exceptions do exist (Brown and Alcala, 1970), but many of these have turned out to represent invasive species with suspected histories of human mediated introductions (Diesmos et al., 2006; Brown et al., 2010). It is clear that the diversity of *Brachymeles* is vastly underestimated, and detailed morphological comparisons are needed to revise the taxonomy within the genus.

Finally, the phylogeny supports dispersal events into the Southeast Asian mainland (Thailand) from Borneo and subsequent dispersal into the Philippines, some level of uncertainty remains in the species diversity of *Brachymeles* outside of the Philippines (Fig. 1.4). The apparent disjunct distribution of *Brachymeles* in Southeast Asia may be an artifact of high levels of extinction outside of the Philippines or an absence of discovery. The phylogeny suggests at least one genetically distinct, undescribed limbless species in the southern regions of Borneo (Kalimantan, Indonesia; Fig. 1.4), and it is highly probable that other undescribed species will eventually be discovered in other regions of Asia. It is remarkable to note that the entire diversity of limbed, pentadactyl, reduced limbed, and limbless body forms are found in the Philippines (Fig. 1.4); we take this pattern as a testament to the richness of processes of diversification found within this small but remarkable island archipelago (Brown and Diesmos, 2009).

Diversification and body form evolution within a semi-fossorial genus

Previous surveys of body plan diversity within *Brachymeles* have focused solely on morphological variation (Brown and Rabor, 1967; Brown and Alcala, 1980; Brown and Alcala, 1995), mentioning the potential for undocumented cryptic diversity within the genus as an ancillary possibility, not an expectation, much less a predominant phenomenon. However, a number of studies have shown that the evolution of a burrowing lifestyle is correlated with decreasing dispersal abilities (Selander et al., 1974; Patton and Yang, 1977; Patton and Feder, 1978) as well as changes in body form (see Crottini et al., 2009 for review). Several lineages of *Brachymeles* have experienced a reduction in limb size and digit numbers (Fig. 1.4), which may further reduce their vagility (Daniels et al., 2005; Mulvaney et al., 2005). Over time, reduced dispersal abilities may lead to an increasingly patchy distribution, reduction in gene flow among populations, and the accumulation of inter-population genetic differences (Nevo, 1979). This process also could be amplified within an island archipelago or a geographically complex island such as Luzon or Mindanao. We expect that this process has contributed to cryptic lineage diversification in this unique southeast Asian radiation.

The results of phylogenetic analyses provide evidence for three losses of external limb elements, and three distinct instances of changes in digit states. Although five species of *Brachymeles* are externally limbless (*B. apus, B. minimus, B. miriamae, B. lukbani, B. vermis*), it is currently unknown whether internal girdle elements are present in any of the five species, an indication that the species have retained some vestigial limb elements. Additionally, there is evidence for up to four independent losses of auricular openings, with the openings being completely covered by scales in *B. apus*, *B.* cf. *apus, B. miriamae*, all species of *Brachymeles* in Clade 3 of Figure 1.4, and *B. muntingkamay*. It is also interesting to note that all species and populations with unequal digit numbers in the fore- and hind limbs have fewer toes than fingers in *Brachymeles* (*B. bonitae, B. cebuensis, B. pathfinderi*, *B. samarensis*), in contrast to many previous studies which have shown that reductions in digit number are more common in the fore-limbs of scincid lizards (Brandley et al. 2008; Skinner and Lee, 2010).

Biogeographic patterns

Although numerous previous studies have observed phylogenetic patterns consistent with PAIC-based models of diversification (e.g., Heaney et al., 1998; Kennedy et al., 2000; Brown & Diesmos, 2002; Brown & Guttman, 2002; Evans et al., 2003; Esselstyn et al., 2004), we rejected all topologies predicted from a PAIC-based model (Fig. 1.3). Additionally, we rejected all hypotheses derived from patterns observed in other taxa (Alfaro et al., 2004; McGuire & Kiew, 2001; Siler et al., 2010c).

Phylogenetic analyses and ancestral state reconstructions provide support for multiple dispersal events in *Brachymeles* leading to complex and biogeographically convoluted distribution patterns observed today. Ancestral range reconstructions unambiguously estimate the ancestral range for 11 nodes in the chronogram, supporting a minimum of five geographic range shifts between major faunal regions in the Philippines (Fig. 1.3). Of these hypothesized inter-PAIC transitions, with the exception of a dispersal out of the Mindanao PAIC, all geographic transitions are hypothesized to have originated in the Luzon or central Visayan PAICs (Fig. 1.3A–C). Additionally we note that although only five inter-PAIC dispersal events are unambiguously reconstructed (Fig. 1.5A–C), an additional 5 instances of between-PAIC dispersal can be inferred with strong statistical support (Bayes factors 6–10; Kass and Raftery 1995; Nylander et al. 2004). Given that the major PAIC platforms of the archipelago have never been connected by dry land (Kloss, 1929, Inger, 1985; Heaney, 1985, Voris, 2000, Yumul et al., 2003, 2008), suggesting that faunal exchange among PAICs necessitates over-water dispersal (review: Brown and Diesmos, 2009), we find it reasonable to conclude that much of the historical dispersion of *Brachymeles* throughout the archipelago has been through the process of waif dispersal over water. Clearly the evolutionary and biogeographic history of semi-fossorial slender lizards has been heavily impacted by over water faunal exchange throughout the archipelago. This may appear at odds with the general assumption of low vagility assumed for reduced-limbed lizards with a burrowing lifestyle, but we find it conceivable, and even plausible, that dispersal between islands is mediated by frequent rafting of mats of vegetation, topsoil, and logs; these possible vectors have frequently observed washing out of the mouths of rivers following heavy storms (CDS and RMB, *personal observations*).

Conclusion

Our data represent a comprehensive, phylogenetic study for a closely related group of lizards. We have included samples from nearly all recognized species within the genus *Brachymeles*, and our intraspecific sampling has uncovered cryptic genetic diversity within many species (e.g., *Brachymeles bonitae* and *B. samarensis*). This study provides the foundation for a robust model system with which to address patterns of body form evolution, processes of diversification, and species delineation. With the exception of the recently published *Lerista* dataset (Skinner et al., 2008; Skinner, 2010; Skinner and Lee, 2010), our estimates of phylogeny represent the most comprehensive dataset for fine-scale studies of limb-reduction and loss in squamate reptiles.

It is clear that the current recognized diversity of *Brachymeles* skinks is vastly underestimated, and that numerous taxonomic revisions will be necessary to fully appreciate the processes of diversification within this nearly endemic Philippine radiation. New species await description (e.g., the new limbless species in southern Borneo; Fig. 4), and likely await discovery, and future survey work should focus on regions outside of the Philippines (e.g., Borneo, Malay Peninsula, Indochina). This study has revealed another case of extensive cryptic diversity in a once recognized assemblage of “widespread” Philippine species (Fig. 1.4). Together with numerous recent studies (Brown et al., 2009; Esselstyn et al., 2009; Esselstyn and Brown, 2009; Oliveros and Moyle, 2010; Siler et al., 2010c; Linkem et al., 2010) this effort has resulted in wholesale discovery of numerous new species and cryptic evolutionary lineages of endemic Philippine vertebrates. Once considered a small radiation of Asian skinks, the recognized species diversity of the genus *Brachymeles* will likely increase by more than 300% over the next five years (Siler et al., unpublished data).

We rejected all PAIC-based models of diversification (e.g., Heaney et al., 1998; Kennedy et al., 2000; Brown & Diesmos, 2002; Brown & Guttman, 2002; Evans et al., 2003; Esselstyn et al., 2004), as well as all patterns observed in other studies (Alfaro et al., 2004; McGuire & Kiew, 2001; Siler et al., 2010c; Fig. 1.3). However, the results of this study provide evidence for five major dispersal events across faunal zone boundaries that have given rise to the major clades of *Brachymeles* species diversity in the Philippines (Fig. 1.5). Surprisingly, all but one of these dispersal events are hypothesized to have originated in the Luzon or central Visayan PAICs (Fig. 1.3A–C). The results of this study, coupled with our knowledge of the geologic history of the region (Kloss, 1929, Inger, 1985; Heaney, 1985, Voris, 2000, Yumul et al., 2003, 2008), suggests that much of the historical faunal exchange of *Brachymeles* throughout the archipelago has been through the process of over-water (waif) dispersal. Without time-calibrated phylogenies, and the absence of closely related fossil calibrations, it is difficult to say when the hypothesized dispersal events occurred, leading to the complex distribution patterns observed today.

The transition from quadrapedal to limbless body plans has occurred repeatedly in independent lineages of squamate reptiles (i.e., snakes, lizards, amphisbaenians; Wiens and

Slingluff, 2001; Greer, 1991; Pough et al., 2004). It is clear that these transitions also occur repeatedly within single radiations of closely related species (Fig. 1.4). The results of this study provide the first evidence of repeated limb, digit, and auricular opening loss in the genus *Brachymeles*. Given our results, and those of other studies that explicitly test morphological patterns of body form change within squamate reptiles (for review, see Wiens and Slingluff, 2001; Brandley et al., 2008), we are left with many unanswered questions. Given the apparent evidence for repeated body form change in *Brachymeles*, can we estimate the number of times characters have been lost (or potentially gained) in *Brachymeles*? Do the patterns of morphological changes observed within this unique radiation of Southeast Asian lizards support previous hypotheses of correlated morphological evolution associated with limb-reduction and loss in squamate reptiles (for review, see Wiens and Slingluff, 2001; Brandley et al., 2008)? Is there evidence for a gradual, evolutionary sequence involved in the process towards limb loss? What inferences can we make from statistical reconstructions (estimates) of ancestral morphology and character state change on the phylogeny? These and other broad-scale evolutionary questions that address the processes of body form evolution must be assessed within a comparative framework, and require the addition of robust morphological datasets.

CHAPTER 2

Evidence for repeated acquisition and loss of complex body form characters in an insular clade of Southeast Asian semi-fossorial skinks

The unidirectional loss of complex characters has been a major theme in the development of theories of evolutionary change of morphology and body plan evolution (Dollo, 1893, 1922; Muller, 1939; Simpson, 1953; Gould, 1970). Dollo's law, or the irreversible loss of complex characters (Dollo, 1893, 1905, 1922; Simpson, 1953; Gould, 1970), has been the subject of many recent empirical studies (for review, see Galis et al., 2010). Although re-acquisition of complex characters historically was believed to be improbable following significant genetic differentiation (Muller, 1939; Simpson, 1953; Marshall et al., 1994; Zufall and Rausher, 2004), Dollo's Law has come into question recently with the advent of phylogenetic methods and new tools for ancestral character state reconstruction (for review, see: Kohlsdorf and Wagner, 2006; Collin and Miglietta, 2008; Goldberg and Igic, 2008; Lynch and Wagner, 2009; Wiens, 2011). For example, in a recent reviews by Galis et al. (2010) and Wiens (2011), numerous examples of studies supporting the re-acquisition of complex traits were discussed, including the re-acquisition of teeth and nipples in mammals (Kurtén, 1964; Gilbert, 1986; Sherman et al., 1999; Lihoreau et al., 2006), teeth in frogs (Wiens, 2011), wings in insects (Whiting et al., 2003), coiling in snails (Collin and Cipriano, 2003; Pagel, 2004), sexuality in orobatid mites (Domes et al., 2007), complex life cycles in marsupial frogs (Wiens et al., 2007), and phalanges and digits in squamate reptiles (Greer, 1992; Kohlsdorf and Wagner, 2006; Brandley et al., 2008). Nevertheless, statistical phylogenetic tests of Dollo's Law have led to questions concerning potential pitfalls and methodological weaknesses (Trueman et al., 2004; Urdy and Chirat, 2005; Goldberg and

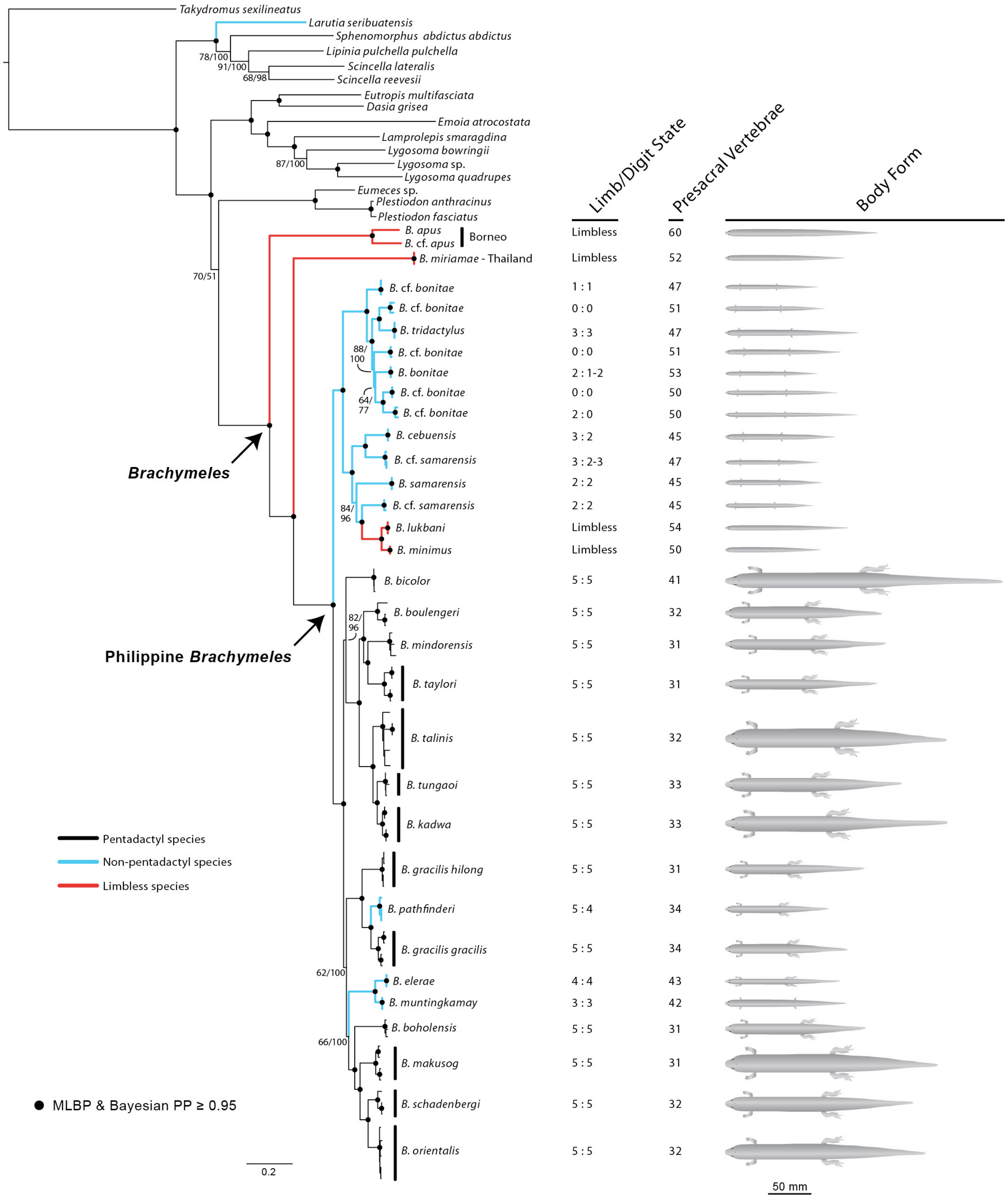
Igic, 2008; Galis et al., 2010; but see Kohlsdorf et al., 2010). Although these potential methodological limitations have been presented, studies continue to find evidence for the re-acquisition of complex traits.

In addition to the studies on the polarity of character change, evolutionary patterns of limb-reduction and loss have provided biologists with a rich suite of hypotheses for tests in a phylogenetic framework (for review, see Brandley et al., 2008). Recent advances in the field of phylogenetics and the availability of molecular data have resulted in a resurgence of interest in the patterns and processes of body form evolution among squamate reptiles (Wiens and Slingluff 2001; Whiting et al. 2003; Kearney and Stuart 2004; Sanger and Brown 2004; Wiens 2004; Schmitz et al. 2005; Kohlsdorf and Wagner 2006; Wiens et al. 2006; Brandley et al. 2008; Skinner et al. 2008; Skinner and Lee 2009, 2010; Skinner 2010; Galis et al. 2010; Kohlsdorf et al. 2010). From studies of development (Shubin and Alberch 1986; Cohn and Tickle 1999; Shapiro 2002) to studies of locomotion (for review, see Bergmann and Irschick 2010), researchers have attempted to address questions concerning the repeated transition from quadrupedal to limbless body plans in independent lineages of squamate reptiles (Greer 1991; Pough et al. 2004; Wiens et al. 2006). Long believed to be an irreversible evolutionary process, recent studies have provided evidence for digit reacquisition (Kohlsdorf and Wagner 2006; Brandley et al. 2008; Kohlsdorf et al. 2010). To date, fine-scale studies of squamate body form evolution have been limited by a paucity of model systems to test the irreversibility of character change (but see Kohlsdorf and Wagner 2006; Skinner et al. 2008; Skinner 2010).

Previous studies of squamate body form evolution have focused most often on broad- scale patterns of limb reduction and loss, and a suite of morphological changes have been identified as associated with this evolutionary transition. These include body elongation, reduction in limb size, loss of digits, miniaturization, increase in the number of presacral vertebrae, loss of external ear openings, and loss of associated limb girdles (for review, see Brandley et al. 2008). Changes in the number of digits have been shown to likely occur through an ordered evolutionary sequence (Alberch and Gale 1985; Shubin and Alberch 1986; Shapiro 2002). Historically, these were assumed to occur through the irreversible loss of the limb and digit character (Brandley et al. 2008). This assumption of irreversibility has had a marked influence on the interpretation of recent findings concerning the re-evolution of multiple digits and limbs from limb-reduced ancestors (Whiting et al. 2003: Kearney and Stuart 2004; Collin and Miglietti 2008). Recent studies focusing on ancestral state reconstructions have highlighted several potential methodological pitfalls by demonstrating well supported but misleading reconstructions of character change; this discussion has focused on extent of outgroup sampling and character states at the root of the phylogeny (Goldberg and Igic 2008; Galis et al. 2010). Finally, the assumption of ordered sequential change has had a significant impact on studies of ancestral squamate digit states (Kohlsdorf and Wagner 2006; Brandley et al. 2008; Skinner et al. 2008; Skinner et al. 2010; Skinner 2010). However, recent findings indicate that an ordered model of digit evolution does not always provide the best-fit model of the evolution of digit change in scincid lizards (Skinner and Lee 2010; Skinner 2010).

There are few genera of scincid lizards that possess both fully limbed and limbless species (*Brachymeles*, *Chalcides*, *Lerista*, and *Scelotes*; Lande 1978; Wiens and Slingluff 2001), providing rare model systems for fine-scale studies of body form evolution. Most studies of these genera have included only morphological data (e.g., Lande 1978; Choquenot and Greer 1987; Greer 1987, 1990, 1991; Caputo et al. 1995; Greer et al. 1998) or limited taxonomic sampling (*Scelotes*: Whiting et al. 2003; *Chalcides*: Brown and Pestano 1998; Pestano and Brown 1999). However, recent studies of *Lerista* addressed patterns of body form evolution

Figure 2.1. Hypothesized relationships of *Brachymeles* from Siler et al. (2011), illustrated by ML estimates (-ln L 60687.493127). Nodes supported by ≥95% Bayesian PP and ML bootstrap support were considered significantly supported and are indicated by black circles. Terminals are labeled with abbreviated taxonomic names, followed by general geographic distribution. Limb and digit states, numbers of presacral vertebrae, and proportionally-drawn body form cartoons are shown for reference. Externally limbless, non-pentadactyl, and pentadactyl species are highlighted by red, blue and black braches, respectively. Alpha and numerical labels correspond to clades referred to in the Results and Discussion.


Takydromus sexilineatus
Larutia seribuatensis
Sphenomorphus abdictus abdictus
Lipinia pulchella pulchella
Scincella lateralis
Scincella reevesii
78/100
91/100
68/98
Eutropis multifasciata
Dasia grisea
Emoia atrocostata
Lamprolepis smaragdina
Lygosoma bowringii
Lygosoma sp.
Lygosoma quadrupes
87/100
Eumeces sp.
Plestiodon anthracinus
Plestiodon fasciatus
70/51
Limb/Digit State
Presacral Vertebrae
Body Form
B. apus
B. cf. apus
Borneo
Limbless
60
B. miriamae - Thailand
Limbless
52
B. cf. bonitae
1 : 1
47
B. cf. bonitae
0 : 0
51
B. tridactylus
3 : 3
47
88/100
B. cf. bonitae
0 : 0
51
B. bonitae
2 : 1-2
53
64/77
B. cf. bonitae
0 : 0
50
B. cf. bonitae
2 : 0
50
B. cebuensis
3 : 2
45
Brachymeles
B. cf. samarensis
3 : 2-3
47
B. samarensis
2 : 2
45
84/96
B. cf. samarensis
2 : 2
45
B. lukbani
Limbless
54
B. minimus
Limbless
50
B. bicolor
5 : 5
41
82/96
B. boulengeri
5 : 5
32
B. mindorensis
5 : 5
31
Philippine Brachymeles
B. taylori
5 : 5
31
B. talinis
5 : 5
32
B. tungaoi
5 : 5
33
B. kadwa
5 : 5
33
Pentadactyl species
Non-pentadactyl species
Limbless species
B. gracilis hilong
5 : 5
31
B. pathfinderi
5 : 4
34
B. gracilis gracilis
5 : 5
34
62/100
B. elerae
4 : 4
43
B. muntingkamay
3 : 3
42
B. boholensis
5 : 5
31
66/100
B. makusog
5 : 5
31
● MLBP & Bayesian PP ≥ 0.95
B. schadenbergi
5 : 5
32
B. orientalis
5 : 5
32
0.2
50 mm

using a molecular and morphological dataset and robust taxonomic sampling (Skinner et al. 2008; Skinner and Lee, 2009, 2010; Skinner 2010). Limb reduction and loss has been shown to occur frequently in *Lerista*, a genus of 94 species, with rates of change suggested to be much higher than previously estimated (Skinner et al. 2008; but see Wiens 2009). In contrast to some recent evidence for digit, and possibly limb, re-evolution (Kohlsdorf and Wager 2006; Brandley et al. 2008; Kohlsdor et al. 2010), studies of *Lerista* support unidirectional loss of digits only (Skinner et al. 2008; Skinner and Lee 2009, 2010; Skinner 2010). Of these four known squamate systems, the genus *Brachymeles* remains the least studied, and to date, patterns of body form evolution among species of this enigmatic lizard radiation have received little attention (but see Siler et al. 2011).

Morphological diversity within the Southeast Asian lizard genus *Brachymeles* has only recently been brought to light by a series of systematic studies (Siler et al. 2009a, 2010a,b; Siler and Brown 2010; Siler et al. 2011, in press c,d). Within this genus, all but two of the 26 recognized species are endemic to the Philippines (Brown and Alcala 1980; Siler et al. 2009a, 2010a,b; Siler and Brown 2010; Siler et al. 2011, in press c,d); the exceptions are *B. apus* from northern Borneo (Hikida 1982) and *B. miriamae* (Heyer 1972) from Thailand (formerly *Davewakeum miriamae*; Siler et al. 2011). Thirteen species are pentadactyl (*bicolor*, *boholensis, boulengeri*, *gracilis*, *kadwa, makusog, mindorensis, orientalis, schadenbergi*, *talinis, taylori, tungaoi,* and *vindumi*), and the remaining thirteen species exhibit limbless or intermediate states, including incompletely developed limbs and reduced numbers of digits (*bonitae*, *cebuensis*, *elerae*, *muntingkamay, pathfinderi*, *samarensis*, *tridactylus*, and *wrighti*). Five of the non-pentadactyl species are completely limbless (*apus*, *minimus, miriamae, lukbani,* and *vermis*). Within the non-pentadactyl species there exists a wide range of limb- and digit-reduced states, from minute limbs that lack full digits (*bonitae*, *cebuensis*, *muntingkamay, samarensis, tridactylus*), to moderately developed limbs with four to five digits on the hands and feet (*elerae, pathfinderi, wrighti*). Because of the body form variation in this clade, and the fact that its many closely related species differ by the presence or absence of digits and characters of the limbs, this group provides an ideal system for testing Dollo's Law and the prediction of unidirectional limb reduction and loss.

Siler et al. (2011) provided the first estimate of phylogenetic relationships among species in the genus *Brachymeles*. The seven-gene dataset included representatives for all but two of the currently known species in the genus as well as broad outgroup sampling (Siler et al. 2011). Results of this study indicated that multiple instances of limb-reduction and loss have occurred in this radiation of burrowing skinks. Additionally, several widespread limb-reduced species (e.g., *B. bonitae, B. samarensis*) were not found to be monophyletic, and were shown to be species complexes with unique digit numbers and morphologies (Siler et al. 2011). However, no morphological data were presented, and the focus remained solely on the phylogenetic relationships, taxonomic stability, and biogeographic patterns. Here we add additional molecular sequence data to the datasets of Siler et al. (2011), and a large, newly acquired, comprehensive morphological dataset, to assess patterns of body form evolution within this unique clade of species. Our combined molecular and morphological datasets represent one the most fine-scaled systems for studying body form evolution in a group of closely related squamates to date.

In order to test hypotheses of body form evolution among squamate reptiles, we investigate patterns of body form change in skinks of the genus *Brachymeles* using a phylogenetic comparative approach, derived from morphological data. We explore the data for evidence of threshold values of morphological features after which changes in body form occur.

Additionally, we test for patterns of correlated evolution of morphological characters. We provide the first exploration of the impact of various methodological choices used in previous studies of body form evolution, including the impact of choice of morphometric variable as a measurement of body size for non-phylogenetic and phylogenetic size-correction as well as the overall method for multivariate principal component analyses. Finally, using our robust estimate of phylogenetic relationships, we explore the prevalence and directionality of evolutionary changes in limb, digit, and ear character states, and the impact of outgroup sampling and ancestral outgroup character states on ancestral state reconstructions. Our results demonstrate one of the best-documented cases of limb reduction, loss, and evolutionary reacquisition of these complex characters in a closely related clade of lizards. We identify the first known case of loss and reacquisition of external ear openings (another trait lost in association with burrowing lifestyles) and highlight the occurrence of taxa occupying two new classes of morphospace: species with minute limbs but with multiple digits and species lacking digits but with longer limbs than congeners with multiple digits. Additionally, our comparative analyses incorporating an historical context via phylogeny revealed significant statistical support for otherwise undetectable patterns of character correlation. Together, our findings provide yet another violation of Dollo's Law in a new, rich model system for future studies of the historical framework for patterns and processes of body form evolution.

Methods

Taxon sampling and data collection

Phylogenetic analyses for this study took advantage of the datasets of Siler et al. (2011); however, we collected 1,323 bp of additional molecular data. Ingroup sampling included 90 individuals collected from 43 localities, with 24 of the 26 currently recognized species of *Brachymeles* represented (Fig. 2.1; Siler et al. 2011). The study incorporated a broad sampling of outgroup scincid species from the subfamilies Lygosominae and "Scincinae", as well as a single outgroup sample from the family Lacertidae (Fig. 2.1; Siler et al. 2011). The phylogeny of Siler et al. (2011) was based on a sequence data for seven-genes: (mitochondrial) NADH Dehydrogenase Subunit 1 (ND1), NADH Dehydrogenase Subunit 2 (ND2), ATPase 8 (ATP8), ATPase 6 (ATP6); (nuclear) Brain-derived Neurotrophic Factor (BDNF), R35, Prostaglandin E receptor 4 (PTGER4). For this study, additional complete or partial sequences were collected for the mitochondrial Cytochrome Oxidase Subunit II (COXII) and Cytochrome Oxidase subunit III (COXIII) genes, and components of seven flanking transfer RNA genes (tRNA^{lys}, tRNA^{leu}, tRNA^{Ile}, tRNA^{gln}, tRNA^{trp}, tRNA^{ala}, tRNA^{asn}) using the primers of Siler et al. (2011). In addition, the two nuclear loci, Glyceraldehyde-3-phosphate Dehydrogenase (GapD) and α-enolase, were completely sequenced for nearly all ingroup samples and many of the outgroup samples using the primers and protocols of Friesen (1997). All newly collected sequences were deposited in GenBank (accession #'s HQ906962–907136).

Sequence alignment and phylogenetic analyses

Initial alignments were produced in Muscle (Edgar, 2004), and manual adjustments made in MacClade 4.08 (Maddison and Maddison, 2005). To assess phylogenetic congruence between the mitochondrial and nuclear data, we inferred the phylogeny for each gene independently using likelihood and Bayesian analyses, and performed pairwise partition homogeneity tests in PAUP 4.0b 10 (Swofford, 2002) with 100 replicates for each pairwise comparison to assess set congruence. Following the observation of no statistically significant incongruence between datasets, we felt justified in using the combined, concatenated, data for subsequent analyses.

Exploratory analyses of the combined dataset of 108 individuals (including outgroup taxa with missing data for several genes) and a reduced dataset of individuals with no missing data exhibited identical relationships; we therefore chose to include all available data (108 individuals) for subsequent analyses of the concatenated dataset. Alignments and resulting topologies were deposited in TreeBase (SN 11274).

Partitioned Bayesian analyses were conducted in MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003). The mitochondrial dataset was partitioned by codon position for the protein-coding region of ND1 and ND2 and by gene region for the short gene regions ATP8 and ATP6. The Akaike Information Criterion (AIC), as implemented in jModeltest v0.1.1 (Guindon and Gascuel, 2003; Posada, 2008), was used to select the best model of nucleotide substitution for each partition (Table 1.2). The best-fit model for each data partition was implemented in subsequent Bayesian analyses. A rate multiplier model was used to allow substitution rates to vary among subsets, and default priors were used for all model parameters. We ran four independent Metropolis-coupled MCMC analyses, each with four chains and an incremental heating temperature of 0.05. All analyses were run for 18 million generations, sampling every 5000 generations. To assess stationarity, all sampled parameter values and log-likelihood scores from the cold Markov chain were plotted against generation time and compared among independent runs using Tracer v1.4 (Rambaut and Drummond, 2007). Finally, we plotted the cumulative and non-overlapping split frequencies of the 20 most variable nodes, and compared split frequencies among independent runs using Are We There Yet? [AWTY (Wilgenbusch et al., 2004)]. Although all samples showed patterns consistent with stationarity after 2.5 million generations (i.e., the first 12.5%), we conservatively discarded the first 20% of samples as burn-in.

Table 2.1. Summary of numbers of specimens examined per species, and adult specimens per species included in this study. The number of x-rays examined per species are provided for reference.

Species or Morphologically Unique Lineage	Specimens Examined	Adult Specimens Included in Analyses	X-rays Examined
Brachymeles apus	1	1	1
Brachymeles bicolor	28	9	5
Brachymeles boholensis	39	18	7
Brachymeles bonitae (central Luzon Island)	11	11	11
Brachymeles cf. *bonitae* (northern Luzon Island population)	2	1	2
Brachymeles cf. *bonitae* (Masbate Island population)	10	6	2
Brachymeles cf. *bonitae* (Mindoro Island population)	23	17	3
Brachymeles cf. *bonitae* (Camiguin Norte Island population)	8	7	4
Brachymeles cf. *bonitae* (Lubang Island population)	6	4	6
Brachymeles boulengeri	26	13	6
Brachymeles cebuensis	9	7	5
Brachymeles elerae	4	3	2
Brachymeles gracilis hilong	20	15	9
Brachymeles gracilis gracilis	62	15	13
Brachymeles lukbani	11	10	6
Brachymeles makusog	14	9	8
Brachymeles mindorensis	35	12	5
Brachymeles minimus	6	4	6
Brachymeles miriamae	2	2	2
Brachymeles muntingkamay	12	10	10
Brachymeles orientalis	53	20	6
Brachymeles pathfinderi	39	29	6
Brachymeles samarensis (Samar Island)	6	6	6
Brachymeles cf. *samarensis* (Leyte Island population)	14	14	7
Brachymeles cf. *samarensis* (Catanduanes Island population)	9	9	9
Brachymeles schadenbergi	49	12	6
Brachymeles talinis	31	14	6
Brachymeles taylori	35	17	6
Brachymeles tridactylus	22	14	10
Brachymeles sp. A	12	5	2
Brachymeles sp. B	33	17	9

In preliminary Bayesian analyses of the combined dataset, the independent runs failed to converge. We tried (1) lowering the incremental heating temperature to 0.02, (2) using an unconstrained branch length prior with an exponential distribution of 25 (Siler et al. 2010c, 2011; Marshall 2006, 2010), and (3) removing outgroup taxa with large amounts of missing data. Although some of the trials of individual permutations of parameters resulted in a failure to converge, the incorporation of the above, plus an unconstrained branch length prior with an exponential distribution and a mean of 25 resulted in convergence. Once complete convergence was achieved, we proceeded with final analyses, presented here.

Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.0 (Stamatakis, 2006) on the concatenated dataset the same partitioning strategy as for Bayesian analysis. The more complex model (GTR + Γ) was used for all subsets, and 100 replicate ML inferences were performed for each analysis. Each inference was initiated with a random starting tree, and employed the rapid hill-climbing algorithm (Stamatakis, 2007). Clade confidence was assessed with 100 bootstrap pseudoreplicates employing the rapid hill climbing algorithm (Stamatakis et al., 2008).

Relative time analyses

To test the combined dataset for deviations from a molecular clock, we optimized likelihood scores in PAUP* 4.0b10 with a molecular clock enforced and not enforced on the maximum-likelihood topology. A likelihood ratio test ([LRT] Arbogast et al. 2002; Felsenstein 2004) significantly rejected a molecular clock ($p = 0.00$), and subsequent analyses were conducted within a relaxed clock framework. The relative rate chronogram used for morphological analyses in this study was inferred in a Bayesian framework using BEAST v1.5.3 (Drummond and Rambaut 2007). The dataset was paired down into individual lineages per species or morphologically distinct, non-monophyletic populations (*B. bonitae* and *B. samarensis*; Siler et al. 2011). Four independent BEAST runs of 50 million generations were completed under the same partitioning strategy as for Bayesian analyses, imposing an uncorrelated lognormal relaxed clock prior on substitution rate (Drummond et al. 2006) and Yule speciation prior. Parameters were sampled every 5000 generations and the initial 50% of each run was discarded as burn-in, leaving a combined 20,000 trees in the posterior distribution. To evaluate convergence among MCMC analyses, trends and distributions of parameters, including the likelihood score, were examined in Tracer (Rambaut and Drummond 2007) and Are We There Yet? [AWTY (Wilgenbusch et al., 2004)].

Testing morphological hypotheses

We test morphology-based hypotheses to address questions concerning the patterns of *Brachymeles* diversity (Fig. 2.2): 1) Did limb reduction occur once? 2) Did the complete loss of external limb elements occur once? 3) Did ear loss occur once? 4) Is there support for a gradual transition from pentadactyl to limbless body forms?

In an attempt to thoroughly evaluate each, we conducted analyses within Bayesian and maximum likelihood (ML) frameworks. The topological constraints for these questions are outlined in Figure 2.2. The ML approach consisted of conducting an approximately unbiased (AU) test (Shimodaira and Hasegawa 2001; Shimodaira 2002), as implemented in Siler et al. (2010c). Using the full, combined dataset, partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.0 (Stamatakis 2006), under the same partitioning strategy used for phylogenetic analyses. A complex model (GTR + Γ) was used for all subsets, and 100 ML searches were performed under each of the 4 constraints. All 500 trees produced by RAxML (100 from the unconstrained analysis and 100 from each of the 4 constrained analyses), were filtered in PAUP to remove identical topologies. A modified version of RAxML (provided by Alexandros Stamatakis) allowed the per-site likelihoods to be estimated for each of the 54 unique topologies under a partitioned model. An AU test was then performed on the per-site likelihoods from all 54 using CONSEL v0.1i (Shimodaira and Hasegawa 2001). The p-value reported for a given hypothesis is the largest p-value of all the trees inferred under that constraint. To automate various steps in the process, Perl and Python scripts were written by J. Oaks and CDS (available by request). For the Bayesian approach, we took the percentage of 11520 post-burnin trees consistent with each hypothesis to represent the posterior probability that the hypothesis is true.

Testing hypotheses of correlated character evolution

We tested the morphological data for phylogenetic signal of morphometric data using Pagel's lambda (Freckelton et al. 2002) and Blomberg's K (Blomberg et al. 2003). Both raw and natural-log transformed morphometric variables were analyzed. The topology and branch lengths from the chronogram estimated in BEAST analyses were imported into R (R Development Team 2008), and the geiger (Harmon et al. 2008) and Picante (Kembel et al. 2010) packages were used to conduct transformations to test for phylogenetic signal. Following the observation of significant phylogenetic signal in all morphometric characters (Fig. 2.3), independent contrasts were used to explore the impact of phylogeny on subsequent analyses of morphology.

Bivariate and multivariate analyses were performed on raw morphometric data as well as independent contrasts of the morphometric variables to explore both raw morphological patterns observed in *Brachymeles* and those observed in a phylogenetic context. Morphometric data were measured for ten characters for twenty-seven lineages of *Brachymeles* (including *B. miriamae*). These lineages corresponded to the species, subspecies, and morphologically unique populations (i.e., *Brachymeles bonitae, B. samarensis*) sampled in phylogenetic analyses (Fig. 2.1). Meristic and mensural characters are based on Siler et al. (2009a, 2010a,b), and include: snout–vent length (SVL), head length (HL), tail length (TL), total length (TotL; SVL + TL), fore- and hind limb length (FLL and HLL), midbody width (MBW), and numbers of presacral vertebrae (PSV), fore-limb digits (Fldig), and hind limb digits (Hldig).

Species, subspecies, or morphologically distinct populations of *Brachymeles* possess limbs with as few as one recognizable digit or up to as many as five recognizable digits. Following the methods of Brandley et al. (2008), we coded limbless species as well as species or populations with limbs consisting of only a small stump and no recognizable digits as having zero digits. We measured the ten morphological characters used in this study from 632 specimens of *Brachymeles*, with an average of 20 specimens per species, subspecies, or morphologically distinct population (Table 2.1). Measurements of juvenile and sub-adult specimens were excluded from analyses (Table 2.1). Additionally, we recorded presacral vertebrae numbers from x-rays for an average of 6 specimens per species, subspecies, or morphologically distinct population (Table 2.1). Minor differences in body size characters between sexes and populations may exist in nature or simply as an artifact of sample size, and we attempted to account for this by combining data from broad geographic sampling for both sexes whenever possible.

Following the methods of Wiens and Slingluff (2001) and Brandley et al. (2008), the value of 1 was added to all variable measurements (some taxa have values of zero for digit numbers), and each measurement was natural log-transformed. Independent contrasts (Felsenstein 1985) were then calculated for each natural log-transformed variable using the Phylogenetic Diversity Analysis Programs (PDAP; Midford et al. 2005) module in Mesquite version 1.06 (Maddison and Maddison 2005). The topology and branch lengths from the chronogram estimated in BEAST analyses were used to calculate contrasts. To check that independent contrasts were adequately standardized, the slopes of the regression lines between the absolute values of the contrasts against the square root of the sum of the corrected branch lengths (or their standard deviations) were inspected (Garland et al. 1992). No significant relationships were observed and the independent contrasts subsequently were considered to be appropriately standardized.

Previous studies corrected for size in body and limb measurements by regressing independent contrasts for each measurement on the contrasts for head length (Wiens and Slingluff 2001; Brandley et al. 2008), based on the observation that relative limb and body lengths vary greatly in lizards compared to the conservative shape of the skull (Stokely 1947). In *Brachymeles*, most species possess what appears to be a conservative body plan, with relatively small limbs even observed in pentadactyl species. We explored whether head length is an appropriate measure with which to standardize morphometric variables, and in doing so account for body size allometry (methodology provided in Appendix III Materials & Methods).

To test for a relationship between body and limb size, as well as body size and presacral vertebrae number, we regressed relative body size measurements against relative limb size and presacral vertebrae number for each of the three sets of size-corrected morphometric variables. Additionally, we regressed digit and presacral vertebrae number against the three sets of relative limb length measurements as well as the raw non-size-corrected limb lengths to test for relationships between limb size and digit number and number of presacral vertebrae. All regressions were made through the origin (Garland et al. 1992).

We used principal components analysis (PCA) on a correlation matrix of raw size-corrected variables following the methods of Wiens and Slingluff (2001) to determine whether any body-form groupings can be recovered without *a priori* designation of groups. All analyses were performed using the seven morphometric variables only, the seven morphometric variables and digit numbers (for the hand and foot), and the seven morphometric variables, digit numbers, and number of presacral vertebrae.

Methods for simultaneously correcting for body size allometry and conducting PCAs, while taking the phylogeny into account have recently been developed (Revell 2009). To explore differences between methodologies, we repeated all bivariate analyses using phylogenetic size-corrected (PSC) data calculated in R using the phyl_resid function provided in Revell (2009), as well as independent contrasts of the PSC data. Additionally, PCAs of raw, size-corrected variables were compared to results of phylogenetic principal component analyses (Revell 2009).

Exploring morphological thresholds

Previous studies of squamate reptiles have reported thresholds of raw morphometric body proportions that appear to mark a demarcation between long, fully pentadactyl limbs and shortened limbs and reduced digit states (Lande 1978; Brandley et al. 2008). To determine whether these hypothesized thresholds occur across the diversity of *Brachymeles*, we created bivariate and overlaid scatterplots of raw digit numbers and presacral vertebrae number against ratios of limb, snout–vent, and total lengths to head length as well as midbody width to head length following the methods of Lande (1978) and Brandley et al. (2008). The plots were subsequently inspected for trends in body form change. As in Brandley et al. (2008), raw data were used for more easily interpretable results and comparison with previous studies.

Testing for evidence of character re-evolution

To explore whether there is evidence of the re-evolution of limbs, digits, or ear openings in *Brachymeles*, we compared empirically observed (extant) character states to estimates of ancestral states using the program BayesTraits version 1.0 (Pagel 1994; Pagel and Lutzoni 2002).

For analyses involving the estimation of ancestral external limb and ear states we examined two models of character evolution: 1) assuming equal rates of character acquisition and loss, 2) assuming independent rates of character acquisition and loss. Following the methods of Skinner and Lee (2010), we examined five disparate models of digit evolution to evaluate which models best fit the data (Table 2.5). For all analyses we seeded the mean and variance of the gamma prior from uniform distributions on the interval 0 to 20 by enforcing the "Hyperpriorall" command of BayesTraits. These analyses were then repeated and compared to runs with uniform priors with upper and lower bounds of 0 and 100 (Skinner and Lee 2010). The LogCombiner v1.5.4 program of BayesTraits was used to combine trees from the posterior distributions of the four independent Beast runs. Of the 20,000 trees in the posterior distribution, we discarded the first 97.5%, producing a file with 2,000 trees from the posterior distribution. All 2,000 chronograms were then used in analyses of morphological data in BayesTraits in an effort to account for phylogenetic uncertainty. We ran MCMC chains for 25 million generations, sampling every 5000th generation, and discarded the first 50% of samples as burn-in. The ratedev parameter was adjusted for each analysis to maintain acceptance rates of 20–40%. The remaining 2,500 samples were used to summarize the posterior probabilities of ancestral character states for all nodes of the tree. Bayes factors comparing the best fit model to all other models of character evolution were applied, accepting more parameterized models when the

Bayes factor shows strong to very strong support (Kass and Raftery 1995; Nylander et al. 2004). The "AddNode" command of BayesTraits was used to specify all nodes in the chronograms for visualization of the posterior probabilities of character states at each node.

We ran a series of additional analyses on nodes with ambiguous estimated ancestral character states. The "fossil" command of BayesTraits was used to sequentially enforce the character states making up 95% of the posterior probability at a single node, prioritizing character states with the highest posterior probability. Bayes factors were again applied, and the state supported at each ambiguous node was summarized with the Bayes factors measure of support for that ancestral state (Figs. 6, 7). To explore the impact of the ancestral character states among outgroup taxa on reconstructions within *Brachymeles* (Goldberg and Igic 2008), additional analyses were conducted in which we assumed the ancestral states for all nodes sister to *Brachymeles* was a limbed, pentadactyl species with external ear openings.

Results

Phylogeny of Brachymeles

Our complete, aligned matrix contain 82 samples of *Brachymeles*, representing 24 of the 26 recognized taxa, and containing both mitochondrial genes and nuclear loci. Seventeen additional outgroup samples included representatives from the subfamilies Lygosominae and "Scincinae" within the family Scincidae as well as a single representative from the lizard family Lacertidae. Following the study of Siler et al. (2011), we rooted the tree using samples of *Takydromus sexilineatus* from China.

All analyses strongly supported five distinct instances of limb reduction in the genus *Brachymeles* (including *B. miriamae*; Fig. 2.1). Complete limb loss is strongly supported to have occurred three separate times (Fig. 2.1). Interestingly, the two non-Philippine species (*B. apus* [Borneo], *B. miriamae* [Thailand]) are always recovered as the two lineages sister to all Philippine *Brachymeles* (Fig. 2.1). Within the Philippines, all limbless species and the majority of limb-reduced species are recovered as part of two reciprocally monophyletic groups, and together are sister to all pentadactyl species and the remaining non-pentadactyl taxa (Fig. 2.1).

The widespread limb-reduced species, *Brachymeles bonitae* and *B. samarensis*, are not recovered as monophyletic groups (Fig. 2.1). Furthermore, with strong statistical support, Siler et al. (2011) rejected the hypothesized monophyly of both of these species complexes. Not only are all of the lineages within these complexes well supported and genetically distinct, but they differ morphologically as well (Fig. 2.1, 2.4). Populations within both species complexes differ in body size, limb and digit characters, and scale counts (Brown and Alcala 1980; Siler et al. 2011), and even the number of digits and presacral vertebrae.

Morphological hypothesis tests

Results from the Bayesian methods and the approximately unbiased (AU) test were highly consistent. Both methods rejected all morphology-based hypotheses (Fig. 2.2). Although we treat the former monotypic genus *Davewakeum miriamae* as the fifth limbless species of *Brachymeles* following Siler et al. (2011), each hypothesis was re-evaluated with both the Bayesian method and by conducting AU tests with *B. miriamae* samples incorporated into excluded from constraint trees. No differences were observed in the resulting support for each of the four hypotheses. Additionally, hypothesis #4 was tested using three topological constraints: 1) A single transition across all *Brachymeles* (with and without *B. miriamae*), 2) Two transitions for Clades 1 and 2, respectively, and 3) A single transition for Clade 1. All three versions of hypothesis #4 were rejected by both analyses (Fig. 2.2).

Analyses of Correlated Character Evolution

Tests for the presence of phylogenetic signal resulted in λ values estimated at 1.0 and K values that were significantly different from 0 (SVL $K = 0.8452$; MBW $K = 1.5540$; TL $K = 0.8877$; HL $K = 1.3734$; HLL $K = 2.4268$; FLL $K = 2.6651$; TotL $K = 0.7828$; Fig. 2.3). Regression analyses show highly consistent results regardless of the variable used for size-correction. Additionally, analyses of size-corrected data based on either residuals from bivariate regressions of phylogenetically independent contrasts (RSC-IC; Lande 1978; Wiens and Slingluff 2001; Brandley et al. 2008), or phylogenetically independent contrasts of phylogenetically size-corrected data (PSC-IC; Revell 2009), show largely similar results (Table 2.2). Multivariate correlation analyses revealed head length to be most correlated to all other variables, an indication that it would be the most appropriate variable for use in size-correction.

Although bivariate regression analyses of raw size-corrected data show highly significant relationships between relative SVL (rSVL), tail length (rTL), total length (rTotal), relative midbody width (rMBW), changes in relative fore- (rFLL) and hind limb (rHLL) lengths, several of these significant relationships disappear when phylogeny is taken into account (Table 2.2). However, the opposite is true of the relationship between several of these characters (rSVL, rTL, rTotal, and rMBW) and raw digit numbers and presacral vertebrae numbers, where regression analyses of all three methods of size-correction result in highly significant relationships only when phylogeny is taken into account (Table 2.2). Finally, regression analyses of raw, non-size-corrected measurements of limb length, digit numbers, and presacral vertebrae numbers show highly significant relationships regardless of whether phylogeny is taken into account (Table 2.3).

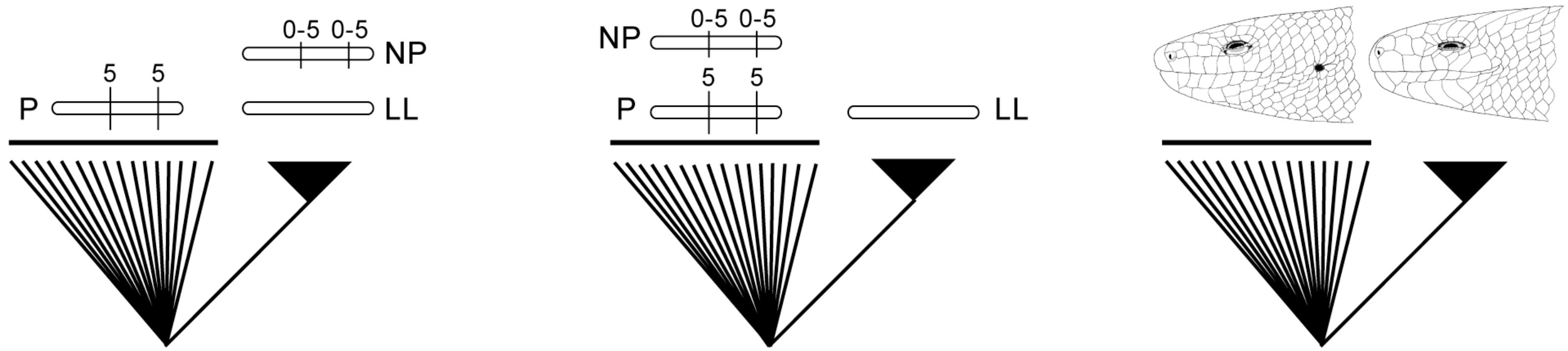
Table 2.2. Bivariate regression analyses of meristic and mensural variables associated with the transition from pentadactyl to limbless body plans in squamates. Each regression analysis was performed using relative size measurements (rSVL, rTL, rTotal, rMBW, rFLL, rHLL) calculated from raw data (Raw), raw data that has been phylogenetically size-corrected (Raw PSC), regression residual-based size-corrected independent contrasts (RSC-IC), and phylogenetic size-corrected independent contrasts (PSC-IC). All phylogenetic size-corrections were conducted in R following the methods of Revell (2009). Significant *P*-values at $\alpha \leq 0.05$ are shown in bold, with *P*-values significant after a table-wide Benjamini and Hochberg (1995) correction marked with an asterisk.

		Raw		Raw PSC		RSC-IC		PSC-IC	
		df = 31		df = 31		df = 30		df = 30	
Independent variable	Dependent variable	R^2	P	R^2	P	R^2	P	R^2	P
rSVL	PSV	0.038	0.284	0.114	0.059	0.447	< **0.001***	0.240	**0.005***
rSVL	rFLL	0.769	< **0.001***	0.530	< **0.001***	0.252	**0.004***	0.277	**0.002***
rSVL	rHLL	0.708	< **0.001***	0.562	< **0.001***	0.220	**0.008***	0.311	**0.001***
rTL	PSV	0.034	0.311	0.030	0.345	0.084	0.113	0.102	0.080
rTL	rFLL	0.551	< **0.001***	0.000	0.939	0.001	0.848	0.004	0.732
rTL	rHLL	0.497	<**0.001***	0.000	0.969	0.002	0.809	0.000	0.960
rTotal	PSV	0.038	0.285	0.004	0.742	0.223	**0.007***	0.164	**0.024***
rTotal	rFLL	0.696	< **0.001***	0.166	**0.021***	0.059	0.190	0.043	0.261
rTotal	rHLL	0.632	< **0.001***	0.191	**0.012***	0.030	0.349	0.074	0.140
rMBW	PSV	0.030	0.340	0.015	0.505	0.196	**0.013***	0.194	**0.013***
rMBW	rFLL	0.636	< **0.001***	0.071	0.141	0.197	**0.012***	0.173	**0.020***
rMBW	rHLL	0.583	< **0.001***	0.063	0.166	0.199	**0.012***	0.168	**0.022***
rFLL	Fingers	0.123	0.049	0.606	< **0.001***	0.396	< **0.001***	0.260	**0.003***
rHLL	Toes	0.154	**0.026***	0.568	< **0.001***	0.406	< **0.001***	0.220	**0.008***
rFLL	PSV	0.029	0.349	0.297	**0.001***	0.429	< **0.001***	0.180	**0.017***
rHLL	PSV	0.026	0.374	0.281	**0.002***	0.397	< **0.001***	0.148	**0.033**
PC1	Fingers	0.173	**0.018***	0.431	< **0.001***	0.108	0.076	0.062	0.185
PC1	Toes	0.213	**0.008***	0.462	< **0.001***	0.261	**0.004***	0.153	**0.032**
PC1	PSV	0.003	0.770	0.141	**0.034**	0.565	< **0.001***	0.324	**0.001***

Table 2.3. Bivariate regression analyses of non-size-corrected meristic and mensural variables associated with the transition from pentadactyl to limbless body plans in squamates for raw values and independent contrasts. Significant *P*-values at $\alpha \leq 0.05$ are shown in bold, with *P*-values significant after a table-wide Benjamini and Hochberg (1995) correction marked with an asterisk.

		Raw		Independent Contrasts	
		df = 31		df = 30	
Independent variable	Dependent variable	R^2	*P*	R^2	*P*
FLL	Fingers	0.936	**< 0.001***	0.346	**< 0.001***
HLL	Toes	0.948	**< 0.001***	0.461	**< 0.001***
Fingers	Toes	0.978	**< 0.001***	0.686	**< 0.001***
FLL	PSV	0.673	**< 0.001***	0.642	**< 0.001***
HLL	PSV	0.697	**< 0.001***	0.661	**< 0.001***

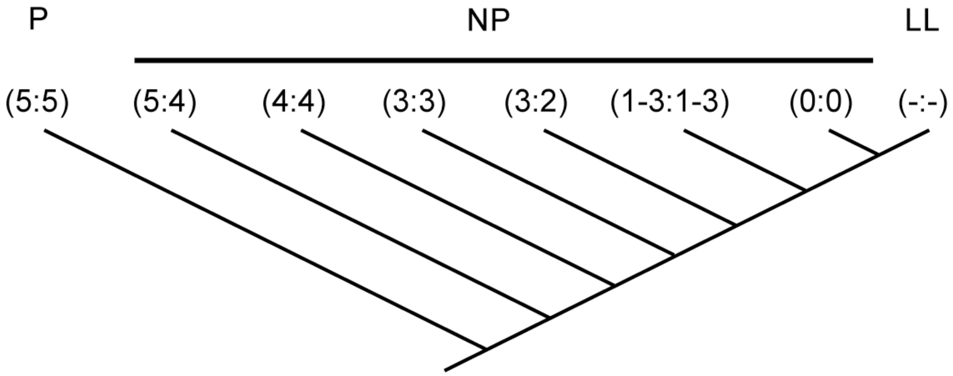
Figure 2.2. Four morphology-based hypotheses tested in the study, derived from hypothesized patterns of body form evolution in squamate reptiles. Each hypothesis is illustrated by constraint trees used in AU and Bayesian tests. The highest P-values recovered from each AU test (AU), and the posterior probabilities (PP) of the constraint topology, are shown. [a]Analyses conducted on constraint topologies with and without the inclusion of *Brachymeles miriamae*. [b]Analyses repeated for individual clades within Philippine *Brachymeles* as well as for the entire genus.



H1: Single origin of limb reduction
AU ≤ 0.000^{a}
PP = 0.0^{a}

H2: Single origin of limb loss
AU ≤ 0.000^{a}
PP = 0.0^{a}

H3: Single origin of ear loss
AU ≤ 0.000^{a}
PP = 0.0^{a}



H4: Gradual transition towards limb loss
AU ≤ $0.000^{a,b}$
PP = $0.0^{a,b}$

Correlation analyses of pairs of variables shown to have significant relationships in bivariate linear regressions revealed positive and negative correlations with changes in body and limb size and changes in limb lengths and numbers of digits and presacral vertebrae.

Multivariate analyses (PCA) of all three sets of data gave highly consistent results, showing strong separation between qualitatively defined (above) body forms of *Brachymeles* (Fig. 2.4, Appendix III). When all ten variables were included in a PCA, the first principal component explains 85.6% of the variation in the non-phylogenetic data. Size-corrected measures of body width and limb lengths, as well as digit numbers show positive loadings on the first principal component, with size-corrected measures of body length and presacral vertebrae numbers loading negatively (Fig. 2.4). The second principal component explains significantly less variation in the data (8.7 %), and shows moderately strong positive loadings for size-corrected body and limb lengths and digit numbers, with size-corrected measures of body width loading negatively (Fig. 2.4). Additional principal components were not retained because cumulative totals of the first two components reached nearly 95%, and subsequent components were associated with low eigenvalues (often well below 1.0), and low levels of explained variance (≤ 2.5%). All non-phylogenetic multivariate analyses support a relationship of body elongation and increased number of presacral vertebrae with decreased body width, limb lengths, and digit numbers (Appendix III). When phylogeny is taken into account, the same general pattern is observed, with the exception of the placement of *Brachymeles bicolor* and *B. pathfinderi* in morphospace. Both of these species are outliers in the observed patterns in *Brachymeles* (Fig. 2.4).

Table 2.4. Correlation analyses of pairs of morphological variables showing significant relationships from bivariate regression analyses. Relative measures of body size are based on regression residual, size-corrected independent contrasts. Values represent the Pearson product-moment correlation coefficients.

Variable 1	Variable 2	PMCC
rSVL	PSV	0.6587
rSVL	rFLL	-0.4770
rSVL	rHLL	-0.5211
rTotal	PSV	0.4643
rMBW	PSV	-0.4592
rMBW	rFLL	0.4459
rMBW	rHLL	0.4426
rFLL	Fingers	0.6346
rHLL	Toes	0.6354
rFLL	PSV	-0.6684
rHLL	PSV	-0.6559
PC1	Toes	-0.3290
PC1	PSV	0.7520
FLL	Fingers	0.6076
HLL	Toes	0.6885
Fingers	Toes	0.8254
FLL	PSV	-0.8153
HLL	PSV	-0.8107

Morphological thresholds

Threshold plots revealed a general trend of increased body length associated with decreased limb lengths and numbers of digits (Fig. 2.5); however, no obvious threshold values exist for which all digits are lost or all external fore- and hind limb elements are lost (Fig. 2.5). There appears to be a general threshold of relative SVL and MBW after which relative limb lengths are greatly reduced and digits are lost. With the exception of *Brachymeles bicolor* and *B. pathfinderi,* species with a SVL > ~ 12 times its head length, and a MBW ≤ ~ 1.3 times its head length, have considerably smaller, non-pentadactyl limbs (Fig. 2.5).

Digit loss was also associated with changes in relative limb lengths as well as raw limb lengths, and general threshold values are observed (Fig. 2.5). Again, with the exception of *B. pathfinderi*, loss of fore-limb digits appears to be initiated in species with fore-limb lengths ≈ head length, and raw fore-limb lengths < ~ 5.8 mm. Loss of hind limb digits appears to be initiated with hind limb lengths ≤ ~ 1.75 times head length, and raw hind limb lengths < ~ 12.2 mm. Additionally, the increase in number of presacral vertebrae is associated with both a loss of digits as well as a decrease in relative limb lengths (Fig. 2.5). No species with greater than 41 presacral vertebrae possessed five fingers, and when we exclude the apparent outlier (*B. bicolor*), fore-limb digit loss appears to be initiated in species with greater than 34 presacral vertebrae. With the exception of *B. pathfinderi*, hind limb digit loss follows an identical pattern. Relative fore-limb and hind limb lengths were observed to decrease by > ~ 40% and > ~ 47% respectively, in species with greater than 41 presacral vertebrae (Fig. 2.5).

With few exceptions, threshold plots revealed numerous cases in which different areas of morphospace were occupied by either pentadactyl or non-pentadactyl species, with little to no overlap.

Figure 2.3. Graphical representation of phylogenetic signal observed for morphometric variables measured for this study. The mean species' values for each measured variable, and body forms for each species of *Brachymeles*, are mapped onto the chronogram for reference.

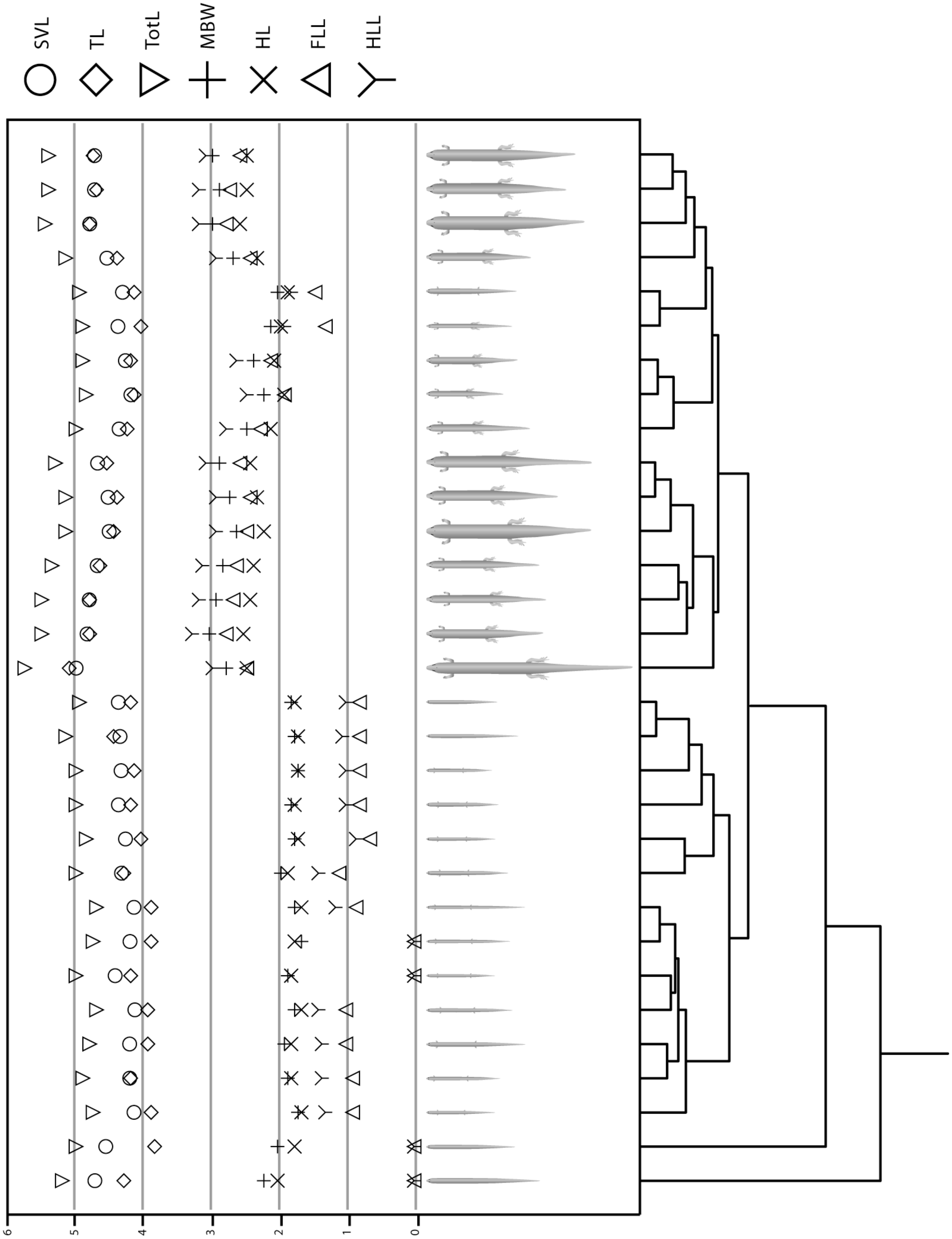

SVL
TL
TotL
MBW
HL
FLL
HLL
6
5
4
3
2
1
0

Figure 2.4. Multivariate plots of morphometric and meristic data showing variable loadings for the first and second components for a phylogenetic PCA. Colored spheres indicate body form groups among *Brachymeles*, with shapes referring to labeled phylogenetic clades in Figure 2.1.

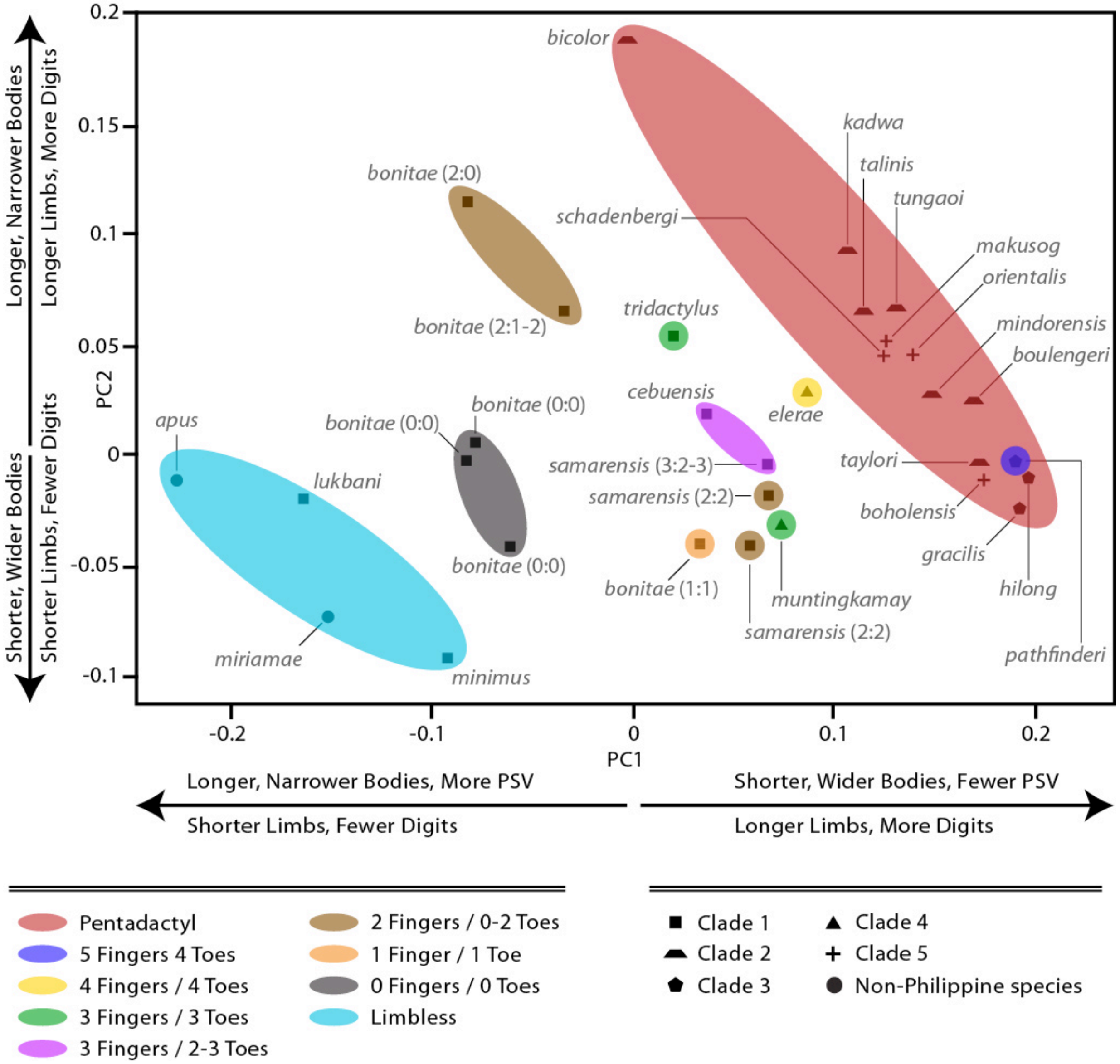
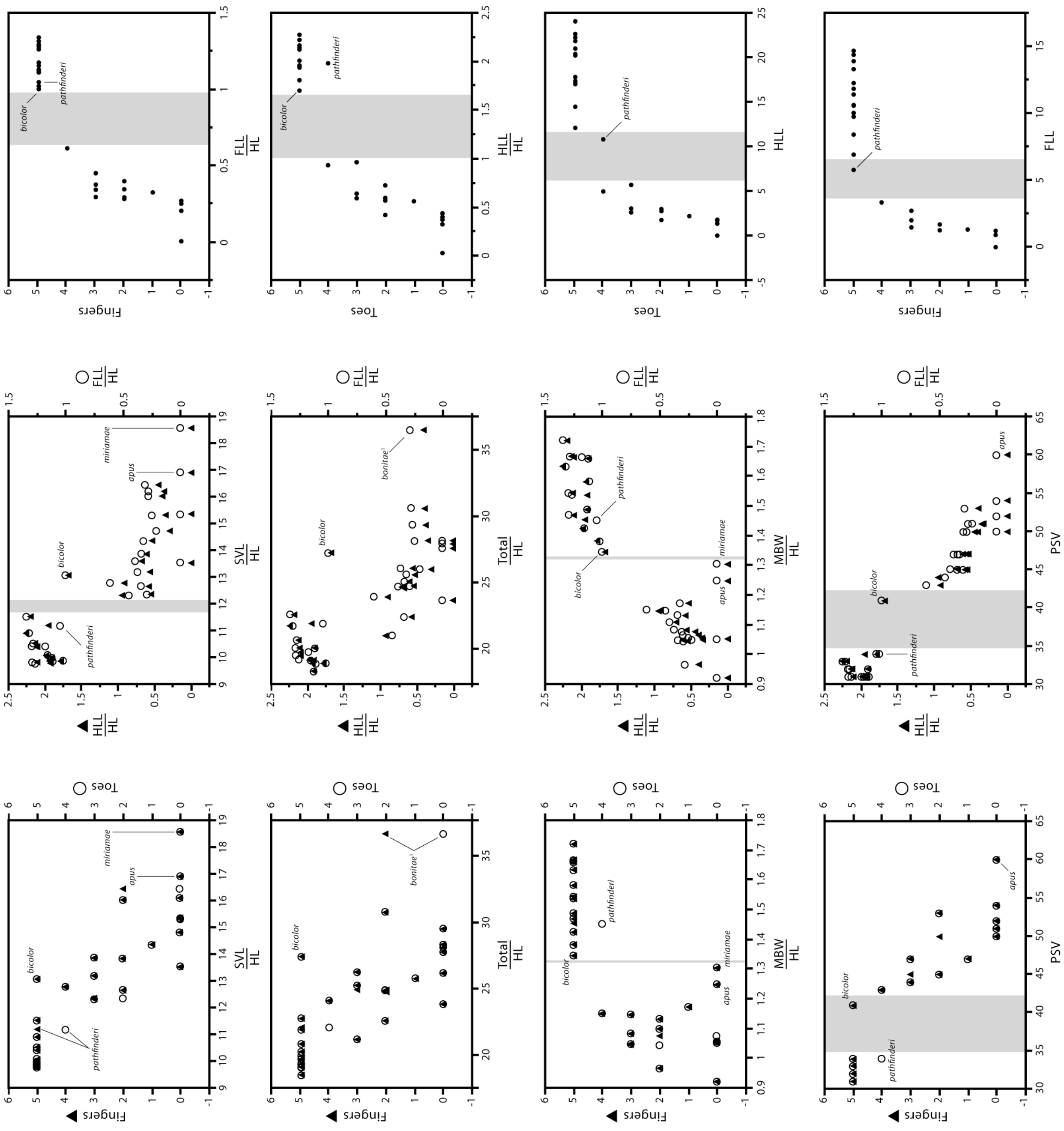

Longer, Narrower Bodies
Longer Limbs, More Digits
Shorter, Wider Bodies
Shorter Limbs, Fewer Digits
PC2
0.2
0.15
0.1
0.05
0
-0.05
-0.1
-0.2
-0.1
0
0.1
0.2
PC1
Longer, Narrower Bodies, More PSV
Shorter Limbs, Fewer Digits
Shorter, Wider Bodies, Fewer PSV
Longer Limbs, More Digits
bicolor
kadwa
talinis
tungaoi
schadenbergi
makusog
orientalis
mindorensis
boulengeri
taylori
boholensis
gracilis
hilong
pathfinderi
bonitae (2:0)
bonitae (2:1-2)
tridactylus
cebuensis
elerae
samarensis (3:2-3)
samarensis (2:2)
bonitae (1:1)
samarensis (2:2)
muntingkamay
bonitae (0:0)
bonitae (0:0)
bonitae (0:0)
apus
lukbani
miriamae
minimus
Pentadactyl
5 Fingers 4 Toes
4 Fingers / 4 Toes
3 Fingers / 3 Toes
3 Fingers / 2-3 Toes
2 Fingers / 0-2 Toes
1 Finger / 1 Toe
0 Fingers / 0 Toes
Limbless
Clade 1
Clade 2
Clade 3
Clade 4
Clade 5
Non-Philippine species

Figure 2.5. Bivariate scatter plots exploring hypothesized thresholds of relative body and limb lengths, relative body width, raw limb lengths, and numbers of presacral vertebrae at which changes in digit number and limb length occur (Brandley et al. 2008). Body proportions are derived from previous studies and were obtained by dividing raw measures of snout–vent length (SVL), fore-limb length (FLL), hind limb length (HLL), and midbody width (MBW) by head length (HL). Hypothesized morphological thresholds indicated by gray boxes, with proposed outliers labeled for reference.


Fingers
Toes
SVL/HL
Total/HL
MBW/HL
PSV
HLL/HL
FLL/HL
HLL
FLL
bicolor
pathfinderi
apus
miriamae
bonitae¹

Evidence of evolutionary re-acquisition of complex characters

Although the placement of *Brachymeles* within the family Scincidae remains somewhat ambiguous (Brandley et al. 2005, 2008; Siler et al. 2011; Fig. 2.1), the impact of ancestral body form for all *Brachymeles* does not appear to heavily impact ancestral reconstructions within the genus (not shown). The results of analyses of limb, digit, and ear opening states are never significantly impacted by placing restrictions on the ancestral character states among outgroup taxa and the node giving rise to all *Brachymeles* (not shown). Exploration of the assumed ancestral character states among outgroup taxa always resulted in highly consistent reconstructions for ingroup nodes. Additionally, our inclusion of a large, diverse group of outgroup taxa aided in avoiding some of the pitfalls of ancestral state reconstructions highlighted by other researchers (Goldberg and Igic 2008).

Ancestral state reconstructions for limbs and ear openings resulted in support for models with equal rates of character gain and loss. The likelihood scores were nearly identical between analyses of a two-rate model versus an equal rates model, with the Bayes factor (limbs, 0.562; ear openings, 0.706) providing non-significant support for the more parameterized models. We therefore used equal rates models for all subsequent analyses. Ancestral limb state reconstruction analyses resulted in four nodes where the reconstructed ancestral state is ambiguous, with the limbed state preferred in all cases with varying degrees of support (Fig. 2.6). These results weakly support the hypothesis of limbed ancestors in *Brachymeles* (Fig. 2.6). The ancestral reconstructions of ear openings supported a minimum of three state changes to have occurred (Fig. 2.6). Unlike the support observed for unidirectional limb loss within *Brachymeles*, we consistently observe strong support for the re-acquisition of ear openings within the Philippine clade, with one or two subsequent losses of the character (Fig. 2.6).

Exploratory analyses of digit evolution resulted in unequivocally strong support for the same two-rate unordered model of character evolution that best explained the data for the hand and foot (Table 2.5). Not only were the resulting likelihood values significantly better than those from analyses of other models, but Bayes factors of pairwise comparisons to the preferred model, with the exception of the unordered model A for toe evolution (Bayes factors = 8.339), were all greater than 10 (Table 2.5). Significantly, both unordered models (those allowing for different rates of character loss and acquisition) provide better fit to the data than ordered or unidirectional models (Table 2.5).

Evidence of digit re-acquisition is observed for both the hand and foot, with strong support for the re-evolution of a pentadactyl hand from a digit-reduced ancestor (Fig. 2.7; Table 2.6). Within the Philippine species, there is moderate to strong evidence for six instances of digit re-acquisition on the hand and five instances on the foot (Fig. 2.7; Table 2.6). Although all analyses provide unequivocal support for several instances of digit re-acquisition, many additional nodes receive ambiguous ancestral state reconstructions, indicating that the potential number of times digits have re-evolved in *Brachymeles* may be higher or lower than the number we currently observe (Fig. 2.7; Table 2.6). As noted in previous studies (Brandley et al. 2008), the results of ordered analyses (not shown) provide highly similar to identical ancestral reconstructions, but at times these reconstructions are more ambiguous. Regardless of the model, all analyses result in strong support for the re-evolution of a fully pentadactyl body form from an ancestor with reduced numbers of digits, with ordered models providing even less support for a pentadactyl ancestor (Fig. 2.7). Digit re-acquisition in *Brachymeles* appears to be equally common on the hand and foot, with evidence for the re- acquisition of 1–5 digits (Fig. 2.7; Table 2.6).

Table 2.5. BayesTraits models of digit evolution explored in ancestral state reconstructions, and subsequent results. Transition descriptions and the number of parameters are shown for reference. Table entries include the mean likelihood for each model followed by the standard deviation, the harmonic mean likelihood value, and the Bayes factors from bivariate comparisons with the model that best explains the data. Preferred model in bold for emphasis.

Model	State transitions	Parameter	$-L_i$	$-HML_i$	2 ln BF
Manus					
A	Unordered (all transitions between digit states occur at equal rates)	q01 = q10	-57.38622 ± 0.906	-58.09153	12.903
B	Ordered (single state transitions allowed only)	q01 = q10	-62.62201 ± 1.076	-63.57498	23.870
C	**Unordered (all state transitions allowed)**	**q01 ≠ q10**	**-50.63118 ± 1.009**	**-51.63983**	**0**
D	Ordered (single state transitions allowed only)	q01 ≠ q10	-57.46331 ± 1.608	-60.10428	16.929
E	Unidirectional (digit gain prohibited)	q10	-63.40825 ± 1.104	-64.62095	25.962
Pes					
A	Unordered (all transitions between digit states occur at equal rates)	q01 = q10	-58.07338 ± 0.846	-58.95081	8.339
B	Ordered (single state transitions allowed only)	q01 = q10	-62.37969 ± 1.033	-63.91871	18.275
C	**Unordered (all state transitions allowed)**	**q01 ≠ q10**	**-53.83906 ± 0.998**	**-54.78141**	**0**
D	Ordered (single state transitions allowed only)	q01 ≠ q10	-57.04622 ± 1.362	-60.12493	10.687
E	Unidirectional (digit gain prohibited)	q10	-69.38824 ± 1.274	-70.72887	31.895

Table 2.6. Statistical support for re-acquisition of digits and ears in *Brachymeles*. Data are only presented for species where moderate to high evidence exists for the re-acquisition of digits or external ear openings. Ancestral character states making up ≥ 0.95 of the posterior probability are listed, with Bayes factors indicating the preferred state in cases of ambiguous state reconstruction. The posterior probability of the preferred ancestral state is provided for reference, with probabilities above 0.95 bolded for emphasis. Clade references refer to those labeled in Figure 2.7.

Lineage	Ancestral state	Extant state	Preferred ancestral state (2 ln BF)	Posterior probability of preferred ancestral state
Fingers				
All *Brachymeles*	0, 1, 2, or 3	0–5	0 (8.54–9.04)	0 (0.890)
Philippine *Brachymeles* + *B. miriamae*	0, 1, 2, or 3	0–5	0 (7.77–12.90)	0 (0.879)
Clade A	0	0, 1, 2, or 3	–	0 (**0.964**)
Clade B	0	0, 1, 2, or 3	–	0 (**0.969**)
Clade C	0	0, 2, or 3	–	0 (**0.998**)
Clade D	0	0 or 2	–	0 (**0.960**)
B. cf. *bonitae* (Luzon)	0	1	–	0 (**0.979**)
B. cf. *bonitae* (Lubang)	0 or 2	2	0 (12.18)	0 (0.892)
B. tridactylus	0 or 3	3	0 (12.43)	0 (0.884)
B. samarensis (Samar)	0 or 2	2	0 (5.29)	0 (0.550)
B. cf. *samarensis* (Catanduanes)	0 or 2	2	0 (7.23)	0 (0.913)
B. elerae	3 or 4	4	3 (5.41)	3 (0.824)
Toes				
Clade E	0	0, 1, 2, or 3	–	0 (**0.957**)
Clade F	0	0, 1, 2, or 3	–	0 (**0.999**)
Clade G	0	0, 1, or 2	–	0 (**0.998**)
B. bonitae (Luzon)	0 or 2	1 or 2	0 (13.70)	0 (0.827)
B. cf. *bonitae* (Luzon)	0	1	–	0 (**0.967**)
B. tridactylus	0 or 3	3	0 (12.14)	0 (0.826)
B. cf. *samarensis* (Leyte)	1, 2, or 3	2 or 3	2 (5.08–5.44)	2 (0.736)
B. elerae	3 or 4	4	3 (4.04)	3 (0.779)
Ears				
All *Brachymeles*	Absent	Absent, present	–	Absent (**0.966**)
Philippine *Brachymeles*	Absent, present	Absent, present	Absent (5.09)	Absent (0.619)
B. elerae	Absent	Present	–	Absent (**0.999**)

Discussion

Patterns of limb reduction and loss

Topology tests rejected single origins of digit reduction, limb loss, and ear loss, and rejected the hypothesis of a gradual transition from pentadactyl to limbless body plans within *Brachymeles*, regardless of the inclusion of *B. miriamae* (Fig. 2.2). Phylogenetic analyses and ancestral state reconstructions provide support for multiple origins of body form changes within *Brachymeles*. We find evidence for three losses of external limb elements, and three distinct instances of changes in digit states. Although five species of *Brachymeles* are externally limbless (*B. apus, B. minimus, B. miriamae, B. lukbani, B. vermis*), internal pectoral and pelvic girdle elements are visible in x-rays of all five species (CDS, pers. obs.), indicating that the species have retained some vestigial elements of limbs. Previous studies have shown that reductions in digit number are more common in the fore-limbs of scincid lizards, with only four genera possessing species with the opposite pattern (*Bipes* [Bipedidae], *Bachia* [Gymnopthalmidae], *Anomolopus* [Scincidae], and *Teius* [Teiidae]; Brandley et al. 2008; Skinner and Lee 2010); however, in contrast all species and populations with unequal digit numbers in the fore- and hind limbs have fewer toes than fingers in *Brachymeles* (*B. bonitae, B. cebuensis, B. pathfinderi*, *B. samarensis*).

The results of regression and correlation analyses are for the most part consistent with the results of previous studies (Tables 2.2–2.4), with many of the general patterns observed across squamates also observed for *Brachymeles*. We find a strong relationship between limb reduction, body elongation, and digit loss (Tables 2.2–2.4). Additionally, body width and vertebral changes are also strongly associated with body and limb length changes and digit loss (Tables 2.2–2.4). Relative measures of tail and total lengths either are not correlated with limb reduction, vertebral changes, and digit loss, or only are correlated with changes in the number of presacral vertebrae

(Table 2.2). This result is consistent with our knowledge of the ecology of *Brachymeles* (Brown and Alcala 1980; Siler 2010; Siler et al. 2009a, 2010a,b; Siler and Brown 2010; Siler et al. 2011, in press a,b,c,d); in this genus, all species are fossorial or semi-fossorial and elongation of the body results predominately from increasing SVL, not TL (Tables 2.2, 2.4).

Multivariate analyses further support the patterns of body form change highlighted in bivariate analyses (Tables 2.2, 2.4; Fig. 2.4, Appendix III). Changes in body shape are moderately correlated with hind limb digit loss and strongly correlated with changes in presacral vertebrae number (Tables 2.2, 2.4). In general, limb reduction and subsequent loss and digit loss are associated with longer, narrower bodies and increased numbers of presacral vertebrae (Fig. 2.4, Appendix III).

We explored patterns of morphological evolution from two points of view: 1) patterns that can be directly observed and empirically quantified, and 2) those that hold regardless of phylogenetic relationships. It is commonly the case that significant relationships and correlations between characters become weaker or non-significant when a phylogenetic context is employed (Cronquist 1981; Kelly and Purvis 1993; Kelly 1995; Kelly and Beerling 1995; Ackerly and Reich 1999; Hutcheon et al. 2002)—a pattern observed in this study. However, our analyses also revealed the opposite pattern to occur as well: numerous significant relationships between morphological characters appeared only after taking phylogeny into account, suggesting that the use of an historical context for comparative analyses incorporated via phylogeny can reveal novel and significant statistical support for otherwise undetectable patterns of character correlation.

Our exploration of morphological thresholds in *Brachymeles* reveals several interesting and unexpected patterns. Brandley et al.'s (2008) study of squamate body form evolution revealed two regions of morphospace to be unoccupied: species with short limbs and multiple digits, and species with long limbs and no digits. For example, no species with limb lengths less than half their HL have been shown to have multiple digits. However, the results of this study provide evidence for both of these morphologies to be occupied by species of *Brachymeles* (Fig. 2.5). For example, with the exception of *B. elerae*, all species with 1–3 fingers have fore-limb lengths less than half their HL, and a population of *B. bonitae* with two toes has a HLL less than half its HL. Additionally, the observed relationships between raw limb lengths and digit loss also do not directly follow previous studies (Brandley et al. 2008). Seven species with fore-limb lengths less than 2 mm possess more than one finger, and six species with hind limb lengths less than 3.1 mm possess more than one toe (Fig. 2.5). Another previously undocumented extreme is also exhibited in *Brachymeles*. To the best of our knowledge, this study is the first to provide evidence for species lacking digits to have longer limb lengths than species with multiple digits (Fig. 2.5). This indicates that even within this relatively small radiation of skinks, there are exceptions to general, previously documented, and widely accepted (see Brandley et al. 2008, for review) patterns of body form change. These findings have general implications, and potentially suggest that whatever functional, mechanical or developmental constraints have shaped morphological evolution among other lizards (except *Bipes*) may have been lost in *Brachymeles*.

In all threshold plots, two outliers were consistently recovered (*B. bicolor* and *B. pathfinderi*; Fig. 2.5). Both of these species represent unique morphologies within the genus, with *B. bicolor* representing by far the longest species of *Brachymeles*, and *B. pathfinderi* being the only digit reduced species to be nested within a clade of pentadactyl species (Fig. 2.1). Despite these outlier species, we observe general patterns of body form change. Loss of fingers appears to occur when relative and raw FLL ≤ 1.0 and 5.8 mm, respectively, and loss of toes occurs when relative and raw HLL ≤ 1.75 times HL and 12.2 mm, respectively (Fig. 2.5). Excluding *B. bicolor* and *B. pathfinderi*, body plan shifts towards limb reduction and digit loss are clearly visible along the spectrum of observed midbody widths and numbers of presacral vertebrae (Fig. 2.5).

We compared two common methods for size correction while exploring whether head length is an appropriate measure with which to correct for size. The results of analyses using size-corrected data from the phylogenetic size-correction method of Revell (2009), or the commonly used size-correction method based on residuals from linear regression analyses of independent contrasts (Garland 1992), were highly consistent (Table 2.2). Although using alternative characters for size correction (SVL, MBW) in regression, correlation, and multivariate analyses showed highly consistent results (not shown), multivariate correlation analyses indicated that, for *Brachymeles*, head length is the most appropriate variable for size correction. Comparisons of principal component analyses with raw, size-corrected data, and phylogenetic PCAs (Revell 2009), showed highly consistent results in the values, loadings, and scores of the analyses, as well as in the partitioning of species in morphospace (Fig. 2.4, Appendix III).

Complex character "re-evolution" and Dollo's Law

Most previous studies of squamate limb and digit evolution have worked within the framework of unidirectional character loss (see Brandley et al. 2008, for review). Although several recent studies have provided numerous lines of evidence for the re-evolution of digits among squamate reptiles (Kohlsdorf and Wagner 2006; Brandley et al. 2008; Kohlsdorf et al. 2010; but see Galis et al. 2010), the hypothesis of digit evolution occurring in an ordered sequence (e.g., Alberch and Gale 1985; Shubin and Alberch 1986; Shapiro 2002) has led to little exploration of disparate models of character evolution. Recently, Skinner and Lee (2010) and

Skinner (2010) showed that unordered models of character evolution provided the best fit data on fore- and hind limb digits in *Lerista* (one of the four genera to possess species with fully limbed, intermediate, and limbless body forms). However, Bayes factors we inferred in this study showed weak positive support for their best-fit model (Kass and Raftery 1995; Nylander et al. 2004). Surprisingly, the studies of *Lerista* did not find evidence for digit re-acquisition (Skinner et al. 2008; Skinner and Lee 2009, 2010; Skinner 2010) whereas in this study, we found one of the first documented cases of high statistical support for complex character re-acquisition in a clade of closely related species.

We considered applying a model that takes into account state-specific rates of speciation and extinction (BiSSE, Maddison et al. 2007). The assumptions of the BiSSE model's original implementation included analyzing trait-dependent diversification for: (1) binary characters only, (2) completely resolved, known phylogenies (= no missing taxa), and (3) large phylogenies. FitzJohn et al. (2009) relaxed one of these assumptions (complete taxon sampling); however, our dataset violates three (original), and both (current), assumptions of the model and preclude its implementation in this study. Evaluations of this model's limitations for smaller datasets are needed in which only a few changes in character states have taken place.

Considering our robust datasets, phylogeny, and best-fit models of character evolution, the phylogenetic results of this study unambiguously support five instances of digit re-acquisition in the hand and four instances of digit re-acquisition in the foot (Fig. 2.7; Table 2.6). Additionally, Bayes factors comparing preferred states for eleven ambiguously reconstructed nodes moderately to highly support an ancestral state with fewer digits than that observed in extant species (Fig. 2.7; Table 2.6). In contrast, the data also support independent instances of complete loss of external limb elements (Fig. 2.7).

Figure 2.6. Maximum clade credibility chronograms and estimated ancestral states of limb and ear opening presence or absence in *Brachymeles* skinks. Ancestral state reconstructions are indicated at each node. Triangles indicate unambiguous reconstructions of a character state (posterior probability ≥ 0.95), colored according to the hypothesized state. Circles represent ambiguous character reconstructions, with colors representing the preferred state and values showing the Bayes factor as an indication of the strength of support for that state. Colored blocks at each ambiguous node represent alternate states supported in analyses.

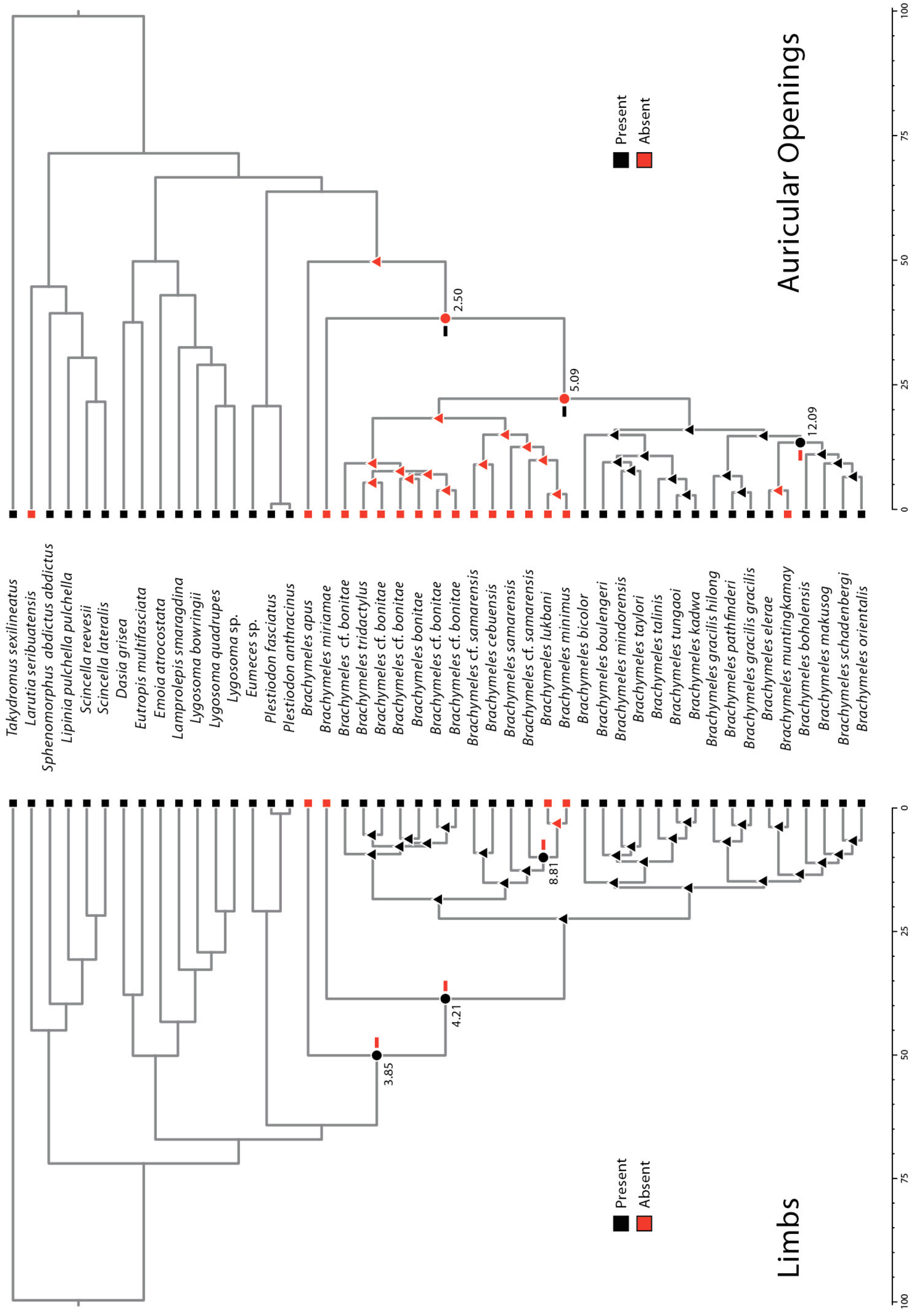
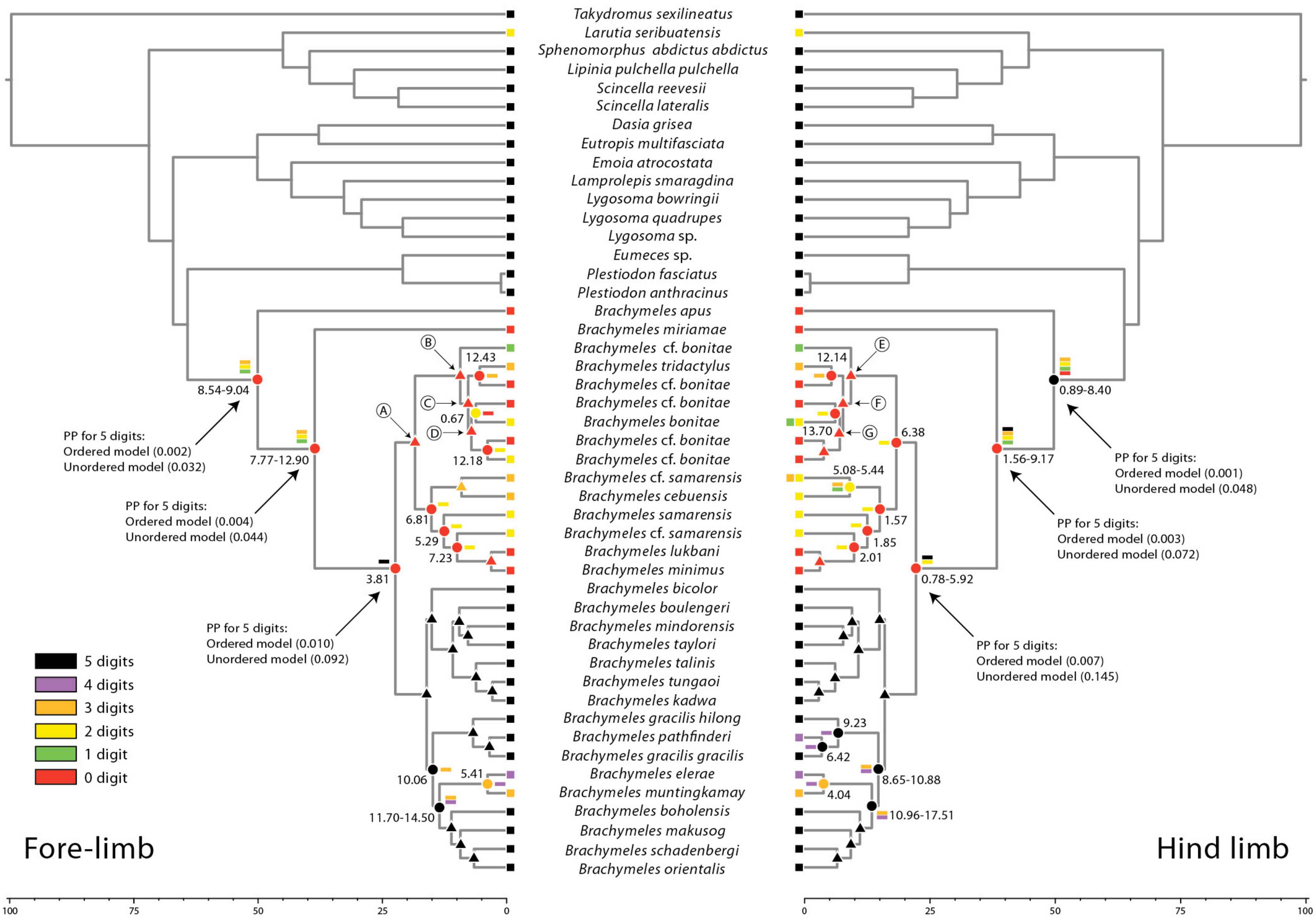

Auricular Openings
Limbs
■ Present
🟥 Absent
■ Present
🟥 Absent
2.50
5.09
12.09
3.85
4.21
8.81
0
25
50
75
100
0
25
50
75
100
Takydromus sexilineatus
Larutia seribuatensis
Sphenomorphus abdictus abdictus
Lipinia pulchella pulchella
Scincella reevesii
Scincella lateralis
Dasia grisea
Eutropis multifasciata
Emoia atrocostata
Lamprolepis smaragdina
Lygosoma bowringii
Lygosoma quadrupes
Lygosoma sp.
Eumeces sp.
Plestiodon fasciatus
Plestiodon anthracinus
Brachymeles apus
Brachymeles miriamae
Brachymeles cf. bonitae
Brachymeles tridactylus
Brachymeles cf. bonitae
Brachymeles cf. bonitae
Brachymeles bonitae
Brachymeles cf. bonitae
Brachymeles cf. bonitae
Brachymeles cf. samarensis
Brachymeles cebuensis
Brachymeles samarensis
Brachymeles cf. samarensis
Brachymeles lukbani
Brachymeles minimus
Brachymeles bicolor
Brachymeles boulengeri
Brachymeles mindorensis
Brachymeles taylori
Brachymeles talinis
Brachymeles tungaoi
Brachymeles kadwa
Brachymeles gracilis hilong
Brachymeles pathfinderi
Brachymeles gracilis gracilis
Brachymeles elerae
Brachymeles muntingkamay
Brachymeles boholensis
Brachymeles makusog
Brachymeles schadenbergi
Brachymeles orientalis

Figure 2.7. Maximum clade credibility chronograms and estimated ancestral states of limb and ear opening presence or absence in *Brachymeles* skinks. Ancestral state reconstructions are indicated at each node. Triangles indicate unambiguous reconstructions of a character state (posterior probability ≥ 0.95), colored according to the hypothesized state. Circles represent ambiguous character reconstructions, with colors representing the preferred state and values showing the Bayes factor as an indication of the strength of support for that state. Colored blocks at each ambiguous node represent alternate states supported in analyses. The posterior probabilities of a 5-digit fore- and hind limb ancestral state to all *Brachymeles*, *B. miriamae* + Philippine *Brachymeles*, and Philippine *Brachymeles* resulting from the ordered model of Brandley et al. (2008) and the best fit, unordered model shown for reference.


Takydromus sexilineatus
Larutia seribuatensis
Sphenomorphus abdictus abdictus
Lipinia pulchella pulchella
Scincella reevesii
Scincella lateralis
Dasia grisea
Eutropis multifasciata
Emoia atrocostata
Lamprolepis smaragdina
Lygosoma bowringii
Lygosoma quadrupes
Lygosoma sp.
Eumeces sp.
Plestiodon fasciatus
Plestiodon anthracinus
Brachymeles apus
Brachymeles miriamae
Brachymeles cf. bonitae
Brachymeles tridactylus
Brachymeles cf. bonitae
Brachymeles cf. bonitae
Brachymeles bonitae
Brachymeles cf. bonitae
Brachymeles cf. bonitae
Brachymeles cf. samarensis
Brachymeles cebuensis
Brachymeles samarensis
Brachymeles cf. samarensis
Brachymeles lukbani
Brachymeles minimus
Brachymeles bicolor
Brachymeles boulengeri
Brachymeles mindorensis
Brachymeles taylori
Brachymeles talinis
Brachymeles tungaoi
Brachymeles kadwa
Brachymeles gracilis hilong
Brachymeles pathfinderi
Brachymeles gracilis gracilis
Brachymeles elerae
Brachymeles muntingkamay
Brachymeles boholensis
Brachymeles makusog
Brachymeles schadenbergi
Brachymeles orientalis
Fore-limb
Hind limb
■ 5 digits
■ 4 digits
■ 3 digits
■ 2 digits
■ 1 digit
■ 0 digit
8.54-9.04
PP for 5 digits:
Ordered model (0.002)
Unordered model (0.032)
7.77-12.90
PP for 5 digits:
Ordered model (0.004)
Unordered model (0.044)
3.81
PP for 5 digits:
Ordered model (0.010)
Unordered model (0.092)
A
B
C
D
12.43
0.67
12.18
6.81
5.29
7.23
10.06
5.41
11.70-14.50
0.89-8.40
PP for 5 digits:
Ordered model (0.001)
Unordered model (0.048)
1.56-9.17
PP for 5 digits:
Ordered model (0.003)
Unordered model (0.072)
0.78-5.92
PP for 5 digits:
Ordered model (0.007)
Unordered model (0.145)
E
F
G
12.14
13.70
6.38
5.08-5.44
1.57
1.85
2.01
9.23
6.42
8.65-10.88
4.04
10.96-17.51
100
75
50
25
0
0
25
50
75
100

One of our most striking findings involve support for the re-evolution of a pentadactyl body form from a digitless or digit-reduced ancestor (Fig. 2.7; Table 2.6). In exploring the impact of the model on this result, we repeated all ancestral state reconstructions with the suite of models compared in Skinner and Lee (2010). Similar to the findings of Brandley et al. (2008), ancestral reconstructions with ordered models of evolution instead of the best-fit undordered models were more ambiguous. However, regardless of the model of character evolution, all analyses preferred digitless or digit-reduced ancestral states for the nodes giving rise to all Philippines species of *Brachymeles* with ≥ 95% of the combined posterior probabilities of digitless and digit-reduced states for each node (Fig. 2.7).

The Philippine radiation of *Brachymeles* includes the known diversity of pentadactyl species in the genus, which are supported to have evolved from digitless or at least digit-reduced ancestors (Fig. 2.7; Table 2.6). Although this finding stands in contrast to expectations derived from Dollo's Law (Dollo 1893, 1905, 1922; Simpson 1953; Gould 1970), preliminary data on the phalangeal formula of species of *Brachymeles* supports the findings of previous studies concerning evidence for digit re-acquisition. Kolsdorf and Wagner (2006) and Brandley et al. (2008) noted several species in which digit re-evolution was reconstructed unambiguously, and phalangeal formulas are uniform among digits when compared with the primitive phalangeal formula among squamates (fore-limb: 2-3-4-5-3; hind limb: 2-3-4-5-4). Among these strongly supported instances of digit, and possibly limb, re-evolution, examples of phalangeal uniformity include *Bachia* (fore-limb, 0-2-2-2-2; hind limb, 2-2-2-2-0; Kolsdorf and Wagner 2006), *Bipes* (fore-limb, 3-3-3-3-3; Zangerl 1945), and *Scelotes* (fore-limb, 2-3-3-3-2; hind limb, 2-3-4-4-2; Brandley et al. 2008). Surprisingly, the phalangeal formulas of all pentadactyl species of *Brachymeles* show striking similarities to those observed in *Scelotes* (fore-limb, 2-3-3-3-2; hind limb, 2-3-4-4-3; C. D. Siler, pers. obs.). Given that pentadactyl species have not lost all digit identity, it remains plausible that the observed phalangeal formulas among extant taxa is simply due to loss of phalangeal elements in the common ancestor. However, the fact that this phalangeal formula has been maintained over significant evolutionary time suggests that there may be a developmental constraint on digit morphology. Regardless of how the pentadactyl state has evolved in *Brachymeles*, this strange, shared phalangeal formula among all pentadactyl members of the genus may be evidence that digits have been re-acquired via a novel evolutionary pathway, unique among pentadactyl lizards.

In addition to the possible re-acquisition of digits and limbs, the results of this study provide unambiguous phylogenetic support for two instances of external ear re-acquisition in *Brachymeles* (Fig. 2.6; Table 2.6). Although the absence of ear openings is common among small, burrowing, or semi-fossorial skinks, external ear openings invariably have been hypothesized to be lost in a unidirectional manner (i.e., present-to-absent), without reversals or re-evolution of exposed tympannae (Greer 2002). Not only do we demonstrate strong evidence for the re-acquisition of external ear openings in *Brachymeles,* but at least one subsequent, additional or secondary, loss of this character is strongly inferred to have taken place leading to the extant character state observed in *B. muntingkamay* (Fig. 2.6). These findings are the first of their kind, and suggest that the previous assumption about the unidirectionality of changes in this character may be incorrect. Presently, it is not clear whether the loss of external ear openings in *Brachymeles* involves a re-structuring of bone or simply a re-structuring of skin, the former process presumably being more complex of a morphological change. If all species with external ear openings possess an atypical inner ear morphology, the finding would lend additional support to members of the genus having re-evolved complex characters via a novel evolutionary pathway.

Conclusions

Our data represent one of the most comprehensive, fine-scaled, studies of body-form evolution to date for a closely related group of lizards. Not only have we sampled nearly every recognized species within the genus *Brachymeles*, but also we have sufficient sampling to investigate intraspecific variation within many species (e.g., *Brachymeles bonitae* and *B. samarensis*). Coupled with this nearly complete taxonomic sampling, our robust morphological and molecular dataset provide a rich system with which to address questions concerning body form evolution within one of the few genera to possess the full suite of body forms extremes, including representatives inhabiting previously undocumented portions of body form morphospace.

Although within the genus, general external morphologies appear conservative, on the whole, *Brachymeles* appears to occupy previously undocumented regions of morphospace (Fig. 2.4, 2.5, Appendix III). Examples of this include species with relatively tiny limbs and multiple digits and species with relatively longer limbs and no digits (Fig. 2.5). Multivariate analyses of morphological data indicate species with similar body forms have evolved into similar regions of morphospace (Fig. 2.4, Appendix III).

Ancestral character state reconstructions are limited in that they provide only a statistical framework with which to investigate data in the context of a reduced tree with branch lengths and a single character per terminus. With that in mind, there are two perspectives to consider when interpreting the results of this study: (1) what do our data, phylogeny, and best-fit models of character evolution tell us about the prevalence and directionality of body form evolution in *Brachymeles*? And (2) what are the limitations of our data and analyses for making these inferences? Although alternative explanations are possible, we believe that the strong statistical support uncovered here for the reversibility of complex characters in a closely related group of lizards is some of the most compelling recent examples of clear exceptions to Dollo's Law. Regardless of the perspective, it is clear that multiple instances of digit and ear state changes have occurred during the evolutionary history of *Brachymeles*. Considering the comprehensive and fine-scale approach to this study, the results of ancestral state reconstructions support the re-acquisition of both digits and external ear openings. Furthermore, all analyses support the re-acquisition of a pentadactyl body form from a digitless or digit-reduced ancestor, regardless of the model enforced.

Although these results are novel, it is important to consider the limitations of our data and methods of inference. Due to disproportional diversification in the archipelago, undiscovered mainland diversity, and/or massive extinction outside the archipelago, nearly all of the known diversity within *Brachymeles* is endemic to the Philippines. The only three non-Philippine species (*Brachymeles apus, Brachymeles* cf. *apus,* and *B. miriamae*) are all limbless and sister to the Philippine radiation (Fig. 2.1). Even with a near complete range of body forms within the genus, the majority of the variation occurs within two major clades (Fig. 2.1, Clade 1, 2), with all pentadactyl species part in Clade 2. With this in mind, it is conceivable that there have been multiple independent losses of limbs, digits, and external ear openings giving rise to the Philippine radiation. If this were plausible, such a scenario would suggest that many of the pentadactyl species with external ear openings gave rise to the currently recognized diversity of *Brachymeles* and have either gone extinct or have yet to be discovered. However, we consider the above scenario unlikely due to the fact that the mainland Southeast Asian herpetofauna has become very well known as a result of extremely active field work in the region (e.g., Van Dijk et al. 1998; Chanard et al. 1999; Malkmus et al. 2002; Pauwels et al. 2003; Grismer et al. 2006a,b; Das 2007, 2010; Manthey and Grossmann 1997; Sang et al. 2009), and no fossil evidence has come to light suggesting otherwise.

With the comprehensive nature of this and previous studies, we are likely approaching a methodological limit to our ability to understand the processes behind body form change in *Brachymeles*. The phylogenetic evidence at hand unambiguously supports the evolution of unique body morphologies and the re-acquisition of complex characters. However, support for the directionality of character change will remain debatable until these patterns are investigated with new approaches, including developmental, ecological, and behavioral studies. Regardless, our results provide new, detailed, insight into heretofore incompletely understood range of diversity in this widespread and conceptually intriguing process of body form evolution among squamate reptiles.

CHAPTER 3

Phylogeny-based species delimitation in Philippine slender skinks (Reptilia: Squamata: Scincidae: *Brachymeles*): taxonomic revision of pentadactyl species groups and description of three new species

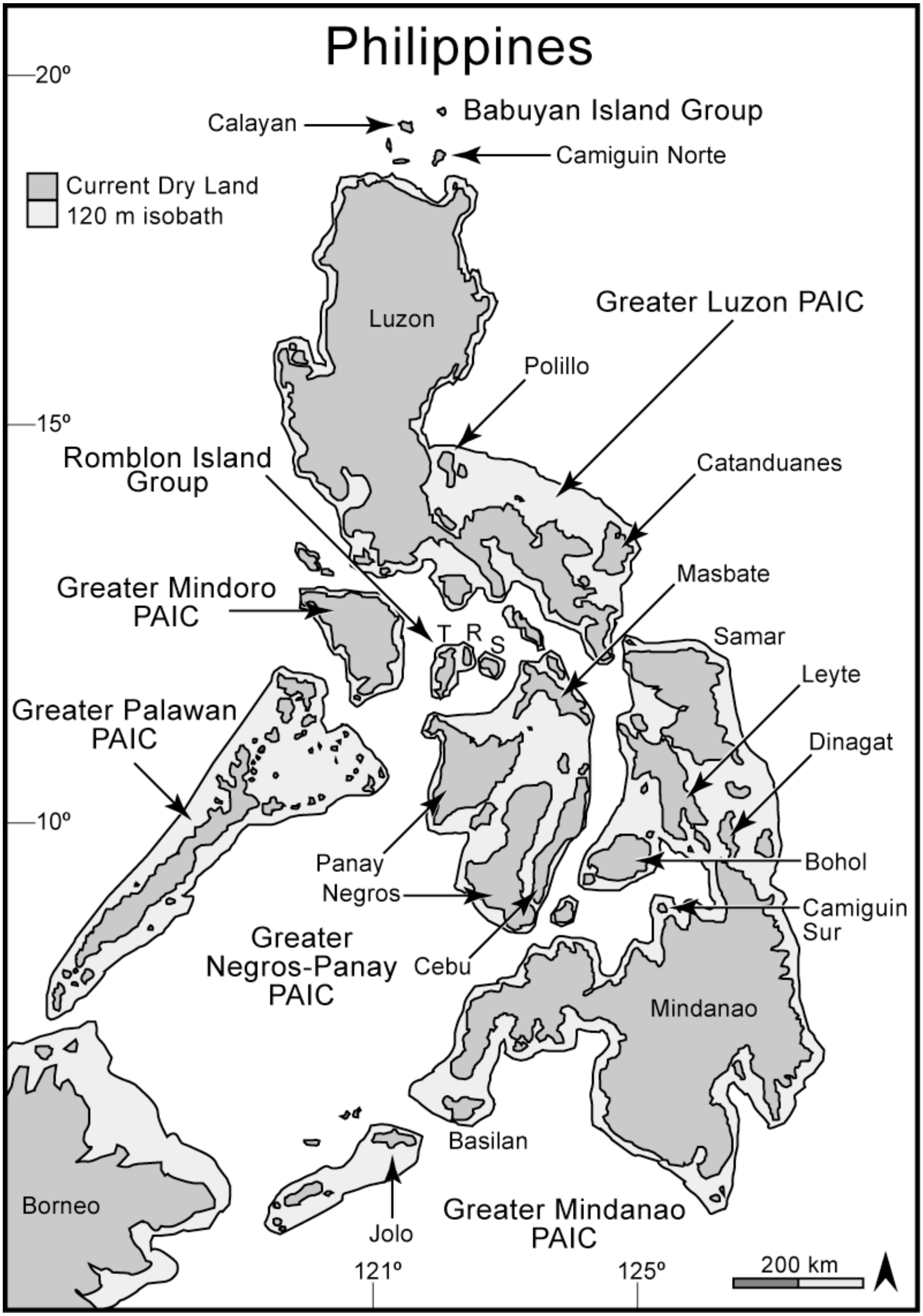
There are only four genera of scincid lizards possessing both fully limbed and limbless species (*Brachymeles*, *Chalcides*, *Lerista*, and *Scelotes*; Lande, 1978; Wiens and Slingluff, 2001; Brandley et al., 2008). Within the genus *Brachymeles*, all but one of the 18 recognized species are endemic to the Philippines. The exception is *B. apus* from northern Borneo (Brown and Alcala, 1980; Hikida, 1982; Siler et al., 2009a, 2010a,b). Six species are pentadactyl (*B. bicolor*, *B. boulengeri*, *B. gracilis*, *B. makusog, B. schadenbergi*, and *B. talinis*), eight are non-pentadactyl, with reduced limbs and numbers of digits (*B. bonitae*, *B. cebuensis*, *B. elerae*, *B. muntingkamay, B. pathfinderi*, *B. samarensis*, *B. tridactylus*, and *B. wrighti*), and four are entirely limbless (*B. apus*, *B. minimus, B. lukbani,* and *B. vermis*). Within the non-pentadactyl species (Duméril and Bibron, 1839; Brown, 1956; Brown and Rabor, 1967; Taylor, 1917, 1925, 1918) exist a wide range of limb- and digit-reduced states, from minute limbs that lack full digits (*B. bonitae*, *B. cebuensis*, *B. muntingkamay, B. samarensis, B. tridactylus*), to moderately developed limbs with four to five digits on the hands and feet (*B. elerae, B. pathfinderi, B. wrighti*: Brown and Alcala, 1980; Hikida, 1982; Siler et al., 2009a, 2010b). All species are semi-fossorial and typically found in dry, rotting material inside decaying logs or in loose soil and leaf litter.

Shared body plans and similar external morphological features among populations of *Brachymeles* has proven problematic for diagnosing species (Brown and Alcala, 1980; Siler et al., 2009a, 2010a,b). Additionally, several rare, mid-to-high elevation species have long been represented by only a few specimens, in some cases without knowledge of their exact type locality (e.g., *Brachymeles bicolor, B. elerae, B. wrighti, B. pathfinderi*). Three species are polytypic: *B. boulengeri* contains four subspecies and *B. gracilis* and *B. schadenbergi* each contain two (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). Several other species are recognized as having widespread distributions that span historical faunal demarcations in the Philippines (Heaney, 1985, 1986; Brown and Guttman, 2002; Brown and Diesmos, 2002), including *B. talinis, B. samarensis,* and *B. bonitae* (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980).

Taxonomic History

The genus *Brachymeles* was first described by Duméril and Bibron (1839) for the small, limb-reduced species *Brachymeles bonitae*. Three additional species (*Senira bicolor* [Gray, 1845], *Eumeces* (*Riopa*) *gracilis* [Fischer, 1885], *E.* (*R.*) *schadenbergi* [Fischer, 1885]) were transferred to the genus by Boettger (1886) and Boulenger (1887). These four species represented the known diversity in the genus for thirty years, until Taylor published a series of herpetofaunal descriptions in the early 1900s. In Taylor's (1917) review of the genus, he revised *B. gracilis* to not only include populations in the Mindanao Faunal Region, but also populations on Negros and Mindoro islands (Fig. 3.1). A few years later, Taylor (1922c) described *B. boulengeri*, based on material from Polillo Island, and included populations from Luzon, Mindoro, and Negros islands as representatives of the species (Fig. 3.1). Thirty years later, Brown (1956) described *B. gracilis taylori*, and included *B. boulengeri* as one of three subspecies of the polytypic species *B. gracilis*. Brown and Rabor's (1967) description of *B. gracilis boholensis* and *B. g. mindorensis* brought the number of subspecies within *B. gracilis* to five. It was not

Figure 3.1. Map of the Philippine islands, with island labels provided for islands with representative samples used for this study. The five recognized major Pleistocene Aggregate Island Complexes (PAICs), major island groups, and additional deep-water islands are labeled for reference. Islands of the Romblon Island Group are designated by the first letter of the island name (T, Tablas Island; R, Romblon Island; S, Sibuyan Island). Current islands in the Philippines are shown in medium grey; light gray areas enclosed in black 120 m bathymetric contours indicate the hypothesized maximum extent of land during the mid- to late Pleistocene.


Philippines
20º
Calayan
Babuyan Island Group
Camiguin Norte
Current Dry Land
120 m isobath
Luzon
Greater Luzon PAIC
Polillo
15º
Romblon Island Group
Catanduanes
Masbate
Greater Mindoro PAIC
T
R
S
Samar
Leyte
Greater Palawan PAIC
Dinagat
10º
Panay
Bohol
Negros
Camiguin Sur
Greater Negros-Panay PAIC
Cebu
Mindanao
Basilan
Borneo
Jolo
Greater Mindanao PAIC
121º
125º
200 km

until 1980 that Brown and Alcala (1980) resurrected the polytypic species *B. boulengeri*, and included four subspecies (*B. b. boulengeri, B. b. boholensis, B. b. mindorensis, B. b. taylori*), all believed to be distinct from *B. gracilis*. This view characterized the taxonomy of *B. boulengeri* for the next 30 years. Numerous authors have mentioned the morphological variation among island populations of *B. boulengeri* and other species (Taylor, 1922b; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980), but all refrained from elevating these subspecies to full species. *Brachymeles boulengeri boulengeri* and *B. b. taylori* have larger geographic distributions across multiple islands within a single faunal region (Taylor, 1922b; Brown and Rabor, 1967; Brown and Alcala, 1980), whereas *B. b. boholensis* and *B. b. mindorensis* are single island endemics (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980).

Although *Brachymeles talinis* was described originally as *B. schadenbergi talinis* (Brown, 1956), and considered it part of the widespread *B. schadenbergi* complex from the Sulu Islands and the Mindanao, Visayan, and Luzon Pleistocene Aggregate Island Complexes (PAICs; Brown and Guttman, 2002; Brown and Diesmos, 2002), the subspecies was described on the basis of material from Negros Island (Brown, 1956). Brown (1956) referred to series of specimens from Jolo and Luzon islands as likely exemplars of *B. schadenbergi talinis*, and hypothesized three explanations for the unusual distribution of *B. schadenbergi* in the Philippines: (1) chance colonization across ocean barriers into distinct faunal regions by two subspecies; (2) morphological convergence within a polytypic species; and (3) prolonged maintenance of two morphologically similar, disjunct distributions of sibling species within the Philippines. At the time, Brown (1956) supported the first hypothesis with reservations; however, in Brown and Rabor's (1967) review of *Brachymeles*, newly available material supported the third hypothesis, and led to the recognition of *B. talinis* from Jolo, Negros, and Luzon islands as a distinct "sibling species" of *B. schadenbergi* populations from Basilan, Mindanao, Bohol, and Leyte islands. When Brown and Alcala (1980) revised the genus, they restricted the geographic distribution of *B. talinis* to the central and northern Philippine islands, and postponed the assignment of the two specimens from Jolo until the morphological variability of that island population was better understood. Although samples from throughout the central and northern range of *B. talinis* have been available, the recognition of this widespread species has continued for more than 40 years (Brown and Alcala, 1980; Siler et al., 2009a, 2010a,b).

Following the separation of *Brachymeles talinis* from the *B. schadenbergi* complex, Brown and Rabor (1967) recognized two subspecies of *B. schadenbergi*, one from western and south-central Mindanao Island and Basilan Island (*B. s. schadenbergi*), and the other from eastern Mindanao, Camiguin Sur, Bohol, and Leyte islands (*B. s. orientalis*). Fischer (1885) had previously designated the type locality for *B. schadenbergi* as southern Mindanao Island, and specimens from south-central Mindanao Island have thus been identified as *B. schadenbergi schadenbergi* (Brown and Rabor, 1967; Brown and Alcala, 1980). In addition to its already broad geographic distribution, Brown and Alcala (1980) predicted that *B. s. orientalis* would also be observed on Samar Island.

Both *Brachymeles boulengeri* and *B. talinis* are distributed across several distinct PAICs, including the Luzon, Mindanao, Mindoro, and Visayan island complexes (Fig. 3.1). Because many recent studies have revealed that few endemic Philippine reptiles actually possess broad distributions spanning these regional faunistic boundaries (Brown et al., 2000a; Brown and Diesmos, 2002, 2009; Siler et al., 2010a; Welton et al., 2009, 2010a,b), we have begun to reevaluate the known polytypic and widespread species in the genus *Brachymeles*. Our goal is to revise the taxonomy such that individual units (species) represent independently evolving, cohesive lineage segments (sensu Simpson, 1961; Wiley 1978; Frost and Hillis, 1990; de Queiroz, 1998, 1999). Careful examination of numerous recently collected specimens from throughout the known ranges of *B. boulengeri, B. schadenbergi,* and *B. talinis*, as well as all relevant name-bearing type material, results in the reorganization of *B. boulengeri*, *B. schadenbergi,* and *B. talinis* into ten distinct species. In this paper we provide a phylogenetic analysis of most of these taxa, fully describe each evolutionary lineage, clarify species boundaries, and provide the first illustrations of most these taxa. We also provide information on each species' natural history, ecology, and geographic distribution.

Materials and Methods

Field work, sample collection, and specimen preservation

Fieldwork was conducted on Bohol, Calayan, Camiguin Norte, Camiguin Sur, Catanduanes, Dinagat, Leyte, Luzon, Masbate, Mindanao, Mindoro, Negros, Panay, Polillo, Romblon, Samar, Sibuyan, and Tablas islands, all in the Philippines (Fig. 3.1) between 1992 and 2009. Specimens were collected between 900 and 1600 hr, euthanized with aqueous chloretone, dissected for genetic samples (liver preserved in 95% ethanol or flash frozen in liquid nitrogen), fixed in 10% buffered-formalin and eventually (< 2 mo) transferred to 70% ethanol. Newly sequenced voucher specimens are deposited in U.S. and Philippine museum collections (Acknowledgments and Specimens Examined); if available, voucher information corresponding to data from GenBank sequences is included in Table 3.1.

Taxon sampling and outgroup selection for phylogenetic analyses

Because our primary goal was to estimate phylogenetic relationships among the subspecies and island populations of *Brachymeles boulengeri, B. schadenbergi,* and *B. talinis*, we sequenced only 1–2 exemplars per species; however, in the case of a species occurring on multiple islands within a single PAIC, or across a large island such as Mindanao, we sampled multiple populations to provide greater geographic resolution. We chose two scincid taxa (*Plestiodon egregius* and *Lygosoma bowringii*) based on relationships presented in a recent phylogenetic analysis of scincid lizards (Brandley et al., 2005) as outgroups. A total of 39 ingroup samples were used to construct phylogenetic inferences. There are no tissue samples of the population of *B. talinis* from Jolo Island, and this population is therefore not included in the phylogenetic analyses.

DNA extraction, purification, and amplification

We extracted total genomic DNA from tissues (Table 3.1) using the modified guanidine thiocyanate extraction method of Esselstyn et al. (2008). The mitochondrial ATPase 8 (ATP8) and ATPase 6 (ATP6) protein coding genes were amplified using standard PCR methods with the primers ATPf (5'-CTCAGARATCTGCGGGYCAAATCACA-3') and ATPr (5'-GTGCYTTCTCGRRTAATRTCYCGTCAT-3'; M. Brandley, unpublished data). PCR products were visualized on 1.0% agarose gels, then purified them with ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ). Purified templates were sequenced with the same primers and the ABI Prism BigDye Terminator chemistry (Ver. 3.1; Applied Biosystems, Foster City, CA). Cycle-sequencing products were purified with Sephadex Medium (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). Sequencing products were run on an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Gene sequences were assembled with Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Table 3.1. Summary of specimens corresponding to genetic samples included in the study, general locality, and GenBank accession number. PNM/CMNH = deposited in the Cincinnati Museum of Natural History; LSUHC = La Sierra University Herpetological Collections; * = currently uncataloged specimen, deposited in the National Museum of the Philippines.

Species	Voucher	Locality	Genbank Accession Numbers
			ATPase 8, 6
Lygosoma bowringi	LSUHC 6970	West Malaysia	HQ239366
Plestiodon egregius	MVZ 11013	Not Available	NC000888
Brachymeles taylori	ACD 862*	Philippines, Cebu Island	HQ239368
Brachymeles taylori	KU 307738	Philippines, Negros Island, Municipality of Valencia, Mt. Talinis	HQ239369
Brachymeles taylori	RMB 3226*	Philippines, Negros Island, Municipality of Valencia, Mt. Talinis	HQ239370
Brachymeles mindorensis	KU 307739	Philippines, Mindoro Island, Municipality of Bongabong	HQ239371
Brachymeles mindorensis	KU 307740	Philippines, Mindoro Island, Municipality of Bongabong	HQ239372
Brachymele boholensis	RMB 2866*	Philippines, Bohol Island, Municipality of Bilar	HQ239373
Brachymele boholensis	RMB 2875*	Philippines, Bohol Island, Municipality of Bilar	HQ239374
Brachymeles boulengeri	KU 307753	Philippines, Polillo Island, Municipality of Polillo	HQ239375
Brachymeles boulengeri	KU 307754	Philippines, Polillo Island, Municipality of Polillo	HQ239376
Brachymeles boulengeri	KU 313831	Philippines, Luzon Island, Municipality of Labo, Mt. Labo	HQ239377
Brachymeles boulengeri	KU 313829	Philippines, Luzon Island, Municipality of Labo, Mt. Labo	HQ239378
Brachymeles boulengeri	KU 320058	Philippines, Luzon Island, Municipality of Laguna, Mt. Makiling	HQ239379
Brachymeles boulengeri	KU 320059	Philippines, Luzon Island, Municipality of Laguna, Mt. Makiling	HQ239380
Brachymeles kadwa	ACD 3290*	Philippines, Luzon Island	HQ239381
Brachymeles kadwa	RMB 4040*	Philippines, Luzon Island, Municipality of Irosin, Mt. Bulusan	HQ239382
Brachymeles kadwa	KU 307965	Philippines, Camiguin Norte Island, Municipality of Calayan	HQ239383
Brachymeles kadwa	KU 307985	Philippines, Camiguin Norte Island, Municipality of Calayan	HQ239384
Brachymeles kadwa	KU 304906	Philippines, Calayan Island, Municipality of Calayan	HQ239385
Brachymeles kadwa	KU 304875	Philippines, Calayan Island, Municipality of Calayan	HQ239386
Brachymeles talinis	RMB 3305*	Philippines, Negros Island, Municipality of Valencia, Mt. Talinis	HQ239387
Brachymeles talinis	KU 303990	Philippines, Sibuyan Island, Municipality of Magdiwang	HQ239388
Brachymeles talinis	KU 306786	Philippines, Panay Island, Municipality of Sibalom	HQ239389
Brachymeles talinis	KU 306781	Philippines, Panay Island, Municipality of Sibalom	HQ239390
Brachymeles talinis	KU 315358	Philippines, Tablas Island, Municipality of Calatrava	HQ239391
Brachymeles talinis	KU 315359	Philippines, Tablas Island, Municipality of Calatrava	HQ239392
Brachymeles tungaoi	KU 323935	Philippines, Masbate Island, Municipality of Mobo	HQ239393
Brachymeles tungaoi	KU 323936	Philippines, Masbate Island, Municipality of Mobo	HQ239394
Brachymeles tungaoi	KU 323933	Philippines, Masbate Island, Municipality of Mobo	HQ239395
Brachymeles tungaoi	KU 323934	Philippines, Masbate Island, Municipality of Mobo	HQ239396
Brachymeles schadenbergi	PNM/CMNH H1457	Philippines, Mindanao Island, Municipality of Kiamba, Mt. Busa	HQ239397
Brachymeles schadenbergi	KU 314980	Philippines, Mindanao Island, Municipality of Zamboanga City	HQ239398

Table 3.1 Continued

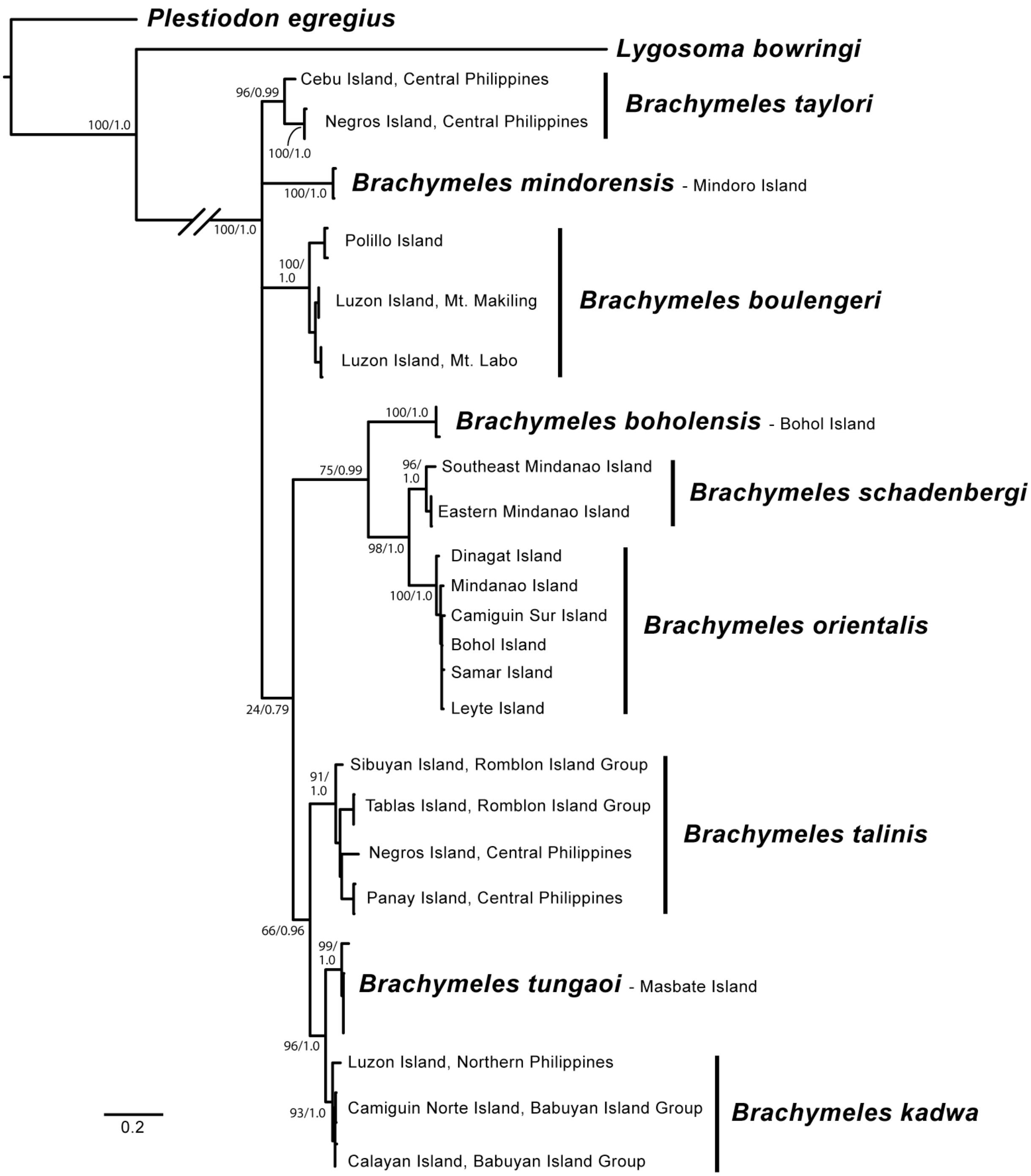
Species	Voucher	Locality	Genbank Accession Numbers
			ATPase 8, 6
Brachymeles schadenbergi	KU 314981	Philippines, Mindanao Island, Municipality of Zamboanga City	HQ239399
Brachymeles orientalis	KU 314092	Philippines, Mindanao Island, Municipality of San Francisco	HQ239400
Brachymeles orientalis	KU 311239	Philippines, Leyte Island, Municipality of Baybay	HQ239401
Brachymeles orientalis	KU 311230	Philippines, Leyte Island, Municipality of Baybay	HQ239402
Brachymeles orientalis	KU 310945	Philippines, Samar Island, Municipality of Taft	HQ239403
Brachymeles orientalis	KU 310357	Philippines, Camiguin Sur Island, Municipality of Mambajao	HQ239404
Brachymeles orientalis	KU 305469	Philippines, Dinagat Island, Municipality of Loreto	HQ239405
Brachymeles orientalis	KU 324028	Philippines, Bohol Island, Municipality of Bilar	HQ239406

Table 3.2. Models of evolution selected by AIC and applied for partitioned, Bayesian phylogenetic analyses[1].

Partition	AIC Model	Number of Characters
ATP8, 1st codon position	HKY + G	53
ATP8, 2nd codon position	HKY + I + G	53
ATP8, 3rd codon position	GTR + G	53
ATP6, 1st codon position	GTR + I	227
ATP6, 2nd codon position	GTR + I + G	227
ATP6, 3rd codon position	GTR + G	227

[1] The model GTR + I + G was used for partitioned RAxMLHPC analyses.

Figure 3.2. Maximum clade credibility tree from a phylognetic analyis of mitochondrial data (ATP 6 and 8; -lnL 5249.903214). Nodes shown with numerical values corresponding to MLBP, and Bayesian PP support values respectively. Terminals are labeled with taxonomic names, and sampling localities.


Plestiodon egregius
Lygosoma bowringi
100/1.0
96/0.99
Cebu Island, Central Philippines
Negros Island, Central Philippines
100/1.0
Brachymeles taylori
100/1.0
Brachymeles mindorensis - Mindoro Island
100/1.0
Polillo Island
100/
1.0
Luzon Island, Mt. Makiling
Luzon Island, Mt. Labo
Brachymeles boulengeri
100/1.0
Brachymeles boholensis - Bohol Island
75/0.99
96/
1.0
Southeast Mindanao Island
Eastern Mindanao Island
Brachymeles schadenbergi
98/1.0
Dinagat Island
100/1.0
Mindanao Island
Camiguin Sur Island
Bohol Island
Samar Island
Leyte Island
Brachymeles orientalis
24/0.79
91/
1.0
Sibuyan Island, Romblon Island Group
Tablas Island, Romblon Island Group
Negros Island, Central Philippines
Panay Island, Central Philippines
Brachymeles talinis
66/0.96
99/
1.0
Brachymeles tungaoi - Masbate Island
96/1.0
Luzon Island, Northern Philippines
93/1.0
Camiguin Norte Island, Babuyan Island Group
Calayan Island, Babuyan Island Group
Brachymeles kadwa
0.2

Alignment and phylogenetic analysis

An initial alignment was produced in Muscle v3.7 (Edgar, 2004), and visual inspections were made in MacClade 4.08 (Maddison and Maddison, 2005). No instances of insertions or deletions, or ambiguously aligned regions, were observed in the data, and all data were used for analyses. The final alignment consisted of 838 aligned nucleotides.

Phylogenetic analyses were conducted using parsimony, likelihood, and Bayesian optimality criteria. Parsimony (MP) analyses were conducted in PAUP* 4.0 (Swofford, 2002) with all characters weighted equally. Most-parsimonious trees were estimated using heuristic searches with 1000 random addition-sequence replicates and tree bisection and reconnection (TBR) branch swapping. To assess heuristic support, nonparametric bootstrapping was conducted using 1000 replicates, each with 100 random addition-sequence replicates and TBR branch swapping.

Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.04 (Stamatakis, 2006). The alignment was partitioned into six regions consisting of the codon positions of ATP8 and ATP6. Analyses that partition protein-coding genes by codon position have been shown to improve resulting inferences (Brandley et al., 2005). The partitions were run under the same model (GTR + I + Γ) with 100 replicate best-tree inferences. Each inference was performed with a random starting tree, and relied on the rapid hill-climbing algorithm (Stamatakis 2006). Clade support was assessed with 1000 bootstrap pseudoreplicates. We considered branches receiving ≥70% bootstrap support to be well-supported (Hillis and Bull, 1993; see also Wilcox et al., 2002). The Akaike Information Criterion (AIC), as implemented in MrModelTest 2.2 (Nylander, 2004), was used to find appropriate models of sequence evolution. The best-fit model for each of the six partitions (Table 3.2) was used for Bayesian analyses performed in MrBayes 3.1 (Ronquist and Huelsenbeck, 2003). The same partitioning strategy used for maximum likelihood analyses was used for Bayesian inferences. Searches over tree space were conducted with four runs, each with four chains, and were run for 2×10^7 generations. Trees were sampled every 1000 generations, with 4000 samples discarded as burn-in; this left 16001 post-burn-in trees from each run included in the summary. Visual inspection for chain stationarity and high ESS values was conducted within the program Tracer v1.4 (Rambaut and Drummond, 2007). Additionally, correlations of split frequencies and cumulative split frequencies were examined using the program AWTY (Nylander et al., 2008). We considered topologies with posterior probabilities ≥0.95 to be well-supported (Wilcox et al., 2002).

Morphological data

We examined fluid-preserved specimens (Appendix IV) for variation in qualitative and mensural characters. Sex was determined by gonadal inspection, and measurements were taken to the nearest 0.1 mm with digital calipers by CDS. Museum abbreviations for specimens examined follow Leviton et al. (1985).

Meristic and mensural characters were chosen based on Siler et al. (2009a, 2010a,b): characters evaluated were snout–vent length (SVL), axilla–groin distance (AGD), total length (TotL), midbody width (MBW), midbody height (MBH), tail length (TL), tail width (TW), tail height (TH), head length (HL), head width (HW), head height (HH), snout–forearm length (SnFa), eye diameter (ED), eye–narial distance (END), snout length (SNL), internarial distance (IND), forelimb length (FLL), hind limb length (HLL), midbody scale-row count (MBSR), paravertebral scale-row count (PVSR), axilla–groin scale-row count (AGSR), Finger-III lamellae count (FinIIIlam), Toe-IV lamellae count (ToeIVlam), supralabial count (SL), infralabial count

(IFL), supraciliary count (SC), and supraocular count (SO). In the description, ranges are followed by mean ± standard deviation in parentheses.

Species concept

We follow the General Lineage Concept of species (de Queiroz, 1998, 1999) as a logical extension of the Evolutionary Species Concept (Simpson, 1961; Wiley, 1978; Frost and Hillis, 1990). We consider as distinct lineages those populations that are morphologically, and genetically distinct. Lineage-based species concepts have been successfully employed in the recognition of Philippine biodiversity (Brown et al., 2000b, 2002, 2008, 2009; Brown and Guttman, 2002; Gaulke et al., 2007; Welton et al., 2009, 2010) due to the highly partitioned nature of the archipelago (Brown and Diesmos, 2009), and because the geological history of the islands has been so well documented (Hall, 2002; Yumul, 2009). In this study we use an estimate of phylogenetic relationships as a guide for delimiting species but restrict our diagnoses of new species to those populations diagnosed by non-overlapping morphological character states.

Results

Phylogeny

Of 838 aligned mitochondrial nucleotide positions, 392 and 306 were variable and parsimony-informative, respectively. Just considering the alignment for *Brachymeles* sequence data, 310 and 279 were variable and parsimony-informative, respectively. The ML analysis resulted in a single optimal tree (–lnL = 5249.903). The resulting topology from the Bayesian analysis is very similar to the ML tree. Trees estimated from ML, MP, and Bayesian analyses are consistent with respect to support for nine unique species of *Brachymeles*.

No inferences support the monophyly of *B. boulengeri*. All analyses recover *B. b. boholensis* as part of a clade with *B. s. orientalis* and *B. s. schadenbergi* with high support (Fig. 3.2). The ML and Bayesian analyses support a close relationship among *B. b. boulengeri*, *B. b. mindorensis,* and *B. b. taylori*, but not their monophyly (Fig. 3.2). Results of both analyses (ML and Bayesian) show a a polytomy with four lineages including *B. b. mindorensis, B. b. taylori, B. b. boulengeri*, and a clade consisting of the remaining species (Fig. 3.2). All analyses support a clade of *B. b. boholensis, B. s. schadenbergi,* and *B. s. orientalis* as sister to a clade of three distinct lineages of *B. talinis* samples, while MP analyses consistently supported the clade of *B. talinis* as sister to a clade of *B. b. mindorensis, B. b. taylori,* and *B. b. boulengeri*. With the inclusion of two short mitochondrial genes for only three of the 18 recognized species in the genus, it is likely that differences in topologies among ML and Bayesian analyses reflect limited taxon and character sampling. Nevertheless, all analyses result in the strong support of nine genetically distinct lineages of *Brachymeles* (Fig. 3.2). Additionally, samples of *B. talinis* cluster into three major clades, each of which is strongly supported in all analyses (Fig. 3.2).

Uncorrected pairwise sequence divergences are low within named taxa and relatively high between these lineages (Table 3.3). Levels of sequence divergence show that the nine mtDNA lineages discovered by our phylogenetic analyses (*B. b. boholensis, B. b. boulengeri, B.* sp. nov. (Masbate Island)*, B.* sp. nov. (Calayan, Camiguin Norte, and Luzon islands)*, B. b. mindorensis, B. talinis, B. b. taylori, B. s. orientalis, B. s. schadenbergi*) are distinguished from congeners by levels of genetic divergence equal to, or greater than, those between previously defined species—viz., *B. boulengeri*, *B. talinis*, *B. schadenbergi* (Table 3.3; Fig. 3.2). The two most genetically similar lineages (*B.* sp. nov. [Masbate Island] and *B.* sp. nov. [northern Philippines]) are separated by 3.8–5.2% sequence divergence, and sequence divergences among all subspecies of *B. boulengeri,* and among both subspecies of *B. schadenbergi,* are greater than 7.3% (Table 3.3; Fig. 3.2). The three lineages with the greatest range of sequence divergence across populations are the presently defined subspecific taxa that occur across multiple islands within a single PAIC (*B. b. boulengeri, B. b. taylori, B. talinis*; Table 3.3; Fig. 3.2, 3.3, 3.5). Sequence divergence among populations in the lineage of northern populations of *B. talinis*, and among populations of *B. schadenbergi orientalis*, are much lower than those of other lineages known to be distributed across multiple islands (Table 3.3; Fig. 3.3, 3.4, 3.5).

Morphology

Variation in morphological characters (Tables 3.4–3.6) mirrors the results observed in phylogenetic analyses, and supports the recognition of nine *Brachymeles* lineages. Additionally, comparison of meristic and mensural morphological characters identified a tenth unique lineage from Jolo Island, previously recognized as a population of *B. talinis*. Characters differing among these ten lineages include: body size, degree of limb development, finger and toe lamellae counts, head and body scale counts and patterns, and pigmentation patterns (Tables 3.4–3.6; species accounts below). We observed no mensural or meristic differences between the sexes of any of the 10 species.

Superficially, subspecies of both *B. boulengeri* and *B. schadenbergi*, and island populations of *B. talinis*, appear morphologically similar, especially in overall body size; however, numerous non-overlapping differences were detected in meristic, mensural, and color pattern characters for each complex member, readily defining ten distinct lineages between the three complexes (Tables 3.4–3.6).

Table 3.3. Uncorrected pairwise sequence divergence (%) for mitochondrial data for *Brachymeles boholensis, B. boulengeri, B. mindorensis, B. taylori*, *B. talinis*, *B. kadwa*, *B. tungaoi, B. orientalis,* and *B. schadenbergi* (Fig. 3.3). Percentages on the diagonal represent intraspecific genetic diversity (bolded for emphasis).

	boholensis	*boulengeri*	*mindorensis*	*taylori*	*talinis*	*kadwa*	*tungaoi*	*orientalis*	*schadenbergi*
boholensis	**0.6**								
boulengeri	15.3–15.9	**0.0–4.7**							
mindorensis	16.1–16.7	10.6–11.5	**0.6**						
taylori	15.6–16.0	10.2–11.6	11.0–11.2	**0.3–4.8**					
talinis	13.0–14.6	10.4–11.8	11.8–12.4	10.3–12.4	**0.1–4.5**				
kadwa	12.7–13.6	10.4–11.7	11.5–12.1	9.3–10.3	6.9–8.6	**0.1–2.2**			
tungaoi	13.2–13.9	10.5–12.1	10.7–11.6	9.7–10.1	7.2–8.3	3.8–5.2	**0.0–1.5**		
orientalis	13.4–14.7	14.7–16.5	15.6–16.7	15.5–16.9	14.3–15.8	15.2–16.2	15.3–16.1	**0.6–2.1**	
schadenbergi	12.6–13.8	14.5–16.0	16.0–17.3	15.2–16.3	13.8–15.4	15.2–16.5	15.2–16.2	7.3–8.5	**0.1–2.6**

Figure 3.3. Hypothesized distributions of *Brachymeles boholensis, B. boulengeri, B. mindorensis,* and *B. taylori* in the Philippines. The sampling localities are indicated by black shapes, and the hypothesized geographic range of each species indicated by shaded islands, with shapes and shades of islands corresponding to the map's key.

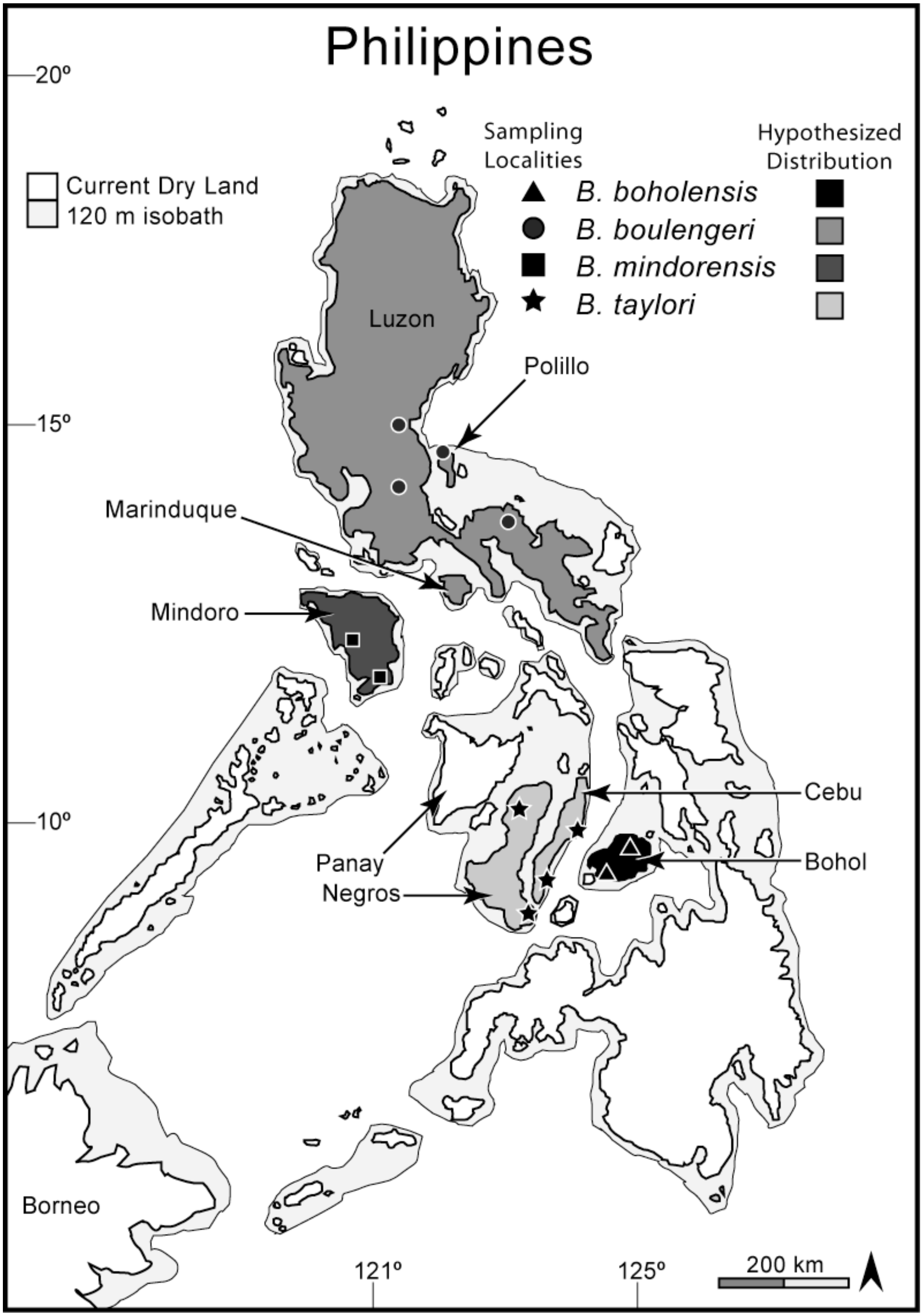

Philippines
20º
15º
10º
121º
125º
Current Dry Land
120 m isobath
Sampling Localities
Hypothesized Distribution
B. boholensis
B. boulengeri
B. mindorensis
B. taylori
Luzon
Polillo
Marinduque
Mindoro
Cebu
Panay
Negros
Bohol
Borneo
200 km

Figure 3.4. Hypothesized distributions of *Brachymeles orientalis, B. schadenbergi,* and *B. vindumi* in the Philippines. The sampling localities are indicated by black shapes, and the hypothesized geographic range of each species indicated by shaded islands, with shapes and shades of islands corresponding to the map's key. Unknown Mindanao Island range boundaries indicated by dashed lines.

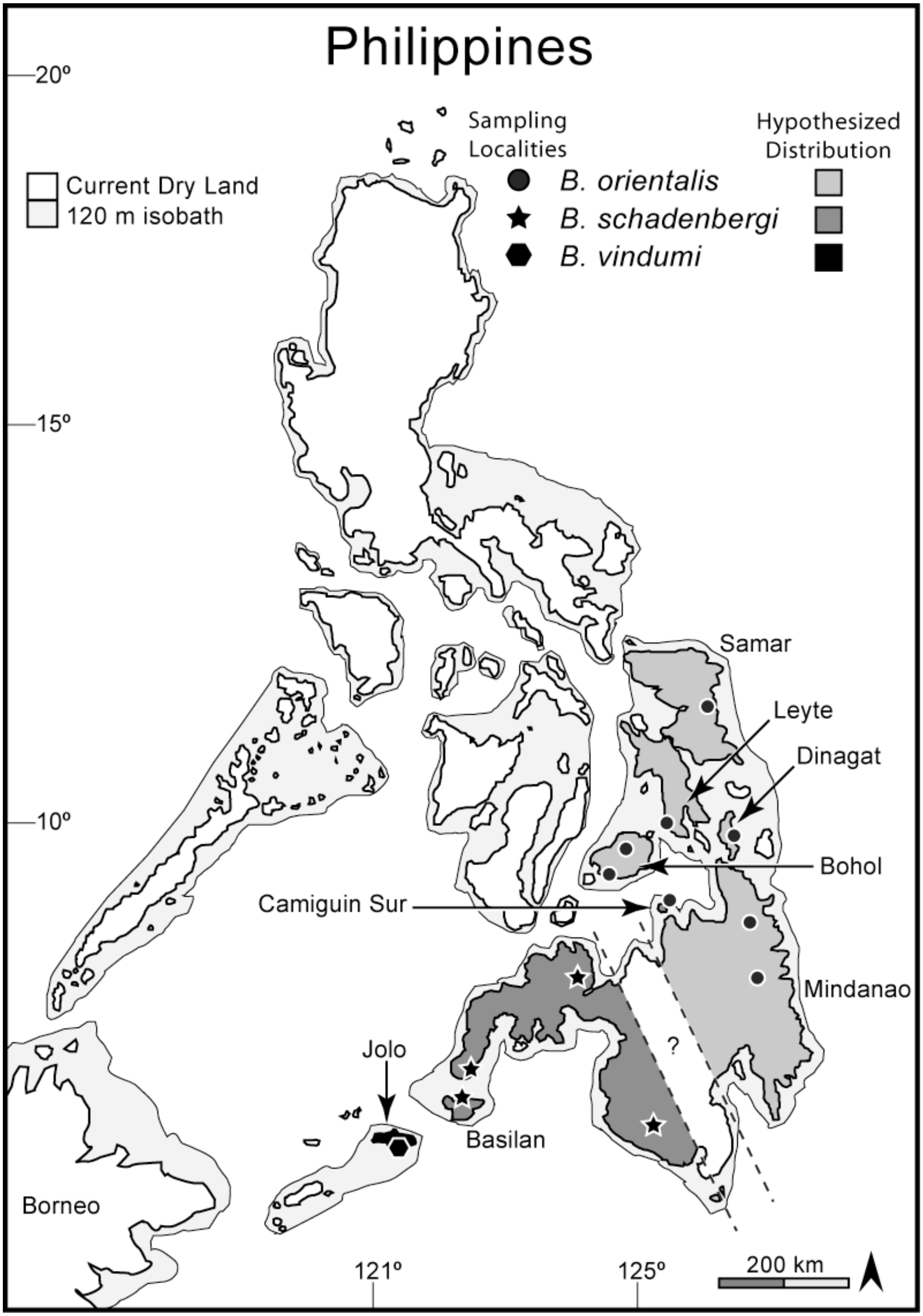
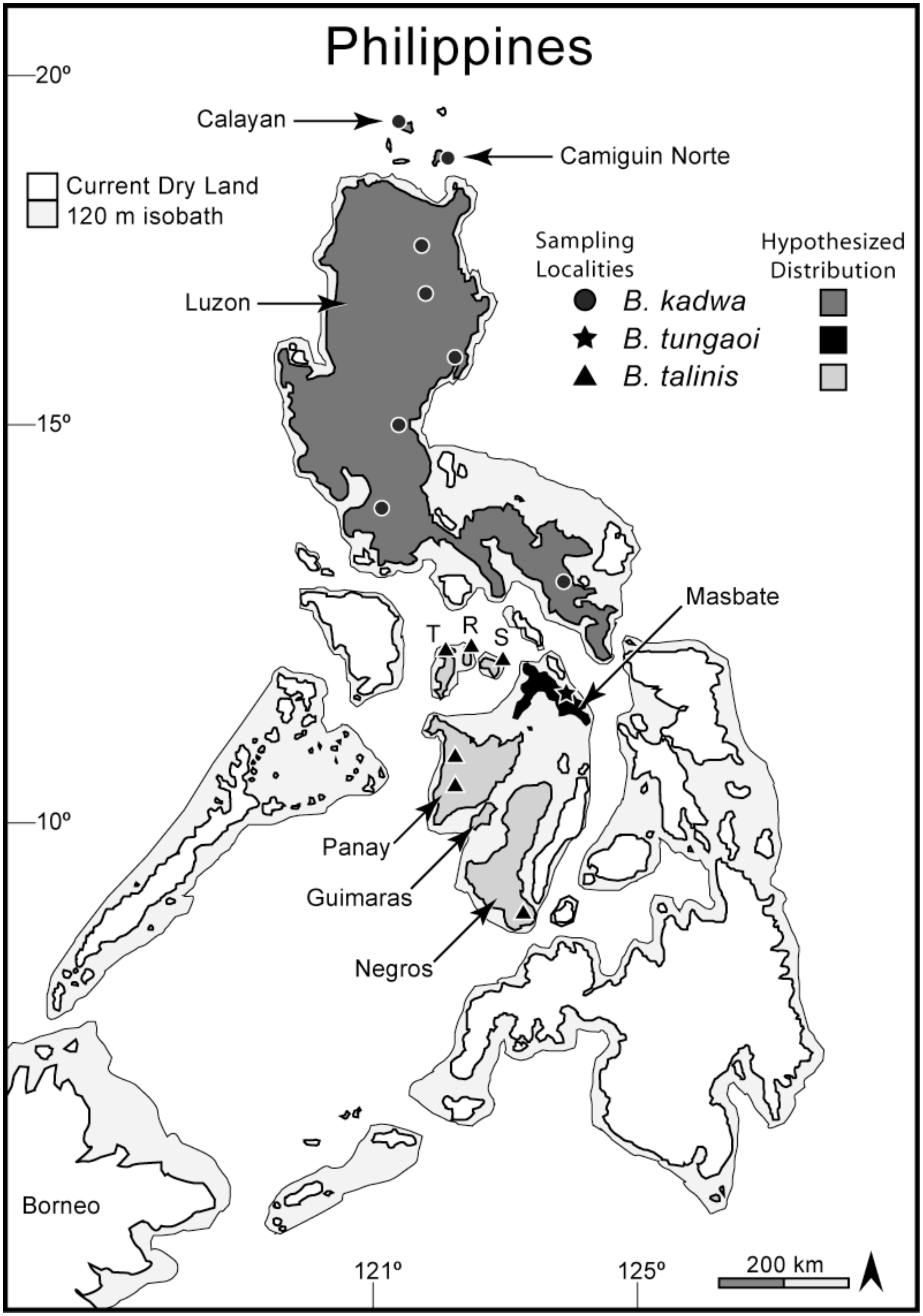

Philippines
20º
15º
10º
121º
125º
Sampling Localities
Hypothesized Distribution
B. orientalis
B. schadenbergi
B. vindumi
Current Dry Land
120 m isobath
Samar
Leyte
Dinagat
Bohol
Camiguin Sur
Mindanao
Jolo
Basilan
Borneo
?
200 km

Figure 3.5. Hypothesized distributions of *Brachymeles tungaoi, B. kadwa,* and *B. talinis* in the Philippines. The sampling localities are indicated by black shapes, and the hypothesized geographic range of each species indicated by shaded islands, with shapes and shades of islands corresponding to the map's key. Islands of the Romblon Island Group are designated by the first letter of the island name (T, Tablas Island; R, Romblon Island; S, Sibuyan Island).


Philippines
20º
Calayan
Camiguin Norte
Current Dry Land
120 m isobath
Sampling Localities
Hypothesized Distribution
Luzon
● B. kadwa
★ B. tungaoi
▲ B. talinis
15º
Masbate
T
R
S
U
10º
Panay
Guimaras
Negros
Borneo
121º
125º
200 km

In summary, each lineage possesses unique and non-overlapping suites of diagnostic character states of morphology, perfectly corresponding to nine of the clades defined in phylogenetic analyses of DNA sequence data (tissues unavailable for *B.* cf. *talinis* from Jolo Island). Combined with biogeographic evidence, and clearly separate geographical ranges, our data suggest the presence of ten evolutionary lineages, worthy of taxonomic recognition.

Taxonomic conclusions

Our inferred phylogeny (Fig. 3.2), biogeographically separate ranges of island endemic species; diagnostic, non overlapping morphological character states; and genetic divergences between the taxa (Table 3.3) indicate the distinctiveness of a new species from Luzon, Calayan, and Camiguin Norte islands, a new species from Masbate Island, and a new species from Jolo Island. Additionally, the molecular and morphological data strongly support the elevation of all subspecies of *Brachymeles boulengeri* and *B. schadenbergi* to full species (Table 3.3; Fig. 3.2). Each of the ten species is morphologically distinct from each other and all other known species in the genus, and each of the nine species included in phylogenetic analyses are also genetically distinct. With the exception of *B. talinis*, each lineage is endemic to one of four isolated PAICs, thereby providing additional support for the distinctiveness of each lineage's evolutionary history and integrity. Accordingly, we recognize all four subspecies of the former polytypic species *B. boulengeri*, and both subspecies of the former polytypic species *B. schadenbergi*, as full species.

TAXONOMIC ACCOUNTS

Brachymeles boulengeri Taylor 1922b: 246

Figs. 3.*3,* 3.*6,* 3.*11A*

Brachymeles boulengeri *(part), Taylor, 1922b, Type locality: Polillo Island, Philippines (holotype presumed lost).*

Brachymeles gracilis *Boulenger (part), Brown, 1956; Brown and Rabor, 1967.*

Brachymeles gracilis *(part), Brown and Alcala, 1970.*

Brachymeles boulengeri boulengeri *(part), Brown and Alcala, 1980.*

Designation of a neotype for Brachymeles boulengeri.—Taylor's holotype for B. boulengeri (Philippine Bureau of Science Publication No. 17:246, collected 15 July 1920) was destroyed in the destruction of the Philippine Bureau of Science in WWII, with no mention of a repository for the holotype. In the absence of an existing holotype and in accordance with article No. 75 of the International Code of Zoological Nomenclature (ICZN, 1979), we designate a neotype for this species. Accordingly, we choose an adult male specimen from the type locality of Polillo Island. Preserved adult specimens from Taylor's (1915) type locality (Polillo Island) have been examined in the collections at CAS; unfortunately these original specimens are either poorly preserved, incomplete or not sexually mature. However, recent collections from Polillo Island (Fig. 3.1) have resulted in well preserved adult individuals that clearly exhibit the diagnostic characters for the species. From these collections we have chosen a male neotype collected as part of a series that contains adults of both sexes and agrees with Taylor's (1922a) holotype description.

Neotype.—PNM 9720 (RMB Field No. 5647, formerly KU 307756), adult male, collected from a fallen, rotting log in secondary growth forest (10:00–12:30 hr) in Barangay Pinaglubayan, Municipality of Polillo, Quezon Province, Polillo Island, Philippines (14°45'09" N, 121°58'06" E; WGS-84), by RMB, J. Fernandez, Y. Vicente, and M. Vicente.

Diagnosis.—*Brachymeles boulengeri* can be distinguished from congeners by the following combination of characters: (1) body size moderate (SVL 60.5–93.1 mm); (2) pentadactyl; (3) Finger-III lamellae five or six; (4) Toe-IV lamellae nine or ten; (5) moderate limb length; (6) supralabials six or seven; (7) infralabials seven; (8) pineal eye spot present; (9) supranasals not contacting on midline; (10) prefrontals not contacting on midline; (11) midline contact of first pair of chin shields; (12) enlarged chin shields in two pairs; (13) nuchal scales undifferentiated; (14) fourth and fifth supralabial below eye; (15) auricular opening present; (16) continuous, light dorsolateral stripes present; and (17) mid-dorsal stripes absent (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing *Brachymeles boulengeri* from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles boulengeri* most closely resembles *B. boholensis, B. mindorensis,* and *B. taylori*, but differs from these three taxa by having six or seven supralabials and five or six supraciliaries, and by the absence of continuous, dark mid-dorsal stripes (Tables 3.4, 3.5). *Brachymeles boulengeri* further differs from *B. boholensis* by having a relatively longer tail, five or six Finger-III lamellae, the fourth and fifth supralabial below the eye, midline contact between the first pair of enlarged chin shields, and by lacking a third pair of enlarged chin shields (Tables 3.4, 3.5); from *B. mindorensis* it is differentiated by its smaller body size, shorter hind limbs, and possession of nine or 10 Toe-IV lamellae, seven infralabials, and by having the fourth and fifth supralabial below the eye (Tables 3.4, 3.5); and from *B. taylori* by the midline contact between the first pair of enlarged chin shields, and the presence of continuous, light dorsolateral stripes (Tables 3.4, 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*)*, B. boulengeri* differs by having a pentadactyl body form (vs. non-pentadactyl), greater forelimb lengths (> 8.2 mm vs. < 6.9 mm), greater hind-limb lengths (> 14.3 mm vs. < 12.9 mm), Toe-IV lamellae nine or 10 (vs. eight or fewer), a midbody scale row count of 26 or 27 (vs. < 24 in all non-pentadactyl species except for 28 in *B. wrighti* [Taylor, 1925]), and by the presence of a postnasal scale (vs. absence). With the exception of *B. pathfinderi*, *B. boulengeri* differs further from all non-pentadactyl species by the absence of a third pair of enlarged chin shields (vs. presence) and the presence of auricular openings (vs. absence). From all non-pentadactyl species except for *B. pathfinderi*, *B. boulengeri* differs by having a paravertebral scale count of 63–66 (vs. > 84). From *B. apus, B. lukbani, B. minimus,* and *B. vermis*, *B. boulengeri* is distinguished by the presence (vs. absence) of limbs.

Description of neotype.—(Fig. 3.6) Adult male, hemipenes everted; SVL 93.1 mm; body moderate relative to other *Brachymeles*; head weakly differentiated from neck, nearly as wide as body, HW 10.3% SVL, 109.0% HL; HL 36.5% SnFa; SnFa 9.4% SVL; snout moderately long, rounded in dorsal and lateral profile, SNL 52.2% HL; auricular opening present, moderate; eyes moderate, ED 2.2% SVL, 23.5% HL, 72.0% END, pupil subcircular; body slightly depressed, MBW 141.8% MBH; body scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26; paravertebral scale rows 64; axilla–groin scale rows 43; limbs well developed, pentadactyl, digits small; FinIIIlam 5; ToeIVlam 9; FLL 19.2% AGD, 12.5% SVL; HLL 28.7% AGD, 18.7% SVL; order of digits from shortest to longest for hand: V = I < IV = II < III, for foot: I < V < II < III < IV; tail original, not as wide as body, sharply tapered towards end, TW 70.1% MBW, TL 84.6% SVL.

Rostral projecting dorsoposteriorly to point in line with anterior edge of nasal scale, broader than high, forming a narrow suture with frontonasal; frontonasal wider than long; nostril ovoid, centered in a single rectangular nasal; nasals well separated; supranasals present, large, moderately separated by frontonasal; postnasals present; prefrontals narrowly separated by frontal; frontal suboctagonal, anterior margin in moderate contact with frontonasal and first two anterior supraoculars, 5× wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, in broad medial contact, contact 2–4 supraoculars; interparietal diamond-shaped, slightly wider than long, nearly one half frontal length; parietal eyespot present in posterior one third of scale; parietals separated by interparietal; nuchals non-enlarged, undifferentiated from dorsal scales; loreals two, decreasing in size from anterior to posterior; anterior loreal approximately as long as and slightly higher than posterior loreal, in contact with prefrontal, postnasal, supranasal, second supralabial; posterior loreal and frontonasal; preocular single, nearly two-thirds height of posterior loreal; presubocular single; supraciliaries six, most anterior contacting prefrontal and separating posterior loreal from first supraocular, most posterior extending to midline of last supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials seven, fourth and fifth below the eye, infralabials seven.

Mental wider than long, in contact with first infralabials; postmental single, wider than mental, followed by two pairs of enlarged chin shields; first pair in broad medial contact, second pair slightly wider than first, separated by a single medial scale.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces

of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration of neotype in preservative.—Ground color of body medium brown; lateral and ventral surfaces of body lacking dark pigment; dorsum, from posterior edge of supranasals to tail tip, uniformly dark brown, with color spanning six full and two half rows of scales at midbody and narrowing to cover four rows of scales posterior to parietals; darker pigmentation covers entire surface of dorsal scales, with exception of pigmentation on half rows of scales; head scales uniform brown; lateral half of supraoculars lacking dark pigmentation; rostral, nasal, postnasal, supranasal, and first supralabial dark gray with light brown blotches; pineal eyespot charcoal, surrounded by cream border. Faint, indistinct light dorsolateral stripes, formed by the absence of dark pigmentation, extending from level of anterior edge of eye to base of tail, spanning one full and two half rows of scales; small blotch of dark brown pigment dorsal to auricular opening. Limbs mottled light and medium brown dorsally, yellowish brown ventrally; dorsal and ventral surface of digits dark brown.

Coloration in life.—(Fig. 3.11A). Dorsal ground color homogeneous medium-brown to yellowish-brown; gradual lateral dorsolateral demarcation between dorsal (dark) and ventral (light) coloration; lateral and ventral surfaces of body homogeneous medium-brown to yellowish-brown; dark-brown spots and longitudinal lines of spots absent from lateral surfaces.

Measurements of neotype in mm.—SVL 93.1; AGD 60.7; TotL 171.9; MBW 14.7; MBH 10.4; TL 78.8; TW 10.3; TH 8.3; HL 8.8; HW 9.6; HH 7.2; SnFa 24.0; ED 2.1; END 2.9; SNL 4.6; IND 3.1; FLL 11.7; HLL 17.5; MBSR 26; PVSR 64; AGSR 43; FinIIIlam 5; ToeIVlam 9; SL 7; IFL 7; SC 6; SO 5.

Variation.—Variation in mensural characters is summarized in Table 3.6. Among the 19 specimens examined for the degree of contact between parietal scales, nine specimens possessed parietals separated by the interparietal (KU 307750, 307758, 320060, 322315–20) and 10 possessed parietals in moderate to broad medial contact (KU 307438–9, 307751–4, 307757, 320058–9, 322314) behind the interparietal.

Scale counts were observed to vary among the measured series. With the exception of a single specimen with five supraciliaries (KU 307752), all specimens examined had six supraciliaries. The number of supralabials varied between six (CAS 61297, 62272–3, 62276–7, KU 307438–9, 307752–4, 307757–8) and seven (CAS 61096, KU 307751). Specimens were observed to have midbody scale row counts of 26 (CAS 61096, 31297, 62273, 62276–7, KU 307439, 307751–4, 307758) and 27 (CAS 62272, KU 307750, 307757); axilla–groin scale row counts of 42 (KU 307439, 307758), 43 (KU 307750–4, 307757), 44 (CAS 61096, 62272–3, 62276–7), and 46 (CAS 61297); and paravertebral scale row counts of 63 (KU 307439, 307750, 307752, 307754, 307757–8), 64 (CAS 61096, 62272–3, 62277, KU 307751, 307753), 65 (CAS 62276), and 66 (CAS 61297).

We also observed lamellae counts to vary among the measured series. With the exception of a single specimen with six Finger-III lamellae (KU 307750), all specimens examined had five. Two specimens examined had ten Toe-IV lamellae (KU 307750, 307757), while the remaining specimens examined had nine.

Distribution.—Brachymeles boulengeri occurs in central and southern Luzon, and on Marinduque and Polillo islands (Fig. 3.3). The species has been collected in the Camarines Norte Province of the Bicol Peninsula, and may eventually be found to occur further south on the Bicol Peninsula and even on Catanduanes Island.

Ecology and natural history.—Brachymeles boulengeri occurs in disturbed and secondary-growth forest. Little or no original, low elevation forest remains throughout the range of *B. boulengeri*, but we assume the species once also occurred in first growth forest when this forest type extended into low elevation areas. Individuals have been observed under piles of rotting coconut husks, in the humus material within rotting logs, and in loose soil and leaf litter surrounding the root networks of trees. This species is quite common at the type locality, which has been virtually completely converted to coconut plantations. When disturbed, individuals immediately move in a rapid serpentine manner, attempting to burrow into loose soil or humus.

Sympatric lizard species observed on Luzon, Polillo, and Marinduque islands include: (Agamidae) *Bronchocela cristatella, Draco spilopterus, Gonocephalus sophiae, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus philippinicus, Gehyra mutilata, Gekko gecko, Gekko mindorensis, Hemidactylus frenatus, H. garnoti, H. luzonensis, H. platyurus, Pseudogekko compressicorpus, P. smaragdina*; (Scincidae) *Brachymeles bonitae, B. bicolor, B. elerae, B. lukbani, B. makusog, B. muntingkamay, B. samarensis, B. kadwa, B. wrighti, Emoia atrocostata, Eutropis bontocensis, E. multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella, Sphenomorphus cumingi, S. decipiens, S. jagori, S. leucospilos, S. luzonensis, S. steerei, S. stejnegeri, Tropidophorus grayi*; (Varanidae) *Varanus marmoratus, and Varanus olivaceus.*

Brachymeles boholensis Brown and Rabor 1967

Figs. 3.3, 3.6, 3.11C

Brachymeles gracilis boholensis, *Brown and Rabor, 1967, Type locality: 6 km southeast of Sierra Bullones, Teacher's Park, Bohol Island, Philippines, 400–433 m elevation,* *9°47'32.53" N, 124°18'14.4" E (holotype: CAS-SU24528).*

Brachymeles gracilis *(part), Brown and Alcala, 1970.*

Brachymeles boulengeri boholensis *(part), Brown and Alcala, 1980.*

Diagnosis.—Brachymeles boholensis can be distinguished from congeners by the following combination of characters: (1) body size moderate (SVL 83.8–93.6 mm); (2) limbs pentadactyl; (3) Finger-III lamellae six; (4) Toe-IV lamellae nine or ten; (5) limb length moderate; (6) supralabials seven; (7) infralabials seven; (8) pineal eye spot present; (9) supranasals not contacting on midline; (10) prefrontals not contacting on midline; (11) enlarged chin shields in three pairs; (12) nuchal scales undifferentiated; (13) fifth and sixth supralabial below eye; (14) auricular opening present; (15) continuous, light, dorsolateral stripes present; and (16) continuous, dark mid-dorsal stripes present (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing *Brachymeles boholensis* from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles boholensis* most closely resembles *B. boulengeri, B. mindorensis,* and *B. taylori*, but differs from them by having six lamellae on Finger-III and by the presence of three pairs of enlarged chin shields (Tables 3.4, 3.5). *Brachymeles boholensis* differs further from *B. boulengeri* by having seven supralabials, six supraciliaries, and the fifth and sixth supralabial below the eye, and by the presence of continuous, dark mid-dorsal stripes (Tables 3.4, 3.5); from *B. mindorensis* by having a smaller body size, shorter hind limbs, nine or 10 Toe-IV lamellae, seven infralabials, and by the absence of contact between supranasals, and the absence of contact between prefrontals (Tables 3.4, 3.5); and from *B. taylori* by having seven supralabials, the fifth and sixth supralabial below the eye, and the presence of continuous, light dorsolateral stripes (Tables 3.4, 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*), *B. boholensis* differs by having pentadactyl (vs. non-pentadactyl) limbs, greater forelimb lengths (greater than 9.0 mm vs. less than 6.9 mm), greater hind limb lengths (greater than 15.4 mm vs. less than 12.9 mm), Toe-IV lamellae nine or 10 (vs. eight or fewer), fifth and sixth supralabial below the eye (vs. fourth and fifth), and by presence of a postnasal scale (vs. absence). Additionally, *Brachymeles boholensis* differs from all non-pentadactyl species except *B. wrighti* by having 26–28 midbody scale rows (vs. fewer than 24); from all non-pentadactyl species except *B. pathfinderi* by having 63–66 paravertebrals (vs. greater than 84) and by the presence of auricular openings (vs. absence); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence of limbs (vs. absence).

Description (based on holotype and 38 referred specimens, including 12 paratypes at CAS).—Details of the head scalation of an adult female are shown in Figure 3.6. Measurements of the holotype are provided below in brackets. Body moderate relative to other *Brachymeles*; maximum SVL 93.6 mm for males, 94.0 mm for females [89.5, female] (Tables 3.4, 3.5); head weakly differentiated from neck, nearly as wide as body, HW 10.0–12.4% (11.3 ± 0.7) SVL [11.8], 104.2–131.9% (112.6 ± 6.7) HL [110.7]; HL 35.2–43.6% (38.9 ± 2.3) SnFa [39.3]; SnFa 24.1–28.0% (26.0 ± 1.0) SVL [27.0]; snout moderately long, broadly rounded in dorsal profile, rounded in lateral profile, SNL 54.6–64.6% (59.3 ± 2.8) HL [57.4]; auricular opening present, moderate; eyes small, ED 1.8–2.2% (2.0 ± 0.1) SVL [2.1], 17.6–23.9% (20.3 ± 1.6) HL [19.5], 45.1–61.8% (52.5 ± 3.7) END [52.9], pupil subcircular; body slightly depressed, MBW 98.1–136.2% (113.0 ± 10.3) MBH [131.0]; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26–28 [28]; paravertebral scale rows 63–66 [64]; axilla–groin scale rows 42–46 [44];

limbs well developed, pentadactyl, digits small; FinIIIlam 6 [6]; ToeIVlam 7–10 [7]; FLL 15.6–20.5% (17.6 ± 1.4) AGD [20.5], 10.2–12.9% (11.4 ± 0.8) SVL [12.4]; HLL 27.6–34.6% (30.0 ± 2.3) AGD [32.9], 17.8–21.5% (19.4 ± 1.2) SVL [20.0]; order of digits from shortest to longest for hand: I = V < II = III = IV, for foot: V < I < II < III = IV; tail not as wide as body, sharply tapered towards end, TW 61.6–78.4% (70.3 ± 5.0) MBW [63.5], TL 52.7–90.0% (75.7 ± 13.0) SVL [86.8].

Rostral projecting dorsoposteriorly to point in line with center of nasal;, broader than high, in contact with frontonasal; frontonasal wider than long; nostril ovoid, centered in a single rectangular nasal; nasals well separated; supranasals present, large, moderately separated by frontonasal; postnasals present; prefrontals broadly separated by frontal; frontal nearly diamond shaped, in moderate contact with frontonasal, first two anterior supraoculars, 4× wider than anterior supraocular; supraoculars five; frontoparietals moderate in size, in contact, each frontoparietal in contact with posterior three or four supraoculars; interparietal moderate in size, quadrilaterally shaped, longer than wide, its length slightly greater than midline length of frontoparietals; parietal eyespot present in posterior half of scale; parietals separated by interparietal; nuchals undifferentiated; loreals two, antreior loreal largest, in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal; preocular single, nearly two thirds as high as posterior loreal; supraciliaries six, anterior supraciliary contacting prefrontal and separating posterior loreal from first supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials seven, fifth and sixth beneath center of eye; infralabials seven.

Mental wider than long, in contact with first infralabials; postmental single, enlarged, slightly wider than mental, followed by three pairs of enlarged chin shields, first pair in broad medial contact, second pair equal in width to first pair, broadly separated by single medial scale, third pair separated by three medial scales.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, variably shaped scales, each bearing variably raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative.—Ground color of body medium brown, lateral surface lacking dark pigment, dorsal surface bearing continuous, longitudinal rows of olive-green to brown pigment, spanning six full and two half rows of scales at midbody, narrowing to four full and two half rows of scales posterior to parietals, extending from posterior edge of parietals to tail tip; dark pigmentation covering one half to three fourths of dorsal scales; lateral surface of body with six continuous to discontinuous longitudinal rows of olive-green to brown stripes, extending from posterior edge of eye to base of tail; dorsolateral stripes present, lacking dark pigmentation, spanning two half rows of scales, extending from posterior edge of supraoculars to base of tail. Ventral scales with or without dark spots. Head scales uniform medium brown, darker brown than ventral scales; rostral, nasal, postnasal, supranasal, first supralabial, mental, and first infralabial dark gray; pineal eyespot poorly defined, small, and light to dark brown. Limbs mottled light and medium brown dorsally, yellowish brown ventrally; dorsal and ventral surfaces of digits dark brown.

Coloration in life.—(Fig. 11C). Ground color of body medium brown to tan; longitudinal rows of darker brown pigmentation; dorsolateral stripes light-brown to tan; limbs bearing dark-brown mottling dorsally.

Variation.—Morphometric variation is summarized in Table 3.6. We observed variation among the 20 specimens examined for the degree of contact between head scales. Six specimens were observed to have parietals separated by the interparietal (KU 323944, 323949, 323953, 323962, 323975–6) and 14 specimens possessed parietals in moderate to broad medial contact (KU 323948, 323952, 323954–6, 323960, 323963, 323966, 323970, 323972, 323981, 323982, 323990, 324001) behind the interparietal. Additionally seven specimens do not have the first pair of enlarged chin shields in medial contact (KU 323954–5, 323970, 323975, 323981–2, 324001) and 13 specimens with the first pair of enlarged chin shields in moderate to broad medial contact (KU 323944, 323948–9, 323952–3, 323956, 323960, 323962–3, 323966, 323972, 323976, 323990).

Scale counts were observed to vary among the measured series. Specimens were observed to have midbody scale row counts of 26 (CAS-SU 18709, 18717, 24502, 24523–5, 24541, 24543, 25443–4), 27 (CAS-SU 24503–4, 24522, 24867), and 28 (CAS-SU 24518, 24520–21, 24528, 25447); axilla–groin scale row counts of 42 (CAS-SU 18717, 24502, 24520, 24524), 43 (CAS-SU 24523, 24541, 24543), 44 (CAS-SU 24504, 24518, 24525, 24528, 24867, 25447), 45 (CAS-SU 24503, 24521, 25443), and 46 (CAS-SU 18709, 24522, 25444); and paravertebral scale row counts of 63 (CAS-SU 18717, 24502, 24520, 24524, 24541, 24543), 64 (CAS-SU 24504, 24523, 24525, 24528, 24867, 25447), 65 (CAS-SU 24518), and 66 (CAS-SU 18709, 24503, 24521–2, 25443–4).

We also observed Toe-IV lamellae counts to vary among the measured series. With the exception of a single specimen with seven Two-IV lamellae (CAS-SU 24528, holotype), all specimens examined had either nine (CAS-SU 18709, 24504, 24523–4, 24867, 25444) or ten (CAS-SU 18717, 24502–3, 24518, 24520–2, 24525, 24541, 24543, 25443, 25447). We observed the holotype to have malformed digits, which we believe resulted in fewer Toe-IV lamellae than are observed for all other individuals of this species.

Distribution.—Brachymeles boholensis is known only from Bohol Island (Fig. 3.3).

Ecology and natural history.—Brachymeles boholensis occurs in agricultural habitats, as well as in disturbed and secondary-growth forests. No original, low elevation forest remains on Bohol Island, but we assume the species once also occurred in primary forest at low elevations. Individuals have been observed under piles of rotting coconut husks, in the humus material within rotting logs, and in loose soil and leaf litter surrounding the root networks of trees. Interestingly, this species seems to be a ubiquitous habitat generalist on Bohol, whereas its congener, *B. orientalis,* seems to be restricted to fallen and rotting logs in secondary-growth forest on the same island (CDS personal observations). As is typical for species in the genus, individuals immediately attempt to evade capture by moving to quickly burrow into loose soil or humus.

Although only two species of *Brachymeles* have been confirmed to occur on Bohol Island (*B. boholensis* and *B. orientalis*), populations of *B. samarensis* are known to occur on Lapinig Grande and Lapinig Chico islands just off the northeast coast of Bohol Island (Brown and Alcala, 1980). No individuals of this species lacking fully formed digits occur on Bohol; however, given proximity of these small islands to mainland Bohol, it seems likely that this neighboring, limb-reduced species of *Brachymeles* eventually may be discovered on Bohol.

Sympatric lizard species observed on Bohol Island include: (Agamidae) *Bronchocela cristatella, Draco bimaculatus, D. ornatus, D. reticulates, Gonocephalus semperi, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus annulatus, Gehyra mutilata, Gekko gecko, Hemidactylus frenatus, H. platyurus, Hemiphyllodactylus typus, Lepidodactylus aureolineatus, L. planicaudus,* *Pseudogekko compressicorpus, P. brevipes*; (Scincidae) *Brachymeles schadenbergi orientalis, Emoia atrocostata, Eutropis multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella, L. quadrivittata, Sphenomorphus acutus, S. cumingi, S. fasciatus, S. jagori, S. minanensis, S. steerei, S. variegatus*; (Varanidae) *Varanus cumingi.* Also, *Brachymeles samarensis* (Scincidae) is known to occur on Lipinig Grande and Lipinig Chico islands just off the northeast coast of Bohol Island (Brown and Alcala, 1980).

Brachymeles mindorensis Brown and Rabor 1967

Figs. 3.3, 3.7

Brachymeles gracilis mindorensis, Brown and Rabor, 1967, Type locality: Bank of Tarogin River, 30 km southeast of Calapan, Mindoro Oriental Province, Mindoro Island, Philippines, 0–33 m elevation, 13°11'25.44" N, 121°8'52.8" E (holotype: CAS-SU 24487).

Brachymeles gracilis *(part), Brown and Alcala, 1970.*

Brachymeles boulengeri mindorensis *(part), Brown and Alcala, 1980.*

Diagnosis.—*Brachymeles mindorensis* can be distinguished from congeners by the following combination of characters: (1) body size moderate (SVL 90.0–104.2 mm); (2) pentadactyl; (3) Finger-III lamellae five or six; (4) Toe-IV lamellae eight or nine; (5) moderate limb length; (6) supralabials seven; (7) infralabials six; (8) pineal eye spot present; (9) enlarged chin shields in two pairs; (10) nuchal scales undifferentiated; (11) fifth and sixth supralabial below eye; (12) auricular opening present; (13) continuous, light, dorsolateral stripes present; and (14) continuous, dark mid-dorsal stripes present (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing *Brachymeles mindorensis* from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles mindorensis* most closely resembles *B. boholensis, B. boulengeri,* and *B. taylori*, but differs from these three taxa by having a larger body size, longer hind limbs, eight or nine Toe-IV lamellae, and six infralabials (Tables 3.4, 3.5). *Brachymeles mindorensis* further differs from *B. boholensis* by having five or six Finger-III lamellae and by the absence of a third pair of enlarged chin shields (Tables 3.4, 3.5); from *B. boulengeri* by having seven supralabials, six supraciliaries, and the fifth and sixth supralabial below the eye, and by the presence of continuous, dark mid-dorsal stripes (Tables 3.4, 3.5); and from *B. taylori* by having seven supralabials and the fifth and sixth supralabial below the eye, and by the presence of continuous, light dorsolateral stripes (Tables 3.4, 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*)*, B. mindorensis* differs by having a pentadactyl body form (vs. non-pentadactyl), longer forelimb lengths (greater than 10.0 mm vs. less than 6.9 mm), greater hind limb lengths (greater than 18.8 mm vs. less than 12.9 mm), and the fifth supralabial below the eye (vs. fourth), and by the presence of a postnasal scale (vs. absence). Additionally, *Brachymeles mindorensis* differs from all non-pentadactyl species except *B. wrighti* by having a midbody scale row count 26–28 (vs. fewer than 24); from all non-pentadactyl species except *B. pathfinderi* by having a paravertebral count 63–65 (vs. greater than 84) and by the presence of auricular openings (vs. absence); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence of limbs (vs. absence).

Description (based on holotype and 33 referred paratypes at CAS).—Details of the head scalation of an adult male are shown in Figure 3.7. Measurements of the holotype are included below in brackets. Body moderate relative to other *Brachymeles*, elongate with respect to other lizards; maximum SVL 104.2 mm for males, 106.8 mm for females [106.8, female] (Tables 3.4, 3.5); head weakly differentiated from neck, nearly as wide as body, HW 10.5–12.9% (11.4 ± 0.7) SVL [10.9], 104.2–130.1% (116.1 ± 6.0) HL [114.6]; HL 31.6–42.9% (37.3 ± 3.1) SnFa [39.2]; SnFa 24.1–29.9% (26.5 ± 1.3) SVL [24.1]; snout moderately long, rounded in dorsal and lateral profile, SNL 50.6–68.2% (57.3 ± 4.9) HL [52.2]; auricular opening present, small; eyes moderate, ED 2.0–2.6% (2.2 ± 0.2) SVL [2.0], 19.4–27.4% (22.7 ± 2.0) HL [21.1], 51.8–72.2% (60.7 ± 5.1) END [58.5], pupil nearly round; body slightly depressed, MBW 105.4–156.0% (120.2 ± 14.0) MBH [125.0]; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26–28 [26]; paravertebral scale rows 63–65 [65]; axilla–groin scale rows 42–45 [45]; limbs well developed, pentadactyl, digits small; FinIIIlam 5–6 [5]; ToeIVlam 8–9 [9]; FLL 14.5–21.3% (17.8 ± 1.9) AGD [15.5], 10.1–13.1% (11.5 ± 0.9) SVL [10.9]; HLL 16.7–37.9% (31.5 ± 5.0) AGD [25.1], 10.5–24.0% (20.3 ± 2.9) SVL [17.6]; order of digits from shortest to longest for hand: I = V < II = IV < III, for foot: I < V < II < III = IV; tail not as wide as body, sharply tapered towards end, TW 54.4–80.1% (69.1 ± 8.1) MBW [54.4], TL 60.4–99.3% (84.6 ± 11.5) SVL [93.5].

Rostral projecting dorsoposteriorly to point in line with anterior edge of nasal, broader than high, in narrow contact with frontonasal; frontonasal wider than long; nostril ovoid, centered in a single rectangular nasal; nasals well separated; supranasals present, large, narrowly separated by frontonasal; postnasals present; prefrontals narrowly separated by frontal; frontal octagonal, narrowly contacting frontonasal and first two supraoculars anteriorly, 4× wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, in broad medial contact, each frontoparietal in contact with supraoculars 2–4; interparietal large, quadrilaterally shaped, slightly longer than wide, its length slightly greater than midline length of frontoparietal; parietal eyespot present in posterior one half of scale; parietals moderately separated behind interparietal; nuchals undifferentiated from adjacent dorsal scales; loreals two, anterior loreal in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal; preocular, single, nearly one third as high as posterior loreal; presubocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials seven, fifth and sixth below eye; infralabials six.

Mental wider than long, in contact with first infralabials; single enlarged postmental, equal in width to mental followed by two pairs of enlarged chin shields; first pair in moderate contact, second pair wider than first, moderately separated by single medial scale.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, variably shaped scales, each with variably raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative.—Ground color of body medium brown; dorsal surface of body with eight longitudinal rows of dark-brown stripes, six continuous medial rows, two discontinuous lateral rows, spanning eight full rows of scales at midbody, narrowing to six full rows of scales posterior to parietals, extending from posterior edge of parietals to tail tip; pigmentation covering middle one third of dorsal scales; dorsolateral stripes present, lacking dark pigmentation, spanning one whole and two half rows of scales, extending from posterior edge of supraoculars to base of tail. Lateral surface of body light brown ground color with three or four rows of nearly continuous spots of dark-brown pigmentation, extending from auricular opening to tail tip. Tail striped with longitudinal rows of dark pigmentation. Ventral scales lacking dark spots. Head scales uniform medium brown, darker brown than ventral scales; posteriormost supraocular lacking pigmentation; dark pigmentation surrounding auricular opening, connected to dark pigmentation on head scales; rostral, nasal, postnasal, supranasal, and first supralabial dark gray; pineal eyespot poorly defined, small and light cream. Limbs mottled dark brown dorsally, yellowish brown ventrally; dorsal and ventral surface of digits dark brown.

*Coloration in life***.**—Ground color of body dark- to medium-brown; continuous, dark mid-dorsal stripes dark brown to black; dorsolateral stripes light-brown to tan, gradually become predominately tan on tail; limbs dark-brown dorsally.

Variation.—Morphometric variation of the series is summarized in Table 3.6. We observed variation among the 16 specimens examined for the degree of contact between head scales. Five specimens were have parietals separated by the interparietal (KU 304352, 304354, 304488, 308447–8) and 11 specimens have parietals in moderate to broad medial contact (KU 304351, 304353, 304355, 304412–3, 307739–42, 308404, 308534) behind the interparietal; four specimens have supranasals narrowly separated by the frontonasal (KU 307740–1, 308404, 308448), six specimens have supranasals in medial point contact (KU 304351–4, 307742, 308447), and six specimens have supranasals in moderate medial contact (KU 304355, 304412–3, 304488, 307739, 308534); 13 specimens have prefrontals moderately separated by the frontal (KU 304351–4, 304412–3, 304488, 307739–41, 308447–8, 308534), one specimen has prefrontals narrowly separated by the frontal (KU 308404), and two specimens have prefrontals in medial point contact (KU 304355, 307742).

Scale counts were observed to vary among the measured series. Specimens were observed to have midbody scale row counts of 26 (CAS-SU 24487, 24551, 24561, 24566, 24574, 24577, 24579), 27 (CAS-SU 24549, 24573), and 28 (CAS-SU 24550, 24552–4, 24562, 24564, 24568, 24570, 24578); axilla–groin scale row counts of 42 (CAS-SU 24564), 43 (CAS-SU 24573), 44 (CAS-SU 24553–4, 24561–2, 24568, 24570, 24578), and 45 (CAS-SU 24487, 24549–52, 24566, 24574, 24577, 24579); and paravertebral scale row counts of 63 (CAS-SU 24564, 24573), 64 (CAS-SU 24561–2, 24568), and 65 (CAS-SU 24487, 24549–54, 24566, 24570, 24574, 24577–9).

We also observed lamellae counts to vary among the series. With the exception of two specimens with six Finger-III lamellae (CAS-SU 24561, 24574), all specimens examined had five. Specimens were observed to have Toe-IV lamellae counts of eight (CAS-SU 24549–54, 24561–2, 24564, 24566, 24570, 24573, 24577–8) or nine (CAS-SU 24487, 24568, 24574, 24579).

Distribution.—Brachymeles mindorensis is known only from Mindoro Island (Fig. 3.3).

Ecology and natural history.—Brachymeles mindorensis occurs in disturbed and secondary-growth forest. Individuals have been observed under piles of rotting coconut husks, in the humus material within rotting logs, and in loose soil and leaf litter surrounding the root networks of trees. The species has been observed to be quite common in certain habitats on Mindoro Island (CDS, RMB personal observations). *Brachymeles mindorensis* occurs sympatrically with *B. bonitae* (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980), and is the largest species of the *B. boulengeri* complex. When individuals were disturbed, they attempted to quickly burrow back into loose soil or humus.

Sympatric lizard species observed on Mindoro Island include: (Agamidae) *Bronchocela marmoratus, Draco quadrasi, Gonocephalus interruptus, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus philippinicus, Gehyra mutilata, Gekko gecko, G. mindorensis, Hemidactylus frenatus, H. garnoti, H. platyurus, Hemiphyllodactylus typus, Lepidodactylus naujanensis*; (Scincidae) *Brachymeles bonitae, Dasia olivaceum, Emoia atrocostata, Eutropis multicarinata,* *E. multifasciata, Lamprolepis smaragdina, Lipinia auriculatum, Sphenomorphus cumingi, S. jagori, S. steerei*; (Varanidae) *Varanus marmoratus.*

Brachymeles taylori Brown 1956

Figs. 3, 7, 11B

Brachymeles gracilis taylori, Brown, 1956, Type-locality: Sitio Lunga, 13 km West Dumaguete, 3 km West Valencia, on low ridge on the north side of the Maite River, Negros Oriental Province, Negros Island, Philippines, 600 m elevation, 9°17'32.96" N, 123°14'2.4" E (holotype: CAS-SU 24487).

Brachymeles gracilis *(part), Brown and Alcala, 1970.*

Brachymeles boulengeri taylori *(part), Brown and Alcala, 1980.*

Diagnosis.—*Brachymeles taylori* can be distinguished from congeners by the following combination of characters: (1) body size moderate (SVL 65.8–99.2 mm); (2) pentadactyl; (3) Finger-III lamellae five or six; (4) Toe-IV lamellae nine or ten; (5) moderate limb length; (6) supralabials six; (7) infralabials seven; (8) pineal eye spot present; (9) supranasals not contacting on midline; (10) prefrontals not contacting on midline; (11) enlarged chin shields in two pairs; (12) nuchal scales undifferentiated; (13) fourth and fifth supralabial below eye; (14) auricular opening present; (15) dorsolateral stripes absent; and (16) continuous, dark mid-dorsal stripes present (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing *Brachymeles taylori* from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles taylori* most closely resembles *B. boholensis, B. boulengeri,* and *B. mindorensis*, but differs from these three taxa by the absence of continuous, light dorsolateral stripes (Tables 3.4, 3.5). *Brachymeles taylori* can further be distinguished from *B. boholensis* by having five or six Finger-III lamellae, six supralabials, and the fourth and fifth supralabial below the eye, and by the absence of a third pair of enlarged chin shields (Tables 3.4, 3.5); from *B. boulengeri* by having six supralabials and six supraciliaries, and the presence of continuous, dark mid-dorsal stripes (Tables 3.4, 3.5); and from *B. mindorensis* by having a smaller body size, shorter hind limbs, nine or ten Toe-IV lamellae, six supralabials, seven infralabials, the fourth and fifth supralabial below the eye, and no contact between supranasals and prefrontals (Tables 3.4, 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*), *B. taylori* differs by having pentadactyl limbs (vs. non-pentadactyl), longer forelimbs (greater than 9.0 mm vs. less than 6.9 mm), longer hind limbs (greater than 15.6 mm vs. less than 12.9 mm), and Toe-IV lamellae nine or ten (vs. eight or fewer), and by the presence of a postnasal scale (vs. absence). Additionally, *Brachymeles taylori* differs from all non-pentadactyl species except *B. wrighti* by having a midbody scale row count 26–28 (vs. fewer than 24); from all non-pentadactyl species except *B. pathfinderi* by having a paravertebral count 62–69 (vs. greater than 84) and by the presence of auricular openings (vs. absence); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence of limbs (vs. absence).

Description (based on holotype and 33 referred specimens, including 5 paratypes at CAS).— Details of the head scalation of an adult female are shown in Figure 3.7. Measurements of the holotype are provided below in brackets. Body moderate relative to other *Brachymeles*, elongate with respect to other lizards; maximum SVL 99.2 mm for males, 93.2 mm for females [65.8, female] (Tables 3.4, 3.5); head weakly differentiated from neck, nearly as wide as body, HW 11.3–15.3% (12.3 ± 1.0) SVL [15.3], 104.4–139.5% (120.5 ± 10.2) HL [132.8]; HL 34.8–44.6%

(39.2 ± 2.5) SnFa [36.4]; SnFa 23.4–31.7% (26.2 ± 1.7) SVL [31.7]; snout moderately long, broadly rounded in dorsal profile, depressed in lateral profile, SNL 44.1–62.5% (52.2 ± 4.6) HL [62.5]; auricular opening present, moderate; eyes moderate, ED 1.6–2.8% (2.1 ± 0.2) SVL [2.8], 15.9–24.4% (20.8 ± 2.4) HL [24.4], 48.8–69.5% (59.6 ± 6.1) END [62.7], pupil nearly round; body slightly depressed, MBW 89.1–148.4% (115.1 ± 14.7) MBH [112.9]; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26–28 [27]; paravertebral scale rows 62–69 [64]; axilla–groin scale rows 42–47 [43]; limbs well developed, pentadactyl, digits small; FinIIIlam 5–6 [6]; ToeIVlam 8–10 [9]; FLL 15.7–20.4% (17.8 ± 1.2) AGD [19.9], 10.4–14.1% (11.5 ± 0.9) SVL [14.1]; HLL 26.7–36.8% (31.1 ± 2.5) AGD [35.6], 17.8–25.2% (20.1 ± 1.7) SVL [25.2]; order of digits from shortest to longest for hand: I = V < IV < II = III, for foot: I < V < II < III = IV; tail not as wide as body, sharply tapered posteriorly, TW 54.0–80.3% (68.9 ± 6.7) MBW [75.0], TL 69.2–103.1% (83.3 ± 10.4) SVL [98.2].

Rostral projecting dorsoposteriorly to point in line with anterior edge of nasal, broader than high, in moderate contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single rectangular nasal; nasals well separated; supranasals present, large, narrowly separated by frontonasal; postnasals present; prefrontals moderately separated by frontal; frontal nearly octagonal, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 4.5 × wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, in broad medial contact, each frontoparietal in contact with supraoculars two–four; interparietal moderate, quadrilaterally shaped, longer than wide, its length nearly equal to midline length of frontoparietal; parietal eyespot present in posterior one half of scale; parietals in moderate contact behind interparietal or narrowly separated; nuchals undifferentiated; loreals two, decreasing in size from anterior to posterior, subequal, anterior loreal in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal; preocular single, nearly two thirds as high as posterior loreal; single presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials six, fourth and fifth below the eye; infralabials seven.

Mental wider than long, in contact with first infralabial; postmental single, enlarged, slightly wider than mental, followed by two pairs of enlarged chin shields, scales of first pair separated or in moderate contact, second pair slightly wider than first, broadly separated by a single medial scale.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with irregular raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative.—Ground color of body medium olive-brown; dorsal pigmentation nearly all dark brown, gradually fading into olive-brown lateral surface and yellowish-brown ventral surface of body, ventral surface without dark pigmentation; dark dorsal pigmentation in nearly continuous block across dorsal surface or at times forming ten continuous longitudinal rows of dark-brown pigment, spanning six full rows of scales across dorsal surface, extending from posterior edge of parietals to tail tip, additional three to four scale rows on each lateral surface with dark coloration, covering one half to two thirds of dorsal and lateral scales; dorsolateral stripes absent. Tail coloration matches body coloration. Head scales uniform dark brown, darker brown than ventral scales; rostral, nasal, postnasal, supranasal, and first supralabial dark gray; pineal eyespot poorly defined, small and light cream. Limbs mottled medium brown dorsally, yellowish brown ventrally; dorsal and ventral surface of digits dark brown.

Coloration in life.—(Fig. 3.11B). Ground color of body light to medium-brown; medium to dark brown dorsal pigmentation gradually fading into medium brown lateral pigmentation; limbs mottled medium to dark brown dorsally.

Variation.—Morphometric variation of the series is summarized in Table 3.6. We observed variation among the 14 specimens examined for the degree of contact between head scales. Six specimens have parietals moderately separated by the interparietal (KU 324048, 324050, 324052–5), one specimen has parietals narrowly separated by the interparietal (KU 324051), and seven specimens have parietals in moderate medial contact (KU 306651, 324044–7, 324049, 324056) behind the interparietal; eight specimens do not have the first pair of enlarged chin shields in medial contact (KU 324045, 324048–50, 324053–6), one specimen has the first pair of enlarged chin shields in point medial contact (KU 324046), and five specimens have the first pair of enlarged chin shields in moderate medial contact (KU 306651, 324044, 324047, 324051–2).

Scale counts were observed to vary among the measured series. Specimens were observed to have midbody scale row counts of 26 (CAS-SU 18641, 18656–7, 18748, 21873, 21877, 21880, 21884, 22355, CAS 154971, 154673, 154680–2, 154686), 27 (CAS-SU 18615, 22356, CAS 154679), and 28 (CAS-SU 18649, 21883, CAS 154678); axilla–groin scale row counts of 42 (CAS 154680, 154686), 43 (CAS-SU 18615, 18656, CAS 154682), 44 (CAS-SU 18641, 18748, 21873, 21877, 21880, 22356, CAS 154678, 154679, 154681), 45 (CAS-SU 21884, 22355, CAS 154671), 46 (CAS-SU 18649, 21883, CAS 154673) and 47 (CAS-SU 18657); and paravertebral scale row counts of 62 (CAS 154680, 154686), 64 (CAS-SU 18615, 18656, CAS 154682), 66

(CAS-SU 18641, 18748, 21873, 21877, 21880, 21884, 22356, CAS 154678–9, 154681), 67 (CAS-SU 18649, CAS 154671, 154673), 68 (CAS-SU 21883, 22355), and 69 (CAS-SU 18657).

We also observed lamellae counts to vary among the measured series. Specimens were observed to have Finger-III lamellae counts of five (CAS-SU 18641, 18649, 18656, 18748, 21883–4, 22356, CAS 154671, 154673, 154678–80) or six (CAS-SU 18615, 18657, 21873, 21877, 21880, 22355, CAS 154681–2, 154686); Toe-IV lamellae counts of eight (CAS 154678), nine (CAS-SU 18615, 18649, 18656, 21880, 22356, CAS 154671, 154673, 154682, 154686), and ten (CAS-SU 18641, 18657, 18748, 21873, 21877, 21883–4, 22355, CAS 15479–81).

There is some color variation in the examined series, with the degree and definition of continuous, dark mid-dorsal stripes. All specimens have continuous, dark lines running down the mid-dorsal surface of the body; however, the continuous lines in some specimens are present without a dark, mid-dorsal background coloration (KU 324045–6, 324049–51, 324053–4). The dark lines in other specimens overlay a dark, mid-dorsal region covered by a long streak of dark background pigmentation (KU 324044, 324047–8, 324052, 324055–6).

Distribution.—Brachymeles taylori is known from Negros, Cebu, Inampulugan, Pan de Azucar, Danjugan, Ponson, and Poro Islands (Fig. 3.3).

Ecology and natural history.—Brachymeles taylori occurs in agricultural areas as well as disturbed and secondary-growth forest. Little or no original, low elevation forest remains in the Visayas, but we assume the species once also occurred in primary forest. Individuals have been observed under piles of rotting coconut husks, in the humus material within rotting logs, and in loose soil and leaf litter surrounding the root networks of trees. The species is quite common throughout its range (CDS personal observations), and occurs sympatrically with three other species of *Brachymeles* (*B. cebuensis, B. talinis,* and *B. tridactylus* [Brown, 1956; Brown and

Rabor, 1967; Brown and Alcala, 1980]). Similar to *B. boulengeri*, *B. taylori* appears to have a wider geographic distribution that spans multiple Philippine islands. This is in contrast to the island endemic species, *B. boholensis* and *B. mindorensis*, which are known from just Bohol and Mindoro Islands respectively. As with all members of the genus, when disturbed, individuals move rapidly attempting to burrow into the loose soil or humus.

Sympatric lizard species observed within the range of *Brachymeles taylori* include: (Agamidae) *Bronchocela marmoratus*, *Draco spilopterus, Gonocephalus sophiae, Hydrosaurus pustulatus*; (Dibamidae) *Dibamus argenteus*; (Gekkonidae) *Cyrtodactylus philippinicus, Gehyra mutilata, Gekko gecko, G. mindorensis, G. enrstkelleri, Luperosaurus corfieldi, Pseudogekko brevipes, Hemidactylus frenatus, H. platyurus, Hemiphyllodactylus typus, Lepidodactylus christiani, L. herrei, L. lugubris*; (Scincidae) *Brachymeles cebuensis, B. talinis, B. cebuensis, Emoia atrocostata, Eutropis multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia auriculata, L. pulchella, L. quadrivittata, L. rabori, Sphenomorphus arborens, S. coxi, S. jagori, S. steerei, Tropidophorus grayi*; (Varanidae) *Varanus nuchalis.*

Brachymeles orientalis Brown and Rabor 1967

Figs. 4, 8, 11F,G

Brachymeles schadenbergi orientalis, Brown and Rabor, 1967, Type-locality: Bario Dusita, 11 km southeast of Sierra Bullones, Bohol Province, Bohol Island, Philippines, 533 m elevation, 9°46'57.5" N, 124°18'10.8" E (holotype: CAS-SU 24436).

Brachymeles schadenbergi *(part), Brown and Alcala, 1970.*

Brachymeles schadenbergi *(part), Brown and Alcala, 1980.*

Diagnosis.—Brachymeles orientalis can be distinguished from congeners by the following combination of characters: (1) body large (SVL 97.6–112.3 mm); (2) pentadactyl; (3) Finger-III lamellae six or seven; (4) Toe-IV lamellae eight to ten; (5) limbs relatively long; (6) supralabials six or seven; (7) infralabials six or seven; (8) pineal eye spot present; (9) supranasal contact absent; (10) prefrontals not contacting on midline; (11) enlarged chin shields in two pairs; (12) nuchal scales undifferentiated; (13) fourth and fifth supralabial below eye; (14) auricular opening present; (15) dorsolateral stripes absent; and (16) mid-dorsal stripes absent (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing *Brachymeles orientalis* from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles orientalis* most closely resembles *B. makusog* and *B. schadenbergi,* but differs from both taxa by having six or seven Finger-III lamellae, eight to ten Toe-IV lamellae, and the fourth and fifth supralabial below the eye (Tables 3.4, 3.5), and by the presence (vs. absence) of reddish-orange to salmon-colored scales on the lateral surfaces of the body. *Brachymeles orientalis* can further be distinguished from *B. makusog* by having a greater maximum axilla–groin scale row count and a greater maximum paravertebral scale row count (Table 3.5), and from *B. schadenbergi* by having no contact between supranasals, and by the absence of continuous, dark mid-dorsal stripes and dark lateral stripes (Table 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*)*, B. orientalis* differs by having pentadactyl limbs (vs. non-pentadactyl), longer forelimb lengths (greater than 10.4 mm vs. less than 6.9 mm), greater hind limb lengths (greater than 18.6 mm vs. less than 12.9 mm), and by the presence (vs. absence) of a postnasal scale. Additionally, *B. orientalis* differs from all non-pentadactyl species except *B. pathfinderi* by having Toe-IV lamellae eight to ten (vs. 4 or fewer), a paravertebral scale row count 69–72 (vs. greater than 84), and by the presence (vs. absence) of auricular openings; from all non-pentadactyl species except *B. wrighti* by having a midbody scale row count 26–28 (vs. fewer than 24); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence of limbs (vs. absence).

Description (based on holotype and 52 referred specimens, including 13 paratypes from CAS).—Details of the head scalation of an adult male are shown in Figure 3.8. Measurements of the holotype are provided below in brackets. Body large relative to other *Brachymeles*, elongate with respect to other lizards; maximum SVL 112.3 mm for males, 115.2 mm for females [99.9, female] (Tables 3.4, 3.5); head weakly differentiated from neck, nearly as wide as body, HW 10.2–12.7% (11.2 ± 0.7) SVL [11.9], 87.5–120.0% (108.4 ± 7.3) HL [120.0]; HL 33.7–45.0% (37.6 ± 2.6) SnFa [38.0]; SnFa 25.3–30.2% (27.6 ± 1.1) SVL [26.1]; snout long, rounded in dorsal and lateral profile, SNL 46.6–65.2% (57.5 ± 4.2) HL [62.5]; auricular opening present, moderate; eyes moderate, ED 1.5–2.3% (1.8 ± 0.2) SVL [1.8], 14.8–19.6% (17.3 ± 1.3) HL [18.2], 38.2–56.7% (44.8 ± 3.7) END [45.9], pupil subcircular; body slightly depressed, MBW 93.1–138.2% (114.5 ± 11.4) MBH [124.9]; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26–30 [28]; paravertebral scale rows 69–73 [72]; axilla–groin scale rows 46–49 [48]; limbs well developed, pentadactyl, digits small; FinIIIlam 6–7 [6]; ToeIVlam 8–10 [8]; FLL 17.0–24.8% (20.7 ± 2.0) AGD [18.8], 10.7–15.4% (13.1 ± 1.1) SVL [12.3]; HLL 27.6–42.7% (34.2 ± 3.4) AGD [32.2], 18.4–24.2% (21.6 ± 1.7) SVL [21.2]; order of digits from shortest to longest for hand: I < V < II = IV < III, for foot: I < V < II < III = IV; tail nearly as wide as body, sharply tapered towards end, TW 55.6–86.9% (69.7 ± 6.4) MBW [70.9], TL 62.2–106.0% (85.2 ± 11.6) SVL [106.0].

Table 3.4. Summary of meristic and mensural characters in all known pentadactyl species of *Brachymeles*. Sample size, body length and total length among males and females, and general geographical distribution (PAIC = Pleistocene Aggregate Island Complexes, sensu Brown and Diesmos, 2002) are included for reference (SVL, TotL, MBW, FLL, and HLL given as range over mean ± standard deviation; all body proportions given as percentage over mean ± standard deviation). In cases of scale count variation within species, numbers of individuals showing specific counts are given in parentheses.

	boholensis (5 m, 14 f)	*boulengeri* (7 m, 8 f)	*mindorensis* (6 m, 12 f)	*taylori* (8 m, 13 f)	*gracilis gracilis* (7 m, 11 f)	*gracilis hilong* (8 m, 12 f)	*bicolor* (7 m, 6 f)
Range	Bohol Island	Luzon PAIC	Mindoro Island	Negros & Cebu Island	Mindanao PAIC	Mindanao PAIC	Luzon Island
SVL (f)	83.8–94.0 (88.4 ± 3.1)	60.5–95.5 (84.0 ± 11.2)	90.0–106.8 (98.8 ± 5.3)	65.8–93.2 (83.9 ± 7.4)	62.8–75.8 (67.6 ± 3.7)	59.9–81.5 (71.8 ± 7.0)	125.9–153.3 (139.4 ± 10.1)
SVL (m)	84.1–93.6 (89.1 ± 4.1)	72.3–93.1 (82.5 ± 6.7)	93.9–104.2 (100.2 ± 4.1)	83.1–99.2 (87.0 ± 5.2)	60.1–82.3 (67.5 ± 7.6)	61.5–78.5 (70.5 ± 5.1)	120.4–140.3 (134.0 ± 7.6)
TotL (f)	129.6–174.8 (154.1 ± 14.7)	129.7–167.4 (159.3 ± 13.1)	162.5–206.7 (180.2 ± 14.2)	130.3–168.5 (149.9 ± 13.0)	116.4–134.4 (126.3 ± 5.5)	94.3–159.2 (126.4 ± 17.1)	225.3–290.7 (260.7 ± 30.7)
TotL (m)	154.5–166.2 (160.7 ± 5.9)	124.3–173.1 (151.4 ± 19.4)	165.3–197.0 (184.9 ± 11.5)	149.6–176.7 (164.3 ± 11.3)	113.9–133.7 (123.2 ± 8.8)	116.7–139.4 (127.4 ± 7.8)	233.4–301.4 (280.1 ± 24.9)
MBW	11.9–15.0 (13.4 ± 1.0)	9.9–14.7 (12.4 ± 1.7)	12.8–20.8 (16.0 ± 1.8)	11.0–16.8 (13.8 ± 1.7)	8.1–11.6 (9.5 ± 0.9)	7.9–12.1 (10.1 ± 1.2)	13.6–15.3 (14.4 ± 0.6)
TL/SVL	53–90 (76 ± 13)	67–114 (89 ± 16)	60–99 (85 ± 11)	69–103 (83 ± 10)	69–100 (88 ± 10)	57–98 (78 ± 14)	62–116 (97 ± 22)
TW/MBW	62–78 (70 ± 5)	60–81 (70 ± 6)	54–80 (69 ± 8)	54–80 (69 ± 7)	57–79 (67 ± 6)	57–81 (69 ± 7)	69–84 (76 ± 6)
FLL	9.0–11.2 (10.1 ± 0.7)	8.2–11.7 (10.5 ± 0.8)	10.0–13.0 (11.4 ± 0.8)	9.0–10.4 (9.8 ± 0.4)	5.9–7.9 (6.9 ± 0.6)	7.1–9.3 (8.3 ± 0.6)	9.0–12.0 (10.5 ± 1.1)
FLL/SVL	10–13 (11 ± 1)	12–14 (13 ± 1)	10–13 (11 ± 1)	10–14 (12 ± 1)	9–12 (10 ± 1)	10–14 (12 ± 1)	6.6–8.8 (7.7 ± 0.7)
HLL	15.4–18.7 (17.2 ± 1.0)	14.3–18.7 (17.2 ± 1.1)	18.8–23.1 (20.6 ± 1.2)	15.6–18.7 (17.0 ± 1.0)	10.3–13.6 (12.0 ± 0.7)	12.2–16.0 (14.3 ± 1.0)	16.1–20.5 (17.6 ± 1.3)
HLL/SVL	18–22 (19 ± 1)	18–24 (21 ± 2)	18–24 (21 ± 2)	18–25 (20 ± 2)	15–20 (18 ± 1)	17–23 (20 ± 1)	11.3–14.9 (13.0 ± 1.1)
FinIIIlam	6 (19)	5 (14) 6 (1)	5 (16) 6 (2)	5 (12) 6 (9)	4 (8) 5 (10)	5 (20)	4 (8) 5 (5)
ToeIVlam	9 (7) 10 (12)	9 (13) 10 (2)	8 (14) 9 (4)	9 (10) 10 (11)	7 (4) 8 (14)	8 (13) 9 (7)	6 (2) 7 (11)

TABLE 4.—Continued.

	talinis (11 m, 10 f)	*kadwa* (12 m, 15 f)	*tungaoi* (2 m, 6 f)	*makusog* (7 m, 4 f)	*orientalis* (21 m, 19 f)	*schadenbergi* (14 m, 10 f)	*vindumi* (1 m, 1 f)
Range	Visayan PAIC	Luzon, Babuyan Claro, Calayan Islands	Masbate Island	Luzon PAIC	Mindanao PAIC	Mindanao PAIC	Jolo Island
SVL (f)	103.8–126.7 (116.5 ± 6.8)	90.6–135.7 (109.7 ± 11.7)	78.2–106.2 (95.6 ± 10.7)	98.6–118.0 (108.8 ± 8.0)	97.6–115.2 (104.6 ± 5.9)	93.1–113.5 (104.8 ± 6.7)	104.9
SVL (m)	103.1–123.1 (113.6 ± 7.1)	97.0–128.2 (109.3 ± 9.1)	89.9, 104.8	82.5–123.5 (110.9 ± 13.7)	84.7–112.3 (99.0 ± 8.4)	94.4–115.8 (104.5 ± 6.1)	113.6
TotL (f)	187.5–236.2 (209.4 ± 18.0)	170.4–221.0 (196.3 ± 18.7)	168.9–206.5 (187.2 ± 15.9)	183.8–217.3 (201.5 ± 17.7)	159.7–213.0 (194.3 ± 17.1)	180.8–217.4 (202.4 ± 17.6)	–
TotL (m)	191.7–238.4 (209.0 ± 12.4)	181.9–255.2 (208.3 ± 20.3)	178.3, 203.1	162.3–241.3 (201.5 ± 25.1)	154.6–221.1 (184.8 ± 22.3)	179.2–219.7 (203.0 ± 14.4)	–
MBW	15.9–20.9 (18.5 ± 1.5)	14.3–21.0 (16.9 ± 1.8)	11.9–17.0 (14.4 ± 1.6)	13.0–19.9 (17.5 ± 2.1)	11.0–18.9 (15.1 ± 1.8)	13.5–19.1 (15.2 ± 1.7)	14.2, 14.8
TL/SVL	61–107 (84 ± 12)	68–106 (87 ± 12)	82–116 (97 ± 11)	61–117 (84 ± 16)	62–106 (85 ± 12)	65–103 (92 ± 11)	–
TW/MBW	63–94 (75 ± 6)	66–84 (75 ± 5)	62–80 (70 ± 6)	69–83 (75 ± 4)	56–87 (70 ± 6)	57–77 (68 ± 6)	83, 79
FLL	11.3–17.7 (14.2 ± 1.4)	10.7–15.0 (13.0 ± 1.2)	11.0–13.8 (12.2 ± 0.9)	12.8–17.0 (14.5 ± 1.1)	10.4–15.6 (13.4 ± 1.5)	11.1–13.5 (12.5 ± 0.8)	13.2, 13.3
FLL/SVL	10–15 (12 ± 1)	10–16 (12 ± 1)	11–14 (13 ± 1)	12–17 (13 ± 1)	11–15 (13 ± 1)	10–14 (12 ± 1)	12, 13
HLL	20.5–27.9 (23.7 ± 2.2)	17.9–24.1 (21.8 ± 1.6)	17.0–22.4 (20.0 ± 1.8)	19.4–25.3 (22.1 ± 1.9)	18.6–25.3 (22.1 ± 2.2)	18.5–21.9 (20.6 ± 1.2)	22.7, 22.7
HLL/SVL	18–25 (21 ± 2)	17–26 (20 ± 2)	20–23 (21 ± 1)	18–25 (20 ± 2)	18–24 (22 ± 2)	17–22 (20 ± 1)	20, 22
FinIIIlam	5 (19) 6 (2)	5 (25) 6 (2)	5 (5) 6 (3)	5 (6) 6 (5)	6 (36) 7 (4)	5 (13) 6 (11)	6 (2)
ToeIVlam	8 (2) 9 (12) 10 (7)	7 (1) 8 (14) 9 (11) 10 (1)	9 (5) 10 (3)	9 (6) 10 (5)	8 (4) 9 (29) 10 (7)	8 (14) 9 (10)	9 (1) 10 (1)

Table 3.5. Summary of qualitative diagnostic characters (present, absent) in all known pentadactyl species of *Brachymeles*. The pairs of enlarged scales posterior to the postmental scale are abbreviated as chin shield pairs with reference to the 1st, 2nd, and 3rd pairs (when present).

	boholensis (5 m, 14 f)	*boulengeri* (7 m, 8 f)	*mindorensis* (6 m, 12 f)	*taylori* (8 m, 13 f)	*gracilis gracilis* (7 m, 11 f)	*gracilis hilong* (8 m, 12 f)	*bicolor* (7 m, 6 f)
MBSR	26–28	26–27	26–28	26–28	24–26	27–30	27–29
AGSR	42–46	42–46	42–45	42–47	46–49	44–50	64–72
PVSR	63–66	63–66	63–65	62–69	67–70	66–73	88–92
SL	7 (19)	6 (12) 7 (3)	7 (18)	6 (21)	6 (18)	6 (20)	6 (13)
IFL	7 (19)	7 (15)	6 (18)	7 (21)	7 (18)	6 (20)	6 (13)
SC	6 (19)	5 (1) 6 (14)	6 (18)	6 (21)	6 (18)	6 (20)	6 (13)
SO	5(19)	5 (15)	5 (18)	5 (21)	5 (18)	5 (20)	5 (13)
Pineal eyespot	+	+	+	+	–	+	+
Supranasal contact	–	–	– or +	–	–	–	+
Prefrontal contact	–	–	– or +	–	+	–	–
Frontoparietal contact	+	+	+	+	+	– or +	+
Parietals contact	– or +	– or +	– or +	– or +	+	+	+
1st chin shield pair contact	– or +	+	+	– or +	–	– or +	+
Enlarged chin shield pairs	3	2	2	2	3	3	2
Chin shield pair size	3 < 1 < 2	1 < 2	1 < 2	1 < 2	3 < 1 < 2	3 < 1 < 2	2 < 1
Chin shield pair separation[1]	1(0/1); 2(1); 3(3)	1(0/1); 2(1)	1(0); 2(1)	1(0); 2(1)	1(1); 2(1); 3(3)	1(0/1); 2(1); 3(3/5)	1(0); 2(3)
Subocular supralabial	5th and 6th	4th and 5th	5th and 6th	4th and 5th	4th and 5th	4th and 5th	4th and 5th
Differentiated nuchals	–	–	–	–	–	–	+
Uniform body color	–	–	–	–	+	+	–
Continuous, light dorsolateral stripes	+	+	+	–	+	+	–
Continuous dark mid-dorsal stripes[2]	+	–	+	+	+	– or +	–
Dark lateral stripes[2]	+	+	+	+	+	+	–
Dark ventral pigmentation	+	–	–	–	+	+	–

[1] Parentheses show the number of small ventral scale rows separating each enlarged pair of chin shields.

[2] Character refers to longitudinal rows of dark scale pigmentation, often in the form of spots, aligned into rows.

TABLE 5.—Continued.

	talinis (11 m, 10 f)	*kadwa* (12 m, 15 f)	*tungaoi* (2 m, 6 f)	*makusog* (7 m, 4 f)	*orientalis* (21 m, 19 f)	*schadenbergi* (14 m, 10 f)	*vindumi* (1 m, 1 f)
MBSR	26–30	26–28	26–28	25–28	26–28	26–28	30, 31
AGSR	43–48	47–49	46–49	42–47	46–49	45–50	49, 49
PVSR	67–72	68–70	66–68	60–69	69–72	67–72	74, 74
SL	7 (20)	7 (27)	7 (4)	6 (7) 7 (4)	6 (31) 7 (9)	6 (2) 7 (22)	7 (2)
IFL	7 (21)	6 (27)	6 (4)	6 (10) 7 (1)	6 (7) 7 (33)	6 (10) 7 (14)	6 (2)
SC	6 (21)	6 (27)	6 (4)	6 (11)	6 (40)	6 (24)	6 (2)
SO	5 (21)	5 (27)	5 (4)	5 (11)	5 (40)	5 (24)	5 (2)
Pineal eyespot	+	+	+	+	+	+	+
Supranasal contact	+	+	+	–	–	+	+
Prefrontal contact	–	–	–	–	–	–	–
Frontoparietal contact	+	– or +	+	+	+	+	+
Parietals contact	– or +	– or +	– or +	–	– or +	– or +	+
1st chin shield pair contact	– or +	– or +	+	– or +	– or +	– or +	–
Enlarged chin shield pairs	2	2	2	2	2	2	2
Chin shield pair size	2 < 1	1 < 2	1 = 2	2 < 1	2 < 1	2 < 1	2 < 1
Chin shield pair separation[1]	1(0/1); 2(3)	1(0/1); 2(1)	1(0); 2(1)	1(1); 2(3)	1(0/1); 2(3)	1(0); 2(3)	1(1); 2(1)
Subocular supralabial	5th and 6th	5th and 6th	5th and 6th	4th and 5th or 5th and 6th	4th and 5th	5th and 6th	5th and 6th
Differentiated nuchals	–	–	–	–	–	–	–
Uniform body color	–	–	–	–	–	–	–
Continuous, light dorsolateral stripes	– or +	+, poorly defined	+, poorly defined	–	–	–	+
Continuous dark mid-dorsal stripes[2]	– or +	+	+	–	–	– or +	–
Dark lateral stripes[2]	+	+	+	–	–	– or +	+
Dark ventral pigmentation	–	+	–	–	–	–	+

[1] Parentheses show the number of small ventral scale rows separating each enlarged pair of chin shields.

[2] Character refers to longitudinal rows of dark scale pigmentation, often in the form of spots, aligned into rows.

Table 3.6. Summary of univariate morphological variation among mensural characters in series of *Brachymeles boholensis, B. boulengeri, B. mindorensis, B. taylori, B. talinis, B. kadwa, B. tungaoi, B. orientalis, B. schadenbergi* and *B. vindumi.*

	boholensis (5 m; 14 f)	*boulengeri* (7 m; 8 f)	*mindorensis* (6 m; 12 f)	*taylori* (8 m; 13 f)	*talinis* (11 m; 10 f)
SVL (m)	84.1–93.6 (89.1 ± 4.1)	72.3–93.1 (82.5 ± 6.7)	93.9–104.2 (100.2 ± 4.1)	83.1–99.2 (87.0 ± 5.2)	103.1–123.1 (113.6 ± 7.1)
SVL (f)	83.8–94.0 (88.4 ± 3.1)	60.5–95.5 (84.0 ± 11.2)	90.0–106.8 (98.8 ± 5.3)	65.8–93.2 (83.9 ± 7.4)	103.8–126.7 (116.5 ± 6.8)
AGD (m)	54.7–61.9 (58.1 ± 2.8)	46.3–60.7 (53.0 ± 5.0)	59.5–67.6 (63.3 ± 3.3)	52.8–66.0 (55.9 ± 4.2)	64.2–90.3 (74.6 ± 7.5)
AGD (f)	53.0–61.2 (57.0 ± 2.7)	36.2–61.3 (54.3 ± 8.3)	56.3–74.9 (64.8 ± 5.5)	46.6–60.6 (54.7 ± 4.6)	66.5–81.4 (74.7 ± 4.9)
TotL (m)	154.5–166.2 (160.7 ± 5.9)	124.3–173.1 (151.4 ± 19.4)	165.3–197.0 (184.9 ± 11.5)	149.6–176.7 (164.3 ± 11.3)	191.7–238.4 (209.0

					± 12.4)
TotL (f)	129.6–174.8 (154.1 ± 14.7)	129.7–167.4 (159.3 ± 13.1)	162.5–206.7 (180.2 ± 14.2)	130.3–168.5 (149.9 ± 13.0)	187.5–236.2 (209.4 ± 18.0)
MBW (m)	12.2–13.9 (13.0 ± 0.7)	10.1–14.7 (12.1 ± 1.9)	12.8–16.0 (14.7 ± 1.1)	11.6–16.8 (13.3 ± 1.7)	15.9–20.1 (17.7 ± 1.3)
MBW (f)	11.9–15.0 (13.6 ± 1.1)	9.9–14.6 (12.7 ± 1.7)	14.5–20.8 (16.7 ± 1.8)	11.0–16.6 (14.0 ± 1.8)	17.3–20.9 (19.3 ± 1.1)
MBH (m)	11.7–12.5 (12.1 ± 0.4)	7.9–10.4 (9.0 ± 1.0)	10.2–12.9 (12.0 ± 1.0)	9.4–14.6 (11.8 ± 1.7)	10.4–15.9 (13.5 ± 1.7)
MBH (f)	10.4–14.2 (11.8 ± 1.0)	6.2–10.2 (8.9 ± 1.3)	11.4–16.6 (14.2 ± 1.8)	10.4–15.2 (12.2 ± 1.5)	12.7–18.6 (16.2 ± 2.1)

TL (m)	70.4–74.8 (72.9 ± 2.3)	52.0–88.6 (69.2 ± 14.7)	62.2–94.2 (84.6 ± 12.0)	63.0–85.7 (76.4 ± 9.2)	86.8–115.3 (96.1 ± 8.5)
TL (f)	45.3–82.3 (65.6 ± 13.0)	69.0–86.3 (76.0 ± 6.7)	65.5–99.9 (82.6 ± 11.6)	55.4–76.1 (67.0 ± 7.3)	70.7–115.2 (94.2 ± 17.6)
TW (m)	8.5–10.0 (9.4 ± 0.5)	7.2–10.3 (8.7 ± 1.0)	10.2–11.9 (10.9 ± 0.6)	7.4–12.2 (9.5 ± 1.4)	11.8–15.9 (13.5 ± 1.2)
TW (f)	8.4–10.4 (9.4 ± 0.5)	7.0–9.9 (8.6 ± 1.2)	10.0–12.5 (11.0 ± 0.7)	7.4–12.1 (9.4 ± 1.3)	12.9–15.6 (14.2 ± 0.9)
TH (m)	7.6–8.1 (7.8 ± 0.2)	5.4–8.3 (6.8 ± 0.9)	8.0–9.5 (8.5 ± 0.6)	6.3–10.0 (8.0 ± 1.0)	9.7–11.4 (10.7 ± 0.6)
TH (f)	6.9–8.5 (7.6 ± 0.5)	5.1–8.0 (6.5 ± 0.9)	7.3–10.0 (8.5 ± 0.7)	6.9–10.3 (8.0 ± 1.0)	10.6–13.2

					(11.7 ± 0.9)
HL (m)	8.3–9.0 (8.7 ± 0.4)	7.3–8.9 (8.3 ± 0.7)	8.6–10.5 (9.6 ± 0.7)	8.4–9.0 (8.7 ± 0.2)	9.2–12.2 (10.7 ± 0.9)
HL (f)	8.6–9.8 (9.0 ± 0.4)	7.9–9.2 (8.3 ± 0.5)	8.9–10.9 (9.9 ± 0.7)	7.6–9.9 (8.7 ± 0.8)	9.9–12.6 (11.3 ± 0.9)
HW (m)	9.3–10.9 (10.2 ± 0.6)	9.1–10.3 (9.5 ± 0.5)	10.3–12.1 (11.2 ± 0.6)	9.6–11.6 (10.4 ± 0.8)	11.9–14.5 (13.2 ± 0.8)
HW (f)	9.3–10.5 (10.0 ± 0.4)	7.5–9.9 (9.1 ± 0.8)	10.7–12.4 (11.4 ± 0.5)	9.3–12.0 (10.5 ± 0.9)	12.8–15.8 (14.0 ± 0.9)
HH (m)	7.2–7.9 (7.7 ± 0.3)	6.2–7.5 (6.9 ± 0.4)	8.2–10.1 (9.0 ± 0.6)	7.3–8.8 (7.9 ± 0.5)	8.8–12.7 (9.9 ± 1.1)
HH	7.2–8.0	5.7–7.2	8.1–9.9	7.3–9.7	9.3–

(f)	(7.5 ± 0.3)	(6.6 ± 0.5)	(8.9 ± 0.5)	(8.1 ± 0.7)	12.5 (10.7 ± 1.0)
SnFa (m)	22.9–25.1 (23.7 ± 1.0)	19.1–24.0 (22.4 ± 1.7)	25.9–28.1 (27.0 ± 0.7)	20.7–23.3 (22.1 ± 1.0)	26.2–34.1 (30.6 ± 2.3)
SnFa (f)	21.3–24.2 (22.7 ± 0.8)	17.9–24.4 (22.7 ± 2.1)	24.3–27.5 (25.9 ± 1.0)	20.8–25.1 (22.2 ± 1.1)	29.1–34.7 (31.4 ± 1.9)
ED (m)	1.7–2.1 (1.8 ± 0.2)	1.8–2.3 (2.0 ± 0.2)	2.0–2.5 (2.2 ± 0.2)	1.4–2.0 (1.8 ± 0.2)	2.0–2.3 (2.2 ± 0.1)
ED (f)	1.6–2.0 (1.8 ± 0.1)	1.5–2.3 (1.9 ± 0.3)	2.0–2.6 (2.2 ± 0.2)	1.5–2.1 (1.8 ± 0.2)	2.0–2.5 (2.2 ± 0.1)
END (m)	2.4–2.6 (3.5 ± 0.1)	2.7–3.0 (2.8 ± 0.1)	2.5–2.9 (2.7 ± 0.2)	2.8–3.4 (3.1 ± 0.2)	3.7–5.1 (4.3 ± 0.4)

END (f)	3.0–3.7 (3.4 ± 0.2)	2.1–3.0 (2.8 ± 0.3)	3.4–4.2 (3.6 ± 0.2)	2.7–3.5 (3.0 ± 0.2)	3.7–5.3 (4.5 ± 0.4)
SNL (m)	5.0–5.3 (5.2 ± 0.1)	4.2–4.6 (4.4 ± 0.1)	5.4–6.0 (5.7 ± 0.2)	4.1–4.8 (4.4 ± 0.3)	5.7–7.5 (6.4 ± 0.6)
SNL (f)	4.8–5.6 (5.3 ± 0.2)	3.4–4.8 (4.2 ± 0.4)	5.0–6.4 (5.5 ± 0.4)	4.1–5.0 (4.6 ± 0.3)	5.5–7.5 (6.6 ± 0.5)
IND (m)	3.0–3.2 (3.1 ± 0.1)	2.8–3.1 (2.9 ± 0.1)	3.2–3.6 (3.4 ± 0.1)	2.7–3.2 (2.9 ± 0.2)	3.3–4.3 (3.9 ± 0.3)
IND (f)	3.0–3.3 (3.1 ± 0.1)	2.3–3.2 (2.8 ± 0.3)	3.1–3.8 (3.4 ± 0.2)	2.7–3.2 (2.9 ± 0.2)	3.6–4.4 (3.9 ± 0.2)
FLL (m)	9.6–11.1 (10.5 ± 0.7)	10.0–11.7 (10.5 ± 0.6)	10.7–12.8 (11.4 ± 0.7)	9.3–10.4 (9.9 ± 0.4)	11.3–17.7 (13.9

					± 1.8)
FLL (f)	9.0–11.2 (9.9 ± 0.7)	8.2–11.3 (10.4 ± 1.0)	10.0–13.0 (11.4 ± 0.9)	9.0–10.3 (9.7 ± 0.4)	13.5–18.9 (14.6 ± 0.9)
HLL (m)	16.2–17.5 (16.8 ± 0.5)	16.6–18.5 (17.4 ± 0.6)	20.1–22.6 (20.8 ± 0.9)	16.1–17.9 (16.9 ± 0.7)	20.5–27.9 (23.0 ± 2.4)
HLL (f)	15.4–18.7 (17.3–1.2)	14.3–18.7 (17.0 ± 1.4)	18.8–23.1 (20.6 ± 1.3)	15.6–18.7 (17.1 ± 1.1)	20.5–26.1 (24.4 ± 1.7)

Rostral projecting dorsoposteriorly to point in line with anterior edge of nasal, broader than high, in narrow contact with frontonasal; frontonasal wider than long; nostril ovoid, centered in a single rectangular nasal; supranasals present, large, narrowly separated by frontonasal; postnasals present; prefrontals moderately separated by frontal; frontal nearly diamond shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, in broad medial contact, each frontoparietal in contact with supraoculars two–four; interparietal moderate, quadrilaterally shaped, longer than wide, its length slightly greater than midline length of frontoparietal; parietal eyespot present in posterior half of scale; parietals in narrow contact or separated behind interparietal; nuchals non-enlarged, undifferentiated; loreals two, decreasing in size from anterior to posterior, anterior loreal about as long as and 1.8× higher than posterior loreal, in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal, and occasionally with first supralabial; preocular single, nearly two thirds as high as posterior loreal; presubocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials six or seven [6], first 2× size of other supralabials, fourth and fifth below the eye; infralabials six or seven [7].

Mental wider than long, in contact with first infralabial; single enlarged postmental, wider than mental; followed by two pairs of enlarged chin shields, first pair narrowly separated by single row of undifferentiated scales or in moderate medial contact, scales of second pair narrower than first, broadly separated by three medial scales.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with irregular raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative.—Ground color of body cream; lateral and ventral surfaces of body lacking dark pigment; dorsum of body, from posterior edge of supranasals to tail tip, uniformly dark brown with dark pigmentation spanning six and two half rows of scales at midbody and narrowing to cover four and two half rows of scales posterior to parietals; body dark brown dorsally abruptly changing to cream laterally and ventrally; head scales uniform dark brown; rostral, nasal, postnasal, supranasal, and first supralabial light gray; pineal eyespot charcoal; small dark brown blotch dorsal to auricular openings. Limbs mottled light and medium brown dorsally, cream colored ventrally; dorsal and ventral surface of digits light brown.

Coloration in life.—(Fig. 3.11F,G). Dorsal ground color homogeneous medium-brown; sharp lateral demarcation between dorsal and lateral and ventral coloration; lateral and ventral surfaces of body bright burnt orange, orange-brown, or salmon colored; dark-brown spots and longitudinal lines of spots absent from lateral surfaces. Limbs medium-brown dorsally, burnt orange to orange-brown ventrally. Dorsal head scales uniform medium-brown.

Variation.—Morphometric variation of the series is summarized in Table 3.6. We observed variation among the 19 specimens examined for the degree of contact between head scales. Twelve specimens were observed to have parietals moderately separated by the interparietal (KU 305470, 310734–6, 310942, 310944, 310949, 310951, 311232–5), one specimen has parietals in point medial contact (KU 311231), and six specimens have parietals in moderate medial contact (KU 310739, 310943, 310945–6, 310955, 311241) behind the interparietal; nine specimens do not have the first pair of enlarged chin shields in medial contact (KU 210736, 310942, 310945–6, 310949, 310951, 311231, 311234–5) and ten specimens have the first pair of enlarged chin shields in moderate medial contact (KU 305470, 310734–5, 310739, 310943–4, 310955, 311232–3, 311241).

Scale counts were observed to vary among the measured series. The number of supralabials varied between six (CAS-SU 18702, 24428, 24434, 24436–7, 24442, 24446–9, 24451, 24458, 25452, 25460, 28332, CAS 102404, 110978–81, 133301, 133616, 133749, 133752, 133754, KU 310734, 310736, 310942, 311231–2, 311234) and seven (CAS-SU 24450, 28320–1, 28338, 28370, CAS 110976–7, 110982–3); infralabials varied between six (CAS-SU 24446, KU 310734, 310736, 310942, 311231–2, 311234) and seven (CAS-SU 18702, 24428, 24434, 24436–7, 24442, 24447–51, 24458, 25452, 25460, 28320–1, 28332, 28338, 28370, CAS 102404, 110976–83, 133301, 133616, 133749, 133752, 133754). Specimens were observed to have midbody scale row counts of 26 (CAS-SU 24428, 24446), 27 (CAS-SU 24458, 25460), 28 (CAS-SU 18702, 24434, 24436–7, 24442, 24447–52, CAS 102404, 133301, 133752, 133754), 29 (CAS-SU 28320, 28338, CAS 110976, 110981, 133616, 133749), and 30 (CAS-SU 28231–2, 28370, CAS 110977–80, 110982–3); axilla–groin scale row counts of 46 (CAS-SU 25452, CAS 110983, 133616), 47 (CAS-SU 24450, 24458, 25460, CAS 110979–81, 133301), 48 (CAS-SU 18702, 24428, 24436, 24442, 24446, 24449, 28332, 28338, CAS 110976, 110978, 110982, 133749), and 49 (CAS-SU 24434, 24437, 24447–8, 24451, 28320–1, 28370, CAS 102404, 110977, 133752, 133754); and paravertebral scale row counts of 69 (CAS-SU 25452, CAS 133616), 70 (CAS-SU 24450, 24458, 25460, CAS 133301), 71 (CAS-SU 18702, 24428, 24442, 24446, 24449, 28332, 28338, CAS 110980, 110983, 133749), 72 (CAS-SU 24434, 24436–7, 24447–8, 24451, 28320–1, CAS 102404, 110976–9, 110981–2, 133752, 133754), and 73 (CAS-SU 28370).

We also observed lamellae counts to vary among the measured series. Specimens were observed to have Finger-III lamellae counts of six (CAS-SU 18702, 24428, 24434, 24436–7, 24442, 24446–7, 24449–51, 24458, 25460, 28320–1, 28332, 28338, 28370, CAS 102404, 110976–83, 133301, 133616, 133749, 133754, KU 310734, 311231–2, 311234) or seven (CAS-SU 24448, CAS 133752, KU 310736, 310942); Toe-IV lamellae counts of eight (CAS-SU 24436, 25452, 28320, CAS 102404), nine (CAS-SU 18702, 24428, 24434, 24437, 24442, 24446–51, 24458, 25460, 28321, 28332, 28370, CAS 110976–7, 110979, 110981–3, 133301, 133616, 133754, KU 310734, 310942, 311232, 311234), or ten (CAS-SU 28338, CAS 110978, 110980, 133749, 133752, KU 310736, 311231).

Distribution.—Brachymeles orientalis is known from Bohol, Samar, Leyte, Dinagat, Camiguin Sur islands, and the eastern and central portions of Mindanao Island (Fig. 3.4).

Ecology and natural history.—Brachymeles orientalis occurs in agricultural areas as well as disturbed and secondary growth forest. On Samar, Leyte, Mindanao, and Camiguin Sur islands, we have collected this species in primary forest, and on Bohol Island it is present in mature secondary growth. Individuals have been observed under piles of rotting coconut husks, in the humus material within rotting logs, and in loose soil and leaf litter surrounding the root networks of trees. The species is quite common throughout its range with the exception of Bohol Island (CDS personal observation), and occurs sympatrically with four other species of *Brachymeles* in different parts of its range (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). *Brachymeles orientalis* occurs sympatrically with *B. boholensis* on Bohol Island, *B. gracilis hilong* and *B. samarensis* on Samar and Leyte islands, *B. gracilis hilong* on Mindanao Island, and *B.* cf. *gracilis hilong* on Camiguin Sur Island (CDS pers. observ.). Similar to *B. boulengeri*, *B. orientalis* appears to have a wider geographic distribution that spans multiple Philippine islands. This is in contrast to the pentadactyl, island endemic species, *B. boholensis*, *B. tungaoi,* and *B. mindorensis*, which are known from just Bohol, Masbate, and Mindoro islands respectively. As do all members of the genus, disturbed individuals move in a rapid serpentine manner and always attempt to burrow back into loose soil or humus.

Sympatric lizard species observed within the range of *Brachymeles orientalis* include: (Agamidae) *Bronchocela cristatella, Draco bimactulatus, D. cyanopterus, D. mindanensis, D. ornatus, Gonocephalus interruptus, G. semperi, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus agusanensis, C. annulatus, C. jambangan, Gehyra mutilata, Gekko gecko, Gekko mindorensis, Hemidactylus frenatus, H. platyurus, Pseudogekko compressicorpus*; (Scincidae) *Brachymeles gracilis hilong*, *Brachymeles* cf. *gracilis gracilis*, *Brachymeles samarensis, Eutropis indeprensa, E. multifasciata, Lamprolepis smaragdina, L. pulchella, L. quadrivittata, Sphenomorphus abdictus abdictus, S. acutus, S. cumingi, S.* cf. *mindanensis, S. coxi, S. fasciatus, S. jagori, S. llanosi, S. steerei, S. variegatus, Tropidophorus misaminus*; and (Varanidae) *Varanus cumingi.*

Brachymeles schadenbergi (Fischer 1885)

Figs. 3.4, 3.8, 3.11E

Senira bicolor (part), Gray, 1845.

Eumeces (Riopa) schadenbergi, Fisher, 1885, Type-locality: "Southern Mindanao Island, Philippines" (Reported by Fischer [1885] as No. 845 housed in the Dresden Museum).

Brachymeles schadenbergi *(part), Boettger, 1886; Boulengeri, 1887; Boettger, 1893; Taylor, 1917, 1922b,c; Brown and Alcala, 1970.*

Brachymeles schadenbergi schadenbergi *(part), Brown, 1956; Brown and Rabor, 1967.*

Diagnosis.—Brachymeles schadenbergi can be distinguished from congeners by the following combination of characters: (1) body large (SVL 93.1–115.8 mm); (2) pentadactyl; (3) Finger-III lamellae five or six; (4) Toe-IV lamellae eight or nine; (5) limbs relatively long; (6) supralabials six or seven; (7) infralabials six or seven; (8) pineal eye spot present; (9) supranasals in contact; (10) prefrontals not contacting on midline; (11) enlarged chin shields in two pairs; (12) nuchal scales undifferentiated; (13) fifth and sixth supralabial below eye; (14) auricular opening present; and (15) continuous, light dorsolateral stripes absent (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing *Brachymeles schadenbergi* from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles schadenbergi* most closely resembles *B. makusog* and *B. orientalis,* but differs from both taxa by having eight or nine Toe-IV lamellae, and the fifth and sixth supralabial below the eye, and by contact between supranasals (Tables 3.4, 3.5). *Brachymeles schadenbergi* can further be distinguished from *B. makusog* by having a greater maximum axilla–groin scale row count and a greater maximum paravertebral scale row count (Table 3.5), and from *B. orientalis* by the absence (vs. presence) of reddish-orange to salmon-colored scales on the lateral surfaces of the body.

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*)*, B. schadenbergi* differs by having a pentadactyl body form (vs. non-pentadactyl), longer forelimb lengths (greater than 11.1 mm vs. less than 6.9 mm), greater hind limb lengths (greater than 18.5 mm vs. less than 12.9 mm), and by the presence of a postnasal scale (vs. absence). Additionally, *B. schadenbergi* differs from all non-pentadactyl species except *B. pathfinderi* by having Toe-IV lamellae eight or nine (vs. 4 or fewer), 67–72 paravertebrals (vs. greater than 84), and by the presence (vs. absence) of auricular openings;

from all non-pentadactyl species except *B. wrighti* by having a midbody scale row count 26–28 (vs. fewer than 24); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence (vs. absence) of limbs.

Description (based on holotype description and 34 referred specimens).—Details of the head scalation of an adult male are shown in Figure 3.8. The holotype was not examined by authors; however, measurements of the holotype taken from the original description are provided below in brackets. Body large relative to other *Brachymeles*, elongate with respect to other lizards; maximum SVL 115.8 mm for males, 113.5 mm for females [85] (Tables 3.4, 3.5); head weakly differentiated from neck, nearly as wide as body, HW 10.2–11.7% (11.2 ± 0.5) SVL, 102.0–116.8% (108.7 ± 4.2) HL; HL 37.0–40.2% (38.4 ± 0.9) SnFa; SnFa 25.7–27.4% (26.8 ± 0.5) SVL; snout moderately long, rounded in dorsal and lateral profile, SNL 48.8–58.8% (54.3 ± 2.9) HL; auricular opening present, moderate; eyes moderate, ED 1.8–2.2% (2.1 ± 0.1) SVL, 18.4–21.8% (20.0 ± 1.0) HL, 44.7–57.5% (52.3 ± 4.3) END, pupil nearly round; body slightly depressed, MBW 94.8–135.4% (115.8 ± 13.0) MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26–28 [28 *fide* Fisher, 1885]; paravertebral scale rows 67–72; axilla–groin scale rows 45–50 [46 *fide* Fisher, 1885]; limbs well developed, pentadactyl, digits small; FinIIIlam 5–6; ToeIVlam 8–9; FLL 12.5–21.6% (18.0 ± 2.4) AGD, 10.3–13.7% (12.0 ± 0.9) SVL [12.9 *fide* Fisher, 1885]; HLL 20.1–24.4% (29.7 ± 3.9) AGD, 17.4–22.0% (19.8 ± 1.4) SVL [22.4 *fide* Fisher, 1885]; order of digits from shortest to longest for hand: V = I < II = IV < III, for foot: I < V < II < III < IV; tail not as wide as body, gradually tapered towards end, TW 57.4–76.8% (68.5 ± 5.7) MBW, TL 64.6–102.6% (91.6 ± 10.8) SVL.

Rostral projecting dorsoposteriorly to point in line with anterior edge of nasal, broader than high, separated from frontonasal; frontonasal wider than long; nostril ovoid, centered in a single rectangular nasal; supranasals present, large, in broad medial contact; postnasals present; prefrontals moderately separated by frontal; frontal nearly diamond shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 5× wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, broad contact medially, each frontoparietal in contact with supraoculars two–four; interparietal moderate, quadrilaterally shaped, longer than wide, its length greater than midline length of frontoparietal; parietal eyespot present in posterior half of scale; parietals in moderate to broad contact behind interparietal or moderately separated; nuchals undifferentiated; loreals two, decreasing in size from anterior to posterior, subequal, in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal; preocular single, nearly two thirds as high as posterior loreal; presubocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials six or seven, fifth and sixth beneath center of eye; infralabials six or seven.

Mental wider than long, in contact with first infralabials; single enlarged postmental, wider than mental, followed by two pairs of enlarged chin shields; first pair in slight contact or narrowly separated by single undifferentiated scale, second pair narrower than first, broadly separated by undifferentiated scales.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with irregular raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative.—Ground color of body medium-brown; dorsal surfaces nearly all dark brown, gradually fading into medium-brown lateral and ventral surfaces of body; dark dorsal pigmentation in nearly continuous block across dorsal surface, spanning six full and two half rows of scales at midbody and narrowing to cover four full and two half rows of scales posterior to parietals; lateral surfaces with 1–2 irregular dark-brown lines on posterior half of axilla–groin region; head scales uniform dark-brown; rostral, nasal, postnasal, supranasal, first supralabial, mental, and first infralabial dark-gray; pineal eyespot poorly defined, surrounded by light-cream border. Tail coloration matches body coloration. Limbs mottled dark-brown dorsally, medium-brown ventrally; dorsal and ventral surface of digits dark brown.

Coloration in life.—(Fig. 3.11E). Dorsal ground color homogeneous dark-brown; blotched, irregular, lateral demarcation between dorsal and lighter lateral and ventral coloration; lateral and ventral surfaces of body medium-brown; lateral surfaces with irregularly shaped rows of dark-brown spots. Limbs dark-brown dorsally, medium-brown ventrally. Dorsal head scales blotched dark and medium-brown.

Variation.—Morphometric variation of the series is summarized in Table 3.6. We observed variation among the 36 specimens examined for the degree of contact between head scales. Twenty-one specimens were observed to have parietals moderately separated by the interparietal (KU 314969, 314976, 314984–5, 314988–9, 314992, 314997; MCZ 26552–3, 26556–8, 26561, 26563, 26566, 26568, 26571–2, 26574), one specimen has parietals narrowly separated by the interparietal (KU 314996), and 14 specimens have parietals in moderate medial contact (KU 314967, 314970–5, 314977–8, 314980, 314990–1, 314994; MCZ 26555) behind the interparietal; seven specimens do not have the first pair of enlarged chin shields in medial contact (KU 314971, 314973, 314976, 314990, 314992, 314994; MCZ 26552, 26554, 26563), one specimen has the first pair of enlarged chin shields in point medial contact (KU 314997), and 26 specimens have the first pair of enlarged chin shields in moderate medial contact (KU 314967, 314969, 314970, 314972, 314974–5, 314977–8, 314980, 314984–5, 314988–9, 314991, 314996; MCZ 26553, 26555–8, 26561, 26566, 26568, 26571–2, 26574).

Scale counts were observed to vary among the measured series. The number of supralabials varied between six (CAS 23495, KU 314991) and seven (CAS 23468–9, 23471, 23479–81, 23484–5, 23494, 23496, 60493, KU 314967, 314969, 314974–5, 314977–8, 314980, 314984–5, 314994, 314996); infralabials varied between six (KU 314967, 314969, 314974–5, 314977, 314980, 314984–5, 314991, 314996) and seven (CAS 23468–9, 23471, 23479–81, 23484–5, 23494–6, 60493). Specimens were observed to have midbody scale row counts of 26 (CAS 23468, 23479–81, 23494–6, 60493), 27 (CAS 23469, 23484), and 28 (CAS 23471, 23485); axilla–groin scale row counts of 45 (CAS 23495), 46 (CAS 23469, 23494, 23496), 47 (CAS 23468, 23484), 48 (CAS 23485, 60493), 49 (CAS 23471, 23480), and 50 (CAS 23479, 23481); and paravertebral scale row counts of 67 (CAS 23495), 68 (CAS 23494, 23496), 70 (CAS 23484), 71 (CAS 23468–9, 23471, 23480, 23485, 60493), and 72 (CAS 23479, 23481).

We also observed lamellae counts to vary among the measured series. Specimens were observed to have Finger-III lamellae counts of five (CAS 23469, 23495, 60493, KU 314967, 314969, 314974, 314977–8, 314984–5, 314991, 314994, 314996) or six (CAS 23468, 23471, 23479–81, 23484–5, 23494, 23496, KU 314975, 314980); Toe-IV lamellae counts of eight (CAS 23468, 23494–5, 60493, KU 314967, 314969, 314974–5, 314977, 314984–5, 314991, 314994, 314996), or nine (CAS 23469, 23471, 23479–81, 23484–5, 23496, KU 314978, 314980).

There is a small degree of color variation in the examined series, with the degree and definition of continuous, dark mid-dorsal pigmentation. Most of the examined specimens show patterns consistent with a continuous, dark streak of pigmentation covering the mid-dorsal region of the body (KU 314969, 314974–5, 314977–8, 314980, 314984–5, 314991, 314994, 314996). In several specimens, continuous, dark mid-dorsal stripes are evident overlaying the dark ground coloration (KU 314967).

Distribution.—Brachymeles schadenbergi is known from Basilan and western Mindanao islands (Fig. 3.4).

Ecology and natural history.—Brachymeles schadenbergi occurs in a variety of habitats from disturbed and secondary growth to primary forest and intact climax forest. Individuals have been observed in the humus material within rotting logs and in loose soil and leaf litter surrounding the root networks of trees. Individuals are moderately common in populations sampled (CDS, RMB personal observation), and occur sympatrically with *B. gracilis gracilis* in western Mindanao Island (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). We collected numerous specimens in pitfall traps, indicating some level of surface activity. Although *B. schadenbergi* occurs on multiple islands in the southern Philippines, the species appears to have a more restricted geographic distribution when compared with more widespread pentadactyl species, such as *B. boulengeri, B. talinis, B. orientalis,* and *B. kadwa*. As in other members of the genus, disturbed individuals move in a rapid serpentine manner and always attempt to burrow back into loose soil or humus.

Sympatric lizard species observed within the range of *Brachymeles schadenbergi* include: (Agamidae) *Bronchocela cristatella, Draco bimaculatus, D. cyanopterus, D. mindanensis, Gonocephalus interruptus, Hydrosaurus amboinensis*; (Gekkonidae) *Cyrtodactylus jambangan, Gehyra mutilata, Gekko gecko, Hemidactylus frenatus, H. platyurus, Hemiphyllodactylus typus, Lepidodactylus* sp., *L. quadrivittata, Luperosaurus joloensis, Pseudogekko compressicorpus*;

(Scincidae) *Brachymeles gracilis gracilis, Eutropis indeprensa, E. multicarinata, E. multifasciata, E. englei, Lamprolepis smaragdina, Sphenomorphus atrigularis, S. fasciatus, S. jagori, S. steerei, S. variegatus, Tropidophorus misaminus, T. partelloi*; and (Varanidae) *Varanus cumingi.*

Brachymeles talinis Brown 1956

Figs. 3.5, 3.9, 3.11H

Brachymeles schadenbergi talinis, Brown, 1956, Type-locality: "On the low ridge north side of the Maite River, 5 to 6 km west of Valencia," Negros Oriental Province, Negros Island, Philippines, 933 m elevation, 9°17'19.25" N, 123°11'56.4" E (holotype: CAS-SU 18358).

Brachymeles talinis, *Brown and Rabor, 1967.*

Brachymeles talinis, *Brown and Alcala, 1980.*

Diagnosis.—Brachymeles talinis can be distinguished from congeners by the following combination of characters: (1) body size large (SVL 103.8–123.1 mm); (2) pentadactyl; (3) Finger-III lamellae five or six; (4) Toe-IV lamellae eight to ten; (5) limbs relatively long; (6) paravertebral scale rows 67–72; (7) supralabials seven; (8) infralabials seven; (9) pineal eye spot present; (10) supranasals in contact; (11) prefrontals not contacting on midline; (12) enlarged chin shields in two pairs; (13) nuchal scales undifferentiated; (14) fifth and sixth supralabial below eye; (15) auricular opening present; (16) dark lateral stripes present; (17) venter devoid of dark pigmentation (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing *Brachymeles talinis* from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles talinis* most closely resembles *B. kadwa, B. makusog, B. tungaoi,* and *B. vindumi*, but differs from these four taxa by having the range of paravertebral scale rows reaching greater than 70 but fewer than 74, and seven infralabials (Table 3.5). *Brachymeles talinis* can further be distinguished from *B. kadwa* by having eight to ten Toe-IV lamellae, the first enlarged chin shield wider than the second, frontoparietals in contact, and by the absence of dark ventral pigmentation (Tables 3.4, 3.5); from *B. makusog* by having seven supralabials the fifth and sixth supralabial below the eye, supranasals in contact, and by the presence of dark lateral stripes (Tables 3.4, 3.5); from *B. tungaoi* by having a larger body size, shorter relative tail length, eight to ten Toe-IV lamellae, and the first enlarged chin shield wider than the second (Tables 3.4, 3.5); and from *B. vindumi* by having fewer axilla–groin scale rows, fewer paravertebral scale rows, and by the absence of dark ventral pigmentation (Table 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*), *B. talinis* differs by having a pentadactyl body form (vs. non-pentadactyl), longer forelimb lengths (greater than 11.3 mm vs. less than 6.9 mm), and greater hind limb lengths (greater than 20.5 mm vs. less than 12.9 mm), and by the presence of a postnasal scale (vs. absence). Additionally, *B. talinis* differs from all non-pentadactyl species except *B. wrighti* by having a midbody scale row count 26–30 (vs. fewer than 24); from all non-pentadactyl species except *B. pathfinderi* by having a paravertebral scale row count 68–70 (vs. greater than 84), and by the presence of auricular openings (vs. absence); from all non-pentadactyl species except *B. apus* and *B. wrighti* by having a larger body size (SVL greater than 103.1 mm vs. less than 81.3 mm); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence (vs. absence) of limbs.

Description (based on holotype and 30 referred specimens, including 2 paratypes from CAS).—Details of the head scalation of an adult male are shown in Figure 3.9. Measurements of the holotype are provided below in brackets. Body large relative to other *Brachymeles*, elongate with respect to other lizards; maximum SVL 123.1 mm for males, 116.5 mm for females [118.7, male] (Tables 3.4, 3.5); head weakly differentiated from neck, nearly as wide as body, HW 10.6–13.2% (11.8 ± 0.5) SVL [12.1], 111.7–136.2% (124.1 ± 6.8) HL [130.3]; HL 30.6–40.7% (35.4 ± 2.7) SnFa [33.5]; SnFa 25.1–29.8% (27.0 ± 1.3) SVL [27.6]; snout moderately long, broadly rounded in dorsal and lateral profile, SNL 51.5–65.8% (58.9 ± 4.0) HL [65.8]; auricular opening present, moderate; eyes moderate, ED 1.7–2.2% (1.9 ± 0.1) SVL [1.7], 17.4–24.8% (20.0 ± 1.9) HL [18.2], 40.9–62.1% (50.3 ± 5.7) END [41.5], pupil nearly round; body slightly depressed, MBW 109.3–153.8% (126.7 ± 14.4) MBH [109.6]; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26–30 [29]; paravertebral scale rows 67–72 [72]; axilla–groin scale rows 43–48 [48]; limbs well developed, pentadactyl, digits moderate; FinIIIlam 5–6 [6]; ToeIVlam 8–10 [10]; FLL 15.1–23.9% (19.1 ± 1.8) AGD [19.6], 10.1–15.3% (12.4 ± 1.2) SVL [14.9]; HLL 26.8–38.9% (31.8 ± 3.0) AGD [30.9], 18.0–24.9% (20.6 ± 1.8) SVL [23.5]; order of digits from shortest to longest for hand: V < I < IV < II < III, for foot: I = V < II < III = IV; tail nearly as wide as body at base, sharply tapered towards end, TW 63.4–94.0% (75.1 ± 6.2) MBW [94.0], TL 60.6–107.2% (83.9 ± 12.0) SVL [73.2].

Rostral projecting dorsoposteriorly to point in line with anterior edge of nasal, broader than high, completely separated from frontonasal by broad supranasal contact; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal; supranasals present, large, in broad medial contact; postnasals present; prefrontals moderately separated by frontal; frontal nearly octagonal shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, in moderate medial contact, each frontoparietal in contact with supraoculars two–four; interparietal moderate, quadrilaterally shaped, width nearly equal to length, its length nearly equal to midline length of frontoparietal; parietal eyespot present in posterior one third of scale; parietals in point to moderate contact behind interparietal or narrowly separated; nuchals undifferentiated; loreals two, decreasing in size from anterior to posterior, subequal, in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal; preocular single, nearly three fourths as high as posterior loreal; single presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials seven, fifth and sixth below the eye; infralabials seven.

Mental wider than long, in contact with first infralabials; single enlarged postmental, wider than mental; followed by two pairs of enlarged chin shields; first pair in moderate contact or moderately separated by a single medial scale, wider than second pair; second pair separated by three undifferentiated scales.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with irregular raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative.—Ground color of body medium brown; longitudinal stripes on dorsal surface of body present or absent; when present a total of eight longitudinal dark-brown spot rows, extending from posterior edge of parietals to base of tail: six continuous medial rows and two discontinuous posterolateral rows, together spanning eight full rows of scales at midbody, narrowing to six full rows of scales posterior to parietals; when dark spot rows are absent, pigmentation forms nearly continuous dark dorsal surface, covering one half to entire surface of dorsal scales; dorsolateral stripes present or absent, when present, well defined, continuous, lacking dark pigmentation, spanning two whole and two half row of scales from auricular opening to base of tail. Lateral and ventral surface of body medium-brown. Lateral surface with three to six discontinuous longitudinal rows of dark-brown spots, rows often extending to edge of ventral surface. Ventral surface without dark pigmentation. Tail coloration equal to body coloration, dorsal surface covered with dark brown blotches, ventral surface covered with scattered dark brown spots, fewer than dorsal surface. Head scales homogeneous dark brown; rostral, nasal, postnasal, supranasal, first supralabial, mental and first infralabial dark gray; pigment surrounding pineal eyespot reduced to indistinct, small and medium brown. Limbs mottled medium brown dorsally, yellowish brown ventrally; dorsal and ventral surface of digits dark brown.

Coloration in life.—(Fig. 3.11H). Dorsal ground color medium-brown; when present, longitudinal rows of spots dark-brown to black; dorsolateral stripes light- to medium-brown, bordered mid-dorsally by rows of dark spots; lateral surface ground color light-brown to tan; ventral surfaces of body light-brown to tan. Dorsal surfaces of limbs dark- to medium-brown, ventral surfaces light-brown. Dorsal head scales blotched dark and medium-brown.

Variation.—Morphometric variation of the series is summarized in Table 3.6. We observed variation among the 19 specimens examined for the degree of contact between head scales. Four specimens were observed to have parietals moderately separated by the interparietal (KU 306757, 306763, 306767, 306786), one specimen has parietals narrowly separated by the interparietal

(KU 306758), and 14 specimens have parietals in moderate medial contact (KU 306756, 306759–60, 306762, 306764–6, 306769–71, 306773–6) behind the interparietal; 13 specimens do not have the first pair of enlarged chin shields in medial contact (KU 304756–7, 306759–60, 306762, 306764–6, 306767, 306769–70, 306774–5) and six specimens have the first pair of enlarged chin shields in moderate medial contact (KU 306758, 306763, 306771, 306773, 306776, 306786).

Scale counts were observed to vary among the measured series. Specimens were observed to have midbody scale row counts of 26 (KU 306766), 28 (CAS-SU 22311, 22317, 37996, KU 306765), 29 (CAS-SU 12225, 18358, 22323, 27972, 89813, CAS 133871, KU 306758, 306774) and 30 (CAS-SU 22312, 27997, KU 306756, 306760, 306769, 306772–3, 306786); axilla–groin scale row counts of 43 (KU 306786), 44 (CAS-SU 12225, 22311, 27996–7), 45 (CAS-SU 22323, KU 306756, 306758, 306760, 306765–6, 306772), 46 (CAS-SU 22312, 22317, 27972, 89813, CAS 133871, KU 306773), 47 (KU 306774), and 48 (CAS-SU 18358, KU 306769); and paravertebral scale row counts of 67 (KU 306786), 68 (CAS-SU 12225, 22311, 27996–7, KU 306756, 306758), 69 (CAS-SU 22312, 22323, KU 306760, 306765–6, 306772–3), 70 (CAS-SU 22317, 37972, 89813, CAS 133871, KU 306769), 71 (KU 306774), and 72 (CAS-SU 18358).

We also observed lamellae counts to vary among the measured series. With the exception of two specimens observed to have six Finger-III lamellae (CAS-SU 18358, CAS 133871), all other examined specimens were observed to have five. We also observed Toe-IV lamellae counts of eight (KU 306769, 306786), nine (CAS-SU 22311, 22317, 89813, KU 306756, 306758, 306760, 306765–6, 306772–4), and ten (CAS-SU 12225, 18358, 22312, 22323, 27972, 27996–7, CAS 133871).

Color variation exists in the degree and definition of continuous, dark mid-dorsal stripes. Many specimens show patterns consistent with continuous, mid-dorsal dark lines (KU 306651, 306756–7, 306759, 30676,2 306765–7, 306769–72, 306776, 306786, 306763). The dark lines are obscured in some and irregular in others, where the mid-dorsal region is covered by a long streak of dark pigmentation, with little to moderate line definition (KU 306759–60, 306764, 306774).

Distribution.—Brachymeles talinis is known from Negros, Panay, Romblon, Sibuyan, and Tablas islands (Fig. 3.5). It is also likely to occur on Guimaras Island.

Ecology and natural history.—Brachymeles talinis occurs in a variety of habitats from agricultural areas, to disturbed and secondary growth forest. Little or no original, lowland forest remains in the Visayas, but we assume the species originally occurred in primary forest. Individuals have been observed under piles of rotting coconut husks, in the humus material within rotting logs, and in loose soil and leaf litter surrounding the root networks of trees. The species is moderately common throughout its range (CDS personal observation), and occurs sympatrically with three other species (*B. bonitae, B. talinis,* and *B. tridactylus* [Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980]). Individuals were often encountered in pitfall traps, indicating some level of activity outside of fossorial microhabitats. Similar to *B. boulengeri*, *B. talinis* appears to have a wider geographic distribution that spans multiple Philippine islands. This is in contrast to the island endemic species, *B. boholensis*, *B. tungaoi,* and *B. mindorensis*, which are known from just Bohol, Masbate, and Mindoro Islands respectively. As do all members of the genus, when disturbed, individuals attempt to escape by moving in a rapid serpentine manner and attempting to burrow back into loose soil or humus.

Sympatric lizard species observed within the range of *Brachymeles talinis* include: (Agamidae) *Bronchocela marmoratus, Draco spilopterus, Hydrosaurus pustulatus*; (Dibamidae) *Dibamus argenteus*; (Gekkonidae) *Cyrtodactylus philippinicus, Gehyra mutilata, Gekko gecko, Gekko mindorensis, Gonocephalus sophiae, Hemidactylus frenatus, H. platyurus, Hemiphyllodactylus typus, Lepidodactylus christiani, L. herrei, L. lugubris, Luperosaurus corfieldi, Pseudogekko brevipes*; (Scincidae) *Brachymeles tridactylus, B. taylori, Emoia atrocostata, Eutropis multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia auriculata, L. pulchella, L. quadrivittata, L. rabori, Sphenomorphus arborens, S. coxi, S. jagori, S. steerei, Tropidophorus grayi*; and (Varanidae) *Varanus nuchalis.*

Brachymeles kadwa sp. nov.

Figs. 5, 9, 11D

Holotype.—PNM 9721 (RMB Field No. 12466, formerly KU 323091), adult male, collected under rotting logs in secondary-growth forest (10:00–12:30 hr) on 4 June 2009, on the campus of Aurora State College of Technology, Barangay Zabali, Municipality of Baler, Aurora Province, Luzon Island, Philippines (15°44'31" N, 121°34'34" E; WGS-84), by CDS, RMB, J. Fernandez, L. Welton, J. Brown, J. Siler, Y. Vicente, and M. Vicente.

Paratopotypes.—Three adult males (KU 323092, 323095, 323096) and four adult females (KU 323106, 323094, 323104, 323100), collected between 4 and 7 June 2009.

Paratypes.—Four adult males (KU 304875, 304900, 304915, 304941) and six adult females (KU 304897, 304902–3, 304905–6, 304929) collected between 15 and 22 March 2006 (19°17'38" N, 121°24'32" E; WGS-84; 245 m above sea level) Barangay Magsidel, Municipality of Calayan, Cagayan Province, Calayan Island, Philippines, by RMB, C. Oliveros, and J.

Fernandez; four adult males (KU 304575, 307984, 307996, 307998) and five adult females (KU 304559, 304593, 304708, 304754, 308011), four adult males and five adult females collected between 3 and 11 March 2006 from 300 m elevation (18°55'45" N, 121°53'56" E; WGS-84) Barangay Balatubat, Municipality of Calayan, Cagayan Province, Camiguin Norte Island, Philippines, by RMB, C. Oliveros, and J. Fernandez.

Referred specimens.—CALAYAN ISLAND: CAGAYAN PROVINCE: *Municipality of* Calayan: Barangay Magsidel: KU 304908, , 304899, 304907, 304909, 304921, 304941; CAMIGUIN NORTE ISLAND: CAGAYAN PROVINCE: *Municipality of Calayan*: Barangay Balatubat: KU 304558, 304562–65, 304569, 304571–74, 304627–30, 304643, 304647, 304696–99, 304704–07, 304709–12, 304714, 304753, 304755–59, 307965–66, 307985–86, 307997, 307999–8003, 308006–10, 308012–15, 308017–18; LUZON ISLAND: AURORA PROVINCE: *Municipality of Baler*: Barangay Zabali, ASCOT: KU 323090–91, 323093, 323097–99, 323101–03, 323105, 323107; *Municipality of Casiguran*, IDC property: KU 323108–48; *Municipality of San Luis*: Barangay Real, Sitio Minoli: KU 322320.

Diagnosis.—*Brachymeles kadwa* can be distinguished from congeners by the following combination of characters: (1) body size large (SVL 90.6–128.2 mm); (2) pentadactyl; (3) Finger-III lamellae five or six; (4) Toe-IV lamellae seven to ten; (5) limbs relatively long; (6) paravertebrals 68–70; (7) supralabials seven; (8) infralabials six; (9) pineal eye spot present, small; (10) supranasals in contact; (11) prefrontals not contacting on midline; (12) enlarged chin shields in two pairs; (13) nuchal scales undifferentiated; (14) fifth and sixth supralabial below eye; (15) auricular opening present; (16) continuous, light dorsolateral stripes present, indistinct; (17) continuous, dark mid-dorsal stripes present; (18) dark lateral stripes present; and (19) dark ventral pigmentation present (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing the new species from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles kadwa* most closely resembles *B. makusog, B. tungaoi*, *B. talinis,* and *B. vindumi*, but differs from these four taxa by having seven to ten Toe-IV lamellae and the second enlarged chin shield wider than the first (Tables 3.4, 3.5). *Brachymeles kadwa* can further be distinguished from *B. makusog* by having seven supralabials, the fifth and sixth supralabial below the eye, six infralabials, the presence of supranasal contact, the presence of continuous, light dorsolateral stripes, continuous, dark mid-dorsal stripes, dark lateral stripes, and dark ventral pigmentation (Table 3.5); from *B. tungaoi* by having a greater midbody width, shorter relative tail length, paravertebrals 68–70, and the presence of dark ventral pigmentation (Tables 3.4, 3.5); from *B. talinis* by having 28 or fewer midbody scale rows, 70 or fewer paravertebrals, infralabials six, and by the presence dark ventral pigmentation (Table 3.5); and from *B. vindumi* by having five or six Finger-III lamellae, 26–28 midbody scale rows, paravertebrals 68–70, and by the presence of continuous, dark mid-dorsal stripes (Tables 3.4, 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*), *B. kadwa* differs by having a pentadactyl body form (vs. non-pentadactyl), longer forelimb lengths (greater than 10.7 mm vs. less than 6.9 mm), and greater hind limb lengths (greater than 17.9 mm vs. less than 12.9 mm), and by the presence of a postnasal scale (vs. absence). Additionally, *B. kadwa* differs from all non-pentadactyl species except *B. wrighti* by having 26–28 midbody scales (vs. fewer than 24); from all non-pentadactyl species except *B. pathfinderi* by having 68–70 paravertebrals (vs. greater than 84), and by the presence of auricular openings (vs. absence); from all non-pentadactyl species except *B. apus* and *B. wrighti* by having a larger body size (SVL greater than 90.6 mm vs. less than 81.3 mm); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence of limbs (vs. absence).

Description of Holotype.—(Fig. 3.10) Mature male, hemipenes everted; SVL 106.2 mm; body moderately large relative to other *Brachymeles*, elongate with respect to other lizards; head weakly differentiated from neck, nearly as wide as body, HW 11.0% SVL, 111.1% HL; HL 38.1% SnFa; SnFa 26.0% SVL; snout moderately long, rounded in dorsal and lateral profile, SNL 56.1% HL; auricular opening present, small; eyes moderate, ED 1.9% SVL, 19.6% HL, 54.8% END, pupil nearly round; body slightly depressed, MBW 157.3% MBH; body scales smooth, glossy, imbricate; longitudinal scale rows at midbody 28; paravertebral scale rows 68; axilla–groin scale rows 47; limbs well developed, pentadactyl, digits moderate; FinIIIlam 5; ToeIVlam 10; FLL 20.3% AGD, 13.0% SVL; HLL 32.0% AGD, 20.6% SVL; order of digits from shortest to longest for hand: I = V < II = IV < III, for foot: V < I < II < III = IV; tail nearly as wide as body at base, gradually tapered towards end, TW 73.5% MBW, TL 101.6% SVL.

Rostral projecting dorsoposteriorly to point in line with anterior edge of nostril, broader than high, separated from frontonasal by moderate contact of supranasals; frontonasal wider than long; nostril ovoid, centered in a single rectangular nasal; supranasals large, in moderate medial contact; postnasals present; prefrontals moderately separated by frontal; frontal nearly diamond shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, point contact medially or moderately separated, each frontoparietal in contact with supraoculars two–four; interparietal moderate, quadrilaterally shaped, its length slightly greater than midline length of frontoparietal; parietal eyespot present in posterior one third of scale, indistinct; parietals in moderate contact behind interparietal; nuchals undifferentiated; loreals two, decreasing in size from anterior to posterior, subequal, in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal; preocular single, nearly two thirds as high as posterior loreal; single presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriormost extending to midline of last supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials seven, fifth and sixth below the eye; infralabials six.

Mental wider than long, in contact with first infralabials; single enlarged postmental, slightly wider than mental; followed by two pairs of enlarged chin shields, first pair in moderate medial contact, second pair slightly wider than first, separated by a single undifferentiated scale.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative.—Ground color of body dark brown; dorsal surface of body with eight longitudinal rows of dark-brown spots spanning eight full rows of scales at midbody and extending from posterior edge of parietals to base of tail: six rows in mid-dorsal region, flanked by discontinuous dorsolateral rows; spot rows narrowing to six full rows of scales posterior to parietals; dark coloration covering middle three fourths of dorsal scales; dorsolateral stripes somewhat indistinct, discontinuous, spanning two half rows of scales from auricular opening point just posterior to forelimb insertion; dark dorsal coloration blends gradually into medium brown lateral and ventral surface of body. Lateral surface with six discontinuous, dark-brown spot rows, extending to edge of ventral surface. Ventral surface with scattered dark brown spots.

Tail coloration similar to body coloration, dorsal surface covered with dark brown blotches, ventral surface covered with few dark brown spots. Head scales homogeneous dark brown; rostral, nasal, postnasal, supranasal, first supralabial, mental, and first infralabial dark gray; pineal eyespot indistinct, small and light brown. Limbs mottled dark brown dorsally, yellowish brown ventrally; dorsal and ventral surface of digits dark brown.

Coloration in life.—(Fig. 3.11D). Ground color of body light to medium-brown; dorsal surfaces of limbs medium-brown.

Measurements of holotype in mm.—SVL 106.2; AGD 68.2; TotL 214.0; MBW 15.9; MBH 10.1; TL 107.9; TW 11.7; TH 9.2; HL 10.5; HW 11.7; HH 8.6; SnFa 27.6; ED 2.1; END 3.8; SNL 5.9; IND 3.7; FLL 13.8; HLL 21.8; MBSR 28; PVSR 68; AGSR 47; FinIIIlam 5; ToeIVlam 10; SL 7; IFL 6; SC 6; SO 5.

Variation.—Morphometric variation of the series is summarized in Table 3.6. We observed variation among the 25 specimens examined for the degree of contact between head scales. Fourteen specimens were observed to have parietals moderately separated by the interparietal (KU 304559, 304574–5, 304593, 304630, 304708, 304754–5, 304759, 304906, 307984–5, 307996, 308007), one specimen has parietals in point medial contact (KU 308011), and 10 specimens have parietals in moderate medial contact (KU 304875, 304897, 304900, 304902–3, 304905, 304915, 304929, 304941, 307998) behind the interparietal; two specimens have frontoparietals moderately separated by the frontal (KU 304559, 307984), one specimen has frontoparietals narrowly separated by the frontal (KU 304574), and 22 specimens have frontoparietals in moderate medial contact (KU 304575, 304593, 304630, 304708, 304754–5, 304759, 304875, 304897, 304900, 304902–3, 304905–6, 304915, 304929, 304941, 307985, 307996, 307998, 308007, 308011). We observed the first pair of enlarged chin shields narrowly separated in a single specimen (KU 307996), and in moderate contact for all other examined specimens.

Scale counts were observed to vary among the measured series. Specimens were observed to have midbody scale row counts of 26 (KU 304559, 307996, 323104), 27 (KU 304593, 307984, 307998), and 28 (KU 304575, 304708, 304754, 304875, 304897, 304900, 304902–3, 304905–6, 304915, 304929, 304941, 308011, 323091, 323091–2, 323094–6, 323100, 323106); axilla–groin scale row counts of 47 (KU 304559, 304575, 304593, 304875, 304902, 304929, 307996, 307998, 308011, 323091, 323096), 48 (KU 304708, 304754, 304897, 304900, 304915, 304941, 307984, 323092, 323094–5, 323100, 323104, 323106), 49 (KU 304903, 304905–6); and paravertebral scale row counts of 68 (KU 304559, 304593, 304900, 307996, 323091, 323096), 69 (KU 304575, 304708, 304754, 304875, 304929, 304941, 307984, 307998, 308011, 323092, 323094–5, 323100, 323104, 323106), and 70 (KU 304897, 304902–3, 304905–6, 304915).

We also observed lamellae counts to vary among the measured series. With the exception of two specimens observed to have six Finger-III lamellae (KU 304903, 304906), all other examined specimens were observed to have five. We also observed Toe-IV lamellae counts of seven (KU 304593), eight (KU 304559, 304575, 304708, 304754, 304875, 304897, 304900, 304915, 304929, 304941, 307984, 307996, 307998, 308011), nine (KU 304902–3, 304905–6, 323092, 323094–6, 323100, 323104, 323106), or ten (KU 323091).

Distribution.—Brachymeles kadwa is known from numerous localities on Luzon Island as well as from Calayan and Camiguin Norte Islands of the Babuyan Island Group (Fig. 3.5).

Ecology and natural history.—Brachymeles kadwa occurs in agricultural areas, disturbed secondary growth forest, and first growth forests of Luzon, Camiguin Norte, and Calayan. Individuals have been observed under piles of rotting coconut husks, in the humus material within rotting logs, and in loose soil and leaf litter surrounding the root networks of trees. This species is quite common in all sampling localities, and we have taken large series in pitfall traps, indicating some level of surface activity. When disturbed, individuals immediately moved in a rapid serpentine manner and attempted to burrow back into loose soil or humus.

Sympatric lizard species observed on Luzon, Camiguin Norte, and Calayan Islands include: (Agamidae) *Bronchocela cristatella, Draco spilopterus, Gonocephalus sophiae, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus philippinicus, Gehyra mutilata, Gekko gecko, Gekko mindorensis, Hemidactylus frenatus, H. garnoti, H. luzonensis, H. platyurus, Luperosaurus* cf. *cumingi, L. kubli, Pseudogekko compressicorpus, P. smaragdina*; (Scincidae) *Brachymeles bonitae, B. bicolor, B. elerae, B. lukbani, B. makusog, B. muntingkamay, B. samarensis, B. cf. talinis, B. wrighti, Emoia atrocostata, Eutropis bontocensis, E. multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella, Sphenomorphus cumingi, S. decipiens, S. jagori, S. leucospilos, S. luzonensis, S. steerei, S. stejnegeri, Tropidophorus grayi*; and (Varanidae) *Varanus marmoratus.*

Etymology.—CDS is pleased to name this new species for his loving wife Jessi M. Siler for her endless support that has made all of this research possible. The name of the new species is derived from one of the local dialects spoken in the Philippines. The word "kadwa" is the Ilonggo term for friend and companion. Suggested common name: Jessi's Slender Skink.

Brachymeles tungaoi sp. nov.

Figs. 3.5, 3.10

Holotype.—PNM 9722 (CDS Field No. 5125, formerly KU 323933), adult male, collected in rotting stump in disturbed, residential habitat (10:00–12:30 hr) 4 September, 2009, at 61 m elevation in Municipality of Masbate City, Masbate Province, Masbate Island, Philippines (12°21'01" N, 123°37'42" E; WGS-84), by CDS and J. Fernandez.

Paratopotypes.—KU 323934–36, three adult females, collected between 3 and 7 September, 2009, from 61–99 m elevation by CDS and J. Fernandez.

Paratypes.—One adult male (CAS 144313), three adult females (CAS 144229–30, 144341), and four juvenile specimens of unknown sex (CAS 144290, 144306–7, 144342), collected 2 June 1976 "in humus under rotting log," in Barangay Tugbo, Municipality of Mobo, Masbate Province, Masbate Island, Philippines (12°20'11.04" N, 123°37'58.8" E; WGS-84; 400 m elevation) by A. Alcala.

Diagnosis.—*Brachymeles tungaoi* can be distinguished from congeners by the following combination of characters: (1) body size moderate (SVL 78.2–106.2 mm); (2) relative tail length long; (3) pentadactyl; (3) Finger-III lamellae five or six; (4) Toe-IV lamellae nine or ten; (5) limb length moderate; (6) paravertebral scale rows 66–68; (7) supralabials seven; (8) infralabials six; (9) pineal eye spot present, large; (10) supranasals in contact; (11) prefrontals not contacting on midline; (12) contact between first pair of chin shields; (13) enlarged chin shields in two pairs; (14) nuchal scales undifferentiated; (15) fifth and sixth supralabial below eye; (16) auricular opening present; (17) continuous, light dorsolateral stripes present, indistinct; (18) continuous, dark mid-dorsal stripes present; (19) dark lateral stripes present; and (20) dark ventral pigmentation absent (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing the new species from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles tungaoi* most closely resembles *B. kadwa, B. makusog, B. talinis,* and *B. vindumi,* but differs from these four taxa by having a smaller body size, smaller midbody width, greater relative tail length, the first and second pairs of enlarged chin shields equal in width, and contact between the first pair of enlarged chin shields (Tables 3.4, 3.5). *Brachymeles tungaoi* can be further distinguished from *B. kadwa* by having nine or ten Toe-IV lamellae, paravertebral scale rows 66–68, frontoparietal in contact, and by the absence of dark ventral pigmentation (Tables 3.4, 3.5); from *B. makusog* by having seven supralabials, six infralabials, the fifth and sixth supralabial below the eye, supranasals in moderate contact, the presence of continuous, light dorsolateral stripes, continuous, dark mid-dorsal stripes, and dark lateral stripes (Table 3.5); from *B. talinis* by having nine or ten Toe-IV lamellae, 66–68 paravertebrals, infralabials six (Tables 3.4, 3.5); and from *B. vindumi* by having five or six Finger-III lamellae, 26–28 midbody scale rows, and 66–68 paravertebrals (Tables 3.4, 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*)*, B. tungaoi* differs by having a pentadactyl body form (vs. non-pentadactyl), longer forelimb lengths (greater than 11.0 mm vs. less than 6.9 mm), and greater hind limb lengths (greater than 17.0 mm vs. less than 12.9 mm), and by the presence of a postnasal scale (vs. absence). Additionally, *Brachymeles tungaoi* differs from all non-pentadactyl species except *B. wrighti* by having a midbody scale row count 26–28 (vs. fewer than 24); from all non-pentadactyl species except *B. pathfinderi* by having a paravertebral scale row count 66 (vs. greater than 84), and by the presence of auricular openings (vs. absence); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence of limbs (vs. absence).

Description of Holotype.—(Fig. 10) Mature male, hemipenes everted; SVL 89.2 mm; body moderate relative to other *Brachymeles*, elongate with respect to other lizards; head weakly differentiated from neck, nearly as wide as body, HW 11.3% SVL, 115.9% HL; HL 38.0% SnFa;

SnFa 25.6% SVL; snout moderately long, bluntly rounded in dorsal profile, sharply rounded in lateral profile, SNL 60.1% HL; auricular opening present, moderate; eyes small, ED 1.9% SVL, 19.2% HL, 50.0% END, pupil nearly round; body slightly depressed, MBW 162.0% MBH; body scales smooth, glossy, imbricate; longitudinal scale rows at midbody 28; paravertebral scale rows 66; axilla–groin scale rows 46; limbs well developed, pentadactyl, digits moderate; FinIIIlam 6; ToeIVlam 10; FLL 22.5% AGD, 14.4% SVL; HLL 35.4% AGD, 22.6% SVL; order of digits from shortest to longest for hand: I = V < II = IV < III, for foot: I < V < II < IV < III; tail not as wide as body, gradually tapered towards end, TW 63.7% MBW, TL 99.9% SVL.

Rostral projecting dorsoposteriorly to point in line with anterior edge of nasal, broader than high, moderately separated from frontonasal; frontonasal wider than long; nostril ovoid, centered in a single rectangular nasal; supranasals present, large, in narrow medial contact; postnasals present; prefrontals broadly separated by frontal; frontal nearly octagonal, its anterior margin in broad contact with frontonasal, in contact with first two anterior supraoculars, 5× wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, in broad contact medially, each frontoparietal in contact with supraoculars two–four; interparietal moderate, quadrilaterally shaped, its length nearly equal to midline length of frontoparietal; distinct parietal eyespot present, large, in posterior half of scale; parietals broadly separated by interparietal; nuchals undifferentiated; loreals two, decreasing in size from anterior to posterior, subequal, in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal; preocular single, nearly one half as high as posterior loreal; single presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriormost extending to midline of last supraocular; subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials seven, fifth and sixth below the eye; infralabials six.

Mental wider than long, in contact with first infralabials; single enlarged postmental, wider than mental; followed by two pairs of enlarged chin shields; first pair in broad medial contact, second pair separated by single undifferentiated scale.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration of holotype in preservative.—Ground color of body medium brown; dorsal surface of body with eight continuous, longitudinal rows of dark-brown spots, extending from posterior edge of parietals to base of tail; spot rows span six full and two half rows of scales at midbody, narrowing to four full and two half rows of scales posterior to parietals; pigmentation covering middle one third of dorsal scales; dorsolateral stripes indistinct, discontinuous, spanning one whole and two half row of scales from auricular opening to midbody. Lateral and ventral surface of body light-brown. Lateral surface with three discontinuous rows of dark-brown spots, spanning posterior two thirds of axilla–groin distance. Ventral surface without dark pigmentation. Tail with dark dorsal blotches and spots; dark pigment reduced ventrally. Head scales homogeneous dark brown; rostral, nasal, postnasal, supranasal, first supralabial, mental, and first infralabial light gray; pineal eyespot large distinct, light cream. Limbs mottled medium to dark brown dorsally, yellowish brown ventrally; dorsal and ventral surface of digits dark brown.

*Coloration of holotype in life***.**—Coloration in life is unrecorded; however, because *Brachymeles* specimens do not change significantly during preservation (CDS, RMB personal observation), we suspect that the preserved coloration and patterns are much like those in life.

Measurements of holotype in mm.—SVL 89.2; AGD 56.8; TotL 178.3; MBW 13.9; MBH 8.6; TL 89.1; TW 8.8; TH 8.0; HL 8.7; HW 10.1; HH 7.2; SnFa 22.8; ED 1.7; END 3.3; SNL 5.2; IND 3.0; FLL 12.8; HLL 20.1; MBSR 28; PVSR 66; AGSR 46; FinIIIlam 6; ToeIVlam 10; SL 7; IFL 6; SC 6; SO 5.

Variation.—Morphometric variation of the series is summarized in Table 3.6. Specimens were observed to have parietals moderately separated by the interparietal (CAS 144229–30, 144341, KU 323933, 323935–6) or in point medial contact (CAS 144313, KU 323934).

Scale counts were observed to vary among the measured series. Specimens were observed to have midbody scale row counts of 26 (KU 323935), 27 (CAS 144313), and 28 (CAS 144229–30, 144341, KU 323933–4, 323936); axilla–groin scale row counts of 46 (KU 323933, 323935–6), 47 (CAS 144229–30, 144341, KU 323934), and 49 (CAS 144313); and paravertebral scale row counts of 66 (KU 323933–6), 67 (CAS 144229), and 68 (CAS 144230, 144313, 144341).

We also observed lamellae counts to vary among the measured series. Specimens were observed to have Finger-III lamellae counts of five (CAS 144229–30, 144341, KU 323934–5) or six (CAS 144313, KU 323933, 323936); Toe-IV lamellae counts of nine (CAS 144229, 144313, 144341, KU 323935–6) or ten (CAS 144230, KU 323933–4).

Distribution.—*Brachymeles tungaoi* is known only from Masbate Island (Fig. 3.5).

Ecology and natural history.—Brachymeles tungaoi occurs in agricultural areas as well as disturbed and secondary growth forest habitat. Little or no original, low elevation forest remains on Masbate Island, but we assume the species once also occurred in primary forest. Individuals were collected in the humus material within the rotting stumps of trees. When disturbed, individuals immediately moved in a rapid serpentine manner and attempted to burrow back into loose soil or humus.

Sympatric lizard species observed on Masbate Island include: (Agamidae) *Bronchocela cristatella, Draco spilopterus, Gonocephalus sophiae*; (Gekkonidae) *Cyrtodactylus philippinicus, Gehyra mutilata, Gekko gecko, Hemidactylus frenatus, H. platyurus*; (Scincidae) *Brachymeles bonitae, Emoia atrocostata, E. multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella, Sphenomorphus decipiens, S. jagori*; and (Varanidae) *Varanus marmoratus.*

Etymology.—We take pleasure in naming the new species after our friend and dedicated field collaborator Jason B. "Tungao" Fernandez, with thanks for years of hard work towards the research of semi-fossorial lizards. Suggested common name: Tungao's Slender Skink.

Brachymeles vindumi sp. nov.

Figs. 3.4, 3.10

Holotype.—CAS 60724 (EHT Field No. 1718), adult male, collected between 25 October and 17 November, 1920, in Sulu Province, Jolo Island, Philippines, by Edward H. Taylor.

Paratypes.—One adult female (CAS 60725), one juvenile female (MCZ 26577), and one juvenile of unknown sex (CAS 60723), collected over the same dates and in the same locality as holotype.

Diagnosis.—*Brachymeles vindumi* can be distinguished from congeners by the following combination of characters: (1) body size moderate (SVL 104.9–113.6 mm); (2) pentadactyl; (3) Finger-III lamellae six; (4) Toe-IV lamellae nine or ten; (5) moderate limb length; (6) midbody scale rows 30 or 31; (7) axilla–groin scale rows 49; (8) paravertebral scale rows 74; (9)

supralabials seven; (10) infralabials six; (11) pineal eye spot present, indistinct; (12) supranasals in contact; (13) prefrontals separate; (14) parietal in contact; (15) enlarged chin shields in two pairs; (16) first pair of chin shields separated; (17) nuchals undifferentiated; (18) fifth and sixth supralabials below the eye; (19) auricular opening present; (20) continuous, light dorsolateral stripes present, distinct; (21) dark lateral stripes present; and (22) dark ventral pigmentation present (Tables 3.4, 3.5).

Comparisons.—Characters distinguishing the new species from all pentadactyl species of *Brachymeles* are summarized in Tables 3.4 and 3.5. *Brachymeles vindumi* most closely resembles *B. kadwa, B. talinis,* and *B. tungaoi*, but differs from these three taxa by having six Finger-III lamellae, six supralabials, midbody scale rows 30 or 31, axilla–groin scale rows 49, paravertebral scale rows 74, the first pair of enlarged chin shields separated, and the presence of continuous, light dorsolateral stripes (Tables 3.4, 3.5). *Brachymeles vindumi* can further be distinguished from *B. kadwa* and *B. talinis* by having nine or ten Toe-IV lamellae (Tables 3.4, 3.5); from *B. talinis* by having six infralabials (Table 3.5); from *B. kadwa* by contact between frontoparietals (Table 3.5); and from *B. kadwa* and *B. tungaoi* by contact between parietals (Table 3.5).

From all non-pentadactyl species of *Brachymeles* (*B. apus, B. bonitae, B. cebuensis, B. elerae, B. lukbani, B. minimus, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. vermis,* and *B. wrighti*), *B. vindumi* differs by having a pentadactyl body form (vs. non-pentadactyl), longer forelimb lengths (greater than 13.2 mm vs. less than 6.9 mm), greater hind limb lengths (greater than 22.7 mm vs. less than 12.9 mm), and greater number of midbody scale rows (30 or 31 vs. less than 28), and by the presence of a postnasal scale (vs. absence). Additionally, *B. vindumi* differs from all non-pentadactyl species except *B. pathfinderi* by having a paravertebral scale row count 74 (vs. greater than 84) and by the presence of auricular openings (vs. absence); and from *B. apus, B. lukbani, B. minimus,* and *B. vermis* by the presence of limbs (vs. absence).

Description of Holotype.—(Fig. 3.9) Mature male, hemipenes not everted; SVL 113.6 mm; body moderate relative to other *Brachymeles*, elongate with respect to other lizards; head weakly differentiated from neck, nearly as wide as body, HW 9.5% SVL, 112.5% HL; HL 33.7% SnFa; SnFa 25.1% SVL; snout moderately long, rounded in dorsal and lateral profile, SNL 59.7% HL; auricular opening present, moderate; eyes small, ED 2.0% SVL, 23.5% HL, 58.0% END, pupil nearly round; body slightly depressed, MBW 122.9% MBH; body scales smooth, glossy, imbricate; longitudinal scale rows at midbody 31; paravertebral scale rows 74; axilla–groin scale rows 49; limbs well developed, pentadactyl, digits moderate; FinIIIlam 6; ToeIVlam 9; FLL 18.1% AGD, 11.6% SVL; HLL 31.2% AGD, 20.0% SVL; order of digits from shortest to longest for hand: I < V < II < IV < III, for foot: I = V < II = III < IV; tail regenerated, not as wide as body, sharply tapered towards end, TW 83.1% MBW.

Rostral projecting dorsoposteriorly to point in line with anterior edge of nasal, broader than high, moderately separated from frontonasal by supranasal contact; frontonasal wider than long; nostril ovoid, centered in a single rectangular nasal; supranasals present, large, in moderate medial contact; postnasals present; prefrontals narrowly separated by frontal; frontal nearly octagonal, its anterior margin in narrow contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anteriormost supraocular; supraoculars five; frontoparietals moderate, in broad medial contact, each frontoparietal in contact with supraoculars two–four; interparietal small, diamond shaped, its length equal in size to midline length of frontoparietal; parietal eyespot absent; parietals in broad contact behind interparietal; nuchals undifferentiated;

loreals two, decreasing in size from anterior to posterior, subequal, in contact with prefrontal, postnasal, supranasal, second supralabial, posterior loreal and frontonasal; preocular single, nearly two thirds as high as posterior loreal; single presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriormost extending to midline of last supraocular; single subocular row complete; lower eyelid with one row of scales, lacking an enlarged oval window, largely transparent; supralabials seven, fifth and sixth below the eye; infralabials six.

Mental wider than long, in contact with first infralabials; single enlarged postmental, slightly wider than mental; followed by two pairs of enlarged chin shields, scales of first pair separated by a single undifferentiated scale, second pair separated by three undifferentiated scales.

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration of holotype in preservative.—Ground color of body medium to dark brown; mid-dorsal surface of body covered with dark pigmentation, extending from posterior edge of supranasals to base of tail, made of eight irregular, longitudinal mid-dorsal rows of dark-brown spots, spanning six full and two half rows of scales at midbody, narrowing to six full rows of scales posterior to parietals, pigmentation covering middle one third of dorsal scales; dorsolateral stripes present, clearly defined, continuous, lacking dark pigmentation, spanning one whole and one half row of scales from anterior-most supraocular to base of tail. Lateral and ventral surface of body medium to dark brown. Lateral surface with six to eight irregular dark spot rows, gradually becoming fainter on ventral surface. Ventral surface with irregular dark spots and blotches. Tail with continuous dark blotches and spots dorsally, dark pigment reduced ventrally. Head scales homogeneous mottled medium and dark brown dorsally; rostral, nasal, postnasal, supranasal, first supralabial, mental, and first infralabial light brown to tan; pineal eyespot absent; dark brown blotch of pigmentation on lateral surfaces of head, spanning from posterior edge of eye to posterior edge of auricular openings. Limbs mottled medium to dark brown; dorsal surface of digits dark brown, ventral surface of digits medium brown.

Coloration of holotype in life.—Coloration in life is unrecorded; however, because *Brachymeles* specimens do not change significantly during preservation (CDS, RMB personal observation), we suspect that the preserved coloration and patterns are much like those in life.

Measurements of holotype in mm.—SVL 113.6; AGD 72.7; TotL N/A; MBW 14.2; MBH 11.6; TL N/A; TW 11.8; TH 8.4; HL 9.6; HW 10.8; HH 7.9; SnFa 28.5; ED 2.3; END 3.9; SNL 5.7; IND 3.4; FLL 13.2; HLL 22.7; MBSR 31; PVSR 74; AGSR 49; FinIIIlam 6; ToeIVlam 9; SL 7; IFL 6; SC 6; SO 5.

Variation.—Morphometric variation of the series is summarized in Table 3.6. Specimens were observed to have midbody scale row counts of 30 (CAS 60725) or 31 (CAS 60724), and Toe-IV lamellae counts of nine (CAS 60724) or ten (CAS 60725).

Distribution.—Brachymeles vindumi is known only from Jolo Island (Fig. 3.4).

Ecology and natural history.—Brachymeles vindumi presumably occurs in disturbed habitat as well as secondary growth forest on Jolo Island. Due to security concerns, no recent surveys have been conducted on Jolo Island, and therefore, no information is available on the ecology of this species.

Sympatric lizard species observed on Jolo Island include: (Agamidae) *Draco guentheri*; (Gekkonidae) *Cyrtodactylus annulatus, Gehyra mutilata, Gekko gecko, G. mindorensis,* *Hemidactylus frenatus, H. platyurus, Luperosaurus joloensis*; (Scincidae) *Brachymeles vermis, Eutropis multifasciata, E. rudis, Lamprolepis smaragdina, Lipinia quadrivittata, Lygosoma bowringi, Sphenomorphus biparietalis, S. variegatus*; (Varanidae) *Varanus cumingi.*

Etymology.—We take pleasure in naming the new species for our close friend and colleague, Jens Vindum. The specific epithet is a patronym in the genitive singular, chosen in thanks for the many years of support and assistance he as provided during our research on Philippine amphibians and reptiles. Suggested common name: Jens' Slender Skink.

DISCUSSION

Phylogenetic analyses of the mitochondrial ATPase 8 (ATP8) and ATPase 6 (ATP6) genes resulted in strong support for nine lineages of *Brachymeles* (Fig. 3.2). The phylogeny, combined with morphological data, supports the elevation of all subspecies of the polytypic species *B. boulengeri* and *B. schadenbergi* to full species. However, the inferred relationships between several of the species sampled are weakly supported. This may be indicative of rapid diversification of *Brachymeles* or simply indicate a lack of character support at some internal nodes. Given the use of only mitochondrial data for our phylogenetic analyses, caution must be taken when interpreting inter-species relationships, as a single locus can be subject to random variation, deep coalescence, lineage sorting, and natural selection (Edwards and Beerli, 2002; Galtier et al., 2009; Brown et al., 2010). Regardless of the potential weaknesses of our single-locus approach, our results are strongly supported by an independent, comprehensive dataset of morphological characters.

No analyses supported the monophyly of species formerly part of *Brachymeles boulengeri* (*B. boholensis, B. boulengeri, B. mindorensis, B. taylori*; Fig. 3.2). Another clade including *B.*

talinis, B. kadwa, and *B. tungaoi* was estimated with strong support (Fig. 3.2). As previously recognized *B. talinis* spanned two distinct, recognized faunal regions (Luzon and Visayas). Given this formerly wide geographical distribution, it is not surprising that the northern populations (Luzon and the Babuyan islands) constitute a genetically distinct lineage that we describe here as *B. kadwa*. We were surprised, however, to discover an additional genetically distinct lineage on Masbate Island (Fig. 3.2). The fauna of Masbate Island is recognized as part of the Visayan or central Philippine islands, and has been hypothesized to have shared land bridge connections with the central islands during periods of glacial maxima (Dickerson, 1928; Inger, 1954; Heaney, 1985; Voris, 2000). Although we expected Masbate populations to be more closely related to Visayan (Negros + Panay) populations, all analyses strongly supported the sister relationship between *B. tunagoi* (Masbate) and *B. kadwa* (Luzon), providing additional biogeographic support for the distinctiveness of *B. tungaoi*. We are unaware of phylogeographic or phylogenetic studies including other vertebrate taxa from Masbate. Comparison of the systematic affinities of other Masbate species may provide interesting exceptions to the prevailing PAIC-oriented perspective of Masbate as a faunistic extension of the central Visayas (Heaney, 1985).

The species recognized in this paper increase the total number of known species of *Brachymeles* to 25, all but one of which are endemic to the Philippines. During the last two years, our knowledge of the species diversity in the genus has expanded rapidly as the result of large-scale sampling efforts across the Philippines and the detailed analyses of morphological variation among species and populations (Siler et al., 2009a, 2010a,b). Prior to this effort, estimates of *Brachymeles* species diversity remained nearly constant for more than 30 years (but see Brown and Alcala, 1995), which is a testament to the extent of morphological similarity among species within the genus and a lack of systematic studies of the group. It comes as little surprise that allopatric populations of "*B. boulengeri*" from the Luzon, Mindanao, Mindoro, and Visayan Pleistocene Aggregate Island Complexes have proven to be morphologically diagnosable with increased sampling. To date, few studies have provided evidence of truly "widespread" reptile species that have geographic distributions spanning recognized zoogeographic boundaries in the Philippines (but see Siler et al., 2010c), and as is quite often the case, these species frequently turn out to constitute multiple evolutionary lineages (McGuire and Alcala, 2000; Brown et al., 2002, 2009; Gaulke et al, 2007; Welton et al., 2009, 2010).

All species of *Brachymeles* have a semi-fossorial life style, specializing in dry rotting material within rotten logs. Many are habitat specialists found exclusively in rotting logs, loose soil, or leaf litter, whereas others are common beneath piles of rotting coconut husks in disturbed, agricultural habitat. The species now found in residential and agricultural areas were once native to forested habitats. Prior to recent, focused survey efforts, the relatively low numbers of specimens of *Brachymeles* in museum collections handicapped our efforts at delimiting species. The rarity of *Brachymeles* in collections was due to their secretive, semi-fossorial lifestyle.

This is the first, species-level phylogenetic study of *Brachymeles*. To date, taxonomic reviews of *Brachymeles* have focused solely on morphological variation (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980; Brown and Alcala, 1995; Hikida, 1982). It is apparent that species diversity in the genus has been considerably underestimated; accordingly, discovery of additional undocumented (possibly cryptic) diversity is anticipated in other species groups (e.g., Siler et al., 2009a, 2010a,b). A number of studies have shown that the evolution of a burrowing lifestyle is correlated with decreasing dispersal abilities (Selander et al., 1974; Patton and Yang, 1977; Patton and Feder, 1978; Nevo, 1979; Wiens et al., 2006). Many

Brachymeles lineages have experienced reduction or loss of limbs, which may further reduce vagility (Daniels et al., 2005; Mulvaney et al., 2005; Wiens et al., 2006). Through time, reduced dispersal abilities may lead to increasingly patchy distributions, reduced gene flow between populations, and the accumulation of inter-population differences (Nevo, 1979). However, the role that geological history and complex geography play on the dispersal abilities and diversification patterns of *Brachymeles* species remains unknown. Regardless of what processes produce species diversity, we expect that additional species await discovery. With several species represented by only a few vouchered specimens, and frequent morphological convergence, it is clear that a comprehensive phylogenetic analysis of the genus will be required to assess, with accuracy, the species diversity within *Brachymeles*.

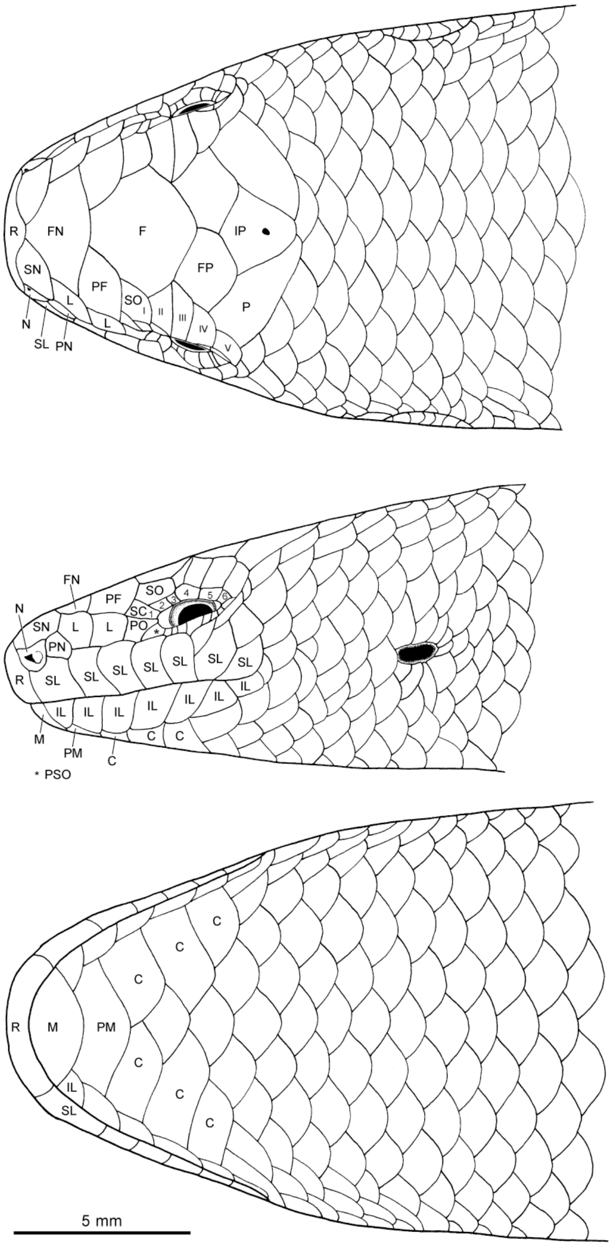
Following the recognition of *Brachymeles boholensis, B. boulengeri, B. tungaoi, B. kadwa, B. mindorensis, B. orientalis, B. schadenbergi, B. taylori*, and *B. vindumi* there are now 13 pentadactyl species of *Brachymeles*. Of these, eight are large-bodied (*B. bicolor, B. tungaoi, B. kadwa, B. makusog, B. orientalis, B. schadenbergi, B. talinis*, and *B. vindumi*) and five (*B. boholensis, B. boulengeri, B. gracilis, B. mindorensis,* and *B. taylori*) have moderately sized bodies. The distribution of pentadactyl species in the Philippines is relatively even across the major recognized faunal regions, with four species known to occur in the Luzon Faunal Region, five in the Mindanao Faunal Region, three in the Visayan Faunal Region, one in the Mindoro Faunal Region, and one in the Sulu archipelago (Brown and Alcala, 1980, Brown and Alcala, 1995; Brown and Diesmos, 2002; Siler et al., 2010a). In contrast, the distribution of total species diversity in the genus is less uniform, with 11 species known from the Luzon Faunal Region versus six in the Mindanao Faunal Region, six in the Visayan Faunal Region, and only one and two in the Sulu archipelago and Mindoro Faunal Region respectively (Brown and Alcala, 1980;

Brown and Alcala, 1995; Brown and Diesmos, 2002; Siler et al., 2009a, 2010a,b). New species discoveries on Luzon Island have occurred with consistency during the last two decades; given the island's complex mountain ranges (Sierra Madres, Cordillera, Zambales, Bicol Peninsula volcanoes) and geographic complexity (Defant et al., 1989; Yumul et al., 2009), the increase in the region's faunal diversity is likely to continue (Ross and Gonzales, 1992; Brown et. al. 1995*a,b*, 1999, 2000*a,b,* 2007; Siler et al., 2009a, 2010a,b). It is worth noting that efforts to survey Mindanao have been less extensive than efforts on Luzon; this may account for some of the differences in diversity between the regions—which may be artifacts of sampling biases.

At present there remains one polytypic species (*B. gracilis*) and two "widespread" species (*B. bonitae* and *B. samarensis*), all with distributions spanning boundaries between recognized faunal regions (Brown and Alcala, 1980). Closer investigation of island populations within each of these species may result in the discovery of new diversity in the genus. As our understanding of the total diversity within *Brachymeles* increases, it is important that continued efforts be made to conduct surveys focused on rotting log and leaf litter microhabitats throughout the ranges of all species. Accurate data on the distributions of these species will allow for a complete assessment of the geographic ranges of the species and appropriate decision of conservation status and actions can be made. At present, all nine species are known or believed to be common throughout their ranges. Although these species currently inhabit highly disturbed, agricultural and residential areas, no studies on the long-term effect of deforestation on populations of *Brachymeles* exist. Therefore, according to the IUCN categories and classification structure, we consider the conservation status of these species as "Least Concern (LC)," pending the collection of additional information that might suggest otherwise.

Figure 3.6. Illustration of head of adult female *Brachymeles boholensis* (KU 323972) and adult male neotype of *Brachymeles boulengeri* (PNM 9720; formerly KU 307756) in dorsal, lateral, and ventral views. Taxonomically diagnostic head scales are labeled as follows: C, chin shield; F, frontal; FN, frontonasal; FP, frontoparietal; IL, infralabial; IP, interparietal; L, loreal; M, mental; N, nasal; P, parietal; PF, prefrontal; PM, postmental; PN, postnasal; PO, preocular; PSO, presubocular; R, rostral; SC, supraciliary; SL, supralabial; SN, supranasal; and SO, supraocular. Roman numerals indicate scales in the supraocular series, with Arabic numbers indicating scales in the supraciliary series. Illustrations by CDS.

Brachymeles boholensis



Brachymeles boulengeri

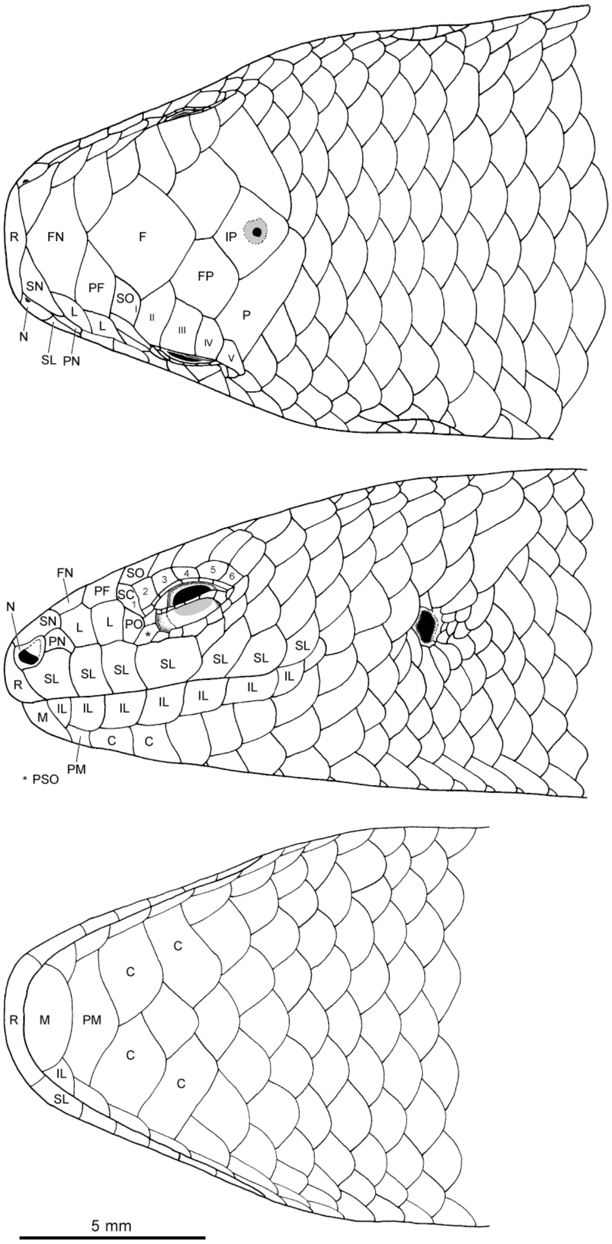


Figure 3.7. Illustration of head of adult male *Brachymeles mindorensis* (KU 304343) and adult female *Brachymeles taylori* (KU 324049) in dorsal, lateral, and ventral views. Labels for taxonomically diagnostic head scales follow those shown in Figure 3.6. Illustrations by CDS.

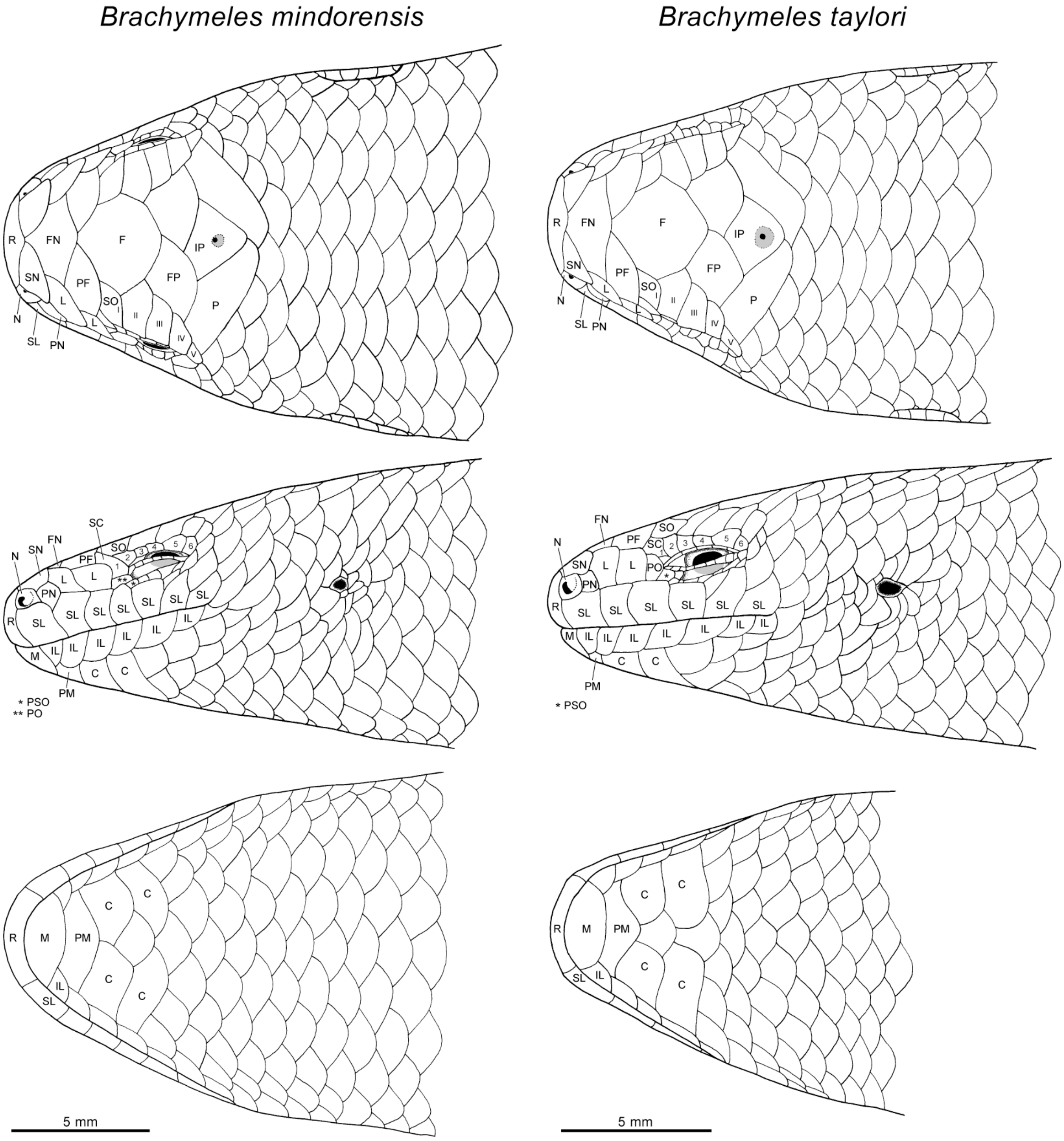
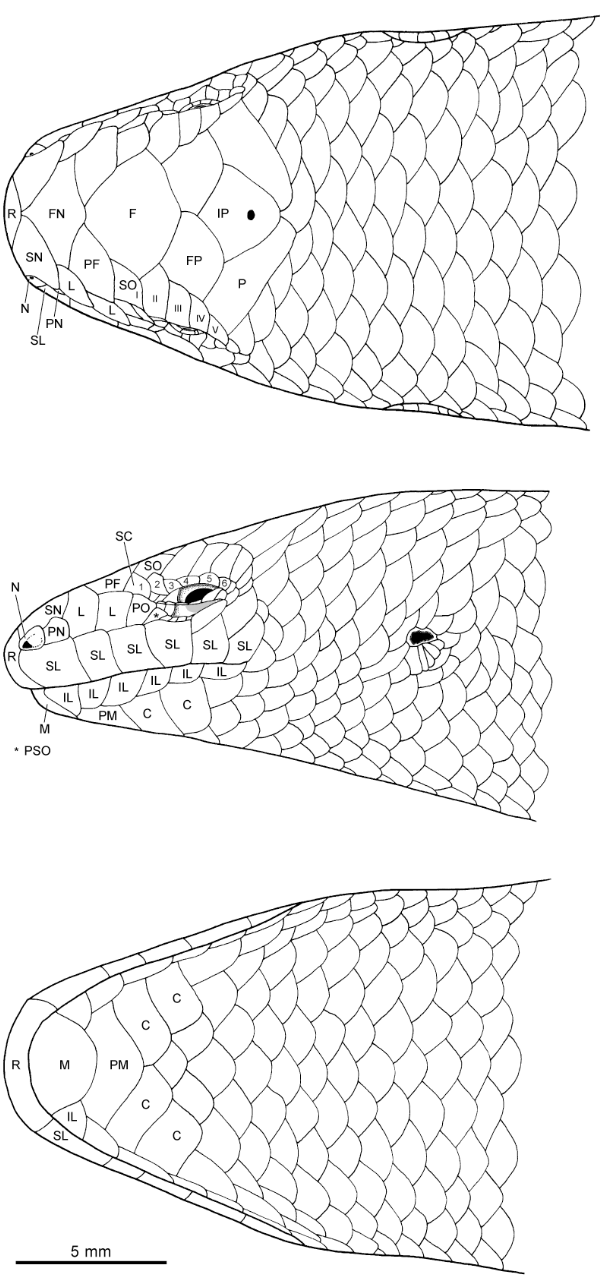

Brachymeles mindorensis
Brachymeles taylori
R
FN
F
IP
SN
PF
FP
L
SO
I
II
III
IV
V
P
N
SL
PN
SC
PO
PM
M
IL
C
* PSO
** PO
1
2
3
4
5
6
5 mm
5 mm

Figure 3.8. Illustration of head of adult male *Brachymeles orientalis* (KU 311241) and adult male *Brachymeles schadenbergi* (KU 314992) in dorsal, lateral, and ventral views. Labels for taxonomically diagnostic head scales follow those shown in Figure 3.6. Illustrations by CDS.

Brachymeles orientalis



Brachymeles schadenbergi

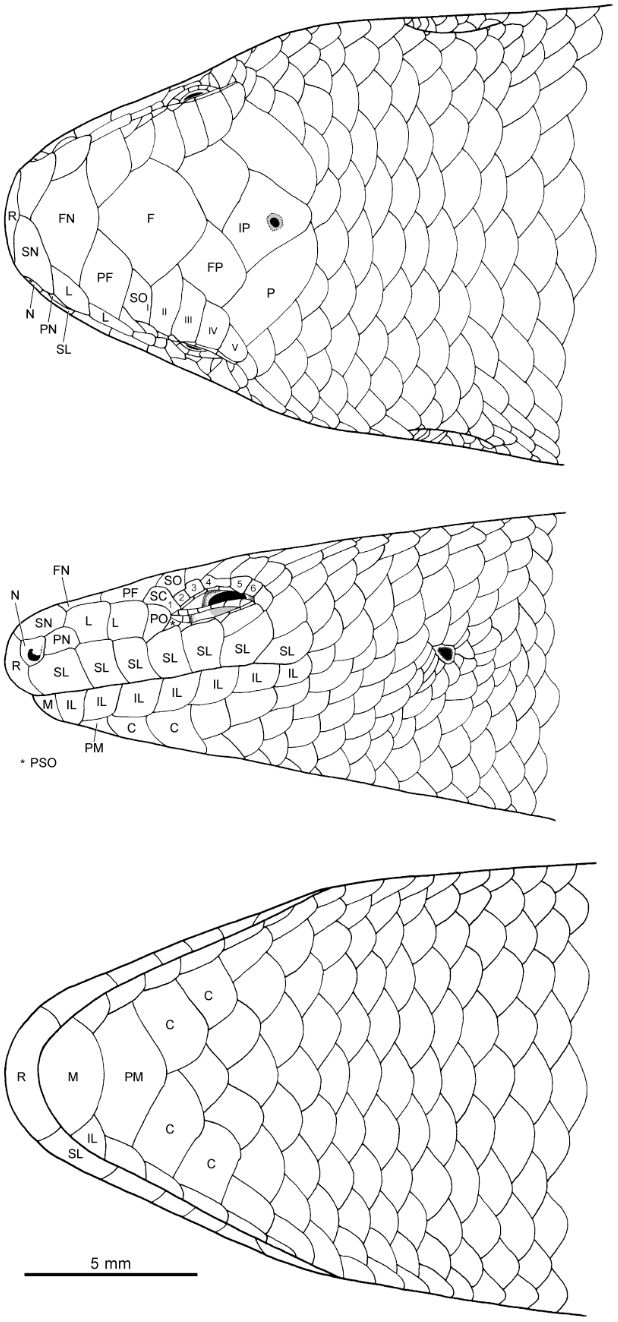
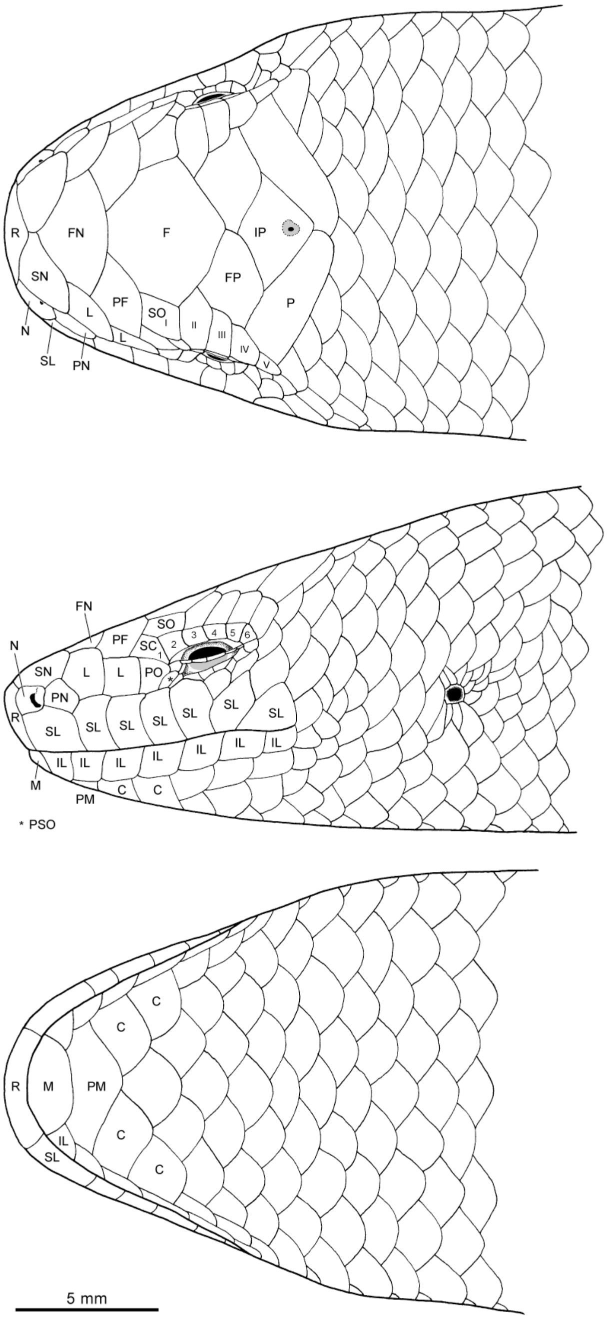


Figure 3.9. Illustration of head of adult male *Brachymeles talinis* (KU 306769) and adult male holotype of *Brachymeles kadwa* (PNM 9721; formerly KU 323091) in dorsal, lateral, and ventral views. Labels for taxonomically diagnostic head scales follow those shown in Figure 3.6. Illustrations by CDS.


Brachymeles talinis

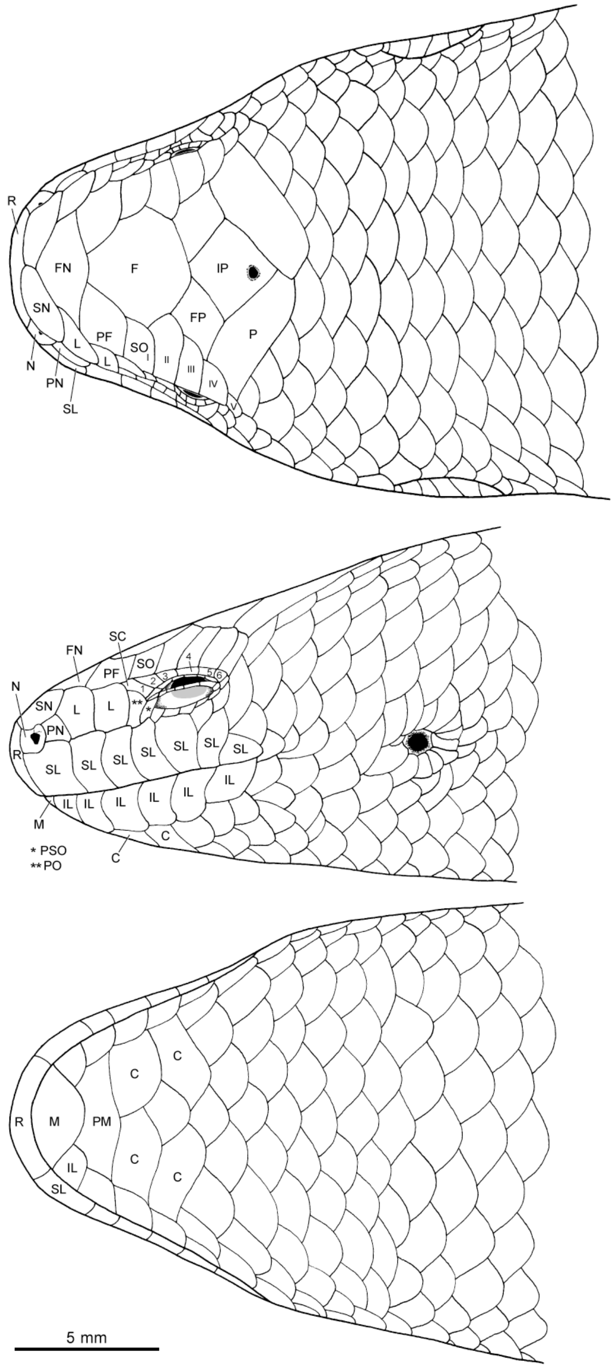
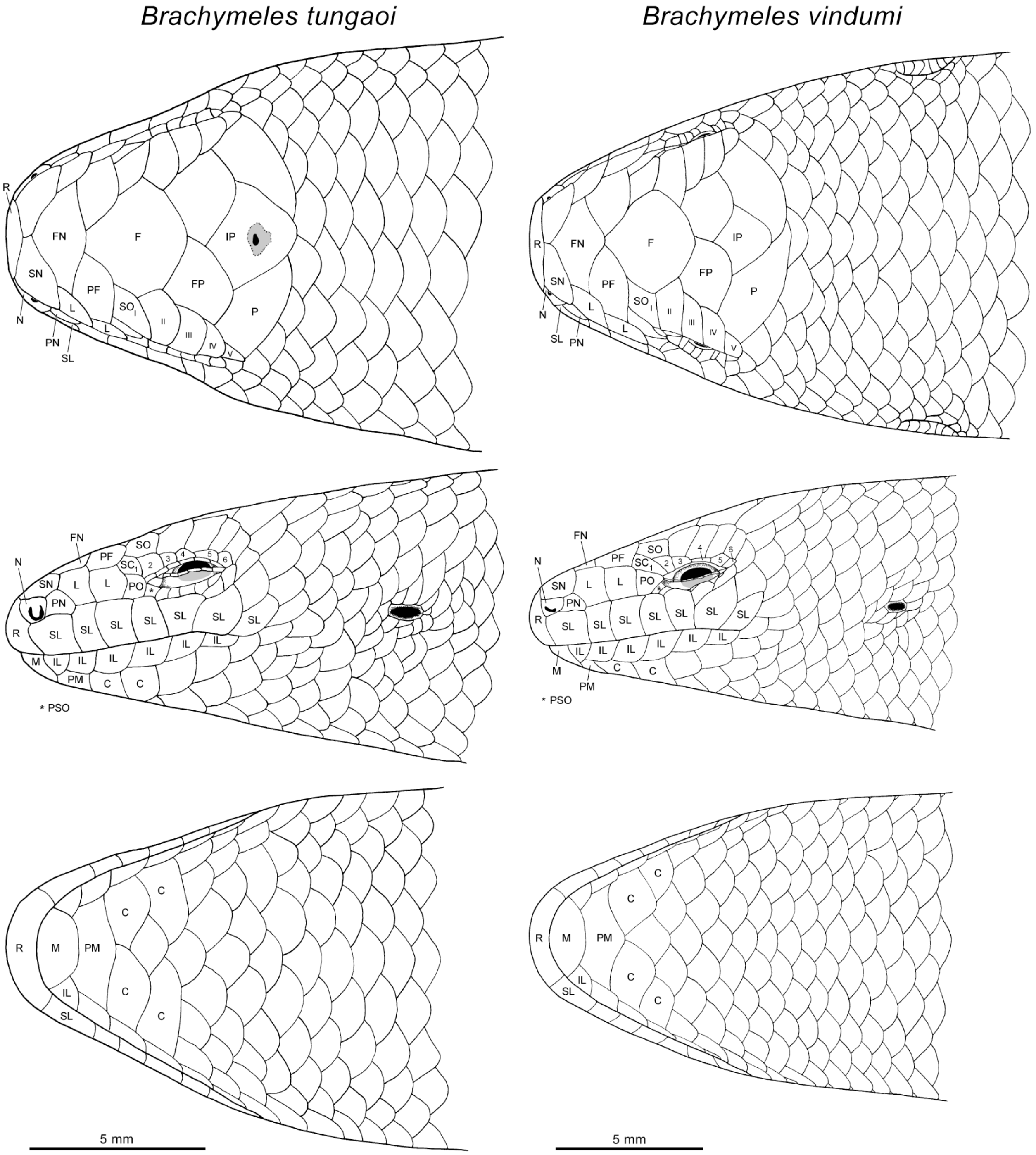

Brachymeles kadwa

Figure 3.10. Illustration of head of adult male holotype of *Brachymeles tungaoi* (PNM 9722; formerly KU 323933) and adult male holotype of *Brachymeles vindumi* (CAS 60724) in dorsal, lateral, and ventral views. Labels for taxonomically diagnostic head scales follow those shown in Figure 3.6. Illustrations by CDS.



Brachymeles tungaoi

Brachymeles vindumi

Figure 3.11. Photographs in life of (A) *Brachymeles boulengeri* (KU 307756), SVL = 98.0 mm, (B) *Brachymeles taylori* (RMB 3283, deposited at PNM), SVL = 81.0 mm, (C) *Brachymeles boholensis* (RMB 2877, deposited at PNM), female, SVL = 89.0 mm, (D) *Brachymeles kadwa* (KU 304593), SVL = 101.0 mm, (E) *Brachymeles schadenbergi* (KU 314973), female, SVL = 107.0 mm, (F) *Brachymeles orientalis* (KU 311240), juvenile, SVL = 51.0 mm, (G) *Brachymeles orientalis* (KU 324029), female, SVL = 91.0 mm, and (H) *Brachymeles talinis* (RMB 3305; deposited at PNM), SVL = 139.0 mm. Photographs by CDS and RMB.


A
E
B
F
C
G
D
H

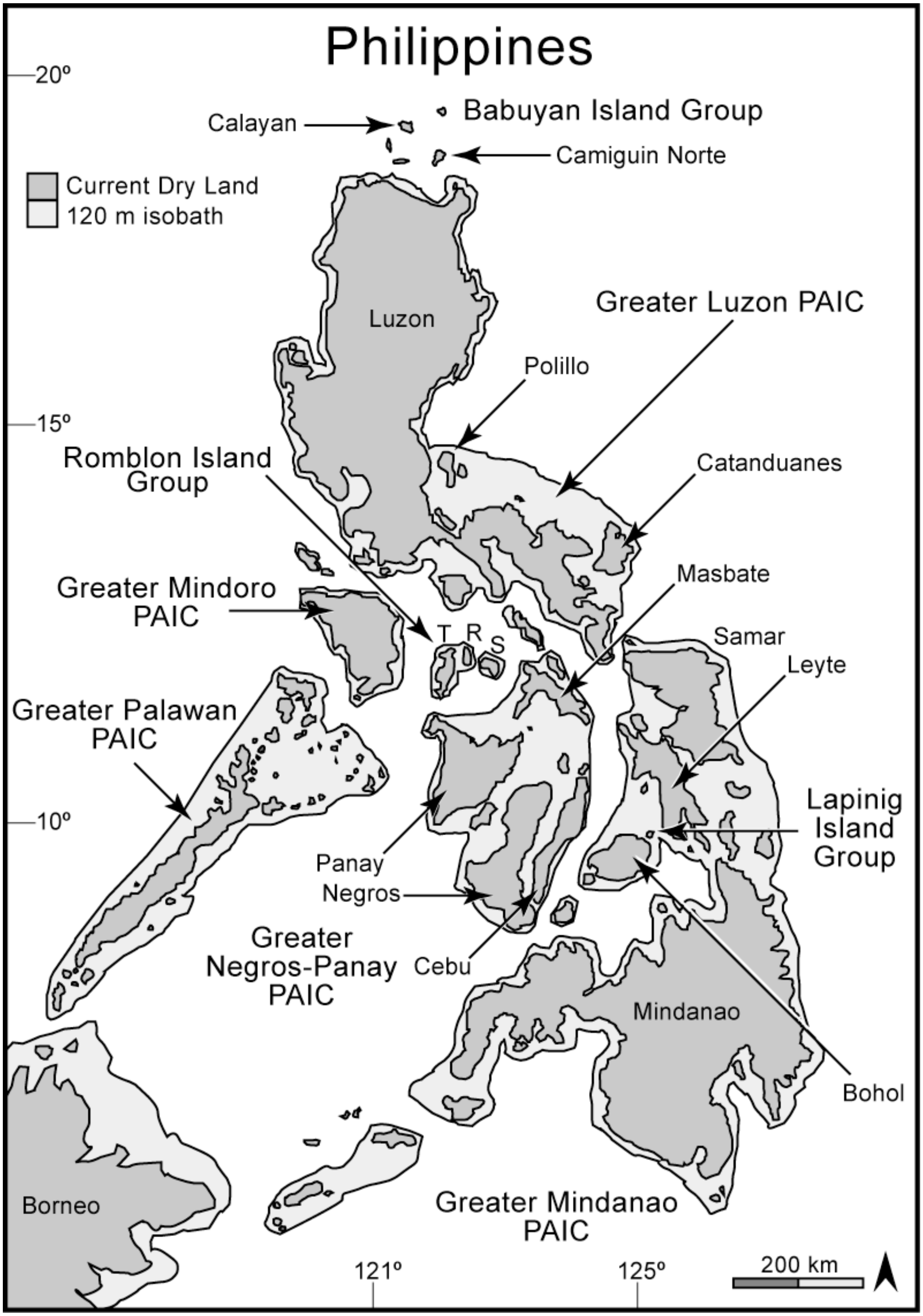
CHAPTER 4

Phylogeny-based species delimitation in Philippine slender skinks (Reptilia: Squamata: Scincidae: *Brachymeles*) II: taxonomic revision of *Brachymeles samarensis* and description of five new species

Few genera of scincid lizards are known to possess species representing a full spectrum of body forms, from fully limbed, pentadactyl species to limbless species (see Siler and Brown, 2010 for review). Within the genus *Brachymeles*, all but two of the 26 recognized species are endemic to the Philippines, with the exceptions being a single species (*B. apus*) from northern Borneo and another (*B. miriamae*) from Thailand (Brown and Alcala, 1980; Hikida, 1982; Siler, 2010; Siler and Brown, 2010, 2011; Siler et al., 2009a, 2010a,b, in press a,b,c,d). Thirteen species are pentadactyl (*bicolor*, *boholensis, boulengeri*, *gracilis*, *kadwa, makusog, mindorensis, orientalis, schadenbergi*, *talinis, taylori, tungaoi,* and *vindumi*), eight are non-pentadactyl, with incompletely developed limbs and reduced numbers of digits (*bonitae*, *cebuensis*, *elerae*, *muntingkamay, pathfinderi*, *samarensis*, *tridactylus*, and *wrighti*), and five are entirely limbless (*apus*, *minimus, miriamae, lukbani,* and *vermis*).

Within the non-pentadactyl species there has been documented a wide range of limb- and digit-reduced states, from minute limbs that lack full digits (*bonitae*, *cebuensis*, *muntingkamay, samarensis, tridactylus*), to moderately developed limbs with four to five digits on the hands and feet (*elerae, pathfinderi, wrighti*: Duméril and Bibron, 1839; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980; Taylor, 1917, 1918, 1925; Siler, 2010; Siler and Brown, 2010, 2011; Siler et al., 2009a, 2010a,b, in press a,b,c,d). All species are semi-fossorial and typically found in dry, rotting material inside or underneath decaying logs or in loose soil, forest floor detritus, and leaf litter.

Figure 4.1. Map of the Philippine islands, with island labels provided for islands with representative samples used for this study. The five recognized major Pleistocene Aggregate Island Complexes (PAICs), major island groups, and additional deep-water islands are labeled for reference. Islands of the Romblon Island Group are designated by the first letter of the island name (T, Tablas Island; R, Romblon Island; S, Sibuyan Island). Current islands in the Philippines are shown in medium grey; light gray areas enclosed in black 120 m bathymetric contours indicate the hypothesized maximum extent of land during the mid- to late Pleistocene.


Philippines
20º
15º
10º
121º
125º
Calayan
Babuyan Island Group
Camiguin Norte
Current Dry Land
120 m isobath
Luzon
Greater Luzon PAIC
Polillo
Romblon Island Group
Catanduanes
Greater Mindoro PAIC
Masbate
T
R
S
Samar
Leyte
Greater Palawan PAIC
Lapinig Island Group
Panay
Negros
Greater Negros-Panay PAIC
Cebu
Mindanao
Bohol
Borneo
Greater Mindanao PAIC
200 km

Although the genus was named well over 150 years ago (Duméril and Bibron, 1839), the rate of *Brachymeles* species descriptions reached an apparent asymptotic maximum in 1980 (Brown and Alcala, 1980). The one exception is *B. minimus*, a legless species described in 1995 (Brown and Alcala, 1995). For more than a century, limited numbers of specimens in museum collections, combined with the similar body plans and external morphological features among species of *Brachymeles* limited assessments of species-level diversity (Taylor, 1917; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). Recent studies have revealed the species-level diversity of *Brachymeles* skinks to be drastically underestimated, and have identified numerous non-monophyletic species complexes within the Philippines (Siler, 2010; Siler and Brown, 2010, 2011; Siler et al., 2009a, 2010a,b, in press a,b,c,d). Additionally, several rare, mid-to-high elevation species long represented by only a few specimens (e.g., *Brachymeles bicolor, B. elerae, B. wrighti, B. pathfinderi*), have recently been rediscovered and redescribed as valid taxa (Siler, 2010; Siler et al., in press a,b). Together, these studies, coupled with increased sampling throughout the Philippines, and a new, robust molecular dataset allow us to begin evalutating variation across the isolated populations of widespread species in the Philippines.

In recent studies Siler and Brown (in press) revised two polytypic species (*B. boulengeri* and *B. schadenbergi*) and one widespread species (*B. talinis*), and inferred the presence of ten genetically and morphologically distinct allopatric evolutionary lineages (species). Several other species are still recognized as having widespread distributions that span historical faunal demarcations in the Philippines (Heaney, 1985; Brown and Guttman, 2002; Brown and Diesmos, 2002, 2009), including *B. samarensis* and *B. bonitae* (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980). One of these species (*B. samarensis*) is the focus of this study.

TAXONOMIC HISTORY

The genus *Brachymeles* was first described by Dumeril and Bibron (1839) for the small, limb-reduced species *Brachymeles bonitae*. Three additional species (*Senira bicolor* [Gray, 1845], *Eumeces* (*Riopa*) *gracilis* [Fischer, 1885], *E.* (*R.*) *schadenbergi* [Fischer, 1885]) were transferred to the genus by Boettger (1886) and Boulenger (1887). These four species represented the known diversity in the genus for thirty years, until Taylor published a series of herpetofaunal descriptions in the early 1900s. It would be fifty years before Brown (1956) described *Brachymeles samarensis* from a single juvenile specimen (FMNH 44472) collected in Guiuan, Samar Island, Philippines in 1945. At the time of description, Brown (1956) hypothesized the species was most closely related to *B. elerae* due to similarities in the number of paravertebral scale rows. This single juvenile would remain the only vouchered, type specimen of this unique, bidactyl species for more than sixty years (Brown and Alcala, 1980).

By the time Brown and Rabor (1967) revised the genus *Brachymeles*, samples of specimens morphologically similar to *B. samarensis* had been collected from the islands of Luzon and Leyte. Additionally, Brown and Rabor (1967) reported on a second specimen from Samar Island; however, no information on where the specimen was deposited or its museum catalog number were provided. Although Brown and Rabor (1967) treated *B. samarensis* as a single widespread species, they referred to the species as a "complex," suggesting they suspected that it contained multiple species, and noted several distinct morphological differences island populations, including differences in fore- and hind limb digit number and head scale patterns.

Additional island populations of *B. samarensis* were subsequently sampled by the time Brown and Alcala (1980) revised the genus, including the Lapinig Group islands off the northeast coast of Bohol Island (Fig. 4.3). Ross and Gonzales (1992) would later report on observations of *B. samarensis* from Catanduanes Island off the northeast coast of the Bicol

Peninsula (Fig. 4.3), and in 2001, RMB recorded *B. samarensis* on the southern tip of the Bicol Peninsula in the foothills of Mt. Bulusan (*unpublished data*); these extralimital range extentions of *B. samarensis* beyond the confines of the Mindanao PAIC (Brown and Diesmos, 2002, 2009) have been interpreted as resulting from recent dispersal events.

To date, *Brachymeles samarensis* remains a widespread species spanning islands of the Luzon and Mindanao Pleistocene Aggregate Island Complexes (PAICs; Brown and Guttman, 2002; Brown and Diesmos, 2002; Fig. 4.1). Widespread distributions such as this have been the focus of many recent studies (Brown et al., 2000a; Siler et al., 2010a,b, 2011; Siler and Brown, 2010, 2011; Welton et al., 2009, 2010a,b), which have revealed that few endemic Philippine reptiles actually possess broad distributions spanning these regional faunistic boundaries (review: Brown and Diesmos, 2009).

The goal of the present study is to revise the taxonomy of the *B. samarensis* complex such that individual units (species) represent independently evolving, cohesive lineage segments (sensu Simpson, 1961; Wiley 1978; Frost and Hillis, 1990; de Queiroz, 1998, 1999). Comprehensive examination of all recently collected specimens from throughout the known range of *B. samarensis* results in the reorganization of the species complex into six distinct evolutionary lineages (species). In this paper we provide a phylogenetic analysis of all of these taxa, fully describe each species, clarify taxonomic boundaries, and provide the first illustrations of all included species. We also provide information on each species' natural history, ecology, and geographic distribution.

Materials and Methods

Field work, sample collection, and specimen preservation

Fieldwork was conducted on Catanduanes, Lapinig Grande, Leyte, Luzon, and Samar islands, all in the Philippines (Fig. 4.1) between 2001 and 2009. Specimens were collected between 900 and 1600 hr, euthenized in aqueous chloretone, dissected for genetic samples (liver preserved in 95% ethanol or flash frozen in liquid nitrogen), fixed in 10% formalin and eventually (< 2 mo) transferred to 70% ethanol. Newly sequenced specimens are deposited in U.S. and Philippine museum collections, the Univrsity of Kansas Natural History Museum (KU), and the Texas Natural History Collections (TNHC) of the Texas Memorial Museum of the University of Texas at Austin. (Acknowledgments and Specimens Examined); voucher information corresponding to data from GenBank sequences is included in Table 4.1.

Taxon sampling and outgroup selection for phylogenetic analyses

Because our primary goal was to estimate phylogenetic relationships among the various populations of *Brachymeles samarensis* we sequenced 2–4 exemplars per sampled population. We included samples of *Lygosoma bowringi* as an outgroup representative based on relationships presented in a recent phylogenetic analyses of the genus *Brachymeles* (Siler and Brown, 2011; Siler et al., 2011). Additionally, we included samples of *Brachymeles apus, B. bonitae, B. minimus, B. lukbani,* and *B. cebuensis* to explore the sister group relationships within the *B. samarensis* complex. A total of 28 ingroup samples were used in phylogenetic inferences.

DNA extraction, purification, and amplification

We extracted total genomic DNA from tissues (Table 4.1) using the modified guanidine thiocyanate extraction method of Esselstyn et al. (2008). The mitochondrial NADH Dehydrogenase Subunit 1 (ND1), NADH Dehydrogenase Subunit 2 (ND2), and the nuclear loci, α-enolase and PTGER4, were completely sequenced for nearly all samples using the primers and protocols provided in Siler et al. (2011). We visualized amplified products on 1.0% agarose gels, then purified them with 1 µL of a 20% solution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ) on the following thermal cycler profile: 31 min at 37°, followed by 15 min at 80°. Upon successful amplification of targeted fragments, cycle-sequencing reactions were completed with the same primers and ABI Prism BigDye Terminator chemistry (Ver. 3.1; Applied Biosystems, Foster City, CA). Cycle-sequencing products were purified with Sephadex Medium (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). We analyzed purified products using an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems), and gene sequences were assembled with Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Alignment and phylogenetic analysis

An initial alignment was produced in Muscle v3.7 (Edgar, 2004), and manual adjustments were made in MacClade 4.08 (Maddison and Maddison, 2005). No instances of insertions or deletions, or ambiguously aligned regions, were observed in the data, and all data were used for analyses. The final alignment thus consisted of 2,570 characters.

Phylogenetic analyses were conducted using parsimony and likelihood optimality criteria, as well as Bayesian methods. Parsimony (MP) analyses were conducted in PAUP* 4.0 (Swofford, 2002) with all characters weighted equally. Most-parsimonious trees were estimated using heuristic searches with 1000 random addition-sequence replicates and tree bisection and reconnection (TBR) branch swapping. To assess heuristic support, nonparametric bootstrapping was conducted using 1000 replicates, each with 100 random addition-sequence replicates and TBR branch swapping.

Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.04 (Stamatakis, 2006). The alignment was partitioned into eight regions consisting of the codon positions of ND1 and ND2, and the two nuclear loci, α-enolase and PTGER4, following the methods of Siler et al. (in press a). Analyses that partition protein-coding genes by codon position have been shown to improve resulting inferences (Brandley et al., 2005). The partitions were run under the same model (GTR + I) with 100 replicate best-tree inferences. Each inference was performed with a random starting tree, and relied on the rapid hill-climbing algorithm (Stamatakis 2006). Clade support was assessed with 1000 bootstrap pseudoreplicates. We considered branches receiving ≥70% bootstrap support to be well-supported (Hillis and Bull, 1993; see also Wilcox et al., 2002).

The Akaike Information Criterion (AIC), as implemented in jModeltest v0.1.1 (Guindon and Gascuel, 2003; Posada, 2008), was used to select the best model of nucleotide substitution for each partition (Table 4.2). The best-fit model for each of the eight partitions (Table 4.2) was used for Bayesian analyses performed in MrBayes 3.1 (Ronquist and Huelsenbeck, 2003). The same partitioning strategy used for maximum likelihood analyses was used for Bayesian inferences. Searches over tree space were conducted with four runs, each with four chains, and were run for 2×10^7 generations. Trees were sampled every 1000 generations, with 4000 samples discarded as burn-in; this left 16001 post-burn-in trees from each run included in the posterior distribution of topologies. Visual inspection for chain stationarity and high ESS values was conducted within the program Tracer v1.4 (Rambaut and Drummond, 2007). Additionally, correlations of split frequencies and cumulative split frequencies were examined using the program AWTY (Nylander et al., 2008). We considered topologies with posterior probabilities ≥0.95 to be well-supported (Wilcox et al., 2002; Leaché and Reeder, 2002).

Morphological data

We examined fluid-preserved specimens (Appendix V) for variation in qualitative and mensural characters. Sex was determined by gonadal inspection, and measurements were taken to the nearest 0.1 mm with digital calipers by CDS. X-rays were taken with a company cabinet X-ray on Kodak paper exposed at 5 miliampheres and 30 volts for 1 minute 15 seconds. Museum abbreviations for specimens examined follow Leviton et al. (1985).

Meristic and mensural characters were chosen based on Siler et al. (2009a, 2010a,b): snout–vent length (SVL), axilla–groin distance (AGD), total length (TotL), midbody width (MBW), midbody height (MBH), tail length (TL), tail width (TW), tail height (TH), head length (HL), head width (HW), head height (HH), snout–forearm length (SnFa), eye diameter (ED), eye–narial distance (END), snout length (SNL), internarial distance (IND), fore-limb length (FLL), hind limb length (HLL), midbody scale-row count (MBSR), paravertebral scale-row count (PVSR), axilla–groin scale-row count (AGSR), Finger-III lamellae count (FinIIIlam), Toe-IV lamellae count (ToeIVlam), supralabial count (SL), infralabial count (IFL), supraciliary count (SC), and supraocular count (SO). Additionally, we counted the number of presacral vertebrae (PSV) from x-ray images of specimens. In the description, ranges are followed by mean ± standard deviation in parentheses.

Species concept

We follow the General Lineage Concept of species (de Queiroz, 1998, 1999) as a logical extension of the Evolutionary Species Concept (Simpson, 1961; Wiley, 1978; Frost and Hillis, 1990). We consider as distinct lineages those populations that are morphologically, and genetically distinct, especially if allopatric. Lineage-based species concepts have been successfully employed in the recognition of Philippine biodiversity (Brown et al., 2000a, 2002, 2008, 2009; Brown and Guttman, 2002; Gaulke et al., 2007; Welton et al., 2009, 2010a,b; Siler et al., 2011) due to the highly partitioned nature of the archipelago (Brown and Diesmos, 2009), and because the geological history of the islands has been so well documented (Voris, 2000; Hall, 2002; Yumul, 2009). In this study we use an estimate of Phylogenetic relationships as a guide for delimiting species but restrict our diagnoses of new species to those populations diagnosed by differences in non-overlapping morphological character states.

Results

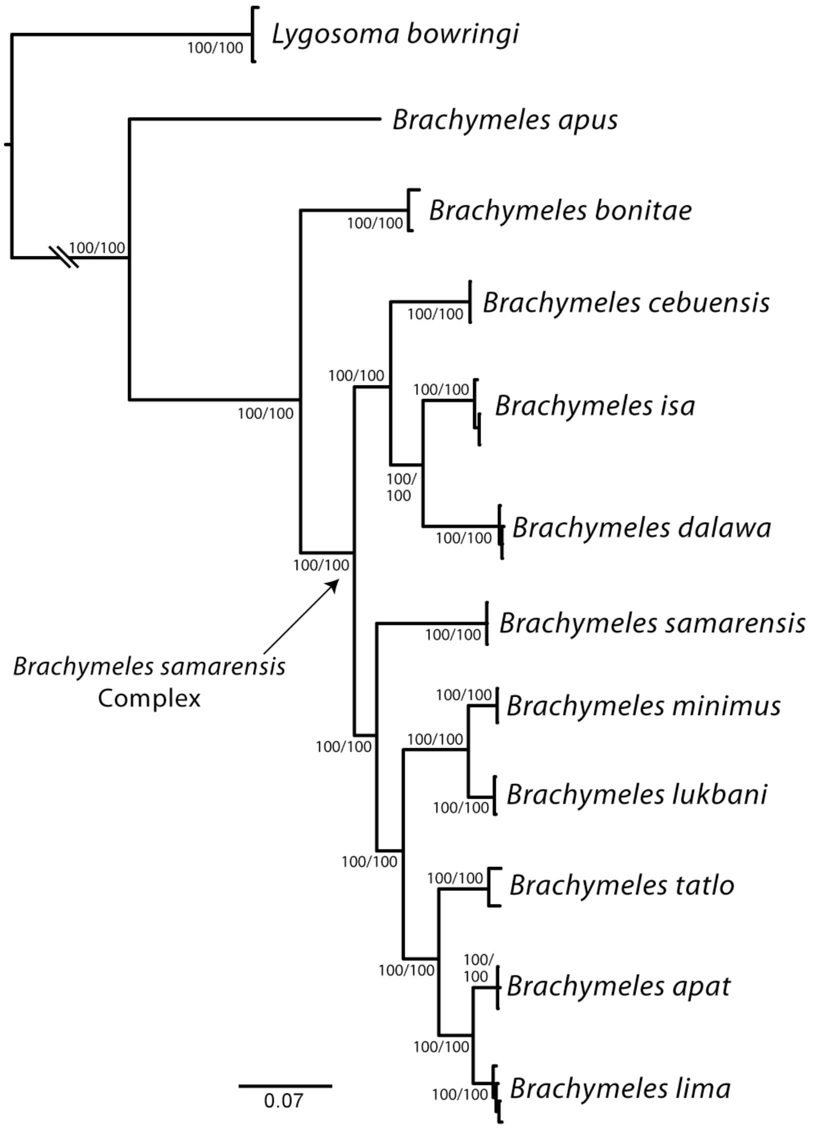
Phylogeny

Of 2,570 mitochondrial characters, 848 were parsimony-informative. The maximum parsimony analysis inferred ten most parsimonious trees (tree length = 2084) that are topologically identical (topology not shown; bootstrap support summarized in Fig. 4.2). The resulting 100 inferences from the partitioned RAxML maximum likelihood analysis show an average likelihood score of –ln *L* 12011.371112, with a single inference having the highest likelihood score of –ln *L* 12011.367644. Trees recovered from ML, MP, and Bayesian analyses are topologically identical. No inferences support the monophyly of *Brachymeles samarensis*. All analyses recover two reciprocally monophyletic clades that include distinct lineages of the *B. samarensis* complex (Fig. 4.2). The Leyte Island and Lapinig Group Islands populations were recovered as a clade, sister to *B. cebuensis* from Cebu Island (Fig. 4.2). True *B. samarensis* from Samar Island was recovered as sister to a clade of two limbless species of *Brachymeles* (*B. minimus* and *B. lukbani*) and the Luzon and Catanduanes island populations of *B. samarensis*

(Fig. 4.2). Two separate lineages are recovered from the Bicol Peninsula of Luzon Island, with no support for their monophyly (Fig. 4.2).

All analyses of result in the strong support of six genetically distinct lineages within the *Brachymeles samarensis* species complex (Fig. 4.2). Uncorrected pairwise sequence divergences are low within the lineages defined here as species and high between these lineages (Table 4.3). Percent divergences for the combined mitochondrial and nuclear data, respectively, show that the monophyletic lineages defined by our phylogenetic analyses (*B. samarensis, B.* sp. nov. [Leyte Island]*, B.* sp. nov. [Lapinig Group Islands]*, B.* sp. nov. [Catanduanes Island]*, B.* sp. nov. [Southern Bicol Peninsula, Luzon Island]*, B.* sp. nov. (Central Bicol Peninsula, Luzon Island]) are distinguished from congeners by levels of genetic divergence equal to, or greater than, those between previously defined species—viz., *B. bonitae, B. cebuensis*, *B. minimus*, *B. lukbani* (Table 4.3; Fig. 4.2). The three most closely related lineages (*B.* sp. nov. [Catanduanes Island]*, B.* sp. nov. [Southern Bicol Peninsula, Luzon Island]*, B.* sp. nov. (Central Bicol Peninsula, Luzon Island]) are separated by 4.1–9.6% mitochondrial sequence divergence. Sequence divergences among the other three lineages within the *B. samarensis* species complex (*B. samarensis* [Samar Island]*, B.* sp. nov. [Lapinig Group islands]*, B.* sp. nov. (Leyte Island]) are greater than 9.2% (Table 4.3; Fig. 4.2). Intraspecific sequence divergences are low in comparison to divergences among monophyletic lineages. Additionally, moderate levels of sequence divergence are observed even when analyses are restricted to only nuclear sequence data (Table 4.3).

Figure 4.2. Maximum likelihood estimate of combined mitochondrial and nuclear data for samples of *Brachymeles* used for this study (preferred ML tree, -ln L 12011.367644; ND1, ND2, α-enolase, PTGER4). Nodes are shown with numerical values corresponding to MPBP, MLBP, and Bayesian PP support values respectively. Terminals are labeled with taxonomic names, fore- and hind limb digit states, and number of presacral vertebrae.



	Digit State	Presacral Vertebrae	Distribution
Lygosoma bowringi			
Brachymeles apus	Limbless	60	Borneo
Brachymeles bonitae	0–2 / 0–2	47–57	Central/Northern Philippines
Brachymeles cebuensis	3 / 2	45	Cebu Island
Brachymeles isa	3 / 3	47	Leyte Island
Brachymeles dalawa	3 / 3	47	Lapinig Group Islands
Brachymeles samarensis	2 / 2	45	Samar Island
Brachymeles minimus	Limbless	50	Catanduanes Island
Brachymeles lukbani	Limbless	54	Northern Bicol Peninsula, Luzon Island
Brachymeles tatlo	2 / 2	47, 48	Southern Bicol Peninsula, Luzon Island
Brachymeles apat	2 / 2	45	Catanduanes Island
Brachymeles lima	2 / 2	46–49	Central Bicol Peninsula, Luzon Island

Figure 4.3. (Left) Map of the Philippine islands showing previously recognized distribution of *Brachymeles samarensis* (indicated by black shaded islands), and recognized distributions of other members of the *B. samarensis* Complex (indicated by dark gray shapes). (Right) Hypothesized distributions of *B. lima*, *B. tatlo*, *B. apat*, *B. dalawa*, *B. isa*, and *B. samarensis* in the eastern-central Philippines. The sampling localities are indicated by black or white shapes, and the hypothesized geographic range of each species indicated by shaded islands and dashed lines, with shapes and shades of islands corresponding to the map's key.

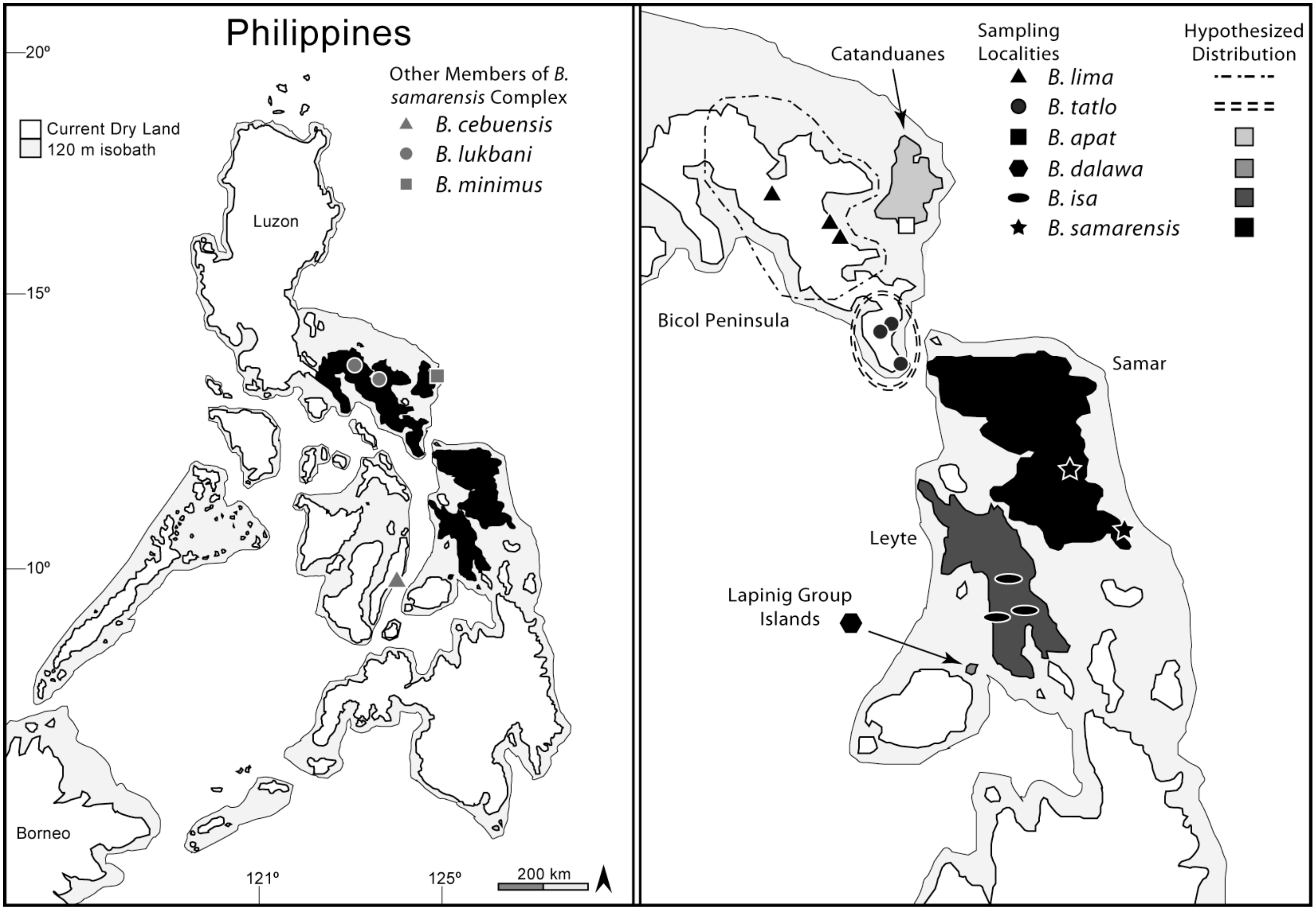

Philippines
20º
15º
10º
121º
125º
Current Dry Land
120 m isobath
Other Members of B. samarensis Complex
B. cebuensis
B. lukbani
B. minimus
Luzon
Borneo
200 km
Catanduanes
Bicol Peninsula
Samar
Leyte
Lapinig Group Islands
Sampling Localities
B. lima
B. tatlo
B. apat
B. dalawa
B. isa
B. samarensis
Hypothesized Distribution

Table 4.1. Summary of specimens corresponding to genetic samples included in the study, general locality, and GenBank accession number. SP = Sabah Parks Reference Collection; KU = University of Kansas Natural History Museum; LSUHC = La Sierra University Herpetological Collections; TNHC = Texas Natural History Collections of the Texas Memorial Museum of the University of Texas at Austin.

Species	Voucher	Locality	Genbank Accession Numbers			
			ND1	ND2	α-enolase	PTGER4
Lygosoma bowringi	LSUHC 6970	West Malaysia				
Lygosoma bowringi	LSUHC 6998	West Malaysia				
Brachymeles apus	SP 06915	Malaysia, Borneo, Sabah, Mt. Kinabalu National Park				
Brachymeles bonitae	KU 307747	Philippines, Polillo Island, Municipality of Quezon				
Brachymeles bonitae	KU 326080	Philippines, Polillo Island, Municipality of Quezon				
Brachymeles minimus	KU 308131	Philippines, Catanduanes Island, Municipality of Gigmoto				
Brachymeles minimus	KU 308129	Philippines, Catanduanes Island, Municipality of Gigmoto				
Brachymele lukbani	KU 313602	Philippines, Luzon Island, Municipality of Labo				
Brachymele lukbani	KU 313596	Philippines, Luzon Island, Municipality of Labo				
Brachymeles cebuensis	KU 320419	Philippines, Cebu Island, Municipality of Carcar				
Brachymeles cebuensis	KU 320421	Philippines, Cebu Island, Municipality of Carcar				
Brachymeles dalawa[2]	KU 320430	Philippines, Lapinig Grande Island, Municipality of Carlos P. Garcia				
Brachymeles dalawa[2]	KU 320458	Philippines, Lapinig Grande Island, Municipality of Carlos P. Garcia				
Brachymeles dalawa[1]	KU 320466	Philippines, Lapinig Grande Island, Municipality of Carlos P. Garcia				
Brachymeles dalawa[2]	KU 320445	Philippines, Lapinig Grande Island, Municipality of Carlos P. Garcia				
Brachymeles lima[1]	KU 324003	Philippines, Luzon Island, Municipality of Tobaco				
Brachymeles lima[2]	KU 324016	Philippines, Luzon Island, Municipality of Tobaco				
Brachymeles lima[2]	KU 324010	Philippines, Luzon Island, Municipality of Tobaco				
Brachymeles lima[2]	KU 324003	Philippines, Luzon Island, Municipality of Tobaco				
Brachymeles tatlo[3]	TNHC 62469	Philippines, Luzon Island, Municipality of Sorsogon				
Brachymeles tatlo[1]	KU 324017	Philippines, Luzon Island, Municipality of Sorsogon				
Brachymeles apat[2]	KU 324025	Philippines, Catanduanes Island, Municipality of San Miguel				
Brachymeles apat[2]	KU 324020	Philippines, Catanduanes Island, Municipality of San Miguel				
Brachymeles apat[2]	KU 324022	Philippines, Catanduanes Island, Municipality of San Miguel				
Brachymeles samarensis	KU 310850	Philippines, Samar Island, Municipality of Taft				
Brachymeles samarensis	KU 310851	Philippines, Samar Island, Municipality of Taft				
Brachymeles samarensis	KU 310849	Philippines, Samar Island, Municipality of Taft				
Brachymeles isa[2]	KU 311225	Philippines, Leyte Island, Municipality of Baybay				
Brachymeles isa[2]	KU 311226	Philippines, Leyte Island, Municipality of Baybay				
Brachymeles isa[2]	KU 311227	Philippines, Leyte Island, Municipality of Baybay				

[1] Holotype; [2] Paratopotype; [3] Paratype

Table 4.2. Models of evolution selected by AIC and applied for partitioned, Bayesian phylogenetic analyses[1].

Partition	AIC Model	Model Applied	Number of Characters
ND1, 1st codon position	GTR + I + G	GTR + G	322
ND1, 2nd codon position	GTR + I + G	GTR + G	322
ND1, 3rd codon position	GTR + I + G	GTR + G	322
ND2, 1st codon position	TVM + I + G	GTR + G	287
ND2, 2nd codon position	GTR + I + G	GTR + G	287
ND2, 3rd codon position	TVM + I + G	GTR + G	287
α-enolase	TVMef + G	GTR + G	261
PTGER4	HKY + I + G	HKY + G	490

[1] The model GTR + G was used for partitioned RAxMLHPC analyses.

Table 4.3. Uncorrected pairwise sequence divergence (%) for mitochondrial data (below diagonal) and nuclear data (above diagonal), for *Brachymeles samarensis, B. isa, B. dalawa, B. lima*, *B. apat*, *B. tatlo*, *B. bonitae, B. cebuensis, B. lukbani,* and *B. minimus* (Fig. 4.2). Percentages on the diagonal represent intraspecific genetic diversity (bolded for emphasis).

	samarensis	*isa*	*dalawa*	*lima*	*apat*	*tatlo*	*bonitae*	*cebuensis*	*lukbani*	*minimus*
samarensis	**0.0**	2.2	1.8–2.8	1.1–1.5	1.6	1.5	2.4	1.2	2.7–3.1	3.4
isa	14.3	**0.0–0.7**	0.2–2.8	1.8–2.2	2.0	1.6–2.0	2.6	1.3	3.0	3.3
lapinig	14.6–15.2	9.2–10.5	**0.0–0.1**	1.4–2.8	1.6–3.6	1.2–3.3	2.2–4.8	1.4–2.8	3.0–3.6	3.2–4.4
lima	14.5–14.7	14.1–14.5	14.9–15.8	**0.4–0.7**	0.5–0.9	0.4–1.1	2.3–2.7	1.1–1.6	2.6–3.2	3.2–3.6
apat	14.4–14.5	14.4–14.6	14.5–14.8	4.1–4.7	**0.0–0.2**	0.7–1.2	2.7	1.5	2.8–3.1	3.5
tatlo	14.9–15.0	14.6–14.9	14.7–15.4	9.4–9.6	9.3–9.5	**1.9**	2.6–2.8	1.4–1.6	2.7–3.1	3.4–3.5
bonitae	16.9–17.3	15.0–15.6	15.5–16.5	15.8–16.5	15.7–16.2	15.7–16.3	**1.4**	2.2	2.6–3.0	3.2
cebuensis	16.2	11.6–11.7	12.0–12.4	14.6–14.8	14.7	14.8–14.9	16.5–16.7	**0.0**	2.8–3.0	3.2
lukbani	14.1	14.1–14.4	14.8–15.3	11.5–11.9	11.2	11.8–11.9	15.0–15.1	13.4	**0.1**	0.7–0.8
minimus	14.1	14.0–14.2	13.8–14.3	11.6–12.0	11.0–11.2	11.6	15.0–15.1	13.7	4.9–5.0	**0.0**

Morphology

Variation in morphological characters (Tables 4.4–4.6) mirrors the results observed in phylogenetic analyses, and supports the recognition of six *Brachymeles samarensis* group lineages. Characters differing among these six lineages include: digit number, presacral vertebrae number, degree of digit development, head and body scale counts and patterns, and pigmentation patterns (Tables 4.4–4.6; species accounts below), all of which are typical morphological diagnostic characters employed historically by taxonomists working with this genus (review: Brown and Alcala, 1980). We observed no intraspecific mensural or meristic differences between the sexes of any of the 6 species.

Superficially, the six lineages within the *B. samarensis* complex appear morphologically similar, especially in overall body size; however, upon closer inspection, three distinct body forms are observed. Among the six lineages, two are observed to be tridactyl (*B.* sp. nov. [Leyte Island] and *B.* sp. nov. [Lapinig Group Islands]), three are observed to be bidactyl (*B. samarensis*, *B.* sp. nov. [Catanduanes Island] and *B.* sp. nov. [Central Bicol Peninsula, Luzon Island]), and one is observed to be bidactyl, but with small, highly-reduced, and near imperceptable claws (*B.* sp. nov. [Southern Bicol Peninsula, Luzon Island]). Additionally, numerous non-overlapping differences were detected in meristic, mensural, osteological, and color pattern characters for each complex member, readily defining six distinct lineages within the complex (Tables 4.4–4.6).

In summary, each lineage (most of which are allopatric) possesses unique and non-overlapping suites of diagnostic character states of morphology, perfectly corresponding to the six clades defined in phylogenetic analyses of DNA sequence data. Combined with biogeographic evidence, and clearly separate geographical ranges, our data suggest the presence of six evolutionary lineages, worthy of taxonomic recognition.

Taxonomic conclusions

Our estimate of phylogeny (Fig. 4.2), biogeographically separate ranges of island or region endemic species, diagnostic, non-overlapping morphological character states, and genetic distances between the taxa (Table 4.3) indicate the distinctiveness of a new species from Catanduanes Island, two new species from the Bicol Peninsula of Luzon Island, a new species from the Lapinig Group Islands, and a new species from Leyte Island (Table 4.3; Fig. 4.2). Each of the six species of the *B. samarensis* complex is morphologically distinct from each other and all other known species in the genus, and each of the eleven species of *Brachymeles* included in phylogenetic analyses also are genetically distinct. Each monophyletic lineage, with the exception of the two occurring on the Bicol Peninsula of Luzon Island, is endemic to single islands within two isolated PAICs, thereby providing additional support for the distinctiveness of each clade's evolutionary history and lineage integrity. Accordingly, we recognize *Brachymeles samarensis* as a species that occurs only on Samar Island in the eastern Visayan (central) Philippine islands (e.g., Mindanao PAIC; Fig. 4.3), and hereby recognize the five additional lineages within the *B. samarensis* species complex each as new species.

TAXONOMIC ACCOUNTS

Brachymeles samarensis Brown 1956: 6

Figs. 4.3, 4. 4

Brachymeles samarensis*, Brown, 1956, Type locality: Guinuan, Samar Island, Philippines*

(FMNH 44472); Brown and Rabor, 1967; Brown and Alcala, 1970; Brown and Alcala, 1980.

Diagnosis.—Brachymeles samarensis can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 57.9–66.1 mm); (2) limbs bidactyl; (3) limb length small; (4) supralabials six; (5) infralabials six; (6) suparciliaries six; (7) supraoculars five; (8) midbody scale rows 19–22; (9) axilla–groin scale rows 66–69; (10) paravertebral scale rows 86–88; (11) pineal eye spot present; (12) prefrontals not contacting on midline; (13) frontoparietals contact; (14) mental/1st infralabial fusion absent; (15) postnasals absent; (16) enlarged chin shields in three pairs; (17) nuchal scales differentiated; (18) fourth and fifth supralabial below eye; (19) auricular opening absent; (20) presacral vertebrae 45; and (21) uniform body color (Tables 4.4, 4.5).

Comparisons.—Characters distinguishing *Brachymeles samarensis* from all non-pentadactyl, limbed species of *Brachymeles* are summarized in Tables 4.4 and 4.5. *Brachymeles samarensis* most closely resembles *B. lima, B. apat, B. tatlo*, and populations of *B. bonitae*, the only other bidactyl species. However, *B. samarensis* differs from these four taxa by having midbody scale rows as few as 19 and axilla–groin scale rows as few as 66 (Table 4.5). *Brachymeles samarensis* further differs from *B. lima* by having fewer presacral vertebrae, six infralabials, the presence of contact between frontoparietals, and non-fusion of mental and first infralabials (Tables 4.4, 4.5); from *B. apat* by having a smaller maximum relative tail length (Table 4.4); from *B. tatlo* by having greater snout–vent lengths among males and females, fewer presacral vertebrae, and fewer paravertebral scale rows (Tables 4.4, 4.5); and from *B. bonitae* by having only bidactyl body forms, longer relative hind limb lengths, fewer presacral vertebrae, fewer paravertebral scale rows, six supralabials, six infralabials, six supraciliaries, five supraoculars, the presence of contact between frontoparietals, and non-fusion of mental and first infralabials (Tables 4.4, 4.5).

Brachymeles samarensis can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all pentadactyl species of *Brachymeles* (*B. boholensis, B. boulengeri, B. bicolor, B. gracilis, B. kadwa, B. makusog, B. mindorensis, B. orientalis, B. schadenbergi, B. talinis, B. taylori, B. tungaoi, B. vindumi*) by having non-pentadactyl (vs. pentadactyl) limbs, shorter fore-limb lengths (less than 2.6 mm vs. greater than 5.9 mm), shorter hind limb lengths (less than 3.1 mm vs. greater than 10.3 mm), a narrower body (less than 6.4 mm vs. greater than 7.9 mm), and by the absence of a postnasal scale and auricular opening (vs. presence).

Description (based on holotype description and six referred specimens).—Details of the head scalation of an adult female are shown in Figure 4.5. Measurements of the holotype are provided below in brackets. Body small, slender; maximum SVL 57.9 mm for males, 66.1 mm for females, [43.5, juvenile] (Tables 4.4, 4.5); head weakly differentiated from neck, nearly as wide as body, HW 7.3–9.2% (8.3 ± 0.7) SVL, 91.4–117.8% (102.7 ± 10.8) HL; HL 36.6–42.5% (38.8 ± 2.1) SnFa; SnFa 18.8–23.5% (20.9 ± 1.6) SVL; snout short, bluntly rounded in dorsal and lateral profile, SNL 50.9–55.3% (53.3 ± 1.8) HL; ear completely hidden by scales; eyes small, ED 1.3–1.6% (1.4 ± 0.1) SVL, 17.0–18.7% (17.6 ± 0.6) HL, 42.6–48.0% (45.8 ± 2.1) END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 109.1–150.6% (130.4 ± 14.9) MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 19–22 [22]; paravertebral scale rows 86–88 [86]; axilla–groin scale rows 66–69; limbs short, poorly developed, with digits reduced to two claws on both fore-limbs and hind limbs, finger and toe lamellae absent; FLL 2.4–5.7% (3.9 ± 1.3) AGD, 1.8–3.9% (2.9 ± 0.9) SVL; HLL 5.3–7.2% (6.2 ± 0.7) AGD, 4.0–5.0% (4.6 ± 0.4) SVL [6.9]; tail not as wide as body, gradually tapered towards end, TW 70.2–82.6% (76.7 ± 5.0) MBW, TL 56.5–80.6% (68.4 ± 11.6) SVL.

Rostral projecting onto dorsal snout to point in line with middle of nasal, broader than high, in contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anteroventrally and posterodorsally; supranasals present, large, broadly separated; postnasals absent; prefrontals moderately separated; frontal octagonal-shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 3× wider than anterior supraocular; supraoculars five; frontoparietals moderate, in broad medial contact, each frontoparietal in contact with interior three supraoculars; interparietal moderate, its length roughly equal to midline length of frontoparietal, longer than wide, diamond-shaped, wider anteriorly; parietals broader than frontoparietals, in broad contact behind interparietal; nuchals enlarged; two loreals, decreasing in size from anterior to posterior, anterior loreal about as long as and slightly higher than posterior loreal; one preocular; one presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to posterior edge of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales; supralabials six, first 2× size of other supralabials, fourth and fifth below eye; infralabials six (Fig. 4.4).

Mental wider than long, in contact with first infralabials; postmental single, enlarged, its width equal to width of mental; followed by three pairs of enlarged chin shields, first pair in broad medial contact, second pair wider than first, broadly separated by single medial scale, third pair separated by three medial scales (Fig. 4.4).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits wrapping around lateral edges of digits; lamellae absent; palmar surfaces of hands and plantar surfaces of feet with several small, irregular scales, each with irregular raised anterior edges; fore-limb digits equal in size; hind limb digits unequal in size, middle digit greatest in length, first and third digits equal in length.

Coloration in preservative.—The ground color of the body is medium brown, with each dorsal scale having a dark, auburn streak on the anterior two thirds to one half of the scale with light brown posterior. Streaks on each individual scale consist of four to seven longitudinal thin lines of auburn pigment with smudges of auburn between streaks. Posterior edge of all body scales transparent. The streaks are present around the entire body and more distinct on the ventrum. Ventral scales have auburn streak at the anterior end with cream color posterior. Caudals and subcaudals coloration matches ventral body coloration. Forelimb and hind limb scales are same color as their surrounding body scales. Precloacal scale coloration matches surrounding ventral scale coloration. Head scales have mottled light and dark brown coloration that match dorsal background coloration. Supraocular scales, rostral, nasal, supranasal, and supralabials are gray-cream color. The mental, infralabial, postmental, and chin shield scales are cream with slight brown mottling with lighter appearance compared to bordering ventral scales.

Coloration in life.—Coloration in life closely matches the coloration in preservative with minor differences, including a dark brown body color and dark brown to black streaks of pigmentation.

Variation.—Morphometric variation of the series is summarized in Table 4.6. We observed a single instance of digit variation, where one specimen (KU 310849) has no fore-limb digits and two hind limb digits. All examined specimens have two loreals with the exception of a single specimen (KU 310852), which has a single loreal on the right side of the body resulting from the fusion of the first and second loreals. Additionally, the first and second pairs of enlarged chin shields are equal in width among all examined specimens with the exception of a single specimen (KU 310850), in which the width of the second pair of enlarged chin shield is greater than the width of the first pair.

Distribution.—Brachymeles samarensis is known only from Samar Island (Fig. 4.3).

Ecology and natural history.—Brachymeles samarensis occurs in primary- and secondary-growth forest habitats. In contrast to the other members of the *B. samarensis* complex, this species appears to be a forest obligate, and was only observed within rotting logs in secondary-growth forest. Three species of *Brachymeles* have been confirmed to occur on Samar Island (*B. gracilis hilong, B. orientalis,* and *B. samarensis* (Brown and Alcala, 1980; Siler and Brown, 2010; Siler et al., 2011, in press c,d).

Other sympatric lizard species observed on Samar Island include: (Agamidae) *Bronchocela cristatella, Draco bimaculatus, D. ornatus, D. reticulates, Gonocephalus semperi, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus annulatus, C. sumoroi, Gehyra mutilata, Gekko gecko, G. mindorensis, Hemidactylus frenatus, H. platyurus, Hemiphyllodactylus typus, Lepidodactylus aureolineatus, L. planicaudus, Pseudogekko compressicorpus*; (Scincidae)*, Emoia atrocostata, Eutropis multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella, L. quadrivittata, Sphenomorphus acutus, S. cumingi, S. fasciatus, S. jagori, S.* cf. *mindanensis, S. steerei, S. variagatus*, *Tropidophorus misaminus*; (Varanidae) *Varanus cumingi samarensis.*

Brachymeles isa sp. nov.

Figs. 4.3, 4.6, 4.7

Holotype.—PNM 9746 (CDS Field No. 3418, formerly KU 311228), adult female, collected under rotting logs in secondary-growth forest (10:00–12:30 hr) on 8 November 2007, in the Sitio

San Vicente Tree Nursery, Barangay Pilim, Baybay City, Leyte Province, Leyte Island, Philippines (10°43'35" N, 124°49'05" E; WGS-84), by CDS and J. Fernandez.

Paratopotypes.—One adult male (KU 311225), one adult female (KU 311229), and three juveniles (KU 311224, PNM 9747–48) collected between 29 October and 8 November 2007.

Paratypes.—One adult male (CAS-SU 26120), four adult females (CAS-SU 26110, 26112, 26121–22), and two juveniles (CAS-SU 26115, 26123) collected between 1 May and 4 June 1964, in Barrio Tambis, Municipality of Burauen, Leyte Province, Leyte Island, Philippines (11°00'37" N, 124°52'19" E; WGS-84), by D. S. Rabor; one adult male (CAS-SU 26771), two adult females (CAS-SU 26770, 26772), and one juvenile (CAS-SU 26773), collected between 10 June and 17 July 1964, in the Municipality of Mahaplag, Leyte Province, Leyte Island, Philippines (10°35'42" N, 124°59'13" E; WGS-84), by D. S. Rabor.

Diagnosis.—*Brachymeles isa* can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 47.2–66.1 mm); (2) limbs tridactyl; (3) limb length small; (4) supralabials six; (5) infralabials five or six; (6) suparciliaries six; (7) supraoculars five; (8) midbody scale rows 21–22; (9) axilla–groin scale rows 71–74; (10) paravertebral scale rows 93–96; (11) pineal eye spot present; (12) prefrontals not contacting on midline; (13) frontoparietals contact; (14) enlarged chin shields in three pairs; (15) nuchals enlarged; (16) fourth and fifth supralabial below eye; (17) auricular opening absent; (18) presacral vertebrae 47; and (19) uniform body color (Tables 4.4, 4.5).

Comparisons.—Characters distinguishing *Brachymeles isa* from all non-pentadactyl, limbed species of *Brachymeles* are summarized in Tables 4.4 and 4.5. *Brachymeles isa* most closely resembles *B. dalawa, B. muntingkamay, and B. tridactylus,* the only other tridactyl species, but differs from these three taxa by having five or six infralabials (Table 4.5). *Brachymeles isa* further differs from *B. dalawa* by having longer body sizes among males, longer relative fore-limb lengths, a greater number of paravertebral scale rows, a uniform body color, and by the absence of contact between prefrontals (Tables 4.4, 4.5); from *B. muntingkamay* by having a shorter maximum body length, shorter fore-limb lengths, shorter hind limb lengths, a greater number of axilla–groin scale rows, a greater number of paravertebral scale rows, six supraciliaries, five supraoculars, the presence of a pineal eyespot, the absence of contact between prefrontals, the presence of contact between frontoparietals, the presence of differentiated nuchals, the presence of a continuous subocular scale row, and the absence of longitudinal rows of spots around the body (Tables 4.4, 4.5); and from *B. tridactylus* by having a shorter maximum body length, shorter relative tail length, shorter fore-limb length, a greater number of presacral vertebrae, six supralabials, six supraciliaries, five supraoculars, the presence of contact between frontoparietals, the presence of a continuous subocular scale row, and the absence of longitudinal rows of spots around the body (Tables 4.4, 4.5).

Brachymeles isa can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all pentadactyl species of *Brachymeles* (*B. boholensis, B. boulengeri, B. bicolor, B. gracilis, B. kadwa, B. makusog, B. mindorensis, B. orientalis, B. schadenbergi, B. talinis, B. taylori, B. tungaoi, B. vindumi*) by having non-pentadactyl (vs. pentadactyl) limbs, shorter fore-limb lengths (less than 1.7 mm vs. greater than 5.9 mm), shorter hind limb lengths (less than 3.0 mm vs. greater than 10.3 mm), a narrower body (less than 5.3 mm vs. greater than 7.9 mm), and by the absence of a postnasal scale and auricular opening (vs. presence).

Description of holotype.—Details of the head scalation are shown in Figure 4.7. Adult female, body small, slender, SVL 59.1 mm; head weakly differentiated from neck, nearly as wide as body, HW 6.5% SVL, 105.5% HL; HL 31.5% SnFa; SnFa 19.5% SVL; snout short, bluntly rounded in dorsal and lateral profile, SNL 71.2% HL; ear completely hidden by scales; eyes small, ED 1.7% SVL, 27.5% HL, 56.2% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 126.7% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 22; paravertebral scale rows 93; axilla–groin scale rows 71; limbs short, poorly developed, with digits reduced to three claws on both fore-limbs and hind limbs, finger and toe lamellae absent; FLL 2.7% AGD, 2.1% SVL; HLL 5.2% AGD, 4.1% SVL; tail not as wide as body, gradually tapered towards end, TW 73.7% MBW, TL 69.4% SVL.

Rostral projecting onto dorsal snout to point in line with posterior edge of nasal, broader than high, in contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anteroventrally and posterodorsally; supranasals present, large, broadly separated; postnasals absent; prefrontals broadly separated; frontal nearly diamond-shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anterior supraocular; supraoculars five; frontoparietals moderate, in narrow medial contact, each frontoparietal in contact with interior three supraoculars; interparietal moderate, its length roughly equal to midline length of frontoparietal, longer than wide, diamond-shaped, wider anteriorly; parietals as broad as frontoparietals, in broad contact behind interparietal; enlarged nuchals present; loreals two, decreasing in size from anterior to posterior, anterior loreal about as long as and slightly higher than posterior loreal; one preocular; one presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to middle of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales; supralabials six, first 2× size of other supralabials, third, fourth, and fifth below eye; infralabials six (Fig. 4.6).

Mental wider than long, in contact with first infralabials; postmental single, enlarged, its width greater than width of mental; followed by three pairs of enlarged chin shields, first pair in broad medial contact, equal in width to third pair, second pair wider than first and third, broadly separated by single medial scale, third pair separated by three medial scales (Fig. 4.6).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits wrapping around lateral edges of digits; lamellae absent; palmar surfaces of hands and plantar surfaces of feet with several small, irregular scales, each with irregular raised anterior edges; fore-limb digits equal in size; hind limb digits unequal in size, middle digit greatest in length, first and third digits equal in length.

Coloration in preservative.—The ground color of the body is medium brown, with each dorsal scale having a dark, auburn streak on the anterior two thirds to one half of the scale with light brown posterior. Posterior edge of all body scales transparent. The streaks are present around the entire body. Ventral scales have smaller streaks restricted to the anterior one third to two-thirds of each scale with cream color posterior. Ventral caudal and subcaudal scales have less cream pigmentation, giving it a darker appearance. Streaks on each individual scale consist of four to six longitudinal thin stripes of auburn piugment with smudges of auburn between them. Forelimb and hind limb scales are darker shade of brown. Forelimb scales have weakly defined scale boundaries. Precloacal scales have slightly lighter coloration than surrounding ventral scales. Head scales have mottled light and dark brown coloration that match dorsal body scales. The rostral, nasal, supranasal, and first supralabial scales have cream coloration slightly lighter than supraocular scales. Supraocular scales and other supralabial scales possses a ligher gray-umber coloration. Supralabial, infralabial, postmental, chin shields are beige with slight light brown mottling.

Coloration in life.—(Fig. 4.7). Coloration in life closely matches the coloration in preservative with minor differences, including a dark brown body color and dark brown to black streaks of pigmentation.

Variation.—Morphometric variation of the series is summarized in Table 4.6. We observed a single instance of digit variation, where one specimen (KU 311225) has two hind limb digits. The pineal eyespot was observed to be absent in a single specimen (CAS 26120), and present in all other examined specimens. The number of infralabials was observed to vary among examined specimens: more than half of the specimens possess six infralabials six (CAS-SU 26110, 26112, 26123, 26772, 26120, 26771, KU 311224–8), and five specimens possess five infralabials (CAS-SU 26121–2, 26770, 26773, KU 311229). Five specimens were observed with enlarged mental scales resulting from fusion with the 1st infralabial (CAS-SU 26121–2, 26770, 26773, KU 311229). Additionally, all specimens have two loreals with the exception of four specimens, which have single, enlarged loreals on both sides of the head (KU 311227) or on only the left side of the head (KU 311224–5, 311229).

Distribution.—Brachymeles isa is known only from Leyte Island (Fig. 4.3).

Ecology and natural history.—Brachymeles isa occurs in agricultural habitats, as well as in disturbed and secondary-growth forest. Little original, forest remains on Leyte Island, but we assume the species once also occurred in first growth forest at low elevations. Individuals have been observed in the rotting material within fallen logs, and leaf litter surrounding the root networks of trees. Similar to *B. samarensis*, this species is found in sympatry with *B. orientalis* and *B. gracilis hilong*.

Other lizard species observed in sympatry on Leyte Island include: (Agamidae) *Bronchocela cristatella, Draco bimaculatus, D. ornatus, D. reticulates, Gonocephalus semperi, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus annulatus, C. gubaot, Gehyra mutilata, Gekko gecko, G. mindorensis, Hemidactylus frenatus, H. platyurus, Hemiphyllodactylus typus, Lepidodactylus aureolineatus, L. planicaudus, Pseudogekko compressicorpus*; (Scincidae)*, Emoia atrocostata, Eutropis multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella, L. quadrivittata, Sphenomorphus acutus, S. cumingi, S. fasciatus, S. jagori, S.* cf. *mindanensis, S. steerei, S. variagatus*, *Tropidophorus misaminus*; (Varanidae) *Varanus cumingi samarensis.*

Etymology.—CDS is pleased to name this new species in honor of the Philippine-American Education Foundation (PAEF), in honor of their continued support and contributions to this research. As the Fulbright Commission in the Philippines, PAEF is responsible for leading the advancement of international exchange programs between the United States and the Philippines, with the mission of promoting mutual understanding between citizens of both countries. Suggested common name: The PAEF Slender Skink.

Brachymeles dalawa sp. nov.

Figs. 4.3, 4.6, 4.8

Holotype.—PNM 9749 (CDS Field No. 3700, formerly KU 320466), adult male, collected under rotting coconut husks in secondary-growth forest (10:00–12:30 hr) on 21 March 2009, in Barangay Villa Milagrosa, Municipality of President Carlos P. Garcia, Bohol Province, Bohol Island, Philippines (10°07'16" N, 124°34'30" E; WGS-84), by CDS and J. Fernandez.

Paratopotypes.—Nine adult males (KU 320435, 320444–6, 320451, 320462, 320466, PNM 9754–55), 21 adult females (KU 320428–30, 320438–40, 320442, 320447, 320449–50, 320452–

5, 320457–61, 320463, 320467), and 10 juveniles (KU 320436–7, 320441, 320443, 320448, 320456, PNM 9750–53) collected between 19 and 21 March 2009.

Paratypes.—One adult male (CAS-SU 28453) collected on 11 April 1967, under rotting coconut tree, 0.5 km SW of Barrio Pitogo, in the Municipality of Ubay, Bohol Province, Lapinig Grande Island, Philippines (10°07'05" N, 124°33'04" E; WGS-84), by A. C. Alcala; one adult female (CAS-SU 27554) collected on 15 April 1967, under rotting log in secondary-growth forest, in the Municipality of Ubay, Bohol Province, Polong Dako Island, Philippines (10°04'11" N, 124°30'14" E; WGS-84), by A. C. Alcala; three adult females (CAS-SU 27556, 28454–5) collected on 20 April 1967, under rotting logs and leaves in a patch of secondary-growth trees, in the Municipality of Ubay, Bohol Province, Lapinig Chico Island, Philippines (10°05'22" N, 124°30'32" E; WGS-84), by A. C. Alcala.

Diagnosis.—*Brachymeles dalawa* can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 52.7–66.1 mm); (2) limbs tridactyl; (3) limb length small; (4) supralabials six; (5) infralabials five; (6) suparciliaries six; (7) supraoculars five; (8) midbody scale rows 22–23; (9) axilla–groin scale rows 72–75; (10) paravertebral scale rows 90–92; (11) pineal eye spot present; (12) frontoparietals contact; (13) enlarged chin shields in three pairs; (14) nuchal scales differentiated; (15) fourth and fifth supralabial below eye; (16) auricular opening covered with scales; (17) presacral vertebrae 47; (18) fusion of mental and first infralabials; and (19) non-uniform body color (Tables 4.4, 4.5).

Comparisons.—Characters distinguishing *Brachymeles dalawa* from all non-pentadactyl, limbed species of *Brachymeles* are summarized in Tables 4.4 and 4.5. *Brachymeles dalawa* most closely resembles *B. isa, B. muntingkamay, and B. tridactylus,* the only other tridactyl species, but differs from these three taxa by having five infralabials, and fusion of the mental and first infralabials (Table 4.5). *Brachymeles dalawa* further differs from *B. isa* by having shorter body sizes among males, shorter relative fore-limb lengths, fewer paravertebral scale rows, and a non-uniform body color (Tables 4.4, 4.5); from *B. muntingkamay* by having a shorter maximum body length, shorter fore-limb lengths, shorter hind limb lengths, a greater number of axilla–groin scale rows, six supraciliaries, five supraoculars, the presence of a pineal eyespot, the presence of contact between frontoparietals, the presence of differentiated nuchals, the presence of a continuous subocular scale row, and the absence of longitudinal rows of spots around the body (Tables 4.4, 4.5); and from *B. tridactylus* by having a shorter maximum body length, shorter relative tail length, shorter fore-limb length, shorter hind limb lenths, a greater number of presacral vertebrae, six supralabials, five infralabials, six supraciliaries, five supraoculars, the presence of contact between frontoparietals, the presence of a continuous subocular scale row, and the absence of longitudinal rows of spots around the body (Tables 4.4, 4.5).

Brachymeles dalawa can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all pentadactyl species of *Brachymeles* (*B. boholensis, B. boulengeri, B. bicolor, B. gracilis, B. kadwa, B. makusog, B. mindorensis, B. orientalis, B. schadenbergi, B. talinis, B. taylori, B. tungaoi, B. vindumi*) by having non-pentadactyl (vs. pentadactyl) limbs, shorter fore-limb lengths (less than 1.8 mm vs. greater than 5.9 mm), shorter hind limb lengths (less than 2.7 mm vs. greater than 10.3 mm), a narrower body (less than 5.9 mm vs. greater than 7.9 mm), and by the absence of a postnasal scale and auricular opening (vs. presence).

Description of holotype.—Details of the head scalation are shown in Figure 4.7. Adult male, hemipenes everted; body small, slender, SVL 56.3 mm; head weakly differentiated from neck, nearly as wide as body, HW 6.5% SVL, 112.7% HL; HL 31.5% SnFa; SnFa 20.9% SVL; snout short, bluntly rounded in dorsal and lateral profile, SNL 65.0% HL; ear completely hidden by scales; eyes small, ED 1.8% SVL, 28.0% HL, 60.8% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 120.3% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 22; paravertebral scale rows 90; axilla–groin scale rows 73; limbs short, poorly developed, with digits reduced to three claws on both fore-limbs and hind limbs, finger and toe lamellae absent; FLL 3.3% AGD, 2.5% SVL; HLL 5.3% AGD, 3.9% SVL; tail not as wide as body, gradually tapered towards end, TW 81.5% MBW, TL 83.6% SVL.

Rostral projecting onto dorsal snout to point in line with posterior edge of nasal, broader than high, in contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anteroventrally and posterodorsally; supranasals present, large, broadly separated; postnasals absent; prefrontals moderately separated; frontal nearly diamond-shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anterior supraocular; supraoculars five; frontoparietals moderate, in moderate medial contact, each frontoparietal in contact with interior two supraoculars; interparietal moderate, its length roughly equal to midline length of frontoparietal, longer than wide, kite-shaped, wider anteriorly; parietals as broad as frontoparietals, in moderate contact behind interparietal; enlarged nuchals present; two loreals, decreasing in size from anterior to posterior, anterior loreal about as long as and slightly higher than posterior loreal; one preocular; one presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to middle of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales; supralabials six, first 2× size of other supralabials, third, fourth, and fifth below eye; infralabials five (Fig. 4.6).

Mental wider than long, fused with first infralabials on both sides; postmental single, enlarged, its width greater than width of mental; followed by three pairs of enlarged chin shields, first pair in broad medial contact, equal in width to third pair, second pair wider than first and third, separated by single medial scale, third pair separated by three medial scales (Fig. 4.6).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits wrapping around lateral edges of digits; lamellae absent; palmar surfaces of hands and plantar surfaces of feet with several small, irregular scales, each with irregular raised anterior edges; fore-limb digits equal in size; hind limb digits unequal in size, middle digit greatest in length, first and third digits equal in length.

Coloration in preservative.—The ground color of the body is dark brown, with each dorsal scale having a dark, chocolate-brown streak on the anterior one third to one half of the scale with cream posterior. Posterior edge of all body scales transparent. The streaks are present around the entire body. Beige coloration on scales more dominant on ventral scales. Caudals and subcaudals have less beige coloration on scales, giving appearance of a darker tail color. Streaks on each individual scale consist of four to seven longitudinal thin stripes of chocolate-brown pigment, with smudges of brown between each. Forelimb scales are the same color as surrounding body scales. Hind limb scales are dark brown and slightly darker than surrounding body scales. Precloacal scales match surrounding ventral scales. Head scales have mottled light and dark brown coloration and match the body color. The rostral, nasal, supranasal and first supralabial scales have a light gray coloration. Supraocular scales and other supralabial scales possess the darkest brown coloration of all head scales with umber brown color. The mental scale is cream. The chin shields and postmental scale match the bordering ventral scales.

Coloration in life.—(Fig. 4.8). Coloration in life closely matches the coloration in preservative with minor differences. Head scales are mottled medium brown to dark brown or black. The ground color of the body is medium to dark brown. The streaks of pigmentation on each scale are dark brown to black.

Variation.—Morphometric variation of the series is summarized in Table 4.6. We observed variation in the degree of head scale contact: (1) prefrontals were observed in point contact medially in seven specimens (KU 320444, 320449, 320458–60, 320462, 320465), and separated for the remaining examined specimens (CAS-SU 27554, 27556, 28453–5, KU 320428–43, 320445–8, 320450–57, 320461, 320463–4, 320466–7); (2) frontoparietals were observed in point contact for a single specimen (KU 320467), and separated for the remaining examined specimens (CAS-SU 27554, 27556, 28453–5, KU 320428–66); (3) first pair of enlarged chin shiels were observed separated in a single specimen (KU 320451), and in contact medially for the remaining examined specimens (CAS-SU 27554, 27556, 28453–5, KU 320428–50, 320452–67).

Additionally, the degree of fusion between loreals was observed to vary among the type series. The majority of specimens examined have two loreals and no fused scales (CAS-SU 27554, 27556, 28453–55, KU 320431–7, 320439–42, 320445–46, 320448, 320450–51, 320455, 320457–60, 320462, 320464, 320466), five specimens have single, enlarged loreals on both sides of the head (KU 320444, 320449, 320452, 320456, 320467), five specimens have single, enlarged loreals on the left side of the head (KU 320430, 320453–54, 320463, 320465), and six specimens have single, enlarged loreals on the right side of the head (KU 320428–29, 320438, 320443, 320447, 320461).

Distribution.—Brachymeles dalawa is known from Lapinig Chico, Lapinig Grande, Tilmubo, and Tintiman islands off the northeast coast of Bohol Island (Fig. 4.3).

Ecology and natural history.—Brachymeles dalawa occurs in agricultural habitats, and disturbed forest habitat. No original forest remains on any of the Lapinig Group Islands, and common habitat consists of grassland, rice fields, agricultural habitats, and human habitations. Surprisingly, *B. dalawa* on Lapinig Grande Island was observed to be the more common than any other known species of *Brachymeles*. Individuals were regularly observed under piles of rotting cocounuts, in loose soil around trees and root systems, and in loose leaf litter. Interestingly, this species seems to be a ubiquitous habitat generalist on the Lapinig Group Islands, but has not been recorded from the nearby island of Bohol, whereas its congeners, *B. orientalis* and *B. boholensis,* are known. It remains possible that populations of this species will eventually be discovered on the northeast coast of Bohol Island.

Sympatric lizard species observed in the Lapinig Group islands include: (Gekkonidae) *Hemidactylus frenatus* and *H. platyurus*.

Etymology.—We are pleased to name this new species in honor of Carlos Polestico Garcia. Born on Bohol Island, Carlos P. Garcia later became the 8th President of the Philippines. He was the first Philippine president to be laid to rest in the *Libingan ng mga Bayani*, or Cemetary of the Heroes, located within Fort Bonifacio in Manila, Philippines. The municipality of Carlos P. Garcia, and type locality for *Brachymeles dalawa*, was named after this Philippine hero. The word “dalawa” is derived from the phrase *Libingan ng mga Bayani*. Suggested common name: Lapinig Islands’ Slender Skink.

Table 4.4. Summary of meristic and mensural characters in all known limbed, non-pentadactyl species of *Brachymeles*. Sample size, body length and total length among males and females, and general geographical distribution (PAIC = Pleistocene Aggregate Island Complexes, sensu Brown and Diesmos, 2002) are included for reference (SVL, TotL, MBW, FLL, and HLL given as range over mean ± standard deviation; all body proportions given as percentage over mean ± standard deviation). In cases of scale count variation within species, numbers of individuals showing specific counts are given in parentheses.

	samarensis (1 m, 5 f)	*isa* (3 m, 9 f)	*dalawa* (10 m, 25 f)	*lima* (6 m, 10 f)	*apat* (9 f)	*tatlo* (1 m, 2 f)
Range	Samar Island	Leyte PAIC	Lapinig Group Islands	Central Bicol Peninsula	Catanduanes Island	Southern Bicol Peninsula
SVL (f)	62.4–66.1 (63.4 ± 1.5)	47.2–61.4 (56.5 ± 4.2)	52.8–66.1 (58.6 ± 3.3)	46.4–67.4 (59.0 ± 6.7)	54.0–64.4 (58.7 ± 3.5)	54.0, 60.0
SVL (m)	57.9	62.4–66.1 (63.4 ± 1.5)	52.7–57.4 (56.0 ± 1.6)	56.4–66.1 (61.7 ± 3.5)	—	56.8
TotL (f)	97.7–112.9 (107.3 ± 8.3)	99.5–108.5 (102.6 ± 5.1)	91.4–111.2 (102.2 ± 6.4)	94.1–112.7 (102.1 ± 8.8)	102.2–109.4 (106.2 ± 2.7)	92.3, 95.2
TotL (m)	93.0	106.7–114.6 (110.6 ± 5.6)	92.1–103.4 (99.4 ± 4.5)	99.6–107.9 (104.1 ± 4.2)	—	102.0
TL/SVL	57–81 (68 ± 12)	69–79 (75 ± 4)	63–84 (77 ± 6)	58–93 (75 ± 12)	76–96 (88 ± 8)	59–80 (70 ± 11)
FLL	1.1–2.6 (1.8 ± 0.5)	1.3–1.7 (1.5 ± 0.1)	1.1–1.8 (1.3 ± 0.2)	1.1–1.9 (1.4 ± 0.3)	1.4–2.1 (1.7 ± 0.2)	1.1–1.5 (1.5 ± 0.2)
FLL/SVL	2–4 (3 ± 1)	2–4 (3 ± 0)	2–3 (2 ± 0)	2–4 (2 ± 0)	3 (3 ± 0)	2–3 (3 ± 0)
HLL	2.5–3.1 (2.9 ± 0.2)	2.3–3.0 (2.6 ± 0.3)	2.0–2.7 (2.4 ± 0.2)	1.9–3.1 (2.6 ± 0.3)	2.5–3.6 (3.0 ± 0.3)	2.1– 2.7 (2.5 ± 0.3)
HLL/SVL	4–5 (5 ± 0)	4–5 (4 ± 0)	3–5 (4 ± 0)	3–5 (4 ± 1)	4–6 (5 ± 1)	4–5 (4 ± 0)
ToeIVlam	0	0	0	0	0	0

Table 4.4.—Continued.

	muntingkamay (12 f)	*tridactylus* (9 m, 11 f)	*bonitae* (6 m, 7 f)	*cebuensis* (8 f)	*elerae* (2 m, 1 f)	*pathfinderi* (14 m, 23 f)	*wrighti* (1 m, 1 f)
Range	Luzon Island	Visayan PAIC	Mindoro & Luzon PAICs	Cebu Island	Luzon Island	Mindanao Island	Luzon Island
SVL (f)	61.8–81.3 (73.6 ± 5.9)	45.5–59.1 (52.1 ± 5.0)	49.7–59.8 (56.4 ± 3.9)	51.5–67.9 (61.8 ± 5.3)	68.2, 71.9	55.8–68.3 (62.0 ± 3.4)	113.0
SVL (m)	N/A	55.7–78.3 (68.5 ± 7.4)	65.1–80.0 (73.5 ± 6.4)	N/A	71.5	54.5–65.1 (59.4 ± 3.8)	125.8
TotL (f)	107.4–136.0 (124.0 ± 8.6)	102.6–154.1 (132.6 ± 14.0)	93.4–150.4 (126.7 ± 19.9)	104.3–128.0 (119.0 ± 8.5)	109.9, 131.9	111.1–133.2 (119.7 ± 8.2)	205.6
TotL (m)	N/A	105.3–133.67 (115.9 ± 15.4)	102.6–144.5 (121.3 ± 15.6)	N/A	N/A	101.4–107.0 (104.2 ± 4.0)	216.4
TL/SVL	50–79 (65 ± 10)	69–112 (92 ± 12)	35–93 (69 ± 18)	78–115 (92 ± 13)	61–84 (72 ± 16)	69–95 (84 ± 10)	72, 82
FLL	2.4–3.0 (2.7 ± 0.2)	1.5–2.5 (2.0 ± 0.3)	1.0–1.5 (1.3 ± 0.1)	1.1–1.8 (1.5 ± 0.3)	3.3–3.5 (3.4 ± 0.1)	4.4–6.9 (5.8 ± 0.5)	7.5, 7.5
FLL/SVL	3–4 (4 ± 0)	2–3 (3 ± 0)	1–2 (2 ± 0)	2–3 (2 ± 0)	5–5 (5 ± 0)	8–11 (10 ± 1)	6, 7
HLL	5.3–6.0 (5.7 ± 0.2)	2.6–3.6 (3.1 ± 0.3)	1.3–2.0 (1.6 ± 0.2)	2.3–3.0 (2.7 ± 0.3)	4.3–5.4 (5.0 ± 0.6)	8.4–12.9 (10.8 ± 1.0)	10.9, 13.9
HLL/SVL	7–9 (8 ± 1)	3–6 (5 ± 1)	2–3 (2 ± 0)	3–5 (4 ± 0)	6–8 (7 ± 1)	15–21 (18 ± 1)	10, 11
ToeIVlam	0	0	0	0	3	5–8	4, 5

Table 4.5. Summary of qualitative diagnostic characters (present, absent) in all known limbed, non-pentadactyl species of *Brachymeles*. The pairs of enlarged scales posterior to the postmental scale are abbreviated as chin shield pairs with reference to the 1st, 2nd, and 3rd pairs (when present).

	samarensis (1 m, 5 f)	*isa* (3 m, 9 f)	*dalawa* (10 m, 25 f)	*lima* (6 m, 10 f)	*apat* (9 f)	*tatlo* (1 m, 2 f)
Number of digits (fore/hind)	2/2	3/3	3/3	2/2	2/2	2/2
PSV	45	47	47	46–49	45	47–48
MBSR	19–22	21–22	22–23	20–22	21–22	20
AGSR	66–69	71–74	72–75	68–73	68–72	73–77
PVSR	86–88	93–96	90–92	85–90	85–89	90–94
SL	6 (6)	6 (12)	6 (35)	6 (16)	6 (9)	6 (3)
IFL	6 (6)	5 (4) 6 (8)	5 (35)	5 (11) 6 (5)	6 (9)	6 (3)
SC	6 (6)	6 (12)	6 (35)	6 (16)	6 (9)	6 (3)
SO	5 (6)	5 (12)	5 (35)	5 (16)	5 (9)	5 (3)
Pineal eyespot	Present	Present	Present	Present	Present	Present
Prefrontal contact	Absent	Absent	Point contact or Absent	Absent	Absent	Absent
Frontoparietal contact	Present	Present	Present	Present or Absent	Present	Present
1st chin shield pair contact	Present	Present or Absent	Present or Absent	Present or Absent	Present	Absent
3rd chin shield pair	Present	Present	Present	Present	Present	Present
Chin shield pair size	$3 < 1 \leq 2$	$3 < 1 \leq 2$	$3 < 1 < 2$	$3 < 1 < 2$	$3 < 1 \leq 2$	$3 < 1 < 2$
Chin shield pair separation[1]	1(0); 2(1); 3(3)	1(0/1); 2(1); 3(3)	1(0/1); 2(1); 3(3)	1(0/1); 2(1); 3(3)	1(0); 2(1); 3(3)	1(0); 2(1); 3(3)
1st/2nd loreal fusion	Present or Absent	Present or Absent	Present or Absent	Present or Absent	Absent	Absent
Mental/1st IFL fusion	Absent	Present or Absent	Present	Present or Absent	Absent	Absent
Differentiated nuchals	Present	Present	Present	Present	Present	Present
Continuous subocular scale row	Present	Present	Present	Present	Present	Present
Auricular opening	Absent	Absent	Absent	Absent	Absent	Absent
Dorsolateral stripes	Absent	Absent	Absent	Absent	Absent	Absent
Longitudinal rows of dark spots	Absent	Absent	Absent	Absent	Absent	Absent

[1] Parentheses show the number of small ventral scale rows separating each enlarged pair of chin shields.

TABLE 4.5.—Continued.

	muntingkamay (12 f)	*tridactylus* (9 m, 11 f)	*bonitae* (6 m, 7 f)	*cebuensis* (8 f)	*elerae* (2 m, 1 f)	*pathfinderi* (14 m, 23 f)	*wrighti* (1 m, 1 f)
Number of digits (fore/hind)	3/3	3/3	0–2/0–2	3/2	4/4	5/4	4/4
PSV	42, 44	47	47–57	45	43	34	—
MBSR	22–24	22–24	21–23	22–24	22–24	23–25	28, 28
AGSR	65–70	70–79	73–90	65–69	63–67	44–48	85, 85
PVSR	85–90	88–98	90–109	84–88	84–87	64–67	106, 108
SL	6 (12)	6 (12) 7 (8)	6 (12) 7 (1)	6 (8)	6 (3)	6 (37)	6 (1) 7 (1)
IFL	6 (12)	6 (12) 7 (8)	5 (1) 6 (10) 7 (2)	6 (5) 7 (3)	6 (3)	6 (37)	7 (2)
SC	6 (10) 7 (2)	5 (20)	5 (12) 6 (1)	6 (8)	5 (2) 6 (1)	5 (17) 6 (19)	6
SO	5 (11) 6 (1)	4 (20)	4 (13)	5 (8)	4 (2) 5(1)	5 (37)	5
Pineal eyespot	Absent	Present	Present	Present	Absent	Present	Present
Prefrontal contact	Present	Absent	Absent	Present or Absent	Present	Absent	Present or Absent
Frontoparietal contact	Absent	Absent	Absent	Present	Present	Present or Absent	Present
1st chin shield pair contact	Absent	Present or Absent	Absent	Present	Absent	Absent	Absent
3rd chin shield pair	Present	Present	Present	Present	Present	Absent	Present
Chin shield pair size	$3 < 1 < 2$	$3 < 1 < 2$	$3 < 2 < 1$	$1 = 3 < 2$	$1 < 3 < 2$	$1 < 2$	$2 < 1$
Chin shield pair separation[1]	1(1); 2(1); 3(3)	1(0/1); 2(1); 3(3)	1(1); 2(1); 3(3)	1(0); 2(1); 3(3)	1(1); 2(1); 3(3)	1(1); 2(1)	1(1); 2(3)
1st/2nd loreal fusion	Absent	Absent	Absent	Absent	Absent	Absent	Absent
Mental/1st IFL fusion	Absent	Absent	Present or Absent	Absent	Absent	Absent	Absent
Differentiated nuchals	Absent	Present	Present	Present	Absent	Absent	Present[2]
Continuous subocular scale row	Absent	Absent	Present	Present	Present	Present	Present
Auricular opening	Absent	Absent	Absent	Absent	Absent	Present	Absent
Dorsolateral stripes	Absent	Absent	Absent	Absent	Absent	Present	Absent
Longitudinal rows of dark spots	Present, around body	Present, vague to indistinct	Absent	Absent	Present, around body	Present, 6	Present

[1] Parentheses show the number of small ventral scale rows separating each enlarged pair of chin shields.

[2] Due to head damage in the nuchal region for both known specimens of *B. wrighti*, the presence of differentiated nuchals remains tentative.

Table 4.6. Summary of univariate morphological variation among mensural characters in series of *Brachymeles samarensis, B. isa, B. dalawa, B. lima, B. apat,* and *B. tatlo*.

	samarensis (1 m; 5 f)	*isa* (3 m; 9 f)	*dalawa* (10 m; 25 f)	*lima* (6 m; 10 f)	*apat* (9 f)	*tatlo* (1 m; 2 f)
SVL (m)	57.9	59.7–64.1 (61.8 ± 2.2)	52.7–57.4 (56.0 ± 1.6)	56.4–66.1 (61.7 ± 3.5)	—	56.8
SVL (f)	62.4–66.1 (63.4 ± 1.5)	47.2–61.4 (56.5 ± 4.2)	52.8–66.1 (58.6 ± 3.3)	46.4–67.4 (59.0 ± 6.7)	54.0–64.4 (58.7 ± 3.5)	54.0, 60.0
AGD (m)	40.3	44.1–48.2 (46.0 ± 2.1)	39.5–43.6 (42.1 ± 1.2)	42.9–52.0 (47.4 ± 3.4)	—	43.8
AGD (f)	45.3–50.3 (47.6 ± 1.8)	35.6–46.5 (43.2 ± 3.1)	39.4–50.6 (44.7 ± 2.8)	32.9–52.3 (44.8 ± 5.8)	41.0–49.1 (44.6 ± 2.3)	45.5, 45.8
TotL (m)	93.0	106.7–114.6 (110.6 ± 5.6)	92.1–103.4 (99.4 ± 4.5)	99.6–107.9 (104.1 ± 4.2)	—	102.0
TotL (f)	97.7–112.9 (107.3 ±	99.5–108.5 (102.7 ±	91.4–111.2	94.1–112.7	102.2–109.4	92.3, 95.2

	8.3)	5.1)	(102.2 ± 6.4)	(102.1 ± 8.8)	(106.2 ± 2.7)	
MBW (m)	5.7	5.0–5.3 (5.1 ± 0.2)	4.0–4.7 (4.4 ± 0.3)	4.2–5.1 (4.5 ± 0.3)	—	4.0
MBW (f)	5.2–6.4 (5.7 ± 0.5)	3.7–5.0 (4.2 ± 0.4)	3.4–5.9 (4.5 ± 0.6)	3.8–4.8 (4.4 ± 0.3)	4.2–5.4 (4.8 ± 0.4)	3.2, 4.8
MBH (m)	4.0	2.9–4.5 (3.8 ± 0.8)	3.2–4.7 (3.6 ± 0.5)	3.0–5.1 (3.6 ± 0.8)	—	3.2
MBH (f)	4.3–4.8 (4.5 ± 0.2)	3.0–4.7 (3.9 ± 0.5)	2.9–5.3 (3.7 ± 0.8)	2.9–5.0 (3.7 ± 0.8)	3.4–4.4 (3.8 ± 0.4)	2.5, 4.3
TL (m)	35.1	45.0–50.5 (47.8 ± 3.9)	39.3–47.1 (43.6 ± 3.4)	38.7–51.5 (43.2 ± 7.2)	—	45.2
TL (f)	35.3–50.4 (44.5 ± 8.1)	41.0–47.1 (43.9 ± 3.1)	38.3–50.1 (44.2 ± 4.1)	32.3–52.1 (42.5 ± 7.4)	45.6–53.5 (49.5 ± 3.1)	38.3, 35.2
TW (m)	4.1	3.8–4.1 (4.0 ± 0.2)	3.1–3.9 (3.4 ± 0.2)	3.4–4.3 (3.7 ± 0.3)	—	3.7
TW (f)	4.1–4.6 (4.4 ± 0.2)	3.3–3.8 (3.4 ± 0.2)	2.8–4.6 (3.5 ± 0.5)	2.8–4.2 (3.5 ± 0.4)	3.6–4.5 (4.0 ± 0.3)	2.4, 3.6
TH (m)	3.5	3.2–3.4 (3.3 ± 0.1)	2.8–3.5 (3.1 ± 0.2)	2.6–3.6 (3.0 ± 0.4)	—	2.6
TH (f)	3.5–3.9	2.9–3.4	2.5–4.5	2.3–3.4	2.7–3.9	2.3, 3.2

	(3.8 ± 0.2)	(3.1 ± 0.2)	(3.1 ± 0.5)	(2.8 ± 0.4)	(3.1 ± 0.4)	
HL (m)	5.3	4.5–4.8 (4.6 ± 0.2)	3.7–4.7 (4.1 ± 0.4)	3.6–4.2 (3.8 ± 0.2)	—	3.9
HL (f)	4.8–5.2 (5.0 ± 0.2)	3.5–4.4 (4.1 ± 0.3)	3.5–4.5 (4.0 ± 0.3)	3.5–5.3 (4.1 ± 0.6)	3.8–5.5 (4.3 ± 0.6)	3.1, 4.2
HW (m)	5.1	4.6–4.7 (4.6 ± 0.1)	3.9–4.6 (4.2 ± 0.2)	3.9–4.9 (4.2 ± 0.4)	—	4.0
HW (f)	4.6–5.8 (5.2 ± 0.5)	3.8–4.6 (4.1 ± 0.2)	3.6–5.2 (4.2 ± 0.4)	3.7–5.4 (4.2 ± 0.5)	4.0–5.3 (4.4 ± 0.4)	3.5, 4.2
HH (m)	3.5	3.0–3.8 (3.4 ± 0.4)	2.7–3.1 (2.9 ± 0.2)	2.8–3.6 (3.0 ± 0.3)	—	2.9
HH (f)	3.4–4.2 (3.9 ± 0.3)	2.9–3.4 (3.1 ± 0.2)	2.5–3.9 (3.0 ± 0.4)	2.5–3.9 (3.0 ± 0.5)	2.9–3.9 (3.3 ± 0.3)	2.5, 3.1
SnFa (m)	13.6	11.6–12.8 (12.0 ± 0.6)	10.9–12.2 (11.6 ± 0.4)	11.3–12.3 (11.8 ± 0.3)	—	11.9
SnFa (f)	11.7–14.1 (12.9 ± 0.9)	10.1–11.9 (11.2 ± 0.6)	10.9–12.5 (11.6 ± 0.5)	10.6–13.0 (11.7 ± 0.8)	11.3–13.2 (11.8 ± 0.6)	11.5, 12.1
ED (m)	0.9	1.0–1.1 (1.0 ± 0.1)	1.0–1.1 (1.0 ± 0.0)	0.8–0.9 (0.9 ± 0.0)	—	0.9
ED (f)	0.8–1.0 (0.9 ± 0.1)	0.8–1.1 (1.0 ± 0.1)	0.9–1.1 (1.0 ± 0.1)	0.8–0.9 (0.9 ± 0.1)	0.9–1.1 (1.0 ± 0.1)	1.0, 1.0

END (m)	1.9	1.1–1.7 (1.5 ± 0.3)	1.5–1.9 (1.7 ± 0.1)	1.6–1.9 (1.7 ± 0.1)	—	1.6
END (f)	1.8–2.2 (1.9 ± 0.1)	1.6–1.8 (1.7 ± 0.1)	1.5–1.9 (1.7 ± 0.1)	1.4–1.9 (1.7 ± 0.2)	1.6–1.9 (1.8 ± 0.1)	1.7, 1.9
SNL (m)	2.7	1.8–2.5 (2.2 ± 0.4)	2.1–2.5 (2.4 ± 0.1)	2.2–2.5 (2.4 ± 0.1)	—	2.3
SNL (f)	2.6–2.9 (2.7 ± 0.1)	2.2–2.6 (2.3 ± 0.1)	2.2–2.6 (2.4 ± 0.1)	2.1–2.7 (2.4 ± 0.2)	2.3–2.6 (2.4 ± 0.1)	2.4, 2.6
IND (m)	1.4	1.2–1.4 (1.3 ± 0.1)	1.2–1.4 (1.3 ± 0.1)	1.1–1.5 (1.3 ± 0.1)	—	1.1
IND (f)	1.1–1.4 (1.3 ± 0.1)	1.2–1.4 (1.3 ± 0.1)	1.1–1.5 (1.3 ± 0.1)	1.0–1.4 (1.3 ± 0.1)	1.1–1.5 (1.3 ± 0.1)	1.1, 1.3
FLL (m)	2.3	1.4–1.7 (1.6 ± 0.1)	1.1–1.5 (1.3 ± 0.1)	1.1–1.6 (1.3 ± 0.2)	—	1.4
FLL (f)	1.1–2.6 (1.7 ± 0.5)	1.2–1.7 (1.4 ± 0.1)	1.1–1.8 (1.3 ± 0.2)	1.1–1.9 (1.5 ± 0.3)	1.4–2.1 (1.7 ± 0.2)	1.1, 1.5
HLL (m)	2.9	2.3–3.0 (2.6 ± 0.4)	2.1–2.4 (2.3 ± 0.1)	2.4–2.8 (2.6 ± 0.2)	—	2.6
HLL (f)	2.5–3.1 (2.8 ± 0.2)	2.3–2.9 (2.6 ± 0.2)	2.0–2.7 (2.4 ± 0.2)	1.9–3.1 (2.7 ± 0.4)	2.5–3.6 (3.0 ± 0.3)	2.1, 2.7

Brachymeles lima sp. nov.

Figs. 4.3, 4.5

Holotype.—PNM 9756 (CDS Field No. 4050, formerly KU 324003), adult male, collected under rotting coconut husks in secondary-growth forest (10:00–12:30 hr) on 1 June 2009, in Barangay Common, Municipality of Tabaco City, Albay Province, Luzon Island, Philippines (13°14' N, 123°38' E; WGS-84), by J. Fernandez.

Paratopotypes.—Four adult males (KU 324015–6, PNM 9759–60), six adult females (KU 323087, 324005–7, 324009–10), and four juveniles (KU 324008, 324011, PNM 9757–58), collected between 1 and 23 June 2009.

Paratypes.—One adult male (CAS 152025) and two adult females (CAS 140065, 152026) collected on 16 December 1991, in an Abaca plantation, Barangay Labnig, Municipality of Malinao, Albay Province, Luzon Island, Philippines (13°22'38" N, 123°40'59" E; WGS-84), by C. A. Ross; two adult females (CAS-SU 24173, 24413) collected between 26 March and 22 April 1961, on Mt. Isarog, Bario Curry, Municipality of Pili, Camarines Sur Province, Luzon Island, Philippines (13°38'35" N, 123°21'4" E; WGS-84), by D. S. Rabor.

Diagnosis.—*Brachymeles lima* can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 46.4–66.1 mm); (2) limbs bidactyl; (3) limb length small; (4) supralabials six; (5) infralabials five or six; (6) suparciliaries six; (7) supraoculars five; (8) midbody scale rows 20–22; (9) axilla–groin scale rows 68–73; (10) paravertebral scale rows 85–90; (11) pineal eye spot present; (12) prefrontals not contacting on midline; (13) postnasals absent; (14) enlarged chin shields in three pairs; (15) nuchals enlarged; (16) fourth and fifth supralabial below eye; (17) mental and first infralabials fused or separated;

(18) auricular opening absent; (19) presacral vertebrae 46–49; and (20) uniform body color (Tables 4.4, 4.5).

Comparisons.—Characters distinguishing *Brachymeles lima* from all non-pentadactyl, limbed species of *Brachymeles* are summarized in Tables 4.4 and 4.5. *Brachymeles lima* most closely resembles *B. samarensis, B. apat, B. tatlo*, and populations of *B. bonitae*, the only other species to be bidactyl or have bidactyl populations. However, *B. lima* differs from these four taxa by having five or six infralabials (Table 4.5). *Brachymeles lima* further differs from *B. samarensis, B. apat, B. tatlo* by the presence or absence of mental and first infralabial fusion (Table 4.5); from *B. samarensis* by having a greater number of presacral vertebrae, and a tendancy towards a greater number of midbody, axilla–groin, and paravertebral scale rows (Table 4.5); from *B. apat* by having a smaller relative fore-limb length and a greater number of presacral vertebrae (Tables 4.4, 4.5); from *B. tatlo* by having a smaller relative fore-limb length, and a tendancy towards having fewer axilla–groin and paravertebral scale rows (Tables 4.4, 4.5); and from *B. bonitae* by having only bidactyl body forms, longer relative fore- and hind limb lengths, six supralabials, five or six infralabials, six supraciliaries, five supraoculars, and a tendancey towards fewer presacral vertebrae, axilla–groin, and paravertebral scale rows (Tables 4.4, 4.5).

Brachymeles lima can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all pentadactyl species of *Brachymeles* (*B. boholensis, B. boulengeri, B. bicolor, B. gracilis, B. kadwa, B. makusog, B. mindorensis, B. orientalis, B. schadenbergi, B. talinis, B. taylori, B. tungaoi, B. vindumi*) by having non-pentadactyl (vs. pentadactyl) limbs, shorter fore-limb lengths (less than 1.9 mm vs. greater than 5.9 mm), shorter hind limb lengths (less than 3.1 mm vs. greater than 10.3 mm), a narrower body (less than 5.1 mm vs. greater than 7.9 mm), and by the absence of a postnasal scale and auricular opening (vs. presence).

Description of holotype.—Details of the head scalation are shown in Figure 4.6. Adult male, body small, slender, SVL 60.2 mm; head weakly differentiated from neck, nearly as wide as body, HW 6.7% SVL, 104.9% HL; HL 33.1% SnFa; SnFa 19.3% SVL; snout short, bluntly rounded in dorsal and lateral profile, SNL 58.2% HL; ear completely hidden by scales; eyes small, ED 1.4% SVL, 22.6% HL, 55.4% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 124.0% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 22; paravertebral scale rows 85; axilla–groin scale rows 68; limbs short, poorly developed, with digits reduced to two claws on both fore-limbs and hind limbs, finger and toe lamellae absent; FLL 2.7% AGD, 2.1% SVL; HLL 6.1% AGD, 4.7% SVL [6.9]; tail nearly as wide as body, gradually tapered at end, TW 88.9% MBW, TL 65.6% SVL.

Rostral projecting onto dorsal snout to point just past poasterior edge of nasal, broader than high, in broad contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anteroventrally and posterodorsally; supranasals present, large, broadly separated; postnasals absent; prefrontals moderately separated; frontal octagonal, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 5× wider than anterior supraocular; supraoculars five; frontoparietals moderate, just barely separated by anterior point of interparietal in contact with frontal, each frontoparietal in contact with interior three supraoculars; interparietal large, its length roughly 1.5× midline length of frontoparietal, longer than wide, diamond-shaped, wider anteriorly; parietals as broad as frontoparietals, in broad contact behind interparietal; enlarged nuchals present; anterior and posterior loreals fused into single, enlarged loreal (Fig. 4.5), or distinct; one preocular; one presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to middle of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales; supralabials six, first 1.5× size of other supralabials, third, fourth, and fifth below eye; infralabials five (Fig. 4.5).

Mental wider than long, fused with first infralabials; postmental single, enlarged, its width less than width of mental; followed by three pairs of enlarged chin shields, first pair in broad medial contact, greater in width than third pair, narrower than second pair, second pair broadly separated by single medial scale, third pair separated by three medial scales (Fig. 4.5).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits wrapping around lateral edges of digits; lamellae absent; palmar surfaces of hands and plantar surfaces of feet with several small, irregular scales, each with irregular raised anterior edges; fore-limb digits equal in size; hind limb digits unequal in size, second digit greatest in length.

Coloration in preservative.—The ground color of the body is medium brown, with each dorsal scale having a dark, auburn streak on the anterior two thirds to one half of the scale with light brown posterior. Posterior edge of all body scales transparent. The streaks are present around the entire body. Ventral scales have more distinct, smaller streaks restricted to the anterior one-third to one half of scale. Ventral scales have sandy brown posterior coloration. Posterior portion of ventral caudal and subcaudal scales have lighter shade of sandy brown. Streaks on each individual scale consist of four to five longitudinal thin stripes of auburn pigment. Forelimb and hind limb scales are dark shade of brown with weakly defined scale boundaries. Auburn streaks are more dominant on precloacal scales, giving them a slightly darker appearance. Head scales have mottled light and dark brown coloration, matching dorsal body scales. Supraocular scales possess the darkest brown coloration of all head scales with brown umber color. The rostral, nasal, supranasal, and first supralabial scales have a cream coloration, lacking any brown color. The mental, infralabial, postmental, and chin shield scales are cream with light brown mottling.

Coloration in life.—Coloration in life is unrecorded; however, because *Brachymeles* specimens do not change significantly during preservation (CDS, RMB personal observation), we suspect that the preserved coloration and patterns are much like those in life.

Variation.—Morphometric variation of the series is summarized in Table 4.6. A single instance of digit variation was observed, where one specimen (KU 324006) has three fore-limb claws and two hind limb claws. We observed variation in the degree of head scale contact and the number of infralabials: (1) frontoparietals were observed in point contact medially for a single specimen (KU 324003), in moderate to broad contact medially for eleven specimens (CAS-SU 24173, 24413, CAS 140065, KU 323087, 324006–8, 324011–3, 324018), and separated for eight specimens (CAS 152025–6, KU 324005, 324014–6, 324009–10); (2) parietals were observed in point contact medially for a single specimen (CAS-SU 24413), in moderate to broad contact medially for seventeen specimens (CAS-SU 24173, CAS 140065, CAS 152025–6, KU 323087, 324003, 324005–9, 324011, 324013–6, 234018), and separated for two specimens (KU 324010, 324012); (3) first pair of enlarged chin shiels were observed in point contact medially for a single specimen (CAS 152025), in moderate to broad contact medially for seventeen specimens (CAS-SU 24173, 24413, CAS 140065, 152026, KU 324003, 324005–13, 324016, 324018), and separated in three specimens (KU 324014–5, 323087); (4) the number of infralabials varied among the type series, with eight specimens observed to have six infralabials

(CAS-SU 24413, KU 324009–14, 324018), and twelve observed to have five infralabials (CAS-SU 24173, CAS 140065, 152025–6, KU 323087, 324003, 324005–8, 324015–6).

Additionally, the degree of fusion between loreals, and between the mental and 1st infralabials, was observed to vary in the type series. All specimens examined have two loreals with the exception of a single specimen (KU 324003) with single, enlarged loreals on both sides of the head. Eleven specimens were observed with enlarged mental scales resulting from fusion with the 1st infralabial on both sides of the head (CAS-SU 24173, CAS 152025–6, KU 323087, 324003, 324005–8, 324015–6), a single specimen was observed with fused scales only on the right side of the head (CAS 140065), and eight specimens were observed to have distinct mentals and infralabials, with no scale fusion (CAS-SU 24413, KU 324009–14, 324018).

Distribution.—Brachymeles lima is known only from the central Bicol Peninsula of Luzon Island (Fig. 4.3).

Ecology and natural history.—Brachymeles lima occurs in agricultural habitats, as well as in disturbed and secondary-growth forest, and is found in sympatry with *B. boulengeri* and *B. makusog*. Three additional species of *Brachymeles* have also been recorded from the Bicol Peninsula of Luzon Island: *B. kadwa*, *B. lukbani*, and *B. tatlo*.

Sympatric lizard species occurring in the Bicol Peninsula include: (Agamidae) *Bronchocela cristatella, Draco spilopterus, Gonocephalus sophiae, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus philippinicus, Hemidactylus frenatus, H. platyurus, Gehyra mutilata, Gekko gecko, G. mindorensis, Luperosaurus cumingii, Pseudogekko smaragdina, P. compressicorpus*; (Scincidae) *Emoia atrocostata, Eutropis multicarinata borealis, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella pulchella, Sphenomorphus abdictus abdictus, S. decipiens, S. cumingi, Sphenomorphus jagori, S. laterimaculatus, S. leucospilos, S. steerei, Tropidophorus* *grayi*; (Varanidae) *Varanus marmoratus, V. olivaceus.*

Etymology.—The specific epithet is chosen in reference to the biogeographically and culturally distinct Bicol Region of southern Luzon Island (Albay, Camarines Norte, Camarines Sur, Catanduanes and Sorsogon Provinces). Inhabited by peaceful and particularly hospitable *Bicolanos*, the unique peninsula is home to many dozens of endemic vertebrates, delicious local cuisine, unique linguistic stock, and rich cultural traditions. Suggested common name: Bicol Slender Skink.

Brachymeles apat sp. nov.

Figs. 4.3, 4.5

Holotype.—PNM 9761 (CDS Field No. 5255, formerly KU 324023), adult female, collected under rotting coconut husks in secondary-growth forest (10:00–12:30 hr) on 8 October 2009, in Barangay Palta Small, Municipality of Virac, Catanduanes Province, Catanduanes Island, Philippines (13°34'44" N, 124°13'52" E; WGS-84), by J. Fernandez.

Paratopotypes.—Eight adult females (KU 306311, 308077, 324019–20, 324025–26, PNM 9562–63) and one juvenile (KU 324021) collected between 4 and 7 June 2009 by CDS and J. Fernandez.

Diagnosis.—*Brachymeles apat* can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 54.0–64.4 mm); (2) limbs bidactyl; (3) limb length small; (4) supralabials six; (5) infralabials six; (6) suparciliaries six; (7) supraoculars five; (8) midbody scale rows 21–22; (9) axilla–groin scale rows 68–72; (10) paravertebral scale rows 85–89; (11) pineal eye spot present; (12) prefrontals not contacting on midline; (13) frontoparietals contact; (14) postnasals absent; (15) enlarged chin shields in three pairs; (16)

nuchals enlarged; (17) fourth and fifth supralabial below eye; (18) auricular opening absent; (19) presacral vertebrae 45; (20) non-fusion of mental and first infralabials; (21) non-fusion of loreals; and (22) uniform body color (Tables 4.4, 4.5).

Comparisons.—Characters distinguishing *Brachymeles apat* from all non-pentadactyl, limbed species of *Brachymeles* are summarized in Tables 4.4 and 4.5. *Brachymeles apat* most closely resembles *B. samarensis, B. lima, B. tatlo*, and populations of *B. bonitae*, the only other species to be bidactyl or have bidactyl populations. However, *B. apat* can be distinguished from *B. samarensis* by having non-fusion of the loreals and a tendancy towards a greater number of axilla–groin scale rows (Table 4.5); from *B. lima* by having a greater relative fore-limb length, fewer presacral vertebrae, six infralabials, the presence of contact between frontoparietals, the presence of contact between the first pair of enlarged chin shields, non-fusion of the loreals, and non-fusion of the mental and first infralabials (Tables 4.4, 4.5); from *B. tatlo* by having fewer presacral vertebrae, a greater number of midbody scale rows, fewer axilla–groin and paravertebral scale rows, and the presence of contact between the first pair of enlarged chin shields (Table 4.5); and from *B. bonitae* by having only bidactyl body forms, longer relative fore- and hind limb lengths, fewer presacral vertebrae, fewer axilla–groin and paravertebral scale rows, six supralabials, six infralabials, six supraciliaries, five supraoculars, the presence of contact between frontoparietals, the presence of contact between the first pair of enlarged chin shields, and non-fusion of the mental and first infralabials (Tables 4.4, 4.5).

Brachymeles apat can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all pentadactyl species of *Brachymeles* (*B. boholensis, B. boulengeri, B. bicolor, B. gracilis, B. kadwa, B. makusog, B. mindorensis, B. orientalis, B. schadenbergi, B. talinis, B. taylori, B. tungaoi, B. vindumi*) by having non-pentadactyl (vs. pentadactyl) limbs, shorter fore-limb lengths (less than 2.1 mm vs. greater than 5.9 mm), shorter hind limb lengths (less than 3.6 mm vs. greater than 10.3 mm), a narrower body (less than 5.4 mm vs. greater than 7.9 mm), and by the absence of a postnasal scale and auricular opening (vs. presence).

Description of holotype.—Details of the head scalation are shown in Figure 4.6. Adult female, body small, slender, SVL 60.2 mm; head weakly differentiated from neck, nearly as wide as body, HW 7.0% SVL, 107.1% HL; HL 33.8% SnFa; SnFa 19.2% SVL; snout short, bluntly rounded in dorsal and lateral profile, SNL 63.0% HL; ear completely hidden by scales; eyes small, ED 1.7% SVL, 26.5% HL, 62.7% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 120.4% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 22; paravertebral scale rows 85; axilla–groin scale rows 68; limbs short, poorly developed, with digits reduced to two claws on both fore-limbs and hind limbs, finger and toe lamellae absent; FLL 3.4% AGD, 2.6% SVL; HLL 6.2% AGD, 4.7% SVL; tail as wide as body, tail tip regenerated, sharply tapered at end, TW 87.6% MBW, TL 75.6% SVL.

Rostral projecting onto dorsal snout to point in line with middle of nasal, broader than high, in contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anteroventrally and posterodorsally; supranasals present, large, broadly separated; postnasals absent; prefrontals moderately separated; frontal octagonal-shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anterior supraocular; supraoculars five; frontoparietals large, in broad medial contact, each frontoparietal in contact with interior three supraoculars; interparietal moderate, its length equal to midline length of frontoparietal, longer than wide, diamond-shaped, wider anteriorly; parietals narrower than frontoparietals, in broad contact behind interparietal;

nuchals enlarged; two loreals, decreasing in size from anterior to posterior, anterior loreal about as long as and slightly higher than posterior loreal; one preocular; one presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending nearly to middle of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales; supralabials six, first 2× size of other supralabials, third, fourth, and fifth below eye; infralabials six (Fig. 4.5).

Mental wider than long, fused with first infralabials; postmental single, enlarged, its width greater than width of mental; followed by three pairs of enlarged chin shields, first pair in broad medial contact, its width greater than width of third pair, narrower than second pair, second pair broadly separated by single medial scale, third pair separated by three medial scales (Fig. 4.5).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits wrapping around lateral edges of digits; lamellae absent; palmar surfaces of hands and plantar surfaces of feet with several small, irregular scales, each with irregular raised anterior edges; fore-limb digits equal in size; hind limb digits unequal in size on right foot, second digit greatest in length, digits absent on left foot.

Coloration in preservative.—The ground color of the body is medium brown, with each dorsal scale having a dark, auburn streak on the anterior two thirds to one half of the scale with light brown posterior. Posterior edge of all body scales transparent. The streaks are present around the entire body. Ventral scales have lighter color, with auburn streaks in anterior and light cream in posterior. Caudals and subcaudals match the bordering body scales. Streaks on each individual scale consist of four to seven longitudinal thin streaks of auburn with smudges of auburn between streaks. Forelimb and hind limb scales are brown and have darker coloration than their surrounding body scales. Forelimb and hind limb scales have weakly defined scale boundaries. Precloacal scale coloration matches surrounding ventral scale coloration. Head scales have mottled light and dark brown coloration that match dorsal body scales. Supraocular scales possess the darkest brown coloration of all head scales with brown umber color. The rostral, nasal, supranasal, and first supralabial scales possess a cream color. The other supralabials have a slightly darker, gray cream coloration. The mental, postmental, and chin shield scales are mottled brown on a light cream background that match bordering body scales.

Coloration in life.—Ground color of body medium to dark brown; streaks of darker pigmentation on body dark-brown.

Variation.—Morphometric variation of the series is summarized in Table 4.6. We observed no variation among the type series in digit number, head scale counts, or in the degree of head scale contact.

Distribution.—Brachymeles apat is known only from Catanduanes Island (Fig. 4.3).

Ecology and natural history.—Brachymeles apat occurs in residential and agricultural habitats, as well as in disturbed and secondary-growth forest. No original, low elevation forest remains on Catanduanes Island, but we assume the species once also occurred in first growth forest at low elevations. Individuals have been observed under piles of rotting coconut husks, in the rotting material within fallen logs, and in loose soil and leaf litter surrounding the root networks of trees. This species occurs sympatrically with the pentadactyl species, *B. makusog*, and the limbless species, *B. minimus*. On Catanduanes Island, both *B. makusog* and *B. minimus* have only been observed in disturbed, secondary-growth forest, whereas *B. apat* appears to be a habitat generalist.

Sympatric lizard species occurring on Catanduanes Island include: (Agamidae) *Bronchocela cristatella, Draco spilopterus, Gonocephalus sophiae, Hydrosaurus pustulatus*; (Gekkonidae)

Cyrtodactylus philippinicus, Hemidactylus frenatus, H. platyurus, Gehyra mutilata, Gekko gecko, G. mindorensis, Luperosaurus cumingii, Pseudogekko smaragdina, P. compressicorpus; (Scincidae) *Dasia atrocostata, Eutropis multicarinata borealis, E. indepresa, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella pulchella, Sphenomorphus abdictus, S.decipiens, S.cumingi, S.jagori, S. laterimaculatus, S. lawtoni, S. leucospilos, S.steerei, Tropidophorus grayi*; (Varanidae) *Varanus marmoratus, V. olivaceus.*

Etymology.—The specific epithet is chosen in recognition of the Catanduanes indigenous people's group for which the first adopted name for the island, "Isla de Apat," was coined. The name was adopted by the Spanish conquistadores who encountered the original Catanduanes tribes living in thatched huts called "apat." Suggested common name: Catanduanes Slender Skink.

Brachymeles tatlo sp. nov.

Figs. 4.3, 4.4

Holotype.—PNM 9764 (CDS Field No. 4099, formerly KU 324017), adult male, collected under pile of rotting coconut husks in secondary-growth forest (10:00–12:30 hr) on 18 June 2009, in the Municipality of Irosin, Sorsogon Province, Luzon Island, Philippines (15°50' N, 123°55' E; WGS-84), by J. Fernandez.

Paratypes.—Adult female (TNHC 62469) collected in a rotting log on ridge above lake Bulusan on 24 November 2001, 500–700 m elevation, Mt. Balusan National Park, Barangay San Roque, Municipality of Irosin, Sorsogon Province, Luzon Island, Philippines, by RMB and B. Fernandez; adult female (PNM 4856) collected 1 July 1995, in Barangay Salvacion, Municipality of Santa Magdalena, Sorsogon Province, Luzon Island, Philippines, by R. V. Sison.

Diagnosis.—*Brachymeles tatlo* can be distinguished from congeners by the following combination of characters: (1) body size small (SVL 54.0–60.0 mm); (2) limbs bidactyl; (3) limb length small; (4) supralabials six; (5) infralabials six; (6) suparciliaries six; (7) supraoculars five; (8) midbody scale rows 20; (9) axilla–groin scale rows 73–77; (10) paravertebral scale rows 90–94; (11) pineal eye spot present; (12) prefrontals not contacting on midline; (13) frontoparietals contact; (14) postnasals absent; (15) enlarged chin shields in three pairs; (16) nuchals elnlarged; (17) fourth and fifth supralabial below eye; (18) auricular opening absent; (19) presacral vertebrae 47–48; (20) non-fusion of mental and first infralabials; (21) non-fusion of loreals; and (22) uniform body color (Tables 4.4, 4.5).

Comparisons.—Characters distinguishing *Brachymeles tatlo* from all non-pentadactyl, limbed species of *Brachymeles* are summarized in Tables 4.4 and 4.5. *Brachymeles tatlo* most closely resembles *B. samarensis, B. lima, B. apat*, and populations of *B. bonitae*, the only other species to be bidactyl or have bidactyl populations. However, *B. tatlo* can be distinguished from *B. samarensis* by having a greater number of presacral vertebrae, a greater number of axilla–groin and paravertebral scale rows, and non-fusion of the mental and the first infralabials (Table 4.5); from *B. lima* by having a greater relative fore-limb length, six infralabials, non-fusion of the mental and the first infralabials, non-fusion of the loreals, a tendancy towards a greater number of axilla–groin and paravertebral scale rows, and by the presence of contact between frontoparietals (Tables 4.4, 4.5); from *B. apat* by having a greater number of presacral vertebrae, fewer midbody scale rows, and a greater number of axilla–groin and paravertebral scale rows (Table 4.5); and from *B. bonitae* by having only bidactyl body forms, longer relative fore- and hind limb lengths, fewer midbody scale rows, six supralabials, six infralabials, six supraciliaries, five supraoculars, the presence of contact between frontoparietals, anda tendancy towards fewer presacral vertebrae, axilla–groin, and paravertebral scale rows (Tables 4.4, 4.5).

Brachymeles tatlo can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all pentadactyl species of *Brachymeles* (*B. boholensis, B. boulengeri, B. bicolor, B. gracilis, B. kadwa, B. makusog, B. mindorensis, B. orientalis, B. schadenbergi, B. talinis, B. taylori, B. tungaoi, B. vindumi*) by having non-pentadactyl (vs. pentadactyl) limbs, shorter fore-limb lengths (less than 2.1 mm vs. greater than 5.9 mm), shorter hind limb lengths (less than 3.6 mm vs. greater than 10.3 mm), a narrower body (less than 5.4 mm vs. greater than 7.9 mm), and by the absence of a postnasal scale and auricular opening (vs. presence).

Description of holotype.—Details of the head scalation are shown in Figure 4.5. Adult male, body small, slender, SVL 56.8 mm; head weakly differentiated from neck, nearly as wide as body, HW 7.0% SVL, 103.6% HL; HL 32.4% SnFa; SnFa 20.9% SVL; snout short, bluntly rounded in dorsal and lateral profile, SNL 59.2% HL; ear completely hidden by scales; eyes small, ED 1.6% SVL, 24.2% HL, 59.6% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 125.2% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 20; paravertebral scale rows 90; axilla–groin scale rows 73; limbs short, poorly developed, with digits highly reduced to two small claws on both fore-limbs and hind limbs, finger and toe lamellae absent; FLL 3.3% AGD, 2.5% SVL; HLL 5.9% AGD, 4.5% SVL; tail nearly as wide as body, gradually tapered at end, TW 91.5% MBW, TL 79.5% SVL.

Rostral projecting onto dorsal snout to point just past posterior edge of nasal, broader than high, in broad contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anterodorsally and posteroventrally; supranasals present, large, broadly separated; postnasals absent; prefrontals broadly separated; frontal octagonal-shaped, its anterior margin in broad contact with frontonasal, in contact with first two anterior supraoculars, 5× wider than anterior supraocular; supraoculars five; frontoparietals large, in moderate medial contact, each frontoparietal in contact with interior three supraoculars; interparietal large, its length greater than midline length of frontoparietal, longer than wide, diamond-shaped, wider anteriorly; parietals as broad as frontoparietals, in broad contact behind interparietal; nuchals enlarged; two loreals, decreasing in size from anterior to posterior, anterior loreal about as long as and slightly higher than posterior loreal; one preocular; one presubocular; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to middle of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales; supralabials six, first 2× size of other supralabials, third, fourth, and fifth below eye; infralabials six (Fig. 4.4).

Mental wider than long, fused with first infralabials; postmental single, enlarged, its width narrower than width of mental; followed by three pairs of enlarged chin shields, first pair in broad medial contact, its width greater than width of third pair, narrower than second pair, second pair broadly separated by single medial scale, third pair separated by three medial scales (Fig. 4.4).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits wrapping around lateral edges of digits; lamellae absent; palmar surfaces of hands and plantar surfaces of feet with several small, irregular scales, each with irregular raised anterior edges; fore-limb digits absent on left hand, highly reduced to two small claw tips on right hand; hind limb digits unequal in size, first digit highly reduced to small claw tip, second digit greatest in length.

Coloration in preservative.—The ground color of the body is medium brown, with each dorsal scale having a dark, auburn streak on the anterior one third to one half of the scale with light brown posterior. Streaks on each individual scale consist of four to six longitudinal thin streaks of auburn with smudges of auburn between streaks. The streaks are present around the entire body. Posterior edge of all body scales transparent. Ventral scales have more distinct streaks, with sandy brown color posterior. Forelimb and hind limb scales are same shade of color as caudal scales. Scales are light sandy brown with brown mottling. Scale boundaries more clearly seen on hind limbs than on forelimbs. Precloacal scales match surrounding ventral scales. Head scales have mottled light and dark brown coloration and slightly lighter appearance compared with bordering dorsal body scales. Supraocular scales possess the darkest brown coloration of all head scales with umber brown color. The rostral, nasal, supranasal and supralabial scales have the lightest coloration of beige-umber. The mental and infralabial scales are cream. The chin shields and postmental scale are cream with slight brown mottling.

Coloration in life.—Coloration in life is unrecorded; however, because *Brachymeles* specimens do not change significantly during preservation (CDS, RMB personal observation), we suspect that the preserved coloration and patterns are much like those in life.

Variation.—Morphometric variation of the series is summarized in Table 4.6. We observed no variation among the type series in digit number, head scale counts, or in the degree of head scale contact.

Distribution.—Brachymeles tatlo is known only from the southern Bicol Peninsula (Fig. 4.3).

Ecology and natural history.—Brachymeles tatlo occurs in disturbed and secondary-growth forest, and is found in sympatry with *B. boulengeri*; however, *B. tatlo*, *B. kadwa*, *B. lukbani*, and *B. makusog* are also recognized to occur on the Bicol Peninsula of Luzon Island.

Sympatric lizard species occurring in the Bicol Peninsula include: (Agamidae) *Bronchocela cristatella, Draco spilopterus, Gonocephalus sophiae, Hydrosaurus pustulatus*; (Gekkonidae) *Cyrtodactylus philippinicus, Hemidactylus frenatus, H. platyurus, Gehyra mutilata, Gekko gecko, G. mindorensis, Luperosaurus cumingii, Pseudogekko smaragdina, P. compressicorpus*; (Scincidae) *Dasia atrocostata, Eutropis multicarinata borealis, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella pulchella, Sphenomorphus abdictus abdictus, S. decipiens, S. cumingi, S. jagori, S. laterimaculatus, S. leucospilos, S. steerei, Tropidophorus grayi*; (Varanidae) *Varanus marmoratus, V. olivaceus.*

Etymology.—The name of the new species is derived from the Latin root word “brevis”, meaning short, and “dactylus,” meaning digit, to represent the species’ small, highly reduced digits. Suggested common name: Southern Bicol Slender Skink.

DISCUSSION

Analyses of the two mitochondrial genes (ND1, ND2) and two nuclear loci (α-enolase, PTGER4) resulted in topologies with high ML bootstrap support and posterior probabilities for six lineages formerly part of the *Brachymeles samarensis* species complex (Fig. 4.2). No analyses supported the monophyly of species formerly part of *Brachymeles samarensis* (*B. isa, B. dalawa, B. lima, B. apat, B. tatlo, and B. samarensis*). However, all analyses show strong support for the sister relationship between *B. isa* and *B. dalawa*, as well as for the clade including the Greater Luzon PAIC species (*B. lima, B. apat, B. tatlo*; Fig. 4.2). All nodes received high support and all analyses resulted in identical topologies.

In addition to the supported paraphyly of species formerly part of *Brachymeles samarensis*, several other recognized species were recovered as part of the *B. samarensis* Complex.

Brachymeles cebuensis, one of only two recognized species to have unequal numbers of fore- and hind limb digits, was supported to be part of a clade of species (*B. cebuensis* + *B. isa* + *B. dalawa*) with three fingers and two or three toes (Fig. 4.2). Sister to this three-finger clade, all analyses recovered *B. minimus* and *B. lukbani*, both limbless species, nested within a didactyl clade of species formerly part of *B. samarensis* (true *B. samarensis, B. lima, B. apat, B. tatlo*; Fig. 4.2). All three previously recognized species (*B. cebuensis, B. lukbani, B. minimus*) have geographical distributions that overlap, or are in close proximity to, the known ranges of other species in the *B. samarensis* Complex (Fig. 4.3).

The six species recognized in this paper are supported to be part of two clades with different body plans (Fig. 4.2). One of these clades, made up of *B. cebuensis*, *B. isa*, and *B. dalawa*, consists of species with three digits on their fore-limbs and two to three digits on their hind limbs (Fig. 4.2). In contrast, the remaining species (*B. samarensis*, *B. tatlo, B. apat, B. lima*) are part of a second clade consisting of limbless and bidactyl body forms (Fig. 4.2). Two of the five recognized species of limbless *Brachymeles* (*B. minimus* and *B. lukbani*) are sister to clade of bidactyl species from the Bicol Peninsula of Luzon Island and Catanduanes Island. As previously recognized, *Brachymeles samarensis* spanned two distinct, recognized faunal regions: Greater Luzon PAIC and Greater Mindanao PAIC. Given this formerly wide geographical distribution, it is not surprising that populations between the two PAICs are distinct; however, we were surprised to discover high levels of intra-PAIC species diversity (Fig. 4.2).

The species recognized in this paper increase the total number of known species of *Brachymeles* to 30, and all but two of these are endemic to the Philippines. The species-level diversity within the genus has doubled in the last two years as the result of large-scale sampling efforts across the Philippines and the detailed analyses of morphological variation among species and populations (Siler, 2010; Siler et al., 2009a, 2010a,b; Siler and Brown, 2010, 2011; Siler et al., 2011, in press a,b,c,d). *Brachymeles* has long been considered a small clade of SE Asian lizards, and estimates of species diversity have remained nearly constant for more than 30 years (but see Brown and Alcala, 1995). This vast underestimation of true diversity within the genus is a testament to the extent of morphological similarity among species and a lack of systematic studies of the group.

Despite the past taxonomic assessments (review: Brown and Alcala, 1980), it comes as little surprise that allopatric populations of "*B. samarensis*" from the Luzon and Mindanao Pleistocene Aggregate Island Complexes have proven with improved sampling to be morphologically diagnosable independent lineages. This study adds to a growing line of evidence suggesting a need for reevaluation of amphibian and reptile species boundaries within the Philippines. Few examples exist of truly "widespread" reptile species that have geographic distributions spanning recognized zoogeographic boundaries, and as is often the case, these species frequently turn out to constitute multiple evolutionary lineages (McGuire and Alcala, 2000; Brown et al., 2009; Gaulke et al, 2007; Welton et al., 2009, 2010a,b; Siler et al., 2010c, 2011). The exceptions, in contrast, appear to be invasive species and human-mediated range expansions (Diesmos et al., 2006; Brown et al., 2010).

All species of *Brachymeles* live a semi-fossorial existence, specializing in dry rotting material inside and underneath fallen decomposing logs, leaf litter, and other forest floor detritus. Many are habitat specialists found exclusively in rotting logs, loose soil, or leaf litter, whereas others are common beneath piles of rotting coconut husks in disturbed, agricultural habitat. We assume that the species now found in residential and agricultural areas were once native to forested habitats and were possibly forest edge specialists.

Prior to recent, focused survey efforts, the modest sample sizes of specimens of *Brachymeles* available in museum collections limited appropriate, lineage-based species delimitations. Although the rarity of *Brachymeles* in collections may be due to their secretive, semi-fossorial lifestyle, focused survey efforts that target the appropriate microhabitat have proven effective in sampling *Brachymeles* in their native environments (CDS pers. observ.; Siler and Brown, 2010; Siler et al., in press a,b,c,d).

Recent fine- and broad-scale phylogenetic analyses of species of the genus *Brachymeles* have made it apparent that species diversity in the clade has been considerably underestimated; accordingly, discovery of additional undocumented (possibly cryptic) diversity is anticipated in other species groups (e.g., Siler et al., 2009a, 2010a,b, in press a,b,c,d; Siler and Brown, 2010, 2011). A number of studies have shown that the evolution of a burrowing lifestyle is correlated with decreasing dispersal abilities (Selander et al., 1974; Patton and Yang, 1977; Patton and Feder, 1978; Nevo, 1979; Siler et al., 2011). Many *Brachymeles* lineages have experienced reduction or loss of limbs, which may further reduce vagility (Siler and Brown, 2010, 2011; Siler et al., 2011). Through time, reduced dispersal abilities and semi-fossorial lifestyles may lead to an increasingly patchy distributions, reduced gene flow among populations, and the accumulation of inter-population differences (Nevo, 1979). Still, the role that reduced dispersal abilities associated with fossoriality play on the dispersal abilities and diversification patterns of *Brachymeles* species remains unknown. Regardless of which processes produce species diversity, we suspect that additional species await discovery.

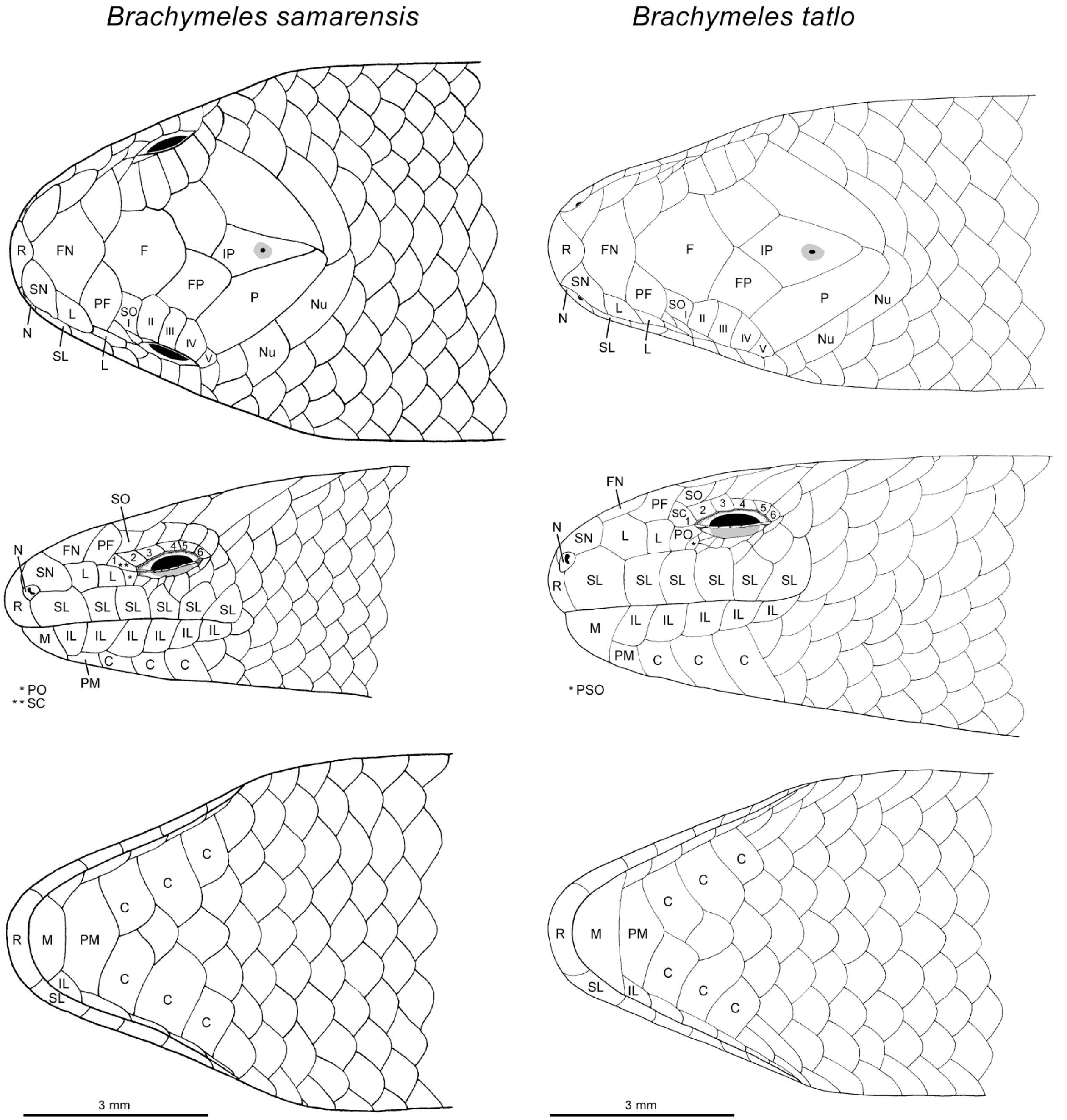
Following the recognition of *Brachymeles samarensis, B. lima, B. tatlo, B. apat, B. isa,* and *B. dalawa* there are now 13 non-pentadactyl, limbed species of *Brachymeles*. Of these, four species are bidactyl (*B. samarensis, B. tatlo, B. lima, B. apat*), four are tridactyl (*B. muntingkamay, B.*

tridactylus, B. isa, B. dalawa), and two are tetradactyl (*B. elerae, B. wrighti*). Additionally, two species have unequal fore- and hind limb digit numbers (*B.* cebuensis, 3/2; *B. pathfinderi*, 5/4), and populations of *B. bonitae* have been observed to have 0–2 fore- and hind limb digits. All non-pentadactyl species have smaller body sizes with the exception of *B. wrighti* (Taylor, 1925; Siler et al., in press b). Interestingly, the distribution of limbed, non-pentadactyl species in the Philippines is relatively uneven across the major biogeographic regions of the Philippines, with seven species known to occur in the Luzon Faunal Region, four in the Mindanao Faunal Region, two in the Visayan Faunal Region, and one in the Mindoro Faunal Region (Brown and Alcala, 1980, Brown and Alcala, 1995; Brown and Diesmos, 2002; Siler et al., 2010a).

Additionally, the distribution of total species diversity in the genus is also uneven, with 13 species known from the Luzon Faunal Region versus eight in the Mindanao Faunal Region, six in the Visayan Faunal Region, and only two and two in the Sulu archipelago and Mindoro Faunal Region respectively (Brown and Alcala, 1980; Brown and Alcala, 1995; Brown and Diesmos, 2002; Siler et al., 2009a, 2010a,b; Siler and Brown, 2010). New species discoveries on Luzon Island have occurred with consistency during the last two decades; given the island's complex mountain ranges (Sierra Madres, Cordillera, Zambales, Bicol Peninsula volcanoes) and geographic complexity (Defant et al., 1989; Yumul et al., 2009), the increase in the faunal region's diversity is likely to continue (Ross and Gonzales, 1992; Brown et. al. 1995*a,b*, 1999, 2000*a*; Linkem et al., 2010; Siler et al., 2009a, 2010a,b,c, in press c,d; Welton et al., 2010a,b). It is worth noting that efforts to survey Mindanao have been less extensive than efforts on Luzon; this may account for some of the differences in diversity between the regons—which may be artifacts of sampling biases.

At present there remains one polytypic species (*B. gracilis*) and one "widespread" species (*B. bonitae*) in the genus, both with distributions spanning boundaries between recognized faunal regions (Brown and Alcala, 1980; Siler and Brown, 2010; Siler et al., in press d). Closer investigation of island populations within each of these species may result in the discovery of new species diversity. Furthermore, recent phylogenetic studies of the genus *Brachymeles* have not supported the monophyly of either of these widespread species, an indication that taxonomic revisions are needed (Siler and Brown, 2011; Siler et al., 2011). As our understanding of the total diversity within *Brachymeles* increases, it is important that continued efforts be made to conduct surveys focused on rotting log and leaf litter microhabitats throughout the ranges of all species. Accurate data on the distributions of these species will allow for a complete assessment of the geographic ranges of the species and appropriate assessment of conservation status can be made. At present, all nine species of the *B. samarensis* Complex are known or believed to be common throughout their ranges. Although these species currently inhabit highly disturbed, agricultural and residential areas, no studies on the long-term effect of deforestation on populations of *Brachymeles* exist. Therefore, according to the IUCN categories and classification structure, we consider the conservation status of these species as "Least Concern (LC)," pending the collection of additional information that might suggest otherwise.

Figure 4.4. Illustration of head of adult female *Brachymeles samarensis* (KU 310849) and adult female *Brachymeles tatlo* (PNM 4856; formerly KU 324004) in dorsal, lateral, and ventral views. Taxonomically diagnostic head scales are labeled as follows: C, chin shield; F, frontal; FN, frontonasal; FP, frontoparietal; IL, infralabial; IP, interparietal; L, loreal; M, mental; N, nasal; Nu, nuchal; P, parietal; PF, prefrontal; PM, postmental; PN, postnasal; PO, preocular; PSO, presubocular; R, rostral; SC, supraciliary; SL, supralabial; SN, supranasal; and SO, supraocular. Roman numerals indicate scales in the supraocular series, with Arabic numbers indicating scales in the supraciliary series. Illustrations by CDS, AMF, and RMJ.

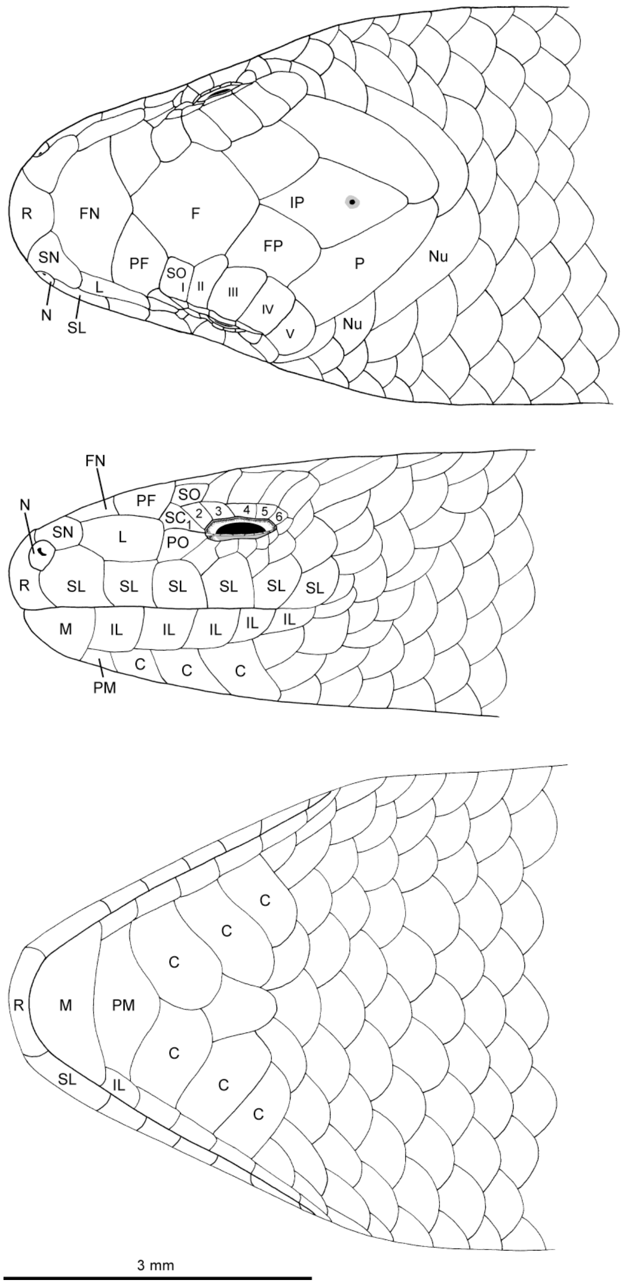


Brachymeles samarensis

Brachymeles tatlo

Figure 4.5. Illustration of head of adult male holotype *Brachymeles lima* (PNM 9756; formerly KU 324003) and adult female holotype *Brachymeles apat* (PNM 9761; formerly KU 324023) in dorsal, lateral, and ventral views. Labels for taxonomically diagnostic head scales follow those shown in Figure 4.4. Illustrations by CDS, AMF, and RMJ.

Brachymeles lima



Brachymeles apat

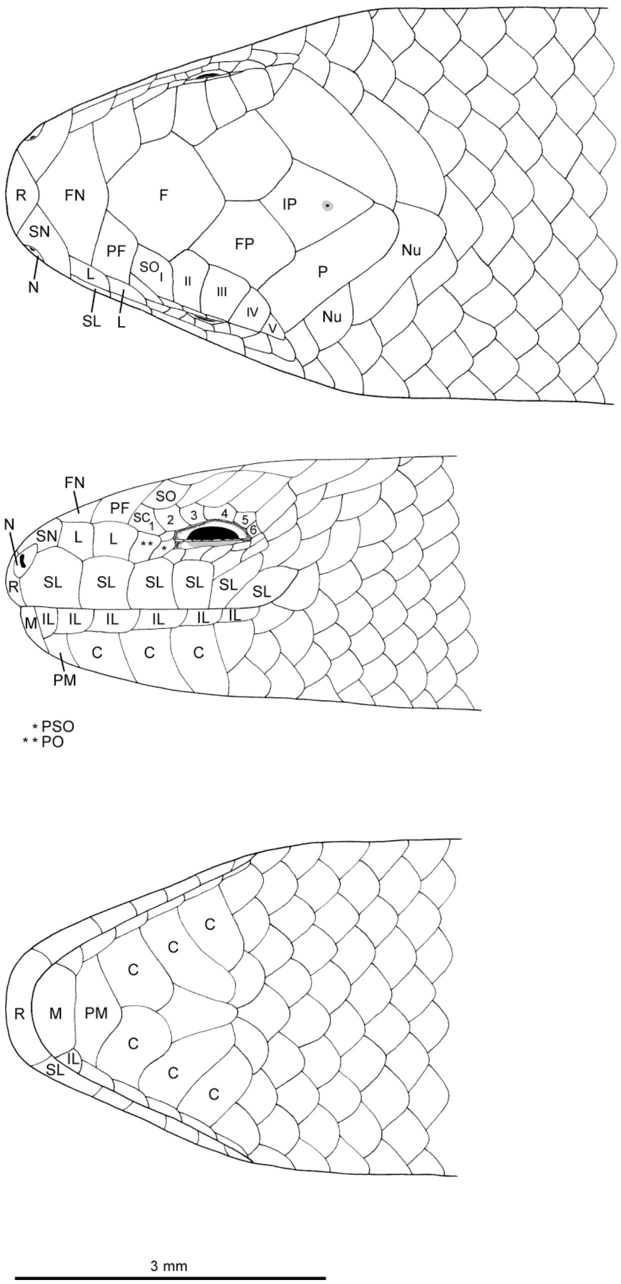
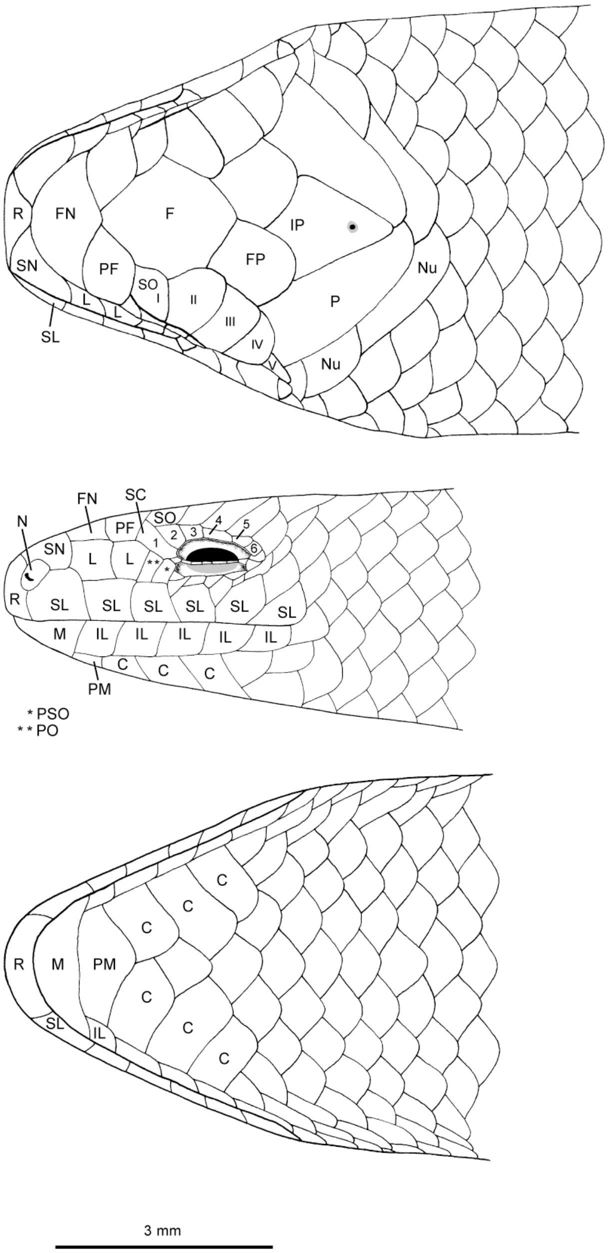


Figure 4.6. Illustration of head of adult female holotype *Brachymeles isa* (PNM 9746; formerly KU 311228) and adult male holotype *Brachymeles dalawa* (PNM 9749; formerly KU 320466) in dorsal, lateral, and ventral views. Labels for taxonomically diagnostic head scales follow those shown in Figure 4.4. Illustrations by CDS, AMF, and RMJ.

Brachymeles dalawa



Brachymeles isa

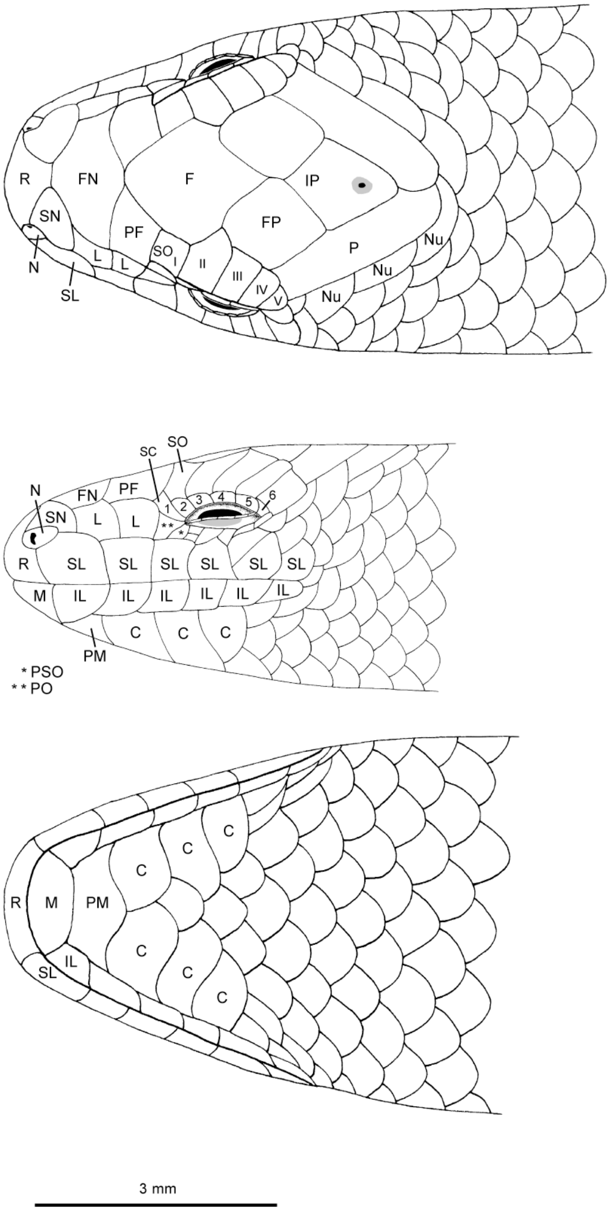
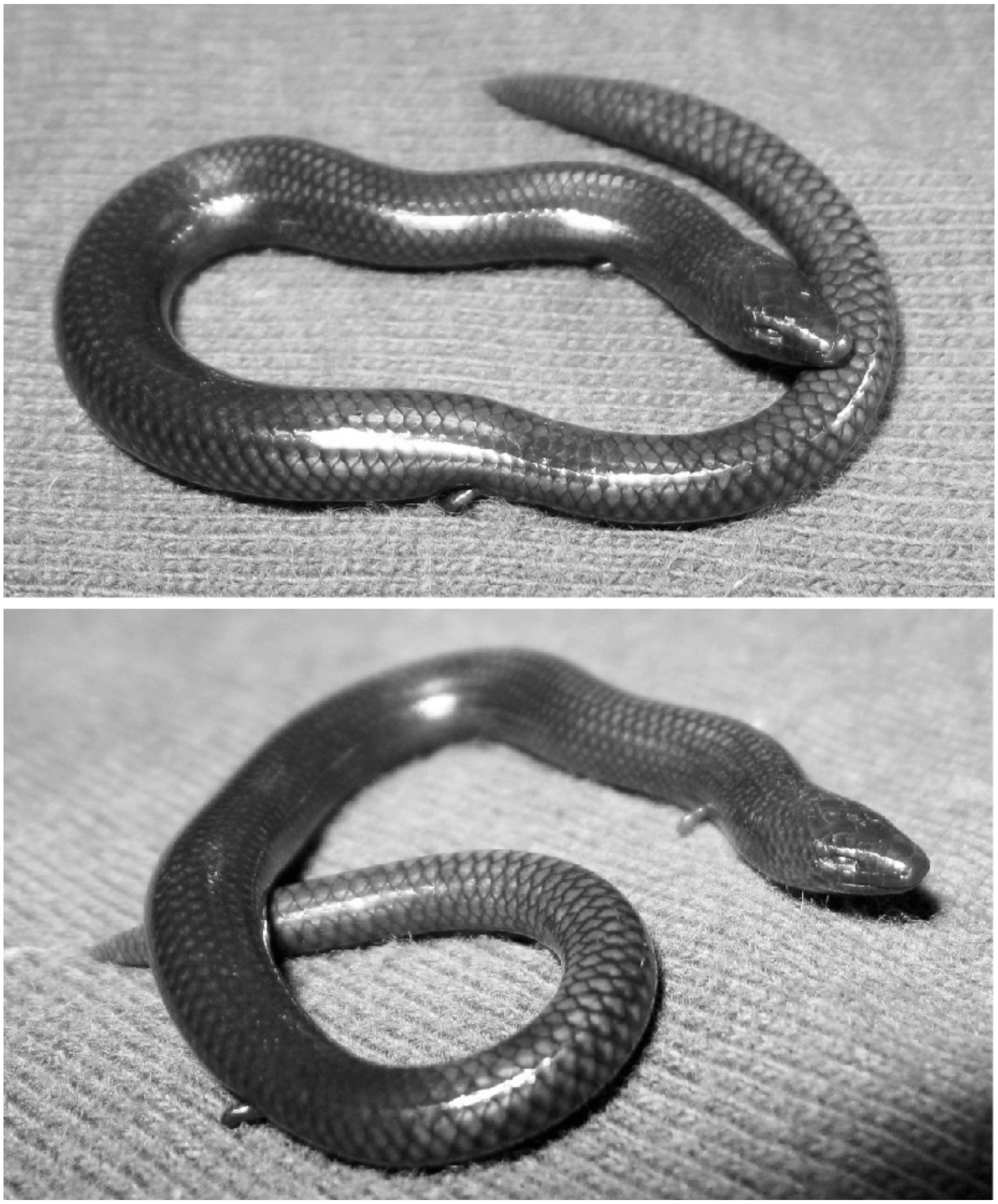


Figure 4.7. Photograph in life of *Brachymeles isa* (PNM 9746; formerly KU 311228), SVL = 59.1 mm. Photograph by CDS.

Figure 4.8. Photographs in life of *Brachymeles dalawa* (PNM 9749; formerly KU 320466), SVL = 56.3 mm. Photographs by CDS.



CHAPTER 5

Phylogeny-based species delimitation in Philippine slender skinks (Reptilia: Squamata: Scincidae: *Brachymeles*) III: taxonomic revision of the *Brachymeles gracilis* Complex, with description of three new species

Few genera of scincid lizards are known to possess species representing a full spectrum of body forms, from fully limbed, pentadactyl species to limbless species (see Siler and Brown, 2010, 2011; Siler et al., 2011). Within one of them, the genus *Brachymeles* Duméril and Bibron, 1839, all but two of the 30 recognized species are endemic to the Philippines, the exceptions being a single species (*B. apus*) from northern Borneo and another (*B. miriamae*) from Thailand (Brown and Alcala, 1980; Hikida, 1982; Siler et al., 2009a, 2010a,b, 2011, in press a,b,c; Siler, 2010; Siler and Brown, 2010, 2011). Thirteen species of *Brachymeles* are pentadactyl (*bicolor*, *boholensis, boulengeri*, *gracilis*, *kadwa, makusog, mindorensis, orientalis, schadenbergi*, *talinis, taylori, tungaoi,* and *vindumi*), thirteen are non-pentadactyl, with incompletely developed limbs and a reduced numbers of digits (*bonitae*, *cebuensis*, *elerae*, *muntingkamay, pathfinderi*, *samarensis*, *tridactylus*, *wright*, sp. nov. [Leyte Island; Siler et al., in press c], sp. nov. [Lapinig Group Islands; Siler et al., in press c], sp. nov. [Catanduanes Island; Siler et al., in press c], sp. nov. [Central Bicol Peninsula, Luzon Island; Siler et al., in press c], and sp. nov. [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c]), and five are entirely limbless (*apus*, *minimus, miriamae, lukbani,* and *vermis*).

The non-pentadactyl species have been the subject of recent studies which have documented a wide range of limb- and digit-reduced states, from minute limbs that lack full digits (*bonitae*, *cebuensis*, *muntingkamay, samarensis, tridactylus,* sp. nov. [Leyte Island; Siler et al., in press c], sp. nov. [Lapinig Group Islands; Siler et al., in press c], sp. nov. [Catanduanes Island; Siler et al., in press c], sp. nov. [Central Bicol Peninsula, Luzon Island; Siler et al., in press c], and sp. nov. [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c]), to moderately developed limbs with four to five digits on the hands and feet (*elerae, pathfinderi, wrighti*: Duméril and Bibron, 1839; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980; Taylor, 1917, 1918, 1925; Siler et al., 2009a, 2010b, 2011, in press a,b,c; Siler, 2010; Siler and Brown, 2010, 2011). All species are semi-fossorial and typically found in dry, rotting material inside or underneath decaying logs or in loose soil, forest floor detritus, and leaf litter. Most species in the genus are recognized from hot, lowland forests; however, several species do occur in cooler high elevation forests (e.g., *B. apus, B. elerae, B. wrighti*).

Named over 150 years ago (Duméril and Bibron, 1839), the genus reached 15 species by 1980 (Brown and Alcala, 1980) and only one additional species, *B. minimus*, a legless species, was described in invervening years (Brown and Alcala, 1995). We assume that until recent work, guided by extensive field based survey work combined with molecular phylogenetic studies, conservative body plans and external morphological features among species of *Brachymeles* led earlier reseachers to conclude that the genus was relatively species-poor (Taylor, 1917; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980).

Recent studies have revealed that this assessment of limited spercies diversity is cleally an underestimate. Phylogeny-based exercises in species delimitation have identified and revised numerous non-monophyletic species complexes within the Philippines (Siler et al., 2009a, 2010a,b, 2011, in press a,b,c; Siler, 2010; Siler and Brown, 2010, 2011). Additionally, several rare, mid-to-high elevation species long represented by only a few specimens (e.g., *Brachymeles bicolor, B. elerae, B. wrighti, B. pathfinderi*), have recently been rediscovered and redescribed as valid taxa (Siler, 2010; Siler et al., in press a,b). Together, these studies, coupled with increased sampling throughout the Philippines, and a new, robust molecular dataset now allows us to begin evalutating variation across the isolated populations of widespread species.

Recently, Siler and Brown (2010) revised two polytypic species (*B. boulengeri* and *B. schadenbergi*) and one widespread species (*B. talinis*), and inferred the presence of ten genetically and morphologically distinct allopatric evolutionary lineages (species). Following this study, Siler et al. (in press c) revised the *B. samarensis* Complex, restricting the range of *B. samarensis* to Samar Island only, and describing five new, non-pentadactyl species. Another another species, *B. bonitae*, is still recognized as having a widespread distribution (Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980) that spans historical faunal demarcations in the Philippines (Heaney, 1985; Brown and Guttman, 2002; Brown and Diesmos, 2002, 2009). Only a single polytypic species still is recognized (*B. gracilis*; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980); this lineage is the focus of the present study.

Taxonomic History

The genus *Brachymeles* was first described by Duméril and Bibron (1839) for the small, limb-reduced species *Brachymeles bonitae*. Three additional species (*Senira bicolor* [Gray, 1845], *Eumeces* (*Riopa*) *gracilis* [Fischer, 1885], *E.* (*R.*) *schadenbergi* [Fischer, 1885]) were transferred to the genus by Boettger (1886) and Boulenger (1887). Fischer's (1885) description of *E. gracilis* was based on single specimen with the collection No. 846 (reported to be deposited in the Dresden Museum), and only a single line drawing of the dorsal view of the head was provided (Fischer, 1885: plate III, Fig. 5.1). Three decades later, in Taylor's (1917) review of the genus, he incorrectly revised *B. gracilis* to include not only populations in the Mindanao

Faunal Region, but also populations on Negros and Mindoro islands (Fig. 5.1). At the time, Taylor did not have access to Fischer's (1885) original description, and based his evaluation on a series of 27 specimens from Negros and Mindoro, inferring that the specimen reported by Fischer (1885) from Mindanao was actually *B. schadenbergi* (*sensu* Siler and Bown, 2010). Taylor (1917) provided an illustration of the ventral view of head likely based on a specimen of *B. taylori* or *B. mindorensis*.

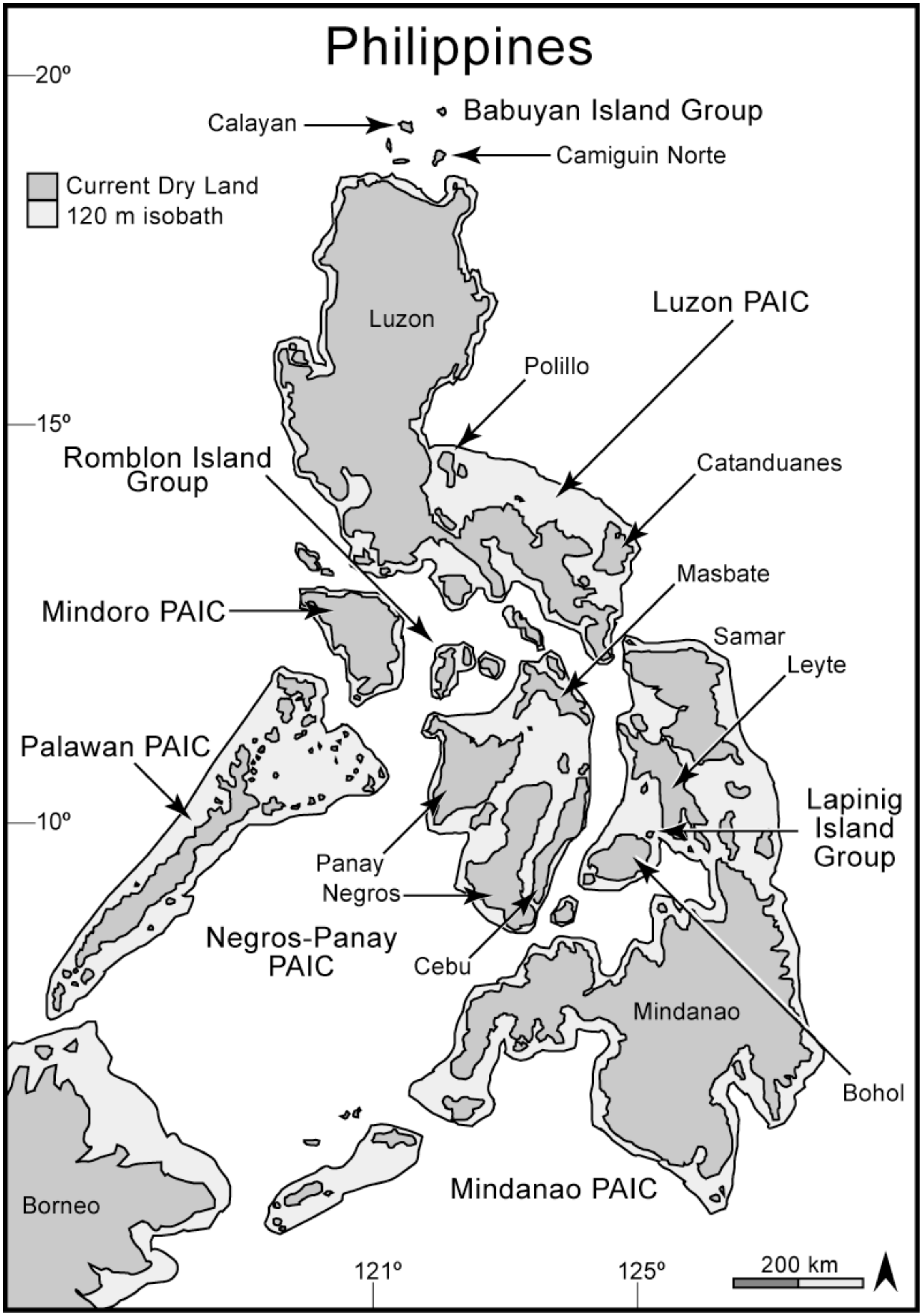
One year later, Taylor (1918) described *B. sampu* based on a single specimen from Bubuan Island of the Tapiantana Island Group off southern the coast of Basilan. He provided line drawings of the dorsal, lateral, and ventral profiles of the head of the type specimen. With what was known of the species diversity in the genus at the time, Taylor (1918) described *B. sampu* as "…another link in the chain of retrogression in the genus *Brachymeles*…between *Brachymeles schadenbergii* and *B. bicolor*." Taylor (1918) described the type specimen (Philippine Bureau of Science collection No. 1989:254) of *B. sampu*; this specimen was lost in the World War II firebombing of Manila (Brown and Alcala, 1978), as were 32 other type specimens of Philippine amphibians and reptiles (Welton et al., 2009). In a subsequent revision Taylor (1922a) placed *B. sampu* in the synonymy of *B. gracilis*. In this revision, Taylor used the original head profile line drawings of *B. sampu* to illustrate head scale patterns for *B. gracilis* (Taylor, 1922a:248), suggesting that he clearly considered *B. sampu* to be a junior synonym of *B. gracilis*.

Thirty years later, Brown (1956) described *B. gracilis taylori*, and included *B. boulengeri* as one of three subspecies of the polytypic species *B. gracilis*. Brown and Rabor's (1967) description of *B. gracilis boholensis* and *B. g. mindorensis* brought the number of subspecies within *B. gracilis* to five. It was not until 1980 that Brown and Alcala (1980) resurrected the polytypic species *B. boulengeri*, and included four subspecies (*B. b. boulengeri, B. b. boholensis,* *B. b. mindorensis, B. b. taylori*), all believed to be distinct from *B. gracilis*. Their restriction of *B. gracilis* to the southern and southeastern islands of the Philippines resulted in the recognition of only two subspecies, *B. gracilis gracilis* and *B. gracilis hilong* (Brown and Alcala, 1980).

This view has characterized the taxonomy of *B. gracilis* for the past 30 years. To date, *Brachymeles gracilis* remains a widespread species spanning most major islands of the Mindanao Pleistocene Aggregate Island Complex (PAICs; Brown and Guttman, 2002; Brown and Diesmos, 2002; Fig. 5.1). Widespread distributions such as this have been the focus of many recent studies (Brown et al., 2000a; Siler et al., 2010a,b, in press c; Siler and Brown, 2010; Welton et al., 2009, 2010a,b), which have revealed that few endemic Philippine reptiles actually possess broad distributions spanning these regional faunistic boundaries (review: Brown and Diesmos, 2009).

The goal of the present study is to revise the taxonomy of the *B. gracilis* complex such that individual units (species) represent independently evolving, cohesive lineage segments (sensu Simpson, 1961; Wiley 1978; Frost and Hillis, 1990; de Queiroz, 1998, 1999). Comprehensive examination of all recently collected specimens from throughout the known range of *B. gracilis*, and historically collected specimens available in museum collections, results in the reorganization of the species complex into six distinct evolutionary lineages (species). In this paper we provide a phylogenetic analysis and the first illustrations of five of these taxa, fully describe each species, and clarify taxonomic boundaries. We also provide information on each species' natural history, ecology, and geographic distribution and comment on additional, presently unrecognized putative new species.

Figure 5.1. Map of the Philippine islands, with island labels provided for islands with representative samples used for this study. The five recognized major Pleistocene Aggregate Island Complexes (PAICs), major island groups, and additional deep-water islands are labeled for reference. Current islands in the Philippines are shown in medium grey; light gray areas enclosed in black 120 m bathymetric contours indicate the hypothesized maximum extent of land during the mid- to late Pleistocene.


Philippines
20º
15º
10º
121º
125º
Calayan
Babuyan Island Group
Camiguin Norte
Current Dry Land
120 m isobath
Luzon
Luzon PAIC
Polillo
Romblon Island Group
Catanduanes
Masbate
Mindoro PAIC
Samar
Leyte
Palawan PAIC
Lapinig Island Group
Panay
Negros
Negros-Panay PAIC
Cebu
Mindanao
Bohol
Borneo
Mindanao PAIC
200 km

Materials and Methods

Field work, sample collection, and specimen preservation

Fieldwork was conducted on Camiguin Sur, Leyte, Mindanao, and Samar islands, all in the Philippines (Fig. 5.1) between 1991 and 2010. Specimens were collected between 900 and 1600 hr, euthenized in aqueous chloretone, dissected for genetic samples (liver preserved in 95% ethanol or flash frozen in liquid nitrogen), fixed in 10% formalin and eventually (< 2 mo) transferred to 70% ethanol. Specimens measured or sequenced in this study are deposited in the University of Kansas Natural History Museum (KU), the Texas Natural History Collections (TNHC) of the Texas Memorial Museum of the University of Texas at Austin, the Philippine National Museum (PNM), the Cincinnati Museum Center (CMC), the California Academy of Sciences (CAS), and the Museum of Comparative Zoology (MCZ) (Acknowledgments and Specimens Examined); voucher information corresponding to data from GenBank sequences is included in Table 5.1.

Taxon sampling and outgroup selection for phylogenetic analyses

Because our primary goal was to estimate phylogenetic relationships among the various populations of *Brachymeles gracilis* we sequenced 2–4 exemplars per sampled population. We included samples of *Plestiodon* and *Lygosoma*, as well as samples of *Brachymeles apus*, *B. bonitae*, and *B. miriamae*, as outgroup representatives based on relationships presented in a recent phylogenetic analyses of the genus *Brachymeles* (Siler et al., 2011). The results of Siler et al. (2011) revealed the *Brachymeles gracilis* species complex to be non-monophyletic, and we therefore included samples of *Brachymeles pathfinderi* to explore the sister group relationships within the *B. gracilis* complex. A total of 21 ingroup samples were used in phylogenetic inferences. Genetic samples of *B. sampu* were not available for inclusion.

DNA extraction, purification, and amplification

We extracted total genomic DNA from tissues (Table 5.1) using the modified guanidine thiocyanate extraction method of Esselstyn et al. (2008). The mitochondrial NADH Dehydrogenase Subunit 1 (ND1), NADH Dehydrogenase Subunit 2 (ND2), and the nuclear loci, Brain-derived Neurotrophic Factor (BDNF) and PTGER4, were completely sequenced for nearly all samples using the primers and protocols provided in Siler et al. (2011). We visualized amplified products on 1.0% agarose gels, then purified them with 1 µL of a 20% solution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ) on the following thermal cycler profile: 31 min at 37°, followed by 15 min at 80°. Upon successful amplification of targeted fragments, cycle-sequencing reactions were completed with the same primers and ABI Prism BigDye Terminator chemistry (Ver. 3.1; Applied Biosystems, Foster City, CA). Cycle-sequencing products were purified with Sephadex Medium (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). We analyzed purified products using an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems), and gene sequences were assembled with Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Alignment and phylogenetic analysis

An initial alignment was produced in Muscle v3.7 (Edgar, 2004), and manual adjustments were made in MacClade 4.08 (Maddison and Maddison, 2005). No instances of insertions or deletions, or ambiguously aligned regions, were observed in the data, and all data were used for analyses. The final alignment thus consisted of 3,032 characters.

Phylogenetic analyses were conducted using likelihood optimality criteria and Bayesian methods. Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.04 (Stamatakis, 2006). The alignment was partitioned into eight regions consisting of the codon positions of ND1 and ND2, and the two nuclear loci, BDNF and PTGER4, following the methods of Siler et al. (2011). Analyses that partition protein-coding genes by codon position have been shown to improve resulting inferences (Brandley et al., 2005). The partitions were run under the same model (GTR + G) with 100 replicate best-tree inferences. Each inference was performed with a random starting tree, and relied on the rapid hill-climbing algorithm (Stamatakis 2006). Clade support was assessed with 1000 bootstrap pseudoreplicates. We considered branches receiving ≥70% bootstrap support to be well-supported (Hillis and Bull, 1993; see also Wilcox et al., 2002).

The Akaike Information Criterion (AIC), as implemented in jModeltest v0.1.1 (Guindon and Gascuel, 2003; Posada, 2008), was used to select the best model of nucleotide substitution for each partition (Table 5.2). The best-fit model for each of the eight partitions (Table 5.2) was used for Bayesian analyses performed in MrBayes 3.1 (Ronquist and Huelsenbeck, 2003). The same partitioning strategy used for maximum likelihood analyses was used for Bayesian inferences. Searches over tree space were conducted with four runs, each with four chains, and were run for 2×10^7 generations. Trees were sampled every 1000 generations, with 4000 samples discarded as burn-in; this left 16001 post-burn-in trees from each run included in the posterior distribution of topologies. Visual inspection for chain stationarity and high ESS values was conducted within the program Tracer v1.4 (Rambaut and Drummond, 2007). Additionally, correlations of split frequencies and cumulative split frequencies were examined using the program AWTY (Nylander et al., 2008). We considered topologies with posterior probabilities ≥0.95 to be well supported (Wilcox et al., 2002; Leaché and Reeder, 2002).

Morphological data

We examined fluid-preserved specimens (Appendix VI) for variation in qualitative and mensural characters. Sex was determined by gonadal inspection, and measurements were taken to the nearest 0.1 mm with digital calipers by CDS. X-rays were taken with a company cabinet X-ray on Kodak paper exposed at 5 miliampheres and 30 volts for 1 minute 15 seconds. Museum abbreviations for specimens examined follow Leviton et al. (1985).

Meristic and mensural characters were chosen based on Siler et al. (2010a): snout–vent length (SVL), axilla–groin distance (AGD), total length (TotL), midbody width (MBW), midbody height (MBH), tail length (TL), tail width (TW), tail height (TH), head length (HL), head width (HW), head height (HH), snout–forearm length (SnFa), eye diameter (ED), eye–narial distance (END), snout length (SNL), internarial distance (IND), fore-limb length (FLL), hind limb length (HLL), midbody scale-row count (MBSR), paravertebral scale-row count (PVSR), axilla–groin scale-row count (AGSR), Finger-III lamellae count (FinIIIlam), Toe-IV lamellae count (ToeIVlam), supralabial count (SL), infralabial count (IFL), supraciliary count (SC), and supraocular count (SO). Additionally, we counted the number of presacral vertebrae (PSV) from x-ray images of specimens. In the description, ranges are followed by mean ± standard deviation in parentheses.

Table 5.1. Summary of specimens corresponding to genetic samples included in the study. PNM/CMNH = deposited in the Cincinnati Museum of Natural History; SP = Sabah Parks Reference Collection; KU = University of Kansas Natural History Museum; LSUHC = La Sierra University Herpetological Collections; * = Holotypes of new species described in this paper.

Species	Voucher	Locality	Genbank Accession Numbers			
			ND1	ND2	PTGER4	BDNF
Lygosoma bowringi	LSUHC 6970	West Malaysia				
Plestiodon fasciatus	KU 289462	United States, Texas, Smith County	—	HQ907423	HQ907526	HQ907224
Brachymeles apus	SP 06915	Malaysia, Borneo, Sabah, Mt. Kinabalu	HQ907331	HQ907433	HQ907533	HQ907233
Brachymeles bonitae	KU 307747	Philippines, Polillo Island, Municipality of Polillo				
Brachymeles bonitae	KU 326080	Philippines, Polillo Island, Municipality of Polillo				
Brachymeles gracilis	PNM/CMNH H-1169	Philippines, Mindanao Island, Municipality of Toril, Mt. Apo				
Brachymeles gracilis	KU 326098	Philippines, Mindanao Island, Municipality of Kiblawan	HQ907391	HQ907494	HQ907594	HQ907294
Brachymeles gracilis	KU 326099	Philippines, Mindanao Island, Municipality of Kiblawan	HQ907392	HQ907495	HQ907595	HQ907594
Brachymeles gracilis	PNM/CMNH H-1175	Philippines, Mindanao Island, Municipality of Toril, Mt. Apo	—	HQ907492	HQ907592	HQ907292
Brachymeles gracilis	PNM/CMNH H-1176	Philippines, Mindanao Island, Municipality of Toril, Mt. Apo	HQ907390	HQ907493	HQ907593	HQ907293
Brachymeles gracilis	PNM/CMNH H-1428	Philippines, Mindanao Island, Malagos Eagle Station				
Brachymeles gracilis	PNM/CMNH H-1641	Philippines, Mindanao Island, Municipality of Kiamba, Mt. Busa				
Brachymeles pito	KU 327935	Philippines, Mindanao Island, Municipality of RTR				
Brachymeles pito	KU 327936	Philippines, Mindanao Island, Municipality of RTR				
Brachymeles pito	KU 327937	Philippines, Mindanao Island, Municipality of RTR				
Brachymeles anim	PNM 9766*	Philippines, Camiguin Sur Island, Municipality of Mambajao				
Brachymeles miriamae	KU 327692	Thailand, Nakhon Ratchasima, Sakaerat Environmental Research Center	HQ907333	HQ907435	HQ907535	HQ907235
Brachymeles pathfinderi	KU 324063	Philippines, Mindanao Island, Municipality of Glan				
Brachymeles pathfinderi	KU 324065	Philippines, Mindanao Island, Municipality of Glan				
Brachymeles pathfinderi	KU 324066	Philippines, Mindanao Island, Municipality of Glan				
Brachymeles syam	KU 310941	Philippines, Samar Island, Municipality of San Jose de Buan				
Brachymeles syam	KU 310825	Philippines, Samar Island, Municipality of Taft				
Brachymeles syam	KU 311216	Philippines, Leyte Island, Municipality of Baybay	HQ907383	HQ907485	HQ907585	HQ907285
Brachymeles syam	KU 311220	Philippines, Leyte Island, Municipality of Baybay	HQ907384	HQ907486	HQ907586	HQ907286
Brachymeles walo	KU 326109	Philippines, Mindanao Island, Municipality of Tubigan				
Brachymeles walo	PNM 9776	Philippines, Mindanao Island, Municipality of Tampakan, Barangay Tablu, Datal Mangisi				
Brachymeles walo	PNM 9777*	Philippines, Mindanao Island, Municipality of Tampakan, Barangay Tablu, Datal Mangisi				

Table 5.2. Models of evolution selected by AIC and applied for partitioned, Bayesian phylogenetic analyses[1].

Partition	AIC Model	Number of Characters
ND1, 1st codon position	GTR + Γ	322
ND1, 2nd codon position	GTR + Γ	322
ND1, 3rd codon position	GTR + Γ	322
ND2, 1st codon position	GTR + Γ	287
ND2, 2nd codon position	GTR + Γ	287
ND2, 3rd codon position	GTR + Γ	287
BDNF	GTR + Γ	715
PTGER4	HKY + Γ	490

[1] The model GTR + I + G was used for partitioned RAxMLHPC analyses.

Table 5.3. Uncorrected pairwise sequence divergence (%) for mitochondrial data (below diagonal) and nuclear data (above diagonal), for *Brachymeles gracilis, B. pito, B. anim, B. syam*, *B. walo*, and *B. pathfinderi* (Fig. 5.2). Percentages on the diagonal represent intraspecific genetic diversity for mitochondrial data (bolded for emphasis).

	gracilis	*pito*	*anim*	*syam*	*walo*	*pathfinderi*
gracilis	**0.4–3.4**	0.5–0.7	1.0	0.0–0.2	0.1–0.4	0.0–0.2
pito	8.7–9.4	**0.0–0.3**	0.4–0.5	0.5–0.7	0.2–0.7	0.3
anim	8.4–8.8	4.2	—	0.4–0.5	0.7–1.0	0.7
syam	9.3–9.9	9.2–9.6	8.9–9.4	**0.3–1.9**	0.5–0.9	0.0–0.2
walo	9.1–10.4	10.1–10.6	8.9–10.1	8.1–10.0	**0.0–5.9**	0.1–0.4
pathfinderi	6.0–6.5	9.2–9.3	9.2	9.1–9.5	9.4–10.0	**0.0**

Species concept

We follow the General Lineage Concept of species (de Queiroz, 1998, 1999) as a logical extension of the Evolutionary Species Concept (Simpson, 1961; Wiley, 1978; Frost and Hillis, 1990). We consider as distinct lineages those populations that are morphologically, and genetically distinct, especially if allopatric. Lineage-based species concepts have been successfully employed in the recognition of Philippine biodiversity (Brown et al., 2000, 2002, 2008, 2009; Brown and Guttman, 2002; Gaulke et al., 2007; Welton et al., 2009, 2010 a,b; Siler and Brown, 2010; Siler et al., 2011) due to the highly partitioned nature of the archipelago (Brown and Diesmos, 2009), and because the geological history of the islands has been so well documented (Voris, 2000; Hall, 2002; Yumul, 2009). In this study we use an estimate of Phylogenetic relationships as a guide for delimiting species but restrict our diagnoses of new species to those populations unambiguously diagnosed by differences in non-overlapping morphological character states.

Results

Phylogeny

Trees recovered from ML and Bayesian analyses are identical in their support for five evolutionary lineages within the *Brachymeles gracilis* Complex (Fig. 5.2). The resulting 100 inferences from the partitioned RAxML maximum likelihood analysis show an average likelihood score of –ln *L* 12804.013201, with a single inference having the highest likelihood score of –ln *L* 12803.989734. No inferences support the monophyly of *Brachymeles gracilis* (Fig. 5.2). All analyses recover four major clades (Fig. 5.2, Clades A–C, F) within the *B. gracilis* Complex; however, we recover only weak support for interclade relationships in most instances. The Camiguin Island population and *B. gracilis hilong* were recovered as a strongly supported clade in all analyses (Fig. 5.2, Clade A), as were populations of *B. gracilis gracilis* and *B. pathfinderi* (Fig. 5.2, Clade E). Populations from northwestern and southwestern Mindanao Island were always recovered as a monophyletic group (Fig. 5.2, Clade B), as were populations from the islands of Samar and Leyte (Fig. 5.2, Clade C). True *B. gracilis hilong* was never recovered as part of a monophyletic group with true *B. gracilis gracilis*.

Uncorrected pairwise sequence divergences are generally low within the lineages defined here as species and high between these lineages (Table 5.3). Percent divergences for the mitochondrial and nuclear data, respectively, show that the monophyletic lineages defined by our phylogenetic analyses (*B. gracilis gracilis, B. gracilis hilong, B.* sp. nov. [Samar and Leyte islands], *B.* sp. nov. [Camiguin Sur Island], and *B.* sp. nov. [western Mindanao Island]) are distinguished from congeners by levels of genetic divergence nearly equal to, or greater than, those between previously defined species—viz., *B. pathfinderi* (Table 5.3; Fig. 5.2). The two most closely related lineages (*B.* sp. nov. [Camiguin Sur Island] and *B. gracilis hilong*) are separated by 4.2% mitochondrial sequence divergence. Sequence divergences among the other lineages within the *B. gracilis* Complex are greater than 8.1% (Table 5.3; Fig. 5.2). Intraspecific sequence divergences are low in comparison to divergences among monophyletic lineages with one exception being *B.* sp. nov. (western Mindanao Island; Table 5.3; Fig. 5.2). Although samples from the southwestern Mindanao populations are genetically similar to each other (Fig. 5.2, Populations 2, 3) and form a monophyletic group, there is a 5.9% sequence divergence between these populations and the northwestern (Fig. 5.2, Population 1) Mindanao population (Table 5.3; Fig. 5.2). We suspect that this highly supported clade (Fig. 5.2, Clade B) actually represents a complex of morphologically similar species; however, only a single juvenile from the northwestern Mindanao population has ever been collected. Therefore, we conservatively consider all western Mindanao popluations (Fig. 5.2, Clade B, Populations 1–3) as members of a single, unique evolutionary lineage, pending the collection of additional samples from throughout western Mindanao Island. Unfortunately, no tissues of *B. sampu* have ever been collected, but we suspect, on the basis of overwhelming morphological similarity, that this species would be recovered within the *B. gracilis* Complex (Fig. 5.2).

Morphology

Superficially, the six lineages within the *B. gracilis* complex appear morphologically similar, especially in overall body size; however, upon closer inspection, numerous non-overlapping differences were detected in meristic, mensural, osteological, and color pattern characters for each complex member, readily defining six distinct lineages within the complex (Tables 5.4–5.6). Variation in morphological characters (Tables 5.4–5.6) mirrors the results observed in phylogenetic analyses, and supports the recognition of six *Brachymeles gracilis* group lineages. Characters differing among these six lineages include: relative tail length, presacral vertebrae number, head and body scale counts and patterns, and pigmentation patterns (Tables 5.4–5.6; species accounts below), all of which are typical morphological diagnostic characters employed historically by taxonomists working with this genus (review: Siler and Brown, 2010; Siler et al., in press c). We observed no intraspecific mensural or meristic differences between the sexes of any of the six species.

In summary, each lineage (all but two of which are allopatric) possesses unique and non-overlapping suites of diagnostic character states of morphology, perfectly corresponding to the six clades defined in phylogenetic analyses of DNA sequence data. Combined with

Figure 5.2. Maximum clade credibility topology of *Brachymeles* inferred in this study resulting from Bayesian analyses of the combined mitochondrial + nuclear dataset (preferred ML tree, -ln L 12803.989734; ND1, ND2, BDNF, PTGER4). Terminals are labeled with taxonomic names, fore- and hind limb digit states, number of presacral vertebrae, and geographic distributions.

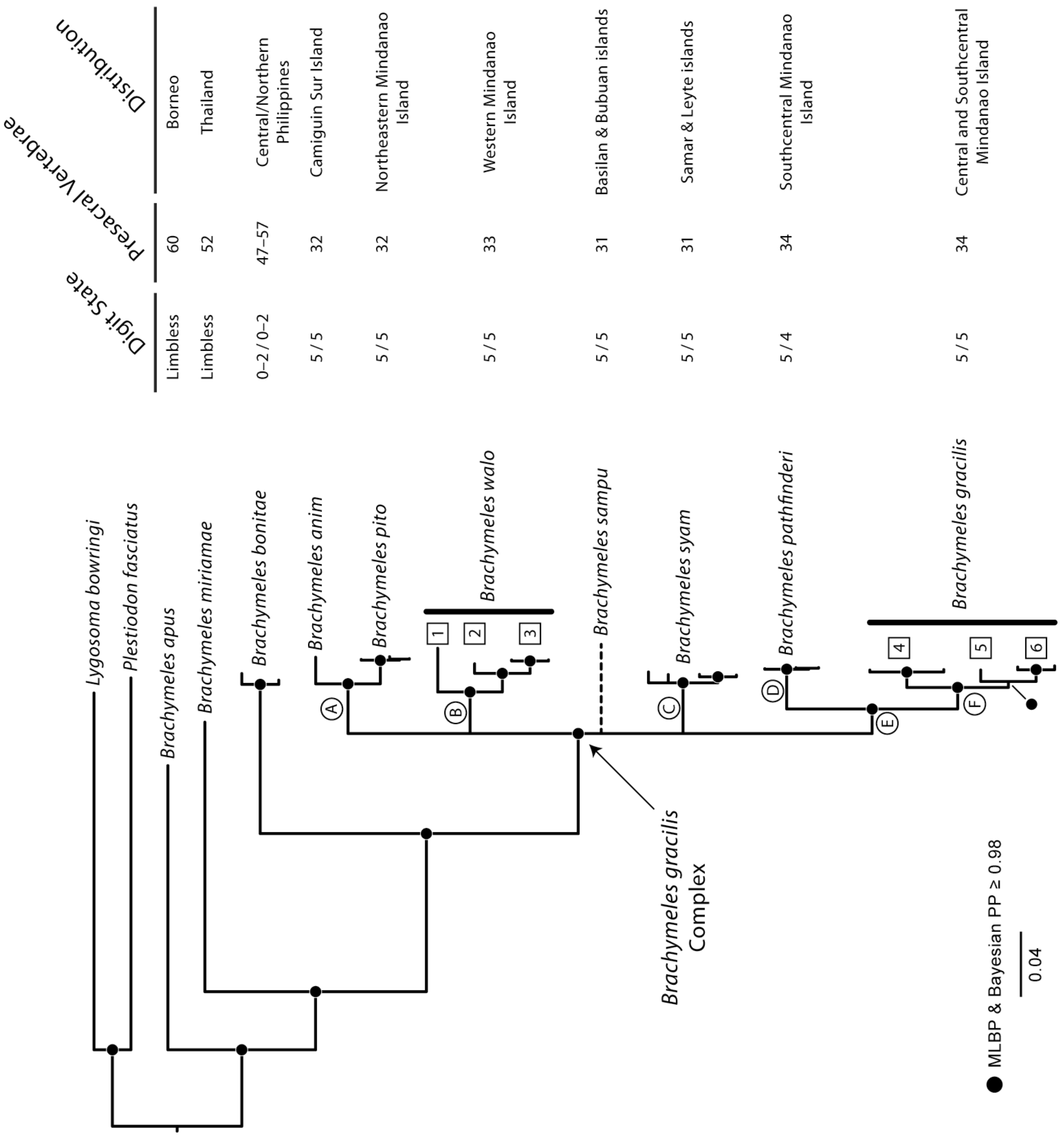

Digit State
Presacral Vertebrae
Distribution
Lygosoma bowringi
Limbless
60
Borneo
Plestiodon fasciatus
Brachymeles apus
Limbless
52
Thailand
Brachymeles miriamae
Brachymeles bonitae
0–2 / 0–2
47–57
Central/Northern Philippines
Brachymeles anim
Brachymeles pito
5 / 5
32
Camiguin Sur Island
A
5 / 5
32
Northeastern Mindanao Island
B
1
2
3
Brachymeles walo
5 / 5
33
Western Mindanao Island
Brachymeles sampu
5 / 5
31
Basilan & Bubuan islands
C
Brachymeles syam
5 / 5
31
Samar & Leyte islands
D
Brachymeles pathfinderi
5 / 4
34
Southcentral Mindanao Island
E
F
4
5
6
Brachymeles gracilis
5 / 5
34
Central and Southcentral Mindanao Island
Brachymeles gracilis Complex
● MLBP & Bayesian PP ≥ 0.98
0.04

Figure 5.3. (Left) Map of the Philippine islands showing previously recognized distribution of *Brachymeles gracilis* (indicated by black shaded islands), and recognized distribution of *B. pathfinderi* (indicated by a star). (Right) Hypothesized distributions of *B. gracilis*, *B. pito*, *B. anim*, *B. syam*, *B. walo*, and *B. sampu* in the southern and southeastern Philippines. Sampling localities are indicated by shapes: black shapes represent sites where both specimens and tissues have been sampled, white shapes represent sites where only specimens have been sampled. Numbered sites correspond to population labels shown in Figure 5.2. The hypothesized geographic range of each species is indicated by shaded polygons. Shapes and color shades correspond to the map's key

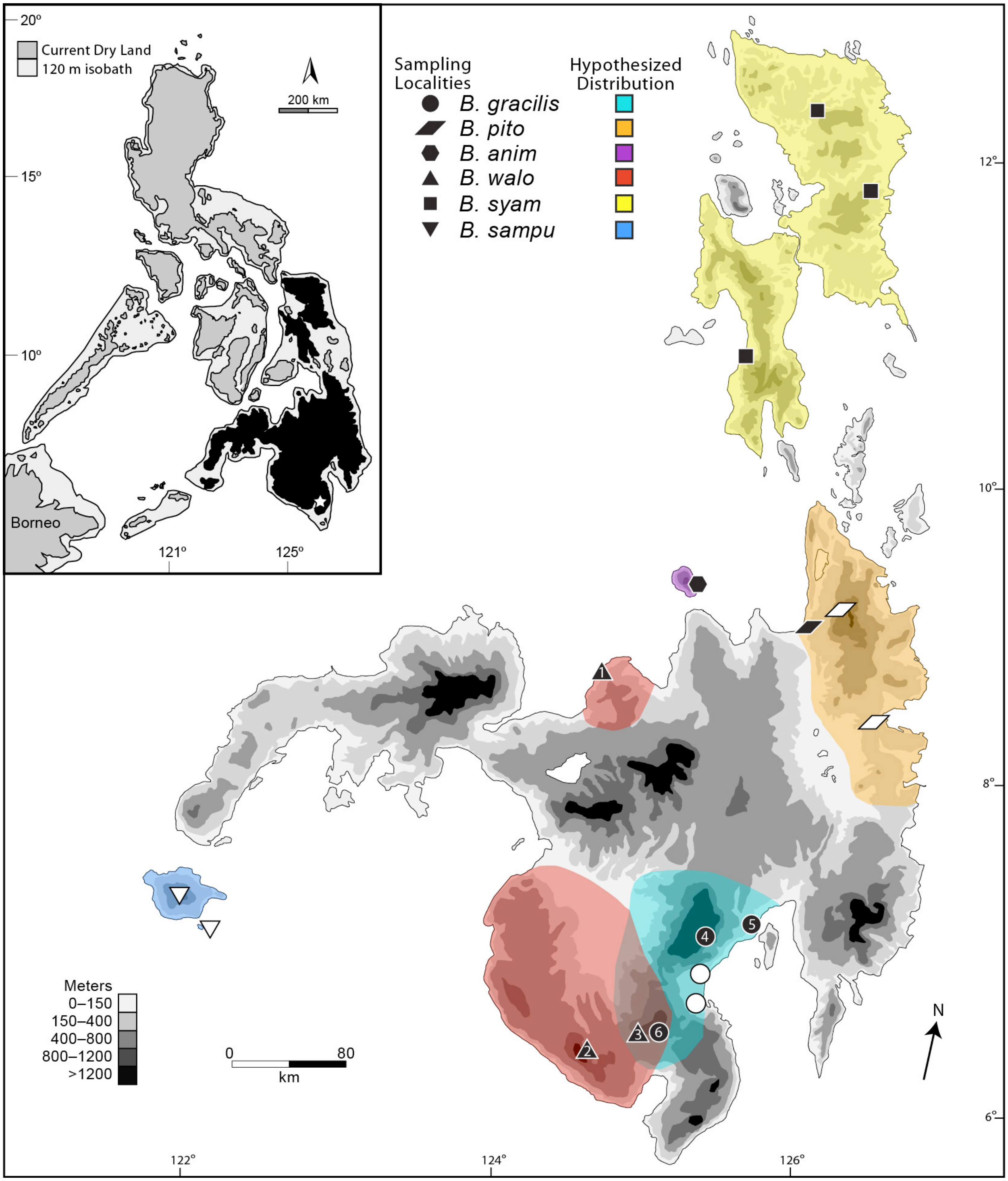

20°
Current Dry Land
120 m isobath
200 km
15°
10°
Borneo
121°
125°
Sampling
Localities
Hypothesized
Distribution
B. gracilis
B. pito
B. anim
B. walo
B. syam
B. sampu
12°
10°
8°
6°
122°
124°
126°
1
2
3
4
5
6
Meters
0–150
150–400
400–800
800–1200
>1200
0
80
km
N

Table 5.4. Summary of meristic and mensural characters in all known medium-sized, pentadactyl species of *Brachymeles*. Sample size, body length and total length among males and females, and general geographical distribution (PAIC = Pleistocene Aggregate Island Complexes, sensu Brown and Diesmos, 2002) are included for reference (SVL, TotL, MBW, FLL, and HLL given as range over mean ± standard deviation; all body proportions given as percentage over mean ± standard deviation). In cases of scale count variation within species, numbers of individuals showing specific counts are given in parentheses.

	gracilis (13 m, 24 f)	*pito* (11 m, 14 f)	*anim* (1 m, 10 f)	*syam* (9 m, 18 f)	*walo* (1 m, 1 f)	*sampu* (1 f)
Range	Southern Mindanao Island	Eastern Mindanao Island	Camiguin Sur Island	Samar & Leyte islands	Western Mindanao Island	Basilan Island Group
SVL (f)	58.6–83.4 (69.9 ± 6.1)	59.9–81.5 (71.7 ± 6.5)	53.6–80.1 (75.4 ± 5.1)	64.2–76.9 (71.5 ± 3.7)	75.5	71.9
SVL (m)	60.1–82.3 (69.6 ± 7.9)	61.5–78.5 (69.8 ± 4.5)	75.8	65.0–74.6 (70.2 ± 3.2)	61.6	—
TotL (f)	116.4–146.0 (127.7 ± 8.0)	117.8–159.2 (132.0 ± 12.0)	117.6–141.4 (128.3 ± 8.7)	135.8–159.7 (147.7 ± 7.9)	142.6	—
TotL (m)	124.4–161.3 (137.8 ± 14.8	116.7–139.4 (128.0 ± 7.5)	—	132.4–146.9 (140.6 ± 7.4)	117.3	—
MBW	8.0–12.0 (9.4 ± 1.0)	7.9–12.1 (9.9 ± 1.1)	8.9–12.3 (10.7 ± 1.1)	7.7–11.2 (9.5 ± 0.8)	8.5, 8.0	8.2
TL/SVL	79–102 (93 ± 6)	57–98 (79 ± 14)	54–84 (72 ± 12)	92–126 (108 ± 9)	90, 89	—
TW/MBW	57–79 (70 ± 5)	57–81 (70 ± 7)	61–82 (70 ± 8)	59–87 (74 ± 6)	87, 86	71
FLL	5.9–8.6 (7.2 ± 0.8)	7.1–9.3 (8.3 ± 0.6)	7.9–9.1 (8.3 ± 0.4)	8.2–9.9 (9.1 ± 0.5)	7.5, 7.1	7.2
FLL/SVL	9–12 (10 ± 1)	10–14 (12 ± 1)	10–12 (11 ± 1)	11–15 (13 ± 1)	12, 9	10
HLL	10.3–14.8 (12.4 ± 1.0)	12.2–16.0 (14.0 ± 1.1)	13.6–15.6 (14.2 ± 0.6)	12.3–16.7 (14.3 ± 1.0)	12.1, 10.3	13.1
HLL/SVL	14–23 (18 ± 2)	17–23 (20 ± 1)	17–21 (19 ± 1)	17–23 (20 ± 2)	20, 14	18
FinIIIlam	4 (11) 5 (26)	5 (25)	5 (11)	5 (27)	4 (1) 5 (1)	5 (1)
ToeIVlam	7 (20) 8 (17)	8 (18) 9 (7)	8 (10) 9 (1)	8 (4) 9 (23)	6 (2)	8 (1)

TABLE 5.4.—Continued.

	boholensis (5 m, 14 f)	*boulengeri* (7 m, 8 f)	*mindorensis* (6 m, 12 f)	*taylori* (8 m, 13 f)
Range	Bohol Island	Luzon PAIC	Mindoro Island	Negros & Cebu Island
SVL (f)	83.8–94.0 (88.4 ± 3.1)	60.5–95.5 (84.0 ± 11.2)	90.0–106.8 (98.8 ± 5.3)	65.8–93.2 (83.9 ± 7.4)
SVL (m)	84.1–93.6 (89.1 ± 4.1)	72.3–93.1 (82.5 ± 6.7)	93.9–104.2 (100.2 ± 4.1)	83.1–99.2 (87.0 ± 5.2)
TotL (f)	129.6–174.8 (154.1 ± 14.7)	129.7–167.4 (159.3 ± 13.1)	162.5–206.7 (180.2 ± 14.2)	130.3–168.5 (149.9 ± 13.0)
TotL (m)	154.5–166.2 (160.7 ± 5.9)	124.3–173.1 (151.4 ± 19.4)	165.3–197.0 (184.9 ± 11.5)	149.6–176.7 (164.3 ± 11.3)
MBW	11.9–15.0 (13.4 ± 1.0)	9.9–14.7 (12.4 ± 1.7)	12.8–20.8 (16.0 ± 1.8)	11.0–16.8 (13.8 ± 1.7)
TL/SVL	53–90 (76 ± 13)	67–114 (89 ± 16)	60–99 (85 ± 11)	69–103 (83 ± 10)
TW/MBW	62–78 (70 ± 5)	60–81 (70 ± 6)	54–80 (69 ± 8)	54–80 (69 ± 7)
FLL	9.0–11.2 (10.1 ± 0.7)	8.2–11.7 (10.5 ± 0.8)	10.0–13.0 (11.4 ± 0.8)	9.0–10.4 (9.8 ± 0.4)
FLL/SVL	10–13 (11 ± 1)	12–14 (13 ± 1)	10–13 (11 ± 1)	10–14 (12 ± 1)
HLL	15.4–18.7 (17.2 ± 1.0)	14.3–18.7 (17.2 ± 1.1)	18.8–23.1 (20.6 ± 1.2)	15.6–18.7 (17.0 ± 1.0)
HLL/SVL	18–22 (19 ± 1)	18–24 (21 ± 2)	18–24 (21 ± 2)	18–25 (20 ± 2)
FinIIIlam	6 (19)	5 (14) 6 (1)	5 (16) 6 (2)	5 (12) 6 (9)
ToeIVlam	9 (7) 10 (12)	9 (13) 10 (2)	8 (14) 9 (4)	9 (10) 10 (11)

Table 5.5. Summary of qualitative diagnostic characters (present, absent) in all known medium-sized, pentadactyl species of *Brachymeles*. The pairs of enlarged scales posterior to the postmental scale are abbreviated as chin shield pairs with reference to the 1st, 2nd, and 3rd pairs (when present).

	gracilis (13 m, 24 f)	*pito* (11 m, 14 f)	*anim* (1 m, 10 f)	*syam* (9 m, 18 f)	*walo* (1 m, 1 f)	*sampu* (1 f, 1 juv.)
PSV	34	32	32	31	33	31
MBSR	24–27	27–30	26–28	25–26	26, 26	24
AGSR	46–49	44–50	44–49	42–45	47, 50	48, 47
PVSR	67–70	66–73	65–70	64–67	70, 72	69
SL	6 (37)	6 (25)	6 (11)	6 (27)	6 (2)	6 (1)
IFL	6 (19) 7 (18)	6 (25)	6 (11)	6 (27)	6 (2)	6 (1)
SC	6 (37)	6 (25)	6 (11)	6 (27)	6 (2)	6 (1)
SO	5 (37)	5 (25)	5 (11)	5 (27)	5 (2)	5 (1)
Pineal eyespot	– or +	+	– or +	+	– or +	+
Supranasal contact	–	–	–	–	–	–
Prefrontal contact	– or +	–	– or point	– or point	– or +	–
Frontoparietal contact	– or +	– or +	+	+	+	–
Parietals contact	+	– or +	+	+	+	– or point
1st chin shield pair contact	– or +	– or +	–	–	– or +	+
Enlarged chin shield pairs	2	2 or 3	2	3	3	3
Chin shield pair size	$1 < 2$ or $1 > 2$	$1 < 2$ or $3 < 1 < 2$	$1 < 2$	$3 < 1 < 2$	$3 < 1 < 2$	$3 < 1 < 2$
Chin shield pair separation[1]	1(0/1); 2(1–3)	1(0/1); 2(1–3) or 1(0/1); 2(1); 3(3)	1(1); 2(1–3)	1(1); 2(1); 3(3)	1(0/1); 2(1); 3(3)	1(0); 2(1); 3(3)
Subocular supralabial	4th and 5th	4th and 5th	4th and 5th	4th and 5th	4th and 5th	4th and 5th
Postnasal	small or absent[2]	small to moderate	small to moderate	small to moderate	small to moderate	small to moderate
Differentiated nuchals	–	–	–	–	–	–

[1] Parentheses show the number of small ventral scale rows separating each enlarged pair of chin shields.

[2] Postnasal/supranasal fusion 31 of 51 specimens (adults and juveniles) examined for this character.

Table 5.5.—Continued.

	boholensis (5 m, 14 f)	*boulengeri* (7 m, 8 f)	*mindorensis* (6 m, 12 f)	*taylori* (8 m, 13 f)
PSV	31	32	31	31
MBSR	26–28	26–27	26–28	26–28
AGSR	42–46	42–46	42–45	42–47
PVSR	63–66	63–66	63–65	62–69
SL	7 (19)	6 (12) 7 (3)	7 (18)	6 (21)
IFL	7 (19)	7 (15)	6 (18)	7 (21)
SC	6 (19)	5 (1) 6 (14)	6 (18)	6 (21)
SO	5(19)	5 (15)	5 (18)	5 (21)
Pineal eyespot	+	+	+	+
Supranasal contact	–	–	– or +	–
Prefrontal contact	–	–	– or +	–
Frontoparietal contact	+	+	+	+
Parietals contact	– or +	– or +	– or +	– or +
1st chin shield pair contact	– or +	+	+	– or +
Enlarged chin shield pairs	3	2	2	2
Chin shield pair size	3 < 1 < 2	1 < 2	1 < 2	1 < 2
Chin shield pair separation[1]	1(0/1); 2(1); 3(3)	1(0/1); 2(1)	1(0); 2(1)	1(0); 2(1)
Subocular supralabial	5th and 6th	4th and 5th	5th and 6th	4th and 5th
Postnasal	moderate	moderate	moderate	moderate
Differentiated nuchals	–	–	–	–

[1] Parentheses show the number of small ventral scale rows separating each enlarged pair of chin shields.

Table 5.6. Summary of univariate morphological variation among mensural characters in series of *Brachymeles gracilis, B. pito, B. anim, B. syam, B. walo* and *B. sampu.*

	gracilis (13 m; 24 f)	*pito* (11 m; 14 f)	*anim* (1 m; 10 f)	*syam* (9 m; 18 f)	*walo* (1 m; 1 f)	*sampu* (1 f)
SVL (m)	60.1–82.3 (69.4 ± 7.9)	61.5–71.5 (69.8 ± 4.5)	75.8	65.0–74.6 (70.1 ± 3.2)	61.6	—
SVL (f)	58.6–83.4 (69.9 ± 3.1)	59.9–81.5 (71.7 ± 6.5)	63.6–80.1 (75.4 ± 5.1)	64.2–76.9 (71.5 ± 3.7)	75.5	71.9
AGD (m)	39.5–58.1 (46.3 ± 6.1)	38.8–54.1 (45.6 ± 3.8)	49.3	41.5–48.7 (44.7 ± 2.4)	38.9	—
AGD (f)	39.6–56.6 (47.5 ± 4.4)	37.9–53.4 (46.0 ± 4.6)	39.8–54.2 (49.7 ± 4.3)	40.4–52.9 (46.6 ± 3.1)	49.3	49.7
TotL (m)	124.4–161.3 (137.8 ± 14.8)	116.7–139.4 (128.0 ± 7.5)	134.2	132.4–146.9 (140.6 ± 7.4)	117.3	—
TotL (f)	116.4–146.0 (127.7 ± 8.0)	117.8–159.2 (132.0 ± 12.0)	117.6–141.4 (128.3 ± 8.7)	135.8–159.7 (147.7 ± 7.9)	142.6	110.1
MBW (m)	8.3–12.0 (9.6 ± 1.2)	8.6–11.6 (9.6 ± 0.9)	9.9	8.8–11.0 (9.4 ± 0.6)	8.5	—

MBW (f)	8.0–10.8 (9.3 ± 0.8)	7.9–12.1 (10.1 ± 1.2)	8.9–12.3 (10.8 ± 1.1)	7.7–11.2 (9.5 ± 0.9)	8.0	8.2
MBH (m)	5.6–9.9 (7.5 ± 1.3)	6.3–9.0 (7.8 ± 1.0)	7.8	6.4–8.4 (7.0 ± 0.7)	6.9	—
MBH (f)	5.6–10.1 (7.3 ± 1.2)	5.3–9.6 (7.8 ± 1.4)	7.8–10.3 (9.2 ± 0.8)	5.6–8.0 (6.8 ± 0.7)	6.8	5.2
TL (m)	53.2–79.4 (63.5 ± 8.6)	44.3–67.0 (57.7 ± 8.2)	58.4	66.5–78.3 (72.9 ± 5.2)	55.7	—
TL (f)	49.4–66.9 (58.9 ± 5.6)	34.4–77.7 (54.6 ± 11.9)	41.3–64.5 (53.8 ± 8.6)	66.5–89.1 (76.7 ± 6.4)	67.1	38.2
TW (m)	5.4–8.7 (6.9 ± 0.9)	6.1–7.7 (6.8 ± 0.4)	8.1	5.7–7.8 (7.0 ± 0.6)	7.4	—
TW (f)	5.7–7.8 (6.4 ± 0.5)	6.2–8.0 (7.0 ± 0.5)	6.7–8.3 (7.5 ± 0.6)	5.9–8.6 (7.0 ± 0.6)	6.9	5.8
TH (m)	4.6–6.7 (5.5 ± 0.6)	5.0–6.4 (5.7 ± 0.4)	6.9	5.1–6.6 (5.8 ± 0.5)	5.1	—
TH (f)	4.4–6.1 (5.3 ± 0.4)	4.6–6.7 (5.6 ± 0.7)	5.5–6.9 (6.1 ± 0.5)	4.7–6.8 (5.6 ± 0.6)	5.6	4.6
HL (m)	5.1–7.7 (6.6 ± 0.7)	6.3–7.5 (7.0 ± 0.4)	7.1	6.0–7.6 (6.7 ± 0.4)	4.8	—
HL (f)	5.1–7.6 (6.5 ± 0.6)	6.4–8.3 (7.2 ± 0.4)	5.9–8.2 (7.3 ± 0.7)	6.3–7.8 (6.8 ± 0.4)	6.1	6.8

HW (m)	6.6–8.4	6.7–8.0	7.8	6.5–7.7	6.4	—
	(7.4 ± 0.5)	(7.4 ± 0.4)		(7.1 ± 0.3)		
HW (f)	6.2–8.2	6.4–9.1	6.7–8.2	6.5–8.4	6.3	6.7
	(7.0 ± 0.4)	(7.7 ± 0.7)	(7.6 ± 0.5)	(7.1 ± 0.5)		
HH (m)	4.1–6.1	4.6–6.4	5.1	4.0–55.5	4.0	—
	(5.1 ± 0.6)	(5.5 ± 0.5)		(5.1 ± 0.5)		
HH (f)	3.9–5.6	4.5–6.5	4.7–6.0	3.9–5.3	4.2	4.6
	(4.9 ± 0.5)	(5.5 ± 0.6)	(5.5 ± 0.4)	(4.6 ± 0.5)		
SnFa (m)	15.6–22.0	16.2–19.6	20.8	18.5–20.8	16.4	—
	(18.3 ± 2.0)	(18.7 ± 1.0)		(19.6 ± 0.8)		
SnFa (f)	16.0–20.7	17.2–20.8	18.4–20.6	183–21.0	19.7	17.5
	(17.7 ± 1.2)	(19.5 ± 1.0)	(19.5 ± 0.6)	(19.6 ± 0.8)		
ED (m)	1.0–1.5	1.2–1.5	1.4	1.2–1.7	1.3	—
	(1.3 ± 0.1)	(1.4 ± 0.1)		(1.4 ± 0.1)		
ED (f)	1.0–1.5	1.3–1.8	1.1–1.6	1.2–1.4	1.4	1.8
	(1.3 ± 0.1)	(1.4 ± 0.2)	(1.4 ± 0.2)	(1.3 ± 0.1)		
END (m)	2.2–3.5	2.8–3.1	3.1	2.7–3.5	2.8	—
	(2.8 ± 0.3)	(2.9 ± 0.1)		(3.1 ± 0.2)		
END (f)	2.3–3.1	2.4–3.1	3.0–3.3	2.9–3.4	3.0	2.6
	(2.6 ± 0.2)	(2.8 ± 0.2)	(3.1 ± 0.1)	(3.1 ± 0.1)		
SNL (m)	3.5–4.7	3.8–4.5	4.4	3.8–4.4	3.9	—
	(4.0 ± 0.4)	(4.1 ± 0.2)		(4.2 ± 0.2)		
SNL (f)	3.3–4.2	3.5–4.2	4.1–4.5	3.8–4.4	3.7	3.8

	(3.8 ± 0.3)	(3.9 ± 0.2)	(4.4 ± 0.1)	(4.1 ± 0.1)		
IND (m)	1.9–2.8	2.1–2.4	2.5	2.1–2.3	2.1	—
	(2.3 ± 0.3)	(2.2 ± 0.1)		(2.2 ± 0.1)		
IND (f)	1.9–2.6	2.1–2.5	2.0–2.5	1.9–2.4	2.6	2.3
	(2.2 ± 0.2)	(2.3 ± 0.1)	(2.4 ± 0.2)	(2.1 ± 0.1)		
FLL (m)	5.9–8.6	7.1–8.8	8.7	8.8–9.8	7.5	—
	(7.3 ± 0.9)	(8.1 ± 0.6)		(9.3 ± 0.3)		
FLL (f)	6.2–8.6	7.5–9.3	7.9–9.1	8.2–9.9	7.1	7.2
	(7.1 ± 0.7)	(8.4 ± 0.5)	(8.3 ± 0.4)	(9.0 ± 0.5)		
HLL (m)	11.3–14.8	12.2–15.7	13.6	12.5–15.7	12.1	—
	(12.4 ± 1.0)	(13.6 ± 1.1)		(14.5 ± 1.0)		
HLL (f)	10.3–14.7	13.1–16.0	13.8–15.6	12.3–16.7	10.3	13.1
	(12.4 ± 1.0)	(14.3 ± 1.0)	(14.3 ± 0.6)	(14.2 ± 1.1)		

biogeographic evidence, and clearly separate geographical ranges (with one exception), our data suggest the presence of six evolutionary lineages, worthy of taxonomic recognition.

Taxonomic conclusions

Our estimate of phylogeny (Fig. 5.2), biogeographically separate ranges on islands or distinct geologic components of islands, diagnostic, non-overlapping morphological character states, and genetic distances between the taxa (Table 5.3) indicate the presence of a new species from Samar and Leyte islands, a new species from Camiguin Sur Island, and a new species from western Mindanao Island (Table 5.3; Fig. 5.2) and the distinctiveness of *B. sampu* from Basilan and Bubuan islands. Each of the six species of the *B. gracilis* complex is morphologically distinct from all others and each of the six species of the *B. gracilis* Complex included in phylogenetic analyses are genetically distinct. Each monophyletic lineage, with the exception of the one occurring on Samar and Leyte islands and the one occurring on Basilan and Bubuan islands, is endemic to single islands within the Mindanao PAIC, thereby providing additional support for the distinctiveness of each clade's evolutionary history and lineage integrity.

Previous descriptions of members of the *B. gracilis* Complex have applied the name *B. gracilis* to southern Mindanao populations (Taylor, 1922a; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980; Siler et al., 2010a; Siler and Brown, 2010). One of the unique diagnostic characters consistently reported for *Brachymeles gracilis* has been the absence of postnasals resulting from the fusion of the postnasal with the supranasal scale (Brown and Rabor, 1967; Brown and Alcala, 1980). Brown and Rabor (1967) and Brown and Alcala (1980) report this fused scale to be present in more than 60% and 50%, respectively, of the *B. gracilis* individuals examined. This unique character (fused postnasal/supranasal) has never been recorded for any other member of the *B. gracilis* Complex. Accordingly, we recognize *Brachymeles gracilis* as a species that occurs only in central and southcentral Mindanao Island, based on a suite of morphological characters that closely allies it with all previously published accounts (Taylor, 1922a; Brown, 1956; Brown and Rabor, 1967; Brown and Alcala, 1980; Siler et al., 2010a; Siler and Brown, 2010): (1) supralabials six; (2) infralabials six or seven; (3) midbody scale rows 24–27; (4) axilla–groin scale rows 46–49; and (5) postnasal/supranasal fusion present in more than 50% of population.

The two examined specimens of *B.* cf. *gracilis* from Basilan Island housed at the California Academy of Sciences closely match Taylor's (1918) description of *B. sampu* based on the following suite of morphological characters: (1) supralabials six; (2) infralabials six; (3) midbody scale rows 24; and (4) supranasals separated; (5) frontoparietals separated; (6) parietals separated or in point contact; (7) first pair of enlarged chin shields moderately to broadly contacting on midline; and (8) enlarged chin shields in three pairs. We therefore recognize *B. sampu* as a species that occurs on Basilan and its surrounding islets (including Buban Island; Fig. 5.2). Finally, we recognize *B. pito* as a species that occurs only in northeast Mindanao Island, and hereby recognize the three additional lineages within the *B. gracilis* species complex each as new species.

TAXONOMIC ACCOUNTS

Brachymeles gracilis (Fischer 1885)

Fig. 5.4

Senira bicolor *(part), Gray, 1845:98.*

Eumeces *(*Riopa*)* gracilis*, Fischer, 1885:85, Type locality: "Mindanao Island," Philippines (No.*

846 reported to be deposited in the Dresden Museum).

Brachymeles gracilis*, Boettger, 1886:103; Boulenger, 1887:378; Boettger, 1893:112; Taylor, 1917:270; 1918:257; 1922 a:247; 1922 b:287; (part) Brown and Alcala, 1970:112.*

Brachymeles gracilis gracilis*, Brown, 1956:10; Brown and Rabor, 1967:537; Brown and Alcala, 1980:37.*

Brachymeles sampu*, Taylor, 1918:254.*

Diagnosis.—*Brachymeles gracilis* can be distinguished from congeners by the following combination of characters: (1) body size medium (SVL 58.6–83.4 mm); (2) limbs pentadactyl; (3) limb length moderate; (4) relative tail length long; (5) Finger-III lamellae four or five; (6) Toe-IV lamellae seven or eight; (7) supralabials six; (8) infralabials six or seven; (9) suparciliaries six; (10) supraoculars five; (11) midbody scale rows 24–27; (12) axilla–groin scale rows 46–49; (13) paravertebral scale rows 67–70; (14) supranasals separate; (15) parietals in contact; (16) postnasal/supranasal fusion present or absent; (17) enlarged chin shields in two pairs; (18) nuchal scales undifferentiated; (19) fourth and fifth supralabial below eye; (20) auricular opening present; and (21) presacral vertebrae 34 (Tables 5.4, 5.5).

Comparisons.—Characters distinguishing *Brachymeles gracilis* from all medium-sized, pentadactyl species of *Brachymeles* are summarized in Tables 5.4 and 5.5. *Brachymeles gracilis* most closely resembles *B. anim, B. walo,* and *B. sampu*. However, *B. gracilis* differs from these three taxa by having seven or eight Toe-IV lamellae (vs. eight or nine [*B. anim*], six [*B. tiboli*], eight [*B. sampu*]), a greater number of presacral vertebrae (34 vs. 31 [*B. sampu*], 32 [*B. anim*], 33 [*B. tiboli*]), six or seven infralabials (vs. six), and the presence or absence of a fused postnasal/supranasal scale (vs. absence; Fig. 5.4). *Brachymeles gracilis* further differs from *B. anim* and *B. sampu* by having four or five Finger-III lamellae (vs. five); from *B. anim* and *B.*

walo by having a tendancy towards a longer relative tail length (TL/SVL up to 102% vs. less than 90%); from *B. walo* and *B. sampu* by having enlarged chind shields in two pairs (vs. 3); and from *B. sampu* by the presence of contact between parietal scales (vs. presence or absence).

Brachymeles gracilis can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all non-pentadactyl species of *Brachymeles* (*B. bonitae, B. cebuensis, B. elerae, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. wright*, sp. nov. [Leyte Island; Siler et al., in press c], sp. nov. [Lapinig Group Islands; Siler et al., in press c], sp. nov. [Catanduanes Island; Siler et al., in press c], sp. nov. [Central Bicol Peninsula, Luzon Island; Siler et al., in press c], and sp. nov. [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c]) by having pentadactyl (vs. non-pentadactyl) limbs.

Description (based on holotype description [Fischer, 1885] and 37 referred specimens).— Details of the head scalation of an adult male (KU 326097) are shown in Figure 5.4. Measurements of the holotype are provided below in brackets. Body medium-sized, moderately slender; maximum SVL 82.3 mm for males, 83.4 mm for females, [67.0, subadult] (Tables 5.4, 5.5); head weakly differentiated from neck, nearly as wide as body, HW 8.7–12.3% (10.2 ± 0.8) SVL, 93.0–130.9% (109.8 ± 9.4) HL; HL 28.9–44.4% (36.8 ± 4.7) SnFa; SnFa 22.5–29.8% (25.6 ± 1.5) SVL; snout short, rounded in dorsal and lateral profile, SNL 47.1–71.4% (59.5 ± 7.2) HL; ear opening visible, small; eyes small, ED 1.3–2.4% (1.8 ± 0.3) SVL, 15.3–25.7% (19.7 ± 2.6) HL, 34.7–58.4% (48.0 ± 6.2) END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 94.2–190.8% (130.4 ± 20.5) MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 24 (CAS 124804, 124808, 124811, 139293, 139300, 139309, CAS-SU 24165, KU 326101, 326103, 326106, MCZ 26539, 26549), 25 (CAS 139295, 139307, MCZ 26550), 26 (CAS 124803, 124806–07, 139294, 139303–05, 139308, CAS-SU 24163, CMC 12170, 12171, KU 326096, 326099, 326104, 326107, 326299, MCZ 26541, 26543, 26548, TNHC 59948, 60016), or 27 (MCZ 26546) [24]; paravertebral scale rows 67 (CAS 124804, 124806, 139293, 139300, 139304, 139309, CAS-SU 24165, MCZ 26549, TNHC 59948), 68 (CAS 124808, 124811, 139295, 139303, CAS-SU 24163, CMC 12171, KU 326101, 326106, MCZ 26543, 26550, TNHC 60016), 69 (CAS 124803, 124807, 139294, 139305, CMC 12170, KU 326096, MCZ 26548), or 70 (CAS 139307–08, KU 326099, 326103–04, 326107, 236299, MCZ 26539, 26541, 26546); axilla–groin scale rows 46 (CAS 124804, 124806, 139293, 139300, 139304, CAS-SU 24165, MCZ 26549), 47 (CAS 124808, 124811, 139295, 139309, CAS-SU 24163, CMC 12171, KU 326101, 326106, MCZ 26543, 26550), 48 (CAS 124803, 124807, 139294, 139303, 139305, CMC 12170, KU 326096, MCZ 26548, TNHC 59948), or 49 (CAS 139307–08, KU 326099, 326103–04, 326107, 326299, MCZ 26539, 26541, 26546, TNHC 60016) [49]; limbs short, well developed, pentadactyl, digits small; FinIIIlam four (CAS 124808, 124811, 139295, 139300, 139304–05, 139307–08, CMC 12171, TNHC 59948, 60016) or five (CAS 124803–04, 124806–07, 139293–94, 139303, 139309, CAS-SU 24163, 24165, CMC 12170, KU 326096, 326099, 326101, 326103–04, 326106–07, 326299, MCZ 26539, 26541, 26543, 26546, 26548–50); ToeIVlam seven (CAS 124808, 124811, 139295, 139305, CMC 12171, KU 326096, 326099, 326101, 326103–04, 326106–07, MCZ 26539, 26541, 26543, 26546, 26548–50, TNHC 59948) or eight (CAS 124803–04, 124806–07, 139293–94, 139300, 139303–04, 139307–09, CAS-SU 24163, 24165, CMC 12170, KU 326299, TNHC 60016); FLL 12.4–19.4% (15.4 ± 1.7) AGD [13.3], 8.6–12.4% (10.3 ± 1.0) SVL [9.0]; HLL 20.6–35.1% (26.5 ± 2.7) AGD [26.7], 14.0–22.6% (17.8 ± 1.6) SVL [17.9]; order of digits from shortest to longest for hand: V = I < IV = II < III, for foot: V = I < II < III < IV; tail not as wide as body, gradually tapered towards end, TW 56.8–78.9% (70.3 ± 5.5) MBW, TL 79.5–102.1% (92.5 ± 5.8) SVL.

Rostral projecting onto dorsal snout to point in line with middle of nasal, broader than high, in contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single pentagonal nasal, longer axis directed anterodorsally and posteroventrally; supranasals present, large, broadly separated; postnasals present and small (CAS 124807, 124812, 139307–08, 139310, CAS-SU 24160, KU 326096, 326100, MCZ 26539, 26541, 26543–44, 26546, 26548–50), present and highly reduced (CAS 124808, 139294, 139301–02), fused to supranasal on one side of the head (CAS 139303, 139306, CAS-SU 24158, 24162, KU 326106), or fused to supranasals on both sides of the head (CAS 124806, 124809–11, 139296–300, 139309, 139311, CAS-SU 24159, 24161, 24163–65, 24171, KU 326089, 326099, 326101–05, 326107–08); prefrontals separated (CAS 124806, 124808, 139293–96, 139299, 139301–05, CMC 12170–71, KU 326089, 326096, 326099, 326100–05, 326107–08, 326299, MCZ 26539, 26541, 26543), in point medial contact (FMNH 52642, KU 326106, MCZ 26544), or in moderate medial contact (FMNH 52647, MCZ 26546, 26548–50); frontal diamond-shaped, its anterior margin in narrow to broad contact with frontonasal, narrowly separated from frontonasal, or in moderate medial contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anterior supraocular; supraoculars five; frontoparietals large, each in contact with supraoculars II–IV, frontoparietals separated (CAS 124806, 124808, 139295, 139301, 139303–05, KU 326299), in point medial contact (KU 326101), or in moderate medial contact (CAS 139293–94, 139296, 139299, 139302, CMC 12170–71, FMNH 52642, 52647, KU 326089, 326096, 326099–100, 326102–08, MCZ 26539, 26543–44, 26546, 26548–50); interparietal large, its length roughly equal to midline length of frontoparietal, longer than wide, subdiamond-shaped, wider anteriorly, with pineal eyespots present and distinct (CAS 139296, CMC 12170–71, FMNH 52642, KU 326089, 326096, 326099, 326100–08, 326299, MCZ 26539, 26541, 26543–44, 26546, 26549–50), present and indistinct (CAS 124806, 124808, 139294–95, 139299, 139302, 139304–05), or absent (FMNH 52647, CAS 139293, 139301, 139303, MCZ 26548); parietals broader than frontoparietals, in broad contact behind interparietal; nuchals undifferentiated; two loreals, decreasing in height from anterior to posterior, anterior loreal slightly narrow than and higher than posterior loreal; preocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to posterior edge of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales on dorsal margin; supralabials six, first 1.5× size of others, fourth and fifth below eye; infralabials six (CMC 12170–71, KU 326096, 326099, 326101, 326103–04, 326106–07, 326299, MCZ 26539, 26541, 26543, 26546, 26548–50, TNHC 59948, 60016) or seven (CAS 124803–04, 124806–08, 124811, 139293–95, 139300, 139303–05, 139307–09, CAS-SU 24163, 24165) (Fig. 5.4).

Mental wider than long, in contact with first infralabials; postmental single, enlarged, its width greater than width of mental; followed by two pairs of enlarged chin shields, first pair of enlarged chin shields separated (CAS 139294, CMC 12170–71, KU 326099, 326299, MCZ 26550), in point medial contact (CAS 124808, 139293, MCZ 26541), or in moderate to broad medial contact (CAS 124806, 139295–96, 139299, 139301–05, FMNH 52642, 52647, KU 326089, 326096, 326100–08, MCZ 26539, 26543–44, 26546, 26548–49); second pair wider than, or narrower than, first, broadly separated by one, two, or three medial scales (Fig. 5.4).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces

of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative (based on holotype description and 37 referred specimens).— Ground color of body is medium brown throughout or with distinctly darker middorsal region (KU 319934–35, 319938–39, 326097, 326105–06, 326108). Light dorsolateral stripes are present in some specimens (KU 326096–98, 326100–04, 326107), absent in remainder. Dorsal surfaces of head, and snout are uniformly medium brown (majority of specimens) or with darker marbling (e.g., KU 319936, 319938, 326100–03). Lateral surfaces of the head are nearly uniformly dark brown; supraocculars are slightly darker than surrounding scales. Postocculr and tympanic regions are distinctly darker than remaining portions of the head and neck in some specimens (KU 326100, 326105–06, 326108). The rostral, supranasals, postnasals, first suprlabials and infralabials and mental scales are all medium gray. Suprlabials are dark brown and infralabials, mental, and chin shields are a lighter shade of orange-brown.

Trunk coloration is variable, with dorsal surfaces dark to medium brown with a series of faint longitudinal streaks, each composed of a series of distinct dark spots either confined to the distal edge of each scale or traversing the whole scale. Lateral surfaces, lack longitudinal streaks and are either homogeneous dark brown or possess equally spaced spots of dark pigment, with each spot on distal tip of each scale.

Ventral surfaces exhibit a wide range of variation with homogeneous dark brown in some specimens (KU 319937–38, 326103, 326106, 326108) to very light orange-brown withalmost no dark pigment in others (KU 319939–40, 326096, 326099, 326104, 326299). In specimens of intermediate hues of pigmentation (KU 319935–36 and remainder of series), ventral surfaces are marked by evenly spaced dark brown spots (corresponding to the distal edge of each scale) on a light ornge-brown background. Ventral surfaces of the head and neck devoid of any dark pigmentation (KU 326096–97, 326099, 326103) or with a light ornge-brown ground coloration with dark streaks composed of dark brown spots on each scale. The posterior portion of trunk with dark brown spots or clusters of striations at the distal edge of each scale, becoming more pronounced posteriorly; subcaudal regions nearly solid dark brown (e.g., KU 326106, 326108), with dark brown spots on the distal edge of each scale (e.g., KU 326100, 326104), or with clusters of faint, dark, striations on the distal edges of scales (remainder). Tail coloration becomes more distinct distally, with contrasting darker shades of brown and lighter ground colration at the tail's tip, which is nearly black in many specimens. Ventral surfaces of hands and feet are light gray to cream, with slightly darker fingers and toes. The precloacals region is slightly lighter than the surrounding ventrals and subcaudals.

Coloration in life.—Coloration in life is unrecorded; however, because *Brachymeles* specimens do not change significantly during preservation (CDS, RMB personal observation), we suspect that the preserved coloration and patterns are much like those in life.

Distribution.—Brachymeles gracilis is known only from central, southern, and southeastern Mindanao Island (Fig. 5.3). No mention of the specific locality, or province, on Mindanao Island was ever given for the holotype (Fischer, 1885). Although we are certain of our identification of *B. gracilis*, that specimens referred here to this species match the type description, and that no other species can possibly be confused with *B. gracilis*, we are unable to pinpoint the type locality on the basis of available specimens.

Ecology and natural history.—Brachymeles gracilis occurs in primary- and secondary-growth forest habitats. In South Cotabato Province, Mindanao Island (Fig. 5.2), *B. gracilis* has been documented to occur in sympatry with *B. schadenbergi* (Siler and Brown, 2010) and *B.*

tiboli. Interestingly, this is the first documented case of two species of *Brachymeles* in the same body form and body size class (*B. gracilis* and *B. tiboli*) occuring in sympatry. All other sympatric communities of *Brachymeles* are made up of distinctly different body forms (e.g., large pentadactyl, medium pentadactyl, non-pentadactyl, limbless). The eastern populations of *B. gracilis* (e.g., Davao Province populations) are documented to occur in sympatry with *B. orientalis* (a large-bodied form; Siler and Brown, 2010). In addition to *B. gracilis, B. tiboli*, *B. orientalis,* and *B. schadenbergi*, two other species of *Brachymeles* have been confirmed to occur on Mindanao Island (*B. pito* and *B. pathfinderi*; Siler and Brown, 2010; Siler et al., in press a).

We have evaluated this species against the IUCN criteria for classification, and find that it does not qualify for Critically Endangered, Endangered, Vulnerable, or Near Threatened status. *Brachymeles gracilis* has been documented to have a broad geographic distribution and is quite abundant at all sampled localities. We therefore classify this species as Least Concern, LC (IUCN, 2010).

Other sympatric scincid species observed on Mindanao Island include: *Eutropis indeprensa, E. multicarinata, E. multifasciata, E. englei, Lamprolepis smaragdina, L. pulchella, L. quadrivittata, Sphenomorphus abdictus abdictus, S. acutus, S. atrigularis, S. cumingi, S.* cf. *mindanensis, S. coxi, S. fasciatus, S. jagori, S. llanosi, S. steerei, S. variegatus, Tropidophorus misaminus, T. partelloi.*

Brachymeles pito Brown and Rabor 1967

Fig. 5.4

Brachymeles pito*, Brown and Rabor, 1967:543 (type locality: Barrio Balang-balang, Mt. Hilong-hilong, Diuata Mountains, Agusan Province, Mindanao Island, Philippines, 9° 03'*

20.77" N, 125° 37' 40.8" E [holotype: CAS-SU 24407]).

Brachymeles gracilis hilong*, Brown and Alcala, 1970:113; Brown and Alcala, 1980:39.*

Diagnosis.—Brachymeles pito can be distinguished from congeners by the following combination of characters: (1) body size medium (SVL 59.9–81.5 mm); (2) limbs pentadactyl; (3) limb length moderate; (4) relative tail length moderate; (5) Finger-III lamellae five; (6) Toe-IV lamellae eight or nine; (7) supralabials six; (8) infralabials six; (9) suparciliaries six; (10) supraoculars five; (11) midbody scale rows 27–30; (12) axilla–groin scale rows 44–50; (13) paravertebral scale rows 66–73; (14) pineal eyespot present; (15) supranasals separate; (16) prefrontals separate; (17) postnasal/supranasal fusion absent; (18) enlarged chin shields in two or three pairs; (19) nuchal scales undifferentiated; (20) fourth and fifth supralabial below eye; (21) auricular opening present; and (22) presacral vertebrae 32 (Tables 5.4, 5.5).

Comparisons.—Characters distinguishing *Brachymeles pito* from all medium-sized, pentadactyl species of *Brachymeles* are summarized in Tables 5.4 and 5.5. *Brachymeles pito* most closely resembles *B. syam*; however, *B. pito* differs from this taxon by having a shorter relative tail length (TL/SVL up to 126% vs. less than 98%), a greater number of presacral vertebrae (32 vs. 31), a greater number of midbody scale rows (27–30 vs. 25–26), a tendency towards a greater number of axilla–groin scale rows (up to 50 vs. less than or equal to 45), a tendency towards a greater number of paravertebral scale rows (up to 73 vs. less than or equal to 67), enlarged chind shields in two or three pairs (vs. three), and the absence of contact between prefrontal scales (vs. presence or absence).

Brachymeles pito can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all non-pentadactyl species of *Brachymeles* (*B. bonitae, B. cebuensis, B. elerae, B. muntingkamay, B. pathfinderi, B.*

samarensis, B. tridactylus, B. wright, sp. nov. [Leyte Island; Siler et al., in press c], sp. nov. [Lapinig Group Islands; Siler et al., in press c], sp. nov. [Catanduanes Island; Siler et al., in press c], sp. nov. [Central Bicol Peninsula, Luzon Island; Siler et al., in press c], and sp. nov. [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c]) by having pentadactyl (vs. non-pentadactyl) limbs.

Description (based on holotype and 25 referred specimens).—Details of the head scalation of an adult female are shown in Figure 5.4. Measurements of the holotype (CAS-SU 22407) are provided below in brackets. Body medium-sized, moderately slender; maximum SVL 78.5 mm for males, 81.5 mm for females, [61.5, subadult] (Tables 5.4, 5.5); head weakly differentiated from neck, nearly as wide as body, HW 9.6–12.9% (10.7 ± 0.8) SVL, 98.9–122.7% (106.3 ± 5.0) HL; HL 32.5–43.5% (37.2 ± 2.2) SnFa; SnFa 23.3–30.1% (27.1 ± 1.5) SVL; snout short, rounded in dorsal and lateral profile, SNL 47.2–71.9% (56.4 ± 5.1) HL; ear opening visible, small; eyes small, ED 1.7–3.0% (2.0 ± 0.3) SVL, 16.9–27.9% (20.0 ± 2.2) HL, 40.4–74.8% (50.0 ± 6.7) END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 102.4–154.7% (128.9 ± 14.9) MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 27 (CAS 102406, 133577–78, 133581, 133692, 133704, KU 319937–38, 319940), 28 (CAS 133582, 133609, 133612, 133693, 133703, 133705–06, 133743, 133745–46, 133747, CAS-SU 24315, 24411, KU 319935–36), or 30 (CAS-SU 24407) [30]; paravertebral scale rows 66 (CAS 102406), 67 (CAS 133704, CAS-SU 24315), 68 (CAS 133578, 133581–82, 133609, 133703, 133745–47, CAS-SU 24411, KU 319936–38, 319940), 69 (CAS 133612, 133692–93, KU 319935), 70 (CAS 133577, 133706, 133743, CAS-SU 24407), or 73 (CAS 133705) [70]; axilla–groin scale rows 44 (CAS 102406), 45 (CAS 133747, CAS-SU 24315), 46 (CAS 133582, 133609, 133612, 133692, 133703, CAS-SU 24411, KU 319936–38, 319940), 47 (CAS 133578, 133581, 133693, 133704, 133743, 133746, CAS-SU 24407, KU 319935), 48 (CAS 133577, 133706, 133745), or 50 (CAS 133705) [47]; limbs short, well developed, pentadactyl, digits short; FinIIIlam 5 [5]; ToeIVlam eight (CAS 102406, 133581, 133609, 133693, 133703–04, 133706, 133743, 133745–47, CAS-SU 24315, 24411, KU 319935–38, 319940) or nine (CAS 133577–78, 133582, 133612, 133692, 133705, CAS-SU 24407) [9]; FLL 15.3–22.0% (18.2 ± 1.7) AGD, 10.3–14.0% (11.8 ± 0.9) SVL; HLL 27.0–37.2% (30.8 ± 2.8) AGD, 17.5–23.4% (19.8 ± 1.5) SVL; order of digits from shortest to longest for hand: I = V < IV = II < III, for foot: V < I < II < IV = III; tail not as wide as body, gradually tapered towards end, TW 56.9–81.4% (70.5 ± 6.6) MBW, TL 57.5–97.9% (78.8 ± 13.8) SVL [89.7].

Rostral projecting onto dorsal snout to point in line with middle of nasal, broader than high, in broad contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anterodorsally and posteroventrally; supranasals present, large, broadly separated; postnasals present, small to moderate; prefrontals moderately separated; frontal nearly diamond-shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 3.5× wider than anterior supraocular; supraoculars five; frontoparietals moderate, each in contact with supraoculars II–IV, frontoparietals separated (CAS 133578, 133704, 133743, KU 319940), in point medial contact (CAS 133579, KU 319937), or in moderate medial contact (CAS 133581, 133705, KU 319934–36, 319938–39); interparietal large, its length roughly 2× length of frontoparietal, longer than wide, subdiamond-shaped, wider anteriorly; parietals roughly as broad as frontoparietals, separated (KU 319935, 319940), in point medial contact (KU 319934–38), or in moderate medial contact (CAS 133578–79, 133581, 133704–05, 133743, KU 319934, 319936, 319939); nuchals undifferentiated; two loreals, decreasing in size from anterior to posterior, anterior loreal about as long and slightly higher than posterior loreal; preocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to midline of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales on dorsal margin; supralabials six, first 1.5× size of others, fourth and fifth below eye; infralabials six (Fig. 5.4).

Mental wider than long, in contact with first infralabials; postmental single, enlarged, its width greater than width of mental; followed by two or three pairs of enlarged chin shields, first pair of enlarged chin shields separated (CAS 133578–79, 133743, KU 319934–40), in point medial contact (CAS 133704), or in moderate medial contact (CAS 133581, 133705), second pair wider than first, broadly separated by single medial scale, third pair absent (CAS 133578, 133581, 133704–05, 133743), or present (CAS 133579, KU 319934–40) and separated by three to five medial scales (Fig. 5.4).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration in preservative (based on holotype description and 25 referred specimens).—The ground color of the body of *B. pito* is medium brown with dark brown longitudinal streaks, with dark streaks traversing each scale. The species lacks any sign of color pattern differentiation between dorsal and lateral surfaces except for a tendency towards more darkly pigmented streaks in middoorsal region and a progressively lighter pattern on ventral surfaces. Light dorsolateral stripes are completely absent. Dorsal surfaces of head, and snout are uniformly light brown (CAS 133704), light brown with darker marbling (CAS 133581, 133704), or are uniformly dark brown (CAS 133579, 133743). Lateral surfaces of the head are uniformly dark brown with light scale sutures; supraocculars are slightly darker than surrounding scales. The rostral, supranasals, postnasals, first suprlabials and infralabials and mental scales are all medium gray. Suprlabials are dark brown and infralabials, mental, and chin shields are a slightly lighter shade of orange-brown.

Trunk coloration is relatively invariant. Lateral surfaces, lack possess longitudinal streaks similar to those of dorsum and become increasingly lighter ventrally.

Ventral surfaces distinctly lighter than lateral and dorsal coloration, either nearly devoid of dark pigment (CAS 133581) or with very faint streaks of diffuse darker brown spots (on per scale). Ventral surfaces of the head and neck devoid of any dark pigmentation (CAS133581, 133704–05) darker brown ground color with light scale margins (CAS133579, 133743). Ventral tail is not distinctly different from ventral trunk coloration, but some specimens exhibit slightly darker tail tips (CAS 133581, 133743). Ventral surfaces of hands and feet are medium gray, with slightly darker fingers and toes. The precloacals region is not noticeably different form the surrounding ventrals and subcaudals.

Coloration in life.—Coloration in life is unrecorded; however, because *Brachymeles* specimens do not change significantly during preservation (CDS, RMB personal observation), we suspect that the preserved coloration and patterns are much like those in life.

Distribution.—Brachymeles pito is known only from northwestern Mindanao Island (Fig. 5.3).

Ecology and natural history.—Brachymeles pito occurs in primary- and secondary-growth forest habitats. In contrast to *B. gracilis* and *B. tiboli*, *B. pito* does not occur in sympatry with any other medium-sized, pentadactyl species of *Brachymeles.* However, *B. orientalis* also occurs throughout the recognized range of *B. pito*. In addition to *B. pito* and *B. orientalis*, four other species of *Brachymeles* have been confirmed to occur on Mindanao Island (*B. gracilis, B. tiboli, B. pathfinderi,* and *B. schadenbergi*; Siler and Brown, 2010; Siler et al., in press a). Based on our expectation that this species will likely qualify for a threatened category in the near future, we would recommend classification of *B. pito* as Near Threatened, NT, based on the following criteria: VU B1ab(iii); D2 (IUCN, 2010).

Other sympatric scincid species observed on Mindanao Island include: *Eutropis indeprensa, E. multicarinata, E. multifasciata, E. englei, Lamprolepis smaragdina, L. pulchella, L. quadrivittata, Sphenomorphus abdictus abdictus, S. acutus, S. atrigularis, S. cumingi, S.* cf. *mindanensis, S. coxi, S. fasciatus, S. jagori, S. llanosi, S. steerei, S. variegatus, Tropidophorus misaminus, T. partelloi.*

Brachymeles sampu Taylor 1918: 254

Fig. 5.5

Brachymeles sampu*, Taylor, 1918:254, Type locality: Bubuan Island, Tapiantana Group, Sulu Province, Philippines.*

Brachymeles gracilis*, Taylor, 1922 a:247; 1922 b:287; (part) Brown and Alcala, 1970:112.*

Brachymeles gracilis gracilis*, Brown, 1956:10; Brown and Rabor, 1967:537; Brown and Alcala, 1980:37.*

Designation of a neotype for Brachymeles sampu.—Taylor (1918) clearly declared a type specimen, deposited at the Philippine Bureau of Science under collection No. 1989, for B. sampu. In a subsequent revision he (Taylor 1922a), synonymized B. sampu with B. gracilis, basing the revised description of B. gracilis on the type specimen of B. sampu which he then (incorrectly) reported to be Philippine Bureau of Science collection No. 1666. We assume that Taylor's (1922a) reference to specimen No. 1666 as the type specimen of B. sampu was in error, that Philippine Bureau of Science No. 1989 was the valid holotype for B. sampu, and that Philippine Bureau of Science No. 1666 was a non-type specimen of B. gracilis. Unfortunately the Philippine Bureau of Science was destroyed and all specimens destroyed during the firebombing of Manila in World War II (see Brown and Alcala, 1978). In the absence of an existing holotype and in accordance with article No. 75 of the International Code of Zoological Nomenclature (ICZN, 1979), we designate a neotype for this species. Accordingly, we choose an adult female specimen from the geographically proximate island of Basilan (Fig. 5.3). Two specimens from Taylor's collections on Basilan Island have been examined in the collections at CAS. Both specimens agree with Taylor's (1918) holotype description; from these collections we have chosen a female neotype.

Neotype.—CAS 60366 (E. H. Taylor Field No. 1173), adult female, collected in Isabela City, Basilan Province, Basilan Island, Philippines, by E. H. Taylor.

Diagnosis.—*Brachymeles sampu* can be distinguished from congeners by the following combination of characters: (1) body size medium (SVL 71.9 mm); (2) limbs pentadactyl; (3) limb length moderate; (4) Finger-III lamellae five; (5) Toe-IV lamellae eight; (6) supralabials six; (7) infralabials six; (8) suparciliaries six; (9) supraoculars five; (10) midbody scale rows 24; (11) axilla–groin scale rows 48; (12) paravertebral scale rows 69; (13) pineal eyespot present; (14) supranasals separate; (15) prefrontals separate; (16) frontoparietals separate; (17) first pair of enlarged chin shields in contact; (18) postnasal/supranasal fusion absent; (19) enlarged chin shields in three pairs; (20) nuchal scales undifferentiated; (21) fourth and fifth supralabial below eye; (22) auricular opening present; and (23) presacral vertebrae 31 (Tables 5.4, 5.5).

Comparisons.—Characters distinguishing *Brachymeles sampu* from all medium-sized, pentadactyl species of *Brachymeles* are summarized in Tables 5.4 and 5.5. *Brachymeles sampu* most closely resembles *B. gracilis, B. anim,* and *B. tiboli*. However, *B. sampu* differs from these three taxa by having eight Toe-IV lamellae (vs. six [*B. tiboli*], seven or eight [*B. gracilis*], eight or nine [*B. anim*]), fewer presacral vertebrae (31 vs. 32 [*B. anim*], 33 [*B. tiboli*], 34 [*B. gracilis*]), the presence of a pineal eyespot (vs. presence or absence), the absence of contact between prefrontal scales (vs. presence or absence), the absence of contact between frontoparietal scales (vs. presence or absence [*B. gracilis*], presence [*B. anim*, *B. tiboli*]), and the presence of contact between the first pair of enlarged chin shields (vs. presence or absence [*B. gracilis*, *B. tiboli*], absence [*B. anim*]). *Brachymeles sampu* further differs from *B. gracilis* and *B. walo* by having five Finger-III lamellae (vs. four or five); from *B. gracilis* and *B. anim* by having enlarged chin shields in three pairs (vs. two); and from *B. gracilis* by having six infralabials (vs. six or seven) and by the absence of a fused postnasal/supranasal scale (vs. presence or absence).

Brachymeles sampu can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all non-pentadactyl species of *Brachymeles* (*B. bonitae, B. cebuensis, B. elerae, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. wright*, sp. nov. [Leyte Island; Siler et al., in press c], sp. nov. [Lapinig Group Islands; Siler et al., in press c], sp. nov. [Catanduanes Island; Siler et al., in press c], sp. nov. [Central Bicol Peninsula, Luzon Island; Siler et al., in press c], and sp. nov. [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c]) by having pentadactyl (vs. non-pentadactyl) limbs.

Description of neotype.—Details of head scalation in CAS 60366 are shown in Figure 5.5. Adult female, body medium in size, moderately slender, SVL 71.9 mm; head weakly differentiated from neck, nearly as wide as body, HW 9.3% SVL, 97.8% HL; HL 38.9% SnFa; SnFa 24.3% SVL; snout short, broadly rounded in dorsal profile, bluntly rounded in lateral profile, SNL 55.2% HL; ear opening visible, small; eyes small, ED 2.4% SVL, 25.8% HL, 69.0% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 158.1% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 24; paravertebral scale rows 69; axilla–groin scale rows 48; limbs short, well developed, pentadactyl, digits small; FinIIIlam 5; ToeIVlam 8; FLL 14.4% AGD, 10.0% SVL; HLL 26.2% AGD, 18.1% SVL; order of digits from shortest to longest for hand: I = V < IV = II < III, for foot: V = I < II < IV = III; tail regenerated, not as wide as body, gradually tapered towards end, TW 70.8% MBW.

Rostral projecting onto dorsal snout to point in line with anterior edge of nasal, broader than high, in broad contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anterodorsally and posteroventrally; supranasals present, large, broadly separated; postnasals present, small; prefrontals moderately separated; frontal suboctagonal-shaped, fragmented posteriorly (Fig. 5), its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 4× wider than anterior supraocular; supraoculars five; frontoparietals moderate, broadly separated, each frontoparietal in contact with supraoculars II–IV; interparietal large, its length roughly 2× length of frontoparietal, longer than wide, diamond-shaped; parietals roughly as broad as frontoparietals, moderately separated behind interparietal; nuchals undifferentiated; two loreals, decreasing in size from anterior to posterior, anterior loreal about as long as and moderately higher than posterior loreal; preocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to midline of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales on dorsal margin; supralabials six, first 1.5× size of other supralabials, fourth and fifth below eye; infralabials six (Fig. 5.5).

Mental wider than long, in contact with first infralabials; postmental single, enlarged, its width greater than width of mental; followed by three pairs of enlarged chin shields, first pair in moderate medial contact, second pair wider than first, moderately separated by single medial scale, third pair narrower than first and second pairs, separated by three medial scales (Fig. 5.5).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration of neotype in preservative.— Ground color of body dark gray-brown, with few color features and no apparent differences between dorsal, lateral and ventral surfaces of trunk and tail. Dorsal surfaces of head, and limbs, colored like trunk, with few lighter brown blotches on head scales; snout slightly darker than remainder of head. Suprlabials slightly darker brown than infralabials, mental, and chin shields. Regenerated portion of tail (distal one third) slightly lighter than remainder.

Trunk coloration invariant; all surfaces medium brown with a series of very faintly indistinct longitudinal streaks, each composed of a series slightly darker spots on the distal edge of each scale.

Ventral body surfaces dark homogeneous gray-brown; subcaudal region similar with slightly lighter regenerated portion towards tail tip. Ventral surfaces of hands and feet light gray; fingers and toes light gray. Precloacals slightly not noticeably lighter than surrounding ventrals. We assume that coloration has considerably faded in the 95 years since the neotype was preserved.

Coloration in life.—"Above and below light brown, each scale with a large slightly darker spot; a lighter stripe from behind eye to hind leg" (Taylor, 1918).

Measurements and scale counts of neotype in mm.—SVL 71.9; AGD 49.7; TotL 110.1; MBW 8.2; MBH 5.2; TL 38.2; TW 5.8; TH 4.6; HL 6.8; HW 6.7; HH 4.6; SnFa 17.5; ED 1.8; END 2.6; SNL 3.8; IND 2.3; FLL 7.2; HLL 13.1; MBSR 24; PVSR 69; AGSR 48; FinIIIlam 5; ToeIVlam 8; SL 6; IFL 6; SC 6; SO 5.

Variation.—Morphometric variation of the series is summarized in Table 5.6. We are aware of only one adult and one subadult specimen of *B. sampu* in museum collections (CAS 60365–66). We observed the following minor variation in scale contact and scale row counts between the neotype and the subadult specimen: axilla–groin scale row counts of 47 (CAS 60365; subadult) or 48 (CAS 60366; neotype); parietals separated (CAS 60366; neotype) or in point medial contact (CAS 60365; subadult); frontal fragmented posteriorly (CAS 60366; neotype) or unbroken (CAS 60365; subadult). The subadult has noticeably more distinct longitudinal streaks on the dorsal survaces of the body (each stream composed of spots, confinded to distal edges of dorsal scales), distint light dorsolateral stripes, a darker tail tip, uniformly brown head scales, and a light brown ventral surfaces of the hed and neck.

Distribution.—Brachymeles sampu is known only from Basilan and Bubuan islands (Fig. 5.3).

Ecology and natural history.—Taylor (1918) did not provide any information regarding the microhabitat preferences of *Brachymeles sampu*; however, we assume that the species occurs in disturbed and secondary-growth forest on the islands of Basilan and Bubuan. On Basilan Island, *B. sampu* is found in sympatry with *B. schadenbergi*. We have evaluated this species against the IUCN criteria for classification, and find that it qualifies for the status of Vulnerable, VU, based on the following criteria: VU B2ab(iii); D2 (IUCN, 2010).

Other sympatric scincid species observed on Basilan Island include: *Emoia atrocostata, Eutropis multicarinata, E. rudis, E. multifasciata, Lamprolepis smaragdina, Lipinia quadrivittata, Sphenomorphus atrigularis, S. fasciatus, S. jagori, S. variagatus*, *Tropidophorus misaminus.*

Brachymeles anim sp. nov.

Figs. 5.3, 5.5

*Holotype.—*PNM 9766 (RMB Field No. 8223, formerly KU 310359), adult male, collected under rotting logs in secondary-growth forest (10:00–12:30 hr) on 19 June 2007, in Sitio Pamahawan, Barangay Pandan, Municipality of Mambajao, Camiguin Sur Province, Camiguin Sur Island, Philippines (09°15'00" N, 124°42'57.6" E; WGS-84), by J. Fernandez.

Paratypes.—Four adult females (CAS-SU 26142, 26144, 26231, 26236) and two juveniles of undetermined sex (CAS-SU 26145–46), collected on 30 June 1966, in Dago-okan, 2 km south of Catibawasan Falls, Municipality of Mambajao, Camiguin Sur Province, Camiguin Sur Island, Philippines (09°11'24.9" N, 124°43'36.01" E; WGS-84), by L. C. Alcala; one juvenile of undetermined sex (CAS-SU 26294) collected on 3 July 1966, in Sitio Basiao, Barrio Naasag, Municipality of Mambajao, Camiguin Sur Province, Camiguin Sur Island, Philippines (09°13'9.95" N, 124°39'18" E; WGS-84), by L. C. Alcala; one juvenile of undetermined sex (CAS-SU 26295) collected on 3 July 1966, on the northwest side of Nasawa crater, Municipality of Mambajao, Camiguin Sur Province, Camiguin Sur Island, Philippines (09°11'14.17" N, 124°41'45.6" E; WGS-84), by L. C. Alcala; two adult females (CAS-SU 26166, 26185), one juvenile female (CAS-SU 26165), one juvenile male (CAS-SU 16184), collected on 4 July 1966, in Barrio Naasag, Municipality of Mambajao, Camiguin Sur Province, Camiguin Sur Island, Philippines (09°13'9.95" N, 124°39'18" E; WGS-84), by L. C. Alcala; three adult females (CAS-SU 28199, 28331, 28358), one juvenile female (CAS-SU 28359), and two juveniles of undetermined sex (CAS-SU 28314, 28329) collected between 15 and 27 May 1967, 4.5–8.0 km NE of Catarman Town, Municipality of Catarman, Camiguin Sur Province, Camiguin Sur Island, Philippines (09°07'32.02" N, 124°40'32.02" E; WGS-84), by L. C. Alcala; one adult female (CAS 139031) collected on 1 March 1973, in Kantinbay, Municipality of Mambajao, Camiguin Sur Province, Camiguin Sur Island, Philippines (09°11'50.1" N, 124°43'12" E; WGS-84), by L. C. Alcala.

Diagnosis.—*Brachymeles anim* can be distinguished from congeners by the following combination of characters: (1) body size medium (SVL 53.6–80.1 mm); (2) limbs pentadactyl; (3) limb length moderate; (4) relative tail length short; (5) Finger-III lamellae five; (6) Toe-IV lamellae eight or nine; (7) supralabials six; (8) infralabials six; (9) suparciliaries six; (10) supraoculars five; (11) midbody scale rows 26–28; (12) axilla–groin scale rows 44–49; (13) paravertebral scale rows 65–70; (14) supranasals separate; (15) frontoparietals in contact; (16) parietals in contact; (17) first pair of enlarged chin shields separate; (18) postnasal/supranasal fusion absent; (19) enlarged chin shields in two pairs; (20) nuchal scales undifferentiated; (21) fourth and fifth supralabial below eye; (22) auricular opening present; and (23) presacral vertebrae 32 (Tables 5.4, 5.5).

Comparisons.—Characters distinguishing *Brachymeles anim* from all medium-sized, pentadactyl species of *Brachymeles* are summarized in Tables 5.4 and 5.5. *Brachymeles anim* most closely resembles *B. gracilis, B. tiboli,* and *B. sampu*. However, *B. anim* differs from these three taxa by having eight or nine Toe-IV lamellae [vs. six [*B. tiboli*], seven or eight [*B. gracilis*], eight [*B. sampu*], 32 presacral vertebrae (vs. 31 [*B. sampu*], 33 [*B. tiboli*], 34 [*B. gracilis*]), and by the absence of contact between the first pair of enlarged chin shields (vs. presence or absence [*B. gracilis*, *B. tiboli*], presence [*B. sampu*]). *Brachymeles anim* further differs from *B. gracilis* and *B. walo* by having a shorter relative tail length (TL/SVL less than 84% vs. up to 102% [*B.* gracilis] and 90% [*B. tiboli*]) and five Finger-III lamellae (vs. four or five); from *B. walo* and *B. sampu* by having enlarged chin shields in two pairs (vs. three); from *B. gracilis* and *B. sampu* by the presence of contact between frontoparietal scales (vs. presence or absence [*B. gracilis*], absence [*B. sampu*]); from *B. gracilis* by having six infralabials (vs. six or seven) and by the absence of a fused postnasal/supranasal scale (vs. presence or absence); and from *B. sampu* by having a greater number of midbody scale rows (26–28 vs. 24).

Brachymeles anim can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all non-pentadactyl species of *Brachymeles* (*B. bonitae, B. cebuensis, B. elerae, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. wright*, sp. nov. [Leyte Island; Siler et al., in press c], sp. nov. [Lapinig Group Islands; Siler et al., in press c], sp. nov. [Catanduanes Island; Siler et al., in press c], sp. nov. [Central Bicol Peninsula, Luzon Island; Siler et al., in press c], and sp. nov. [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c]) by having pentadactyl (vs. non-pentadactyl) limbs.

Description of holotype.—Details of the head scalation are shown in Figure 5.5. Adult male, body medium in size, moderately slender, SVL 75.8 mm; head weakly differentiated from neck, nearly as wide as body, HW 10.2% SVL, 109.6% HL; HL 34.1% SnFa; SnFa 27.4% SVL; snout short, broadly rounded in dorsal and lateral profile, SNL 61.9% HL; ear opening visible, small; eyes small, ED 1.8% SVL, 19.5% HL, 45.1% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 127.0% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26; paravertebral scale rows 68; axilla–groin scale rows 49; limbs short, well developed, pentadactyl, digits small; FinIIIlam 5; ToeIVlam 8; FLL 17.6% AGD, 11.5% SVL; HLL 27.6% AGD, 18.0% SVL; order of digits from shortest to longest for hand: V < I < IV = II < III, for foot: I < V < II < IV = III; tail regenerated, not as wide as body, gradually tapered towards end, TW 81.6% MBW.

Rostral projecting onto dorsal snout to point in line with anterior one third of nasal, broader than high, in broad contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anteroventrally and posterodorsally; supranasals present, large, broadly separated; postnasals present, moderate; prefrontals moderately separated; frontal subdiamond-shaped, its anterior margin in moderate contact with frontonasal, in contact with first two anterior supraoculars, 2.5× wider than anterior supraocular; supraoculars five; frontoparietals moderate, in moderate medial contact, each frontoparietal in contact with interior three supraoculars; interparietal moderate, its length roughly 1.5× length of frontoparietal, slightly longer than wide, subdiamond-shaped, wider anteriorly; parietals roughly as broad as frontoparietals, in broad medial contact behind interparietal; nuchals undifferentiated; two loreals, decreasing in size from anterior to posterior, anterior loreal slightly longer than and about as high as posterior loreal; preocular single; presubocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to posterior edge of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales on dorsal margin; supralabials six, first nearly 2× size of other supralabials, fourth and fifth below eye; infralabials six (Fig. 5.5).

Mental wider than long, in contact with first infralabials; postmental single, enlarged, its width greater than width of mental; followed by two pairs of enlarged chin shields, first pair moderately separated by singl medial scale, second pair wider than first, moderately separated by one, two, or three medial scales (Fig. 5.5).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration of holotype in preservative.—The ground color of the body is light (lateral surfaces) to medium (middorsal surface) brown,with very two faintly lighter dorsolateral stripes enclosing a distinctly darker middorsal region. Dorsal surfaces of the head, forelimbs, hind limbs, and basal tail region darker brown. Head scales mottled light and dark brown, similar to dorsal body scales but slightly darker. Temporal region distinctly darker than remaining portions of the head and neck. Supraocular scales and other supralabial scales ligher gray-umber. Rostral, supranasals, postnasals, first suprlabials and infralabials and mental scale medium gray.

Trunk coloration variable; each dorsal scale with dark brown blotch on the anterior and posterior one fourth to one third of the scale. The resulting color pattern. a field of uniformly distributed dark brown spots not corresponding to underlying scales. Each spot consequently lies at the distal margin of each scale and bleeds over on to the basal edge of the next posteriorly adjacent scale. On lateral surfaces, each spot more or less confined to distal tip of each scale; on the ventrum, distal edge of each scale marked with fine array of three to four radiating lines, together giving the appearance of dark smudge pigmentation at the distal edge of each scale. Ventral body surfaces rich orange-brown; ventral surfaces of head, neck and subcaudal coloration similar to remaining ventrum. Ventral surfaces of hands and feet dark gray; fingers and toes nearly black. Precloacals slightly lighter than surrounding ventrals.

Coloration of holotype in life.—Coloration in life is unrecorded; however, because *Brachymeles* specimens do not change significantly during preservation (CDS, RMB personal observation), we suspect that the preserved coloration and patterns are much like those in life.

Measurements and scale counts of holotype in mm.—SVL 75.8; AGD 49.3; TotL 134.2; MBW 9.9; MBH 7.8; TL 58.4; TW 8.1; TH 6.9; HL 7.1; HW 7.8; HH 5.1; SnFa 20.8; ED 1.4; END 3.1; SNL 4.4; IND 2.5; FLL 8.7; HLL 13.6; MBSR 26; PVSR 68; AGSR 49; FinIIIlam 5; ToeIVlam 8; SL 6; IFL 6; SC 6; SO 5.

Variation.—Morphometric variation of the series is summarized in Table 5.6. Among the 20 specimens examined for the degree of contact between head scales, we observed the following variation: prefrontals in point medial contact (CAS 139031, CAS-SU 26142, 26231, 26236, 28331, 28359, KU 310359) or separated (CAS-SU 16184, 26144–46, 26165–66, 26185, 26294–95, 28199, 28314, 29329, 28358); frontoparietals in moderate to broad medial contact (CAS 139031, CAS-SU 16184, 26142, 26144–46, 26166, 26185, 26231, 26294–95, 28199, 28314, 28329, 28331, 28358, 28359, KU 310359) or in point medial contact (CAS-SU 26165, 26236). A single individual (CAS-SU 26142) was observed to possess a single, large frontoparietal scale, resulting from the fusion of the frontoparietals.

Scale counts were observed to vary among the measured series. Specimens were observed to have midbody scale row counts of 26 (CAS-SU 26166, 28199, 28358, KU 310359) and 28 (CAS 139031, CAS-SU 16184, 26142, 26144, 26165, 26185, 26231, 26236, 26295, 28331); axilla–

groin scale row counts of 44 (CAS-SU 26166), 45 (CAS-SU 28199, 28358), 47 (CAS-SU 26142, 26144, 26231, 26236, 28331), 49 (CAS 139031, CAS-SU 26165, 26185, KU 310359), and 50 (CAS-SU 16184, 26295); and paravertebral scale row counts of 65 (CAS-SU 26166), 66 (CAS-SU 28199, 28358), 68 (CAS-SU 26142, 26144, 26231, 26236, 28331, KU 310359), 69 (CAS 139031, CAS-SU 26165), and 70 (CAS-SU 16184, 26185, 26295).

We also observed lamellae counts and the presence of a pineal eyespot to vary among the specimens examined. The number of Toe-IV lamellae varied between eight (CAS-SU 26142, 26144, 26146, 26166, 26185, 26231, 26236, 26294, 28199, 28314, 28331, 28358, 28359, KU 310359) and nine (CAS 139031, CAS-SU 16184, 26145, 26165, 26295, 28329). Pineal eyespots were observed to be present (CAS 139031, CAS-SU 16184, 26145–46, 26165, 26185, 26231, 26236, 26294–95, 28199, 28329, 28331, 28358–59) or absent (CAS-SU 26142, 26144, 26166, 28314, KU 310359).

Coloration of the type series is generally very consistent. Some specimens (holotype, CAS-SU 26144, 26231) have a distinctly darker temporal and tympanic region; others have well developed dorsolater lines (CAS-SU 26144, 28358). Most specimens possess ventral coloration matching the holotype; four have nearly immaculate cream ventral surfaces (CAS-SU 26166, 28199, 28314, 28359).

Distribution.—Brachymeles anim is known only from Camiguin Sur Island (Fig. 5.3).

Ecology and natural history.—Brachymeles anim occurs in agricultural habitats, as well as in disturbed and secondary-growth forest. Little original, forest remains on Camiguin Sur Island, but we assume the species once also occurred in first-growth forest at low elevations. Individuals have been observed in the rotting material within fallen logs. Over the last several years, multiple herpetological expeditions to Camiguin Sur Island have resulted in the observation of only a single specimen of this island endemic species. However, not enough data is available to determine if this is an indication of a declining population on the island. This species is found in sympatry with *B. orientalis* (Siler and Brown, 2010). We have evaluated this species against the IUCN criteria for classification, and find that it qualifies for the status of Vulnerable, VU, based on the following criteria: VU B2ab(iii); D2 (IUCN, 2010).

Other sympatric scincid species observed on Camiguin Sur Island include: *Eutropis multifasciata, Lamprolepis smaragdina, Sphenomorphus abdictus abdictus, S. coxi, S. fasciatus, S. variegatus, Tropidophorus misaminus.*

Etymology.—The island of Camiguin Sur is volcanic in origin, with five major volcanic structures: Mt. Hibok-Hibok, Mt. Vulcan, Mt. Mambajao, M. Guinsiliban, and Mt. Uhay. Since its formation, the island has experienced regular volcanic activity, with several major eruptions resulting in the death of thousands of the island's inhabitants and the complete destruction of several coastal towns. The specific epithet is chosen in recognition of the island's volatile geologic history, and is derived from the latin word "Vulcan," the ancient Roman god of fire. Suggested common name: Camiguin Sur Slender Skink.

Brachymeles syam sp. nov.

Figs. 5.3, 5.6, 5.7

Holotype.—PNM 9767 (CDS Field No. 2772, formerly KU 310828), adult male, collected under rotting coconut husks in secondary-growth forest (10:00–12:30 hr) on 18 October 2007, in Taft Forest, Barangay San Rafael, Municipality of Taft, Eastern Samar Province, Samar Island, Philippines (11°48'9.18" N, 125°17'33.936" E; WGS-84), by CDS and J. Fernandez.

Paratopotypes.—Five adult males (KU 310826, 310830–31, 310834, 310941), 14 adult females (KU 310731, 310820–21, 310827, 310829, 310835, 310928–31, 310933–34, 310937, 310939), one juvenile male (KU 310838) and 11 juveniles of undetermined sex (KU 310730, 310822–25, 310832–33, 310836–37, 310932, 310935) collected between 11 and 26 October 2007.

Paratypes.—Three adult males (KU 311216, 311218, PNM 9768), four adult females (KU 311223, PNM 9769, 9773–74), and six juveniles of undetermined sex (KU 311220–21, PNM 9770–72, 9775,) collected under rotting logs in secondary-growth forest (10:00–12:30 hr) between 29 October and 7 November 2007, in the Sitio San Vicente Tree Nursery, Barangay Pilim, Baybay City, Leyte Province, Leyte Island, Philippines (10°43'35" N, 124°49'05" E; WGS-84), by CDS and J. Fernandez.

Diagnosis.—*Brachymeles syam* can be distinguished from congeners by the following combination of characters: (1) body size medium (SVL 64.2–76.9 mm); (2) limbs pentadactyl; (3) limb length moderate; (4) relative tail length long; (5) Finger-III lamellae five; (6) Toe-IV lamellae eight or nine; (7) supralabials six; (8) infralabials six; (9) suparciliaries six; (10) supraoculars five; (11) midbody scale rows 25–26; (12) axilla–groin scale rows 42–45; (13) paravertebral scale rows 64–67; (14) pineal eyespot present; (15) supranasals separate; (16) frontoparietals in contact; (17) parietals in contact; (18) first pair of enlarged chin shields separate; (19) postnasal/supranasal fusion absent; (20) enlarged chin shields in three pairs; (21) nuchal scales undifferentiated; (22) fourth and fifth supralabial below eye; (23) auricular opening present; and (24) presacral vertebrae 31 (Tables 5.4, 5.5).

Comparisons.—Characters distinguishing *Brachymeles syam* from all medium-sized, pentadactyl species of *Brachymeles* are summarized in Tables 5.4 and 5.5. *Brachymeles syam* most closely resembles *B. pito*; however, *B. syam* differs from this taxa by having a longer relative tail length (TL/SVL up to 126% vs. less than 98%), fewer presacral vertebrae (31 vs. 32), fewer midbody scale rows (25–26 vs. 27–30), a tendency towards fewer axilla–groin scale rows (less than 45 vs. up to 50), a tendency towards fewer paravertebral scale rows (less than 67 vs. up to 70), enlarged chind shields in three pairs (vs. two or three), the presence of contact between frontoparietal scales (vs. presence or absence), the presence of contact between paretal scales (vs. presence or absence), and the absence of contact between the first pair of enlarged chin shields (vs. presence or absence).

Brachymeles syam can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all non-pentadactyl species of *Brachymeles* (*B. bonitae, B. cebuensis, B. elerae, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. wright*, sp. nov. [Leyte Island; Siler et al., in press c], sp. nov. [Lapinig Group Islands; Siler et al., in press c], sp. nov. [Catanduanes Island; Siler et al., in press c], sp. nov. [Central Bicol Peninsula, Luzon Island; Siler et al., in press c], and sp. nov. [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c]) by having pentadactyl (vs. non-pentadactyl) limbs.

Description of holotype.—Details of the head scalation are shown in Figure 5.6. Adult male, body medium in size, moderately slender, SVL 68.6 mm; head weakly differentiated from neck, nearly as wide as body, HW 10.4% SVL, 113.5% HL; HL 31.6% SnFa; SnFa 29.0% SVL; snout short, broadly rounded in dorsal and lateral profile, SNL 69.8% HL; ear opening visible, small; eyes small, ED 1.9% SVL, 20.3% HL, 37.1% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 140.3% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26; paravertebral scale rows 65; axilla–groin scale rows 43; limbs short, well developed, pentadactyl, digits small; FinIIIlam 5; ToeIVlam 9; FLL 19.9% AGD, 12.9% SVL; HLL 31.2% AGD, 20.3% SVL; order of digits from shortest to longest for hand: I = V < II < IV = III, for foot: I < V < II < III < IV; tail long, not as wide as body, gradually tapered towards end, TW 77.6% MBW; TL 114.1% SVL.

Rostral projecting onto dorsal snout to point in line with midline of nasal, broader than high, in broad contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anteroventrally and posterodorsally; supranasals present, large, moderately separated; postnasals present, moderate; prefrontals in point medial contact; frontal suboctagonal-shaped, its anterior margin narrowly separated from frontonasal, in contact with first two anterior supraoculars, 3× wider than anterior supraocular; supraoculars five; frontoparietals moderate, in moderate medial contact, each in contact with supraoculars II–IV; interparietal moderate, its length roughly equal to length of frontoparietal, slightly longer than wide, subdiamond-shaped, wider anteriorly; parietals roughly as broad as frontoparietals, in broad contact behind interparietal; nuchals undifferentiated; two loreals, increasing in size from anterior to posterior, anterior loreal narrower than and slightly higher than posterior loreal; preocular single; presubocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to posterior edge of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales on dorsal margin; supralabials six, first 1.2× size of other supralabials, fourth and fifth below eye; infralabials six (Fig. 5.6).

Mental wider than long, in contact with first infralabials; postmental single, enlarged, its width greater than width of mental; followed by three pairs of enlarged chin shields, first pair moderately separated, second pair wider than first, moderately separated by single medial scale, third pair narrower than first and second pairs, separated by three medial scales (Fig. 5.6).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration of holotype in preservative.—Ground color of body light (lateral surfaces) to dark (middorsal surface) brown, with distinctly darker middorsal region; light dorsolateral stripes absent. Dorsal surfaces of head, and snout darker brown but dorsal surfaces of limbs match that of trunk. Scales of dorsal and lateral surfaces of head nearly uniformly dark brown; supraoccular nearly black. Nuchal and supratympanic regions distinctly darker than remaining portions of the head and neck. Rostral, supranasals, postnasals, first suprlabials and infralabials and mental scale medium gray. Suprlabials dark brown but infralabials, mental, and chin shields light orange-brown.

Trunk coloration variable; dorsal surfaces medium brown with a series of indistinct longitudinal streaks, each composed of a series of indstinct dark spots either confined to the distal edge of each scale or traversing the whole scale. Lateral surfaces, lack the appearance of longitudinal streaks but instead possess equally spaced spots of dark pigment, with each spot on distal tip of each scale.

Ventral body surfaces rich orange-brown; ventral surfaces of head and neck devoid of any dark pigmentation; posterior portion of trunk with faint brown striations at the distal edge of each scale, becoming more pronounced posteriorly; subcaudal regions with dark brown spots or clusters of striations on distal edge of each scale, becoming more contrasting distally with darker shades of brown and lighter ground colration at the tail's tip. Ventral surfaces of hands and feet light gray; fingers and toes dark gray. Precloacals slightly lighter than surrounding ventrals.

Coloration of holotype in life.—(Differences from preserved specimens; Fig. 5.7). Light, dorsolateral stripes absent to nearly indistinct. Trunk coloration medium to dark brown; dorsal surfaces dark brown with a series of distinct to indistinct longitudinal streaks, each composed of a series of dark brown to black spots confined to the distal edge of each scale or traversing the whole scale. Lateral surfaces possess longitudinal rows of dark spots of pigment, indistinct anteriorly, distinct posteriorly, with each spot on distal tip of each scale. Ventral body surfaces rich orange-brown or medium brown. Ventral surfaces of hands and feet light gray to tan; fingers and toes dark gray.

Measurements and scale counts of holotype in mm.—SVL 68.6; AGD 44.6; TotL 146.9; MBW 9.4; MBH 6.7; TL 78.3; TW 7.3; TH 5.3; HL 6.3; HW 7.2; HH 4.8; SnFa 19.9; ED 1.3; END 3.5; SNL 4.4; IND 2.1; FLL 8.9; HLL 13.9; MBSR 26; PVSR 65; AGSR 43; FinIIIlam 5; ToeIVlam 9; SL 6; IFL 6; SC 6; SO 5.

Variation.—Morphometric variation of the series is summarized in Table 5.6. Among the 45 specimens examined for the degree of contact between head scales, we observed the following variation: prefrontals in point medial contact (KU 310827–29, 310931, 311218) or separated (KU 310730–31, 310820–26, 310830–38, 310929–30, 310932–41, 311214–17, 311219–23). A single individual (KU 310830) was observed to possess a single, large parietal scale, resulting from the fusion of the parietals.

Scale counts were observed to vary among the measured series. Specimens were observed to have midbody scale row counts of 25 (KU 310929, 310936) and 26 (KU 310731, 310820–21, 310826–31, 310834–35, 310928, 310930–31, 310933–34, 310937–39, 310941, 311214–16, 311218, 311223); axilla–groin scale row counts of 42 (KU 310829–30, 310929, 310933, 310938, 311215), 43 (KU 310826, 310828, 310831, 310835, 310931, 310934, 310936–37, 310941, 311214), 44 (KU 310731, 310820–21, 310834, 310928, 310930, 310939, 311223), and 45 (KU 310827, 311216, 311218); and paravertebral scale row counts of 64 (KU 310829–30, 310929, 310933, 310938, 311215), 65 (KU 310826, 310828, 310831, 310835, 310931, 310934, 310936–37, 310941, 311214), 66 (KU 310731, 310820–21, 310834, 310928, 310930, 310939, 311223), and 67 (KU 310827, 311216, 311218).

We also observed lamellae counts to vary among the specimens examined, with the number of Toe-IV lamellae observed to vary between eight (KU 310930, 310937, 311216, 311218) and nine (KU 310820–21, 310826–31, 310834–35, 310928–29, 310931, 310933–34, 310936, 310938–39, 310941, 311214–15, 311223).

Color in the type series is remarkably invariant. Several specimens possess slightly lighter dorsolateral reions, suggesting the presence of dorsolateral “stripes” (KU 310831, 310937, 310928, 310939, 311214); in one small juvenile, this color feature is particularly evident (KU 311211) but in others (KU 310822, 311220, 311222) it is absent. In some specimens, overall pigmentation is markedly darker on both dorsal and ventral surfaces (KU 310820, 310821, 3190931, 310933, 310934, 310936) and in some specimens dorsal coloration is slightly lighter and ventral ground color nerly immaculate orange-brown (KU 310731, 311218). In two specimens ventral surfaces are marked by indistinct midventral streaks of dark minute flecks and spots.

Distribution.—Brachymeles syam is known only from Samar and Leyte islands (Fig. 5.3).

Ecology and natural history.—Brachymeles syam occurs in primary- and secondary-growth forest, as well as disturbed and agricultural habitats. In contrast to the other members of the *B.*

gracilis complex, this species appears to be quite common throughout its range (CDS pers. observ.). Three species of *Brachymeles* have been confirmed to occur on Samar Island (*B. orientalis, B. syam,* and *B. samarensis*; Siler and Brown, 2010; Siler et al., in press c).

We have evaluated this species against the IUCN criteria for classification, and find that it does not qualify for Critically Endangered, Endangered, Vulnerable, or Near Threatened status. *Brachymeles syam* has been documented to have a broad geographic distribution and is quite abundant at all sampled localities. We therefore classify this species as Least Concern, LC (IUCN, 2010).

Other sympatric sincid species observed on Samar and Leyte islands include: *Emoia atrocostata, Eutropis multicarinata, E. multifasciata, Lamprolepis smaragdina, Lipinia pulchella, L. quadrivittata, Sphenomorphus acutus, S. cumingi, S. fasciatus, S. jagori, S.* cf. *mindanensis, S. steerei, S. variegatus*, *Tropidophorus misaminus*.

Etymology.—Prior to the Spanish colonization of the Philippines, numerous names (Samal, Ibabao, Tandaya) had been colloquially given to Samar Island. The name Samar was originally derived from the local dialect “syam”, meaning wound or cut, which described the geographically complex features of the island, and the rough terrain dissected by streams. Suggested common name: Eastern Visayas Slender Skink.

Brachymeles walo sp. nov.

Figs. 5.3, 5.6

Holotype.—PNM 9777 (ACD Field No. 5747), adult female, collected under a rotting log in secondary-growth forest (10:00–12:30 hr) on 23 October 2009, in Barangay Tablu, Municipality of Tampakan, South Cotabato Province, Mindanao Island, Philippines, by ACD and J. Fernandez.

Paratopotype.—One subadult male (PNM 9776) collected on 21 October 2009 by ACD and J. Fernandez.

Paratype.—One juvenile of undetermined sex (KU 326109) collected on 24 May 2001, in Initao National Park, Barangay Initao, Municipality of Tubigan, Misamis Oriental Province, Mindanao Island, Philippines (08°50'2.4" N, 123°52'30" E; WGS-84), by ACD.

Diagnosis.—Brachymeles walo can be distinguished from congeners by the following combination of characters: (1) body size medium (SVL 61.6, 75.5 mm); (2) limbs pentadactyl; (3) limb length moderate; (4) relative tail length moderate; (5) Finger-III lamellae four or five; (6) Toe-IV lamellae six; (7) supralabials six; (8) infralabials six; (9) suparciliaries six; (10) supraoculars five; (11) midbody scale rows 26; (12) axilla–groin scale rows 46–47; (13) paravertebral scale rows 68–70; (14) supranasals separate; (15) frontoparietals in contact; (16) parietals in contact; (17) postnasal/supranasal fusion absent; (18) enlarged chin shields in three pairs; (19) nuchal scales undifferentiated; (20) fourth and fifth supralabial below eye; (21) auricular opening present; and (22) presacral vertebrae 33 (Tables 5.4, 5.5).

Comparisons.—Characters distinguishing *Brachymeles walo* from all medium-sized, pentadactyl species of *Brachymeles* are summarized in Tables 5.4 and 5.5. *Brachymeles walo* most closely resembles *B. gracilis, B. anim,* and *B. sampu*. However, *B. walo* differs from these three taxa by having six Toe-IV lamellae (vs. seven or eight [*B. gracilis*], eight [*B. sampu*], eight or nine [*B. anim*]), a tendency towards a greater number of paravertebral scale rows (up to 72 vs. less than or equal to 70), and 33 presacral vertebrae (vs. 31 [*B. sampu*], 32 [*B. anim*], 34 [*B. gracilis*]). *Brachymeles walo* further differs from *B. anim* and *B. sampu* by having four or five Finger-III lamellae (vs. five); from *B. gracilis* and *B. anim* by having enlarged chin shields in three pairs (vs. two); from *B. gracilis* and *B. sampu* by the presence of contact between frontoparietal scales (vs. presence or absence [*B. gracilis*], absence [*B. sampu*]); from *B. gracilis* by having six infralabials (vs. six or seven) and the absence of a fused postnasal/supranasal scale (vs. presence or absence); and from *B. sampu* by having a greater number of midbody scale rows (26 vs. 24) and by the presence of contact between parietals scales (vs. presence or absence).

Brachymeles walo can be distinguished from all limbless species of *Brachymeles* (*B. apus, B. lukbani, B. minimus, B. miriamae, B. vermis*) by having limbs; and from all non-pentadactyl species of *Brachymeles* (*B. bonitae, B. cebuensis, B. elerae, B. muntingkamay, B. pathfinderi, B. samarensis, B. tridactylus, B. wright*, sp. nov. [Leyte Island; Siler et al., in press c], sp. nov. [Lapinig Group Islands; Siler et al., in press c], sp. nov. [Catanduanes Island; Siler et al., in press c], sp. nov. [Central Bicol Peninsula, Luzon Island; Siler et al., in press c], and sp. nov. [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c]) by having pentadactyl (vs. non-pentadactyl) limbs.

Description of holotype.—Details of the head scalation are shown in Figure 5.6. Adult female, body medium in size, moderately slender, SVL 75.5 mm; head weakly differentiated from neck, nearly as wide as body, HW 8.3% SVL, 103.3% HL; HL 31.0% SnFa; SnFa 26.1% SVL; snout short, rounded in dorsal profile, bluntly rounded in lateral profile, SNL 60.7% HL; ear opening visible, small; eyes small, ED 1.9% SVL, 23.0% HL, 46.7% END, pupil subcircular; body slightly depressed, nearly uniform in thickness, MBW 117.6% MBH; scales smooth, glossy, imbricate; longitudinal scale rows at midbody 26; paravertebral scale rows 72; axilla–groin scale rows 50; limbs short, well developed, pentadactyl, digits small; FinIIIlam 4; ToeIVlam 6; FLL 14.4% AGD, 9.4% SVL; HLL 20.9% AGD, 13.6% SVL; order of digits from shortest to longest for hand: I = V < IV = II < III, for foot: V = I < II < IV = III; tail moderate in length, not as wide as body, gradually tapered towards end, TW 86.3% MBW; TL 88.9% SVL.

Rostral projecting onto dorsal snout to point in line with anterior edge of nasal, broader than high, in broad contact with frontonasal; frontonasal wider than long; nostril ovoid, in center of single trapezoidal nasal, longer axis directed anteroventrally and posterodorsally; supranasals present, large, broadly separated; postnasals present, moderate; prefrontals broadly separated; frontal suboctagonal-shaped, its anterior margin in broad contact with, or narrowly separated from, frontonasal, in contact with first two anterior supraoculars, 4.5× wider than anterior supraocular; supraoculars five; frontoparietals moderate, in moderate medial contact, each in contact with supraoculars II–IV; interparietal large, its length roughly equal to length of frontoparietal, slightly longer than wide, subdiamond-shaped, wider anteriorly; parietals narrower than frontoparietals, in broad contact behind interparietal; nuchals undifferentiated; two loreals, decreasing in size from anterior to posterior, anterior loreal about as long as and moderately higher than posterior loreal; preocular single; supraciliaries six, the anteriormost contacting prefrontal and separating posterior loreal from first supraocular, posteriomost extending to posterior edge of fifth supraocular; single subocular scale row complete, in contact with supralabials; lower eyelid with one row of scales on dorsal margin; supralabials six, first 2× size of other supralabials, fourth and fifth below eye; infralabials six (Fig. 5.6).

Mental wider than long, in contact with first infralabials; postmental single, enlarged, its width greater than width of mental; followed by three pairs of enlarged chin shields, first pair narrowly separated, second pair wider than first, moderately separated by single medial scale, third pair narrower than first and second pairs, separated by three medial scales (Fig. 5.6).

Scales on limbs smaller than body scales; scales on dorsal surfaces of digits large, wrapping around lateral edges of digits; lamellae undivided; palmar surfaces of hands and plantar surfaces

of feet covered by small, irregular scales, each with raised anterior edges; scales on dorsal surface of hands and feet smaller than limb scales, lacking raised edges.

Coloration of holotype in preservative.—Ground color of body dark (lateral surfaces) to miedium (middorsal surface) brown, with distinctly lighter tan dorsolateral stripes, continuing from postorbital region to base of tail. Dorsal surfaces of head, and snout marbled light and dark brown, with distinct tan spots on prefrontals and first supralabials and dark gray to black supraoccular coloration posteriorly. Scales of dorsal and lateral surfaces of snout and lateral surfaces of head homogenous dark brown. Rostral, supranasals, postnasals, first suprlabials and infralabials and mental scale medium gray. Suprlabials medium brown; infralabials orange-brown; mental, and chin shields light immaculate creram.

Trunk coloration variable; middorsal reguion between light tan dorsolateral stripes medium brown with a series of six faint longitudinal dark brown streaks, each composed of a indistinct dark blotches either on the distal edge of each scale and traversing the whole scale in posterior portions of trunk. Lateral surfaces nearly uniformly dark brown, with lighter margins of each scale. Dorsal surfaces of limbs similar to lateral body coloration.

Ventral surfaces of head, neck and body light brown, with light yellowish cream margins to each scale. Subcaudal regions uniform dark brown with slighter scale margins becoming more evident distally. Ventral surfaces of hands and feet dark gray; fingers and toes slightly darker. Precloacals colored as surrounding ventrals.

Coloration of holotype in life.—Coloration in life is unrecorded; however, because *Brachymeles* specimens do not change significantly during preservation (CDS, RMB personal observation), we suspect that the preserved coloration and patterns are much like those in life.

Measurements and scale counts of holotype in mm.—SVL 75.5; AGD 49.3; TotL 142.6; MBW 8.0; MBH 6.8; TL 67.1; TW 6.9; TH 5.6; HL 6.1; HW 6.3; HH 4.2; SnFa 19.7; ED 1.4; END 3.0; SNL 3.7; IND 2.6; FLL 7.1; HLL 10.3; MBSR 26; PVSR 72; AGSR 50; FinIIIlam 4; ToeIVlam 6; SL 6; IFL 6; SC 6; SO 5.

Variation.—Morphometric variation of the series is summarized in Table 5.6. We observed the following variation in the degree of contact between head scales: prefrontals in moderate medial contact (ACD 5727) or separated (KU 326109, ACD 5747); first pair of enlarged chin shields in moderate medial contact (KU 326109, ACD 5727) or separated (ACD 5747).

Scale and lamellae counts were observed to vary among the measured series. Specimens were observed to have axilla–groin scale row counts of 47 (ACD 5727) and 50 (ACD 5747); and paravertebral scale row counts of 70 (ACD 5727) and 72 (ACD 5747). The number of Finger-III lamellae varied between four (ACD 5747) and five (ACD 5727).

Distribution.—*Brachymeles walo* is known only from western Mindanao Island (Fig. 5.3).

Ecology and natural history.—Brachymeles walo occurs in primary- and secondary-growth forest habitats, and occurs in sympatry throughout its currently recognized range with *B. schadenbergi* (Siler and Brown, 2010). The population found in South Cotabato Province, Mindanao Island (Fig. 2) also has been documented to occur in sympatry with *B. gracilis*. As previously mentioned, this is the first documented case of two species of *Brachymeles* in the same body form and body size class occuring in sympatry. In addition to *B. gracilis* and *B. schadenbergi*, four other species of *Brachymeles* have been confirmed to occur on Mindanao Island (*B. pito, B. orientalis,* and *B. pathfinderi*; Siler and Brown, 2010; Siler et al., in press a).

Due to the observation of a high degree of sequence divergence (up to 5.9%; Table 5.3) between the northern and southern populations sampled for this species, we suspect that *B. walo* may actually represent a complex of morphologically similar species. However, due to the absence of additional, adult samples for both populations, currently we cannot evaluate this hypothesis. Given what little we know about this unique species (or species complex), *B. walo* cannot be directly, or indirectly, assessed for risk of extinction based on the IUCN criteria. Therefore, we classify this species as Data Deficient, DD, pending the collection of additional information (IUCN, 2010).

Other sympatric sincid species observed on Mindanao Island include: *Eutropis indeprensa, E. multicarinata, E. multifasciata, E. englei, Lamprolepis smaragdina, L. pulchella, L. quadrivittata, Sphenomorphus abdictus abdictus, S. acutus, S. atrigularis, S. cumingi, S.* cf. *mindanensis, S. coxi, S. fasciatus, S. jagori, S. llanosi, S. steerei, S. variegatus, Tropidophorus misaminus, T. partelloi.*

Etymology.—The specific epithet is chosen to recognize the T'boli indigenous peoples from South Mindanao Island. The T'boli possess ancestral tribal domains from Buluan Lake in the Cotabato Basin to Agusan del Norte Province in northeastern Mindanao Island, encompassing much of the known distribution of this new species. Suggested common name: Western Mindanao Slender Skink.

DISCUSSION

Analyses of the two mitochondrial gene fragments (ND1, ND2) and two unlinked nuclear loci (BDNF, PTGER4) resulted in topologies with high ML bootstrap support and posterior probabilities for five lineages formerly part of the *Brachymeles gracilis* Complex (Fig. 5.2). No analyses supported the monophyly of species formerly part of *Brachymeles gracilis* (*B. gracilis,* *B. pito, B. anim, B. syam,* and *B. tiboli*). However, all analyses show strong support for the sister relationship between *B. anim* and *B. pito* (Fig. 5.2).

In addition to the apparent paraphyly of species formerly part of *Brachymeles gracilis*, *B. pathfinderi* was recovered as part of the *B. gracilis* Complex. *Brachymeles pathfinderi*, one of only two recognized species to have unequal numbers of fore- and hind limb digits, was placed by our analyses sister to *B. gracilis* (Fig. 5.2, Clade E).

Although each of the five genetically sampled species formerly part of the *B. gracilis* Complex were recovered in all analyses with strong support, the interspecific relationships remain incompletely resolved, and the diversity of species within the complex is recovered as a polytomy of four, well supported clades (Fig. 5.2, Clades A–C, E). The previously recognized species *B. pathfinderi* has an abutting distribution with true *B. gracilis* in southcentral Mindanao Island (Fig. 5.3).

The species recognized in this paper increase the total number of known species of *Brachymeles* to 34, and all but two of these are endemic to the Philippines. Having nearly doubled the known number of species of *Brachymeles* in the last several years (Siler, 2010; Siler et al., 2009a, 2010a,b, 2011, in press a,b,c; Siler and Brown, 2010), we are left with two general questions: do many more species in this clade await discovery? And will the results of our studies involving this group extrapolate to generalizations regarding underestimation of Philippine biodiversity?

First, our comprehensive fossorial lizard field studies throughout the archipelago have targeted the major biogeographic components of the Philippines (Brown and Diesmos, 2009) and allowed for a clade-by-clade revisionary approach of the genus *Brachymeles* (Siler and Brown, 2010; Siler et al. in press c). Consequently, we do not expect wholesale discovery of many additional clades of species and we suspect that we will soon (following the revision of the *B. bonitae* Complex) arrive at a reasonably accurate accounting of species diversity. Nevertheless we anticipate that additional species of *Brachymeles* will be discovered with continued fieldwork in isolated regions of the archipelago. To date, despite our efforts and those of our colleagues, the major montane components of Luzon and Mindanao remain poorly sampled for biodiversity due to logistical obstacles to field research. Overcoming many of these bureaucratic hurdles will undoubtedly result in the discovery of additional species of *Brachymeles*. Finally, many small islands (now known to harbor distinct species of *Brachymeles*) have not been adequately surveyed for fossorial lizard species diversity by biologists targeting this distinct microhabitat. As a result, we expect that many areas considered reasonably well known by terrestrial biodiversitry specialists may indeed possess additional undescribed of *Brachymeles.*

This study adds to a growing body of literature suggesting that a reevaluation of amphibian and reptile species boundaries within the Philippines will result in a wholesale reappraisal of archipelago-wide biodiversity (review: Brown et al., 2002; Brown and Diesmos, 2009). In the context of this body of work, few examples of truly widespread reptile species are now known to exist, and most previous examples have turned out to constitute multiple evolutionary lineages (McGuire and Alcala, 2000; Brown et al., 2009, in press; Gaulke et al, 2007; Welton et al., 2009, 2010a,b; Siler and Brown, 2010; Siler et al., in press c) with limited geographical distributions. The exceptions to this generalization appear to be invasive species and human-mediated range expansions (Diesmos et al., 2006; Brown et al., 2010).

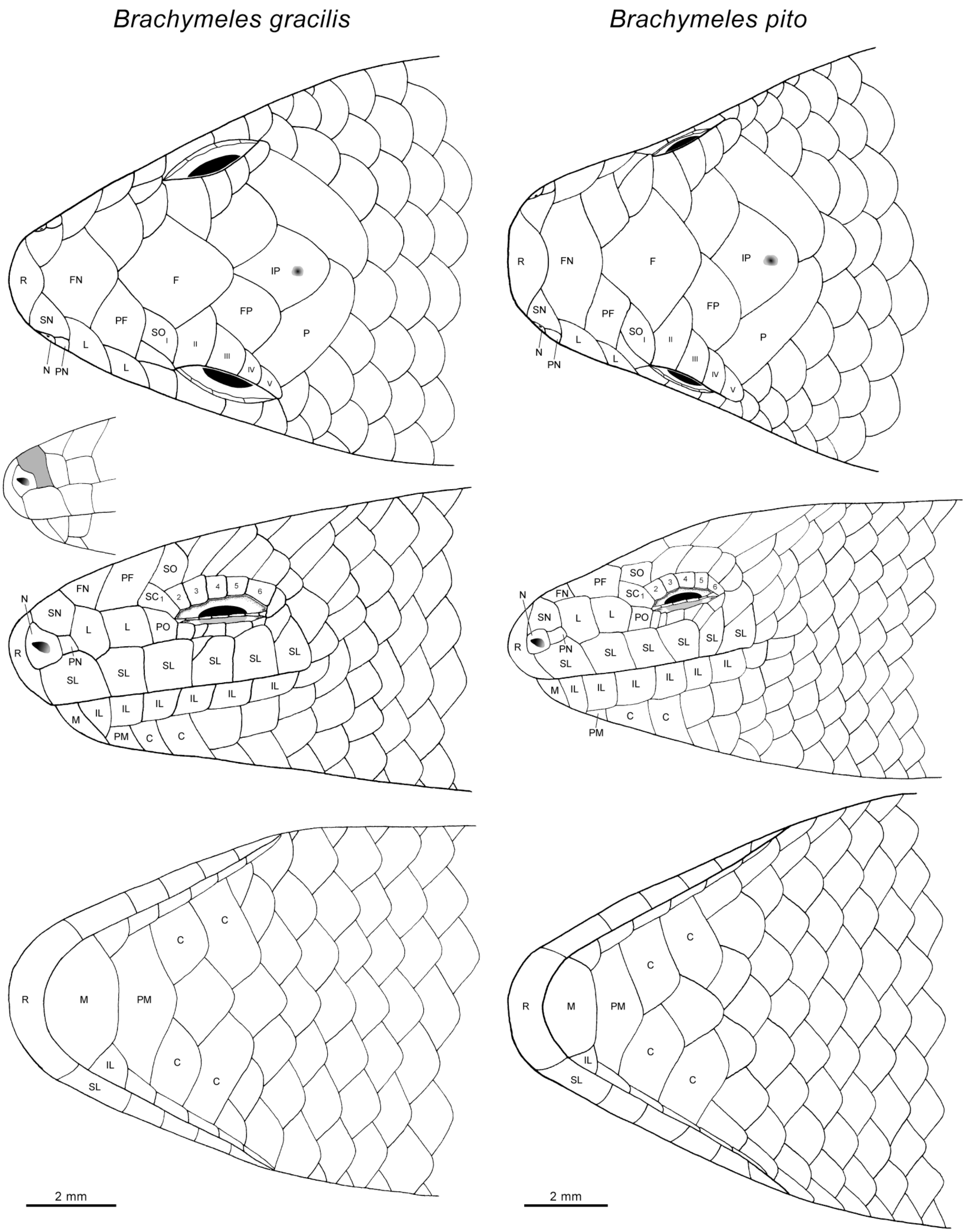
Following the recognition of *B. gracilis, B. pito, B. anim, B. syam, B. tiboli,* and *B. sampu* there are now 18 pentadactyl species of *Brachymeles*. The diversity of pentadactyl species can be broken into three major body size categories. Half of the diversity of pentadactyl taxa consists of medium-sized species (*B. boholensis, B. boulengeri, B. mindorensis, B. taylori, B. gracilis, B. pito, B. anim, B. syam, B. tiboli, and B. sampu*; Siler and Brown, 2010), and the other half consists of larger, more robust species (*B. talinis, B. kadwa, B. tungaoi, B. makusog, B. orientalis, B. schadenbergi, B. vindumi*; Siler and Brown, 2010). Finally, *B. bicolor* represents a unique species in having a large, long body; significantly longer than all other pentadactyl species (Siler et al., in press a). Interestingly, the distribution of pentadactyl species in the Philippines is markedly uneven across the major biogeographic regions of the Philippines, with four species known to occur in the Luzon Faunal Region, nine in the Mindanao Faunal Region, three in the Visayan Faunal Region, one in the Sulu Archipelago, and one in the Mindoro Faunal Region (Siler and Brown, 2010). This observation of the greatest pentadactyl species diversity being distributed across the Mindanao PAIC stands in stark contrast to the patterns observed for the diversity of limbed, non-pentadactyl species, where 13 species are known from the Luzon PAIC versus eight in the Mindanao PAIC (Siler et al., in press c).

A resurgence of species discoveries on Mindanao Island have occurred during the last decade, largely due to increased sociopolitical stability in the southern Philippines resulting in renewed survey efforts. Given the island's complex geography (Defant et al., 1989; Yumul et al., 2009), the increase in the faunal region's diversity is likely to continue (Siler et al., 2009b, in press c; Siler and Brown, 2010; Sanguila et al., in press; Welton et al., 2009, 2010a,b)

Although *B. syam, B. anim, B. pito,* and *B. gracilis* currently can be found in a variety of habitat types, from secondary-growth forest to highly disturbed, agricultural and residential areas, no studies are available on the long-term effect of deforestation on *Brachymeles* populations. In contrast, less is known about the natural history, abundance, and effective range of *B. walo* and *B. sampu*, and both species remain known from three and two vouchered specimens, respectively.

Presently, one “widespread” species complex (*B. bonitae*) remains in the genus, with a distribution spanning boundaries between recognized faunal regions (Brown and Alcala, 1980; Siler and Brown, 2010; Siler et al., 2011, in press c). Recent phylogenetic studies of the genus have statistically rejected the monophyly of the *B. bonitae* species complex (Siler et al., 2011). Closer investigations of island populations of *B. bonitae* will likely result in the discovery of new species diversity, and needed taxonomic revisions for this group of morphologically similar, non-pentadatyl species.

Figure 5.4. Illustration of head of adult male *Brachymeles gracilis* (KU 326079) and adult female *Brachymeles pito* (CAS 133705) in dorsal, lateral, and ventral views. Taxonomically diagnostic head scales are labeled as follows: C, chin shield; F, frontal; FN, frontonasal; FP, frontoparietal; IL, infralabial; IP, interparietal; L, loreal; M, mental; N, nasal; Nu, nuchal; P, parietal; PF, prefrontal; PM, postmental; PN, postnasal; PO, preocular; PSO, presubocular; R, rostral; SC, supraciliary; SL, supralabial; SN, supranasal; and SO, supraocular. Roman numerals indicate scales in the supraocular series, with Arabic numbers indicating scales in the supraciliary series. The partial lateral view for *B. gracilis* highlights (in gray) the absence of a postnasal scale resulting from the fusion of the supranasal and postnasal. Illustrations by RMJ and CDS.


Brachymeles gracilis
Brachymeles pito
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2 mm
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C
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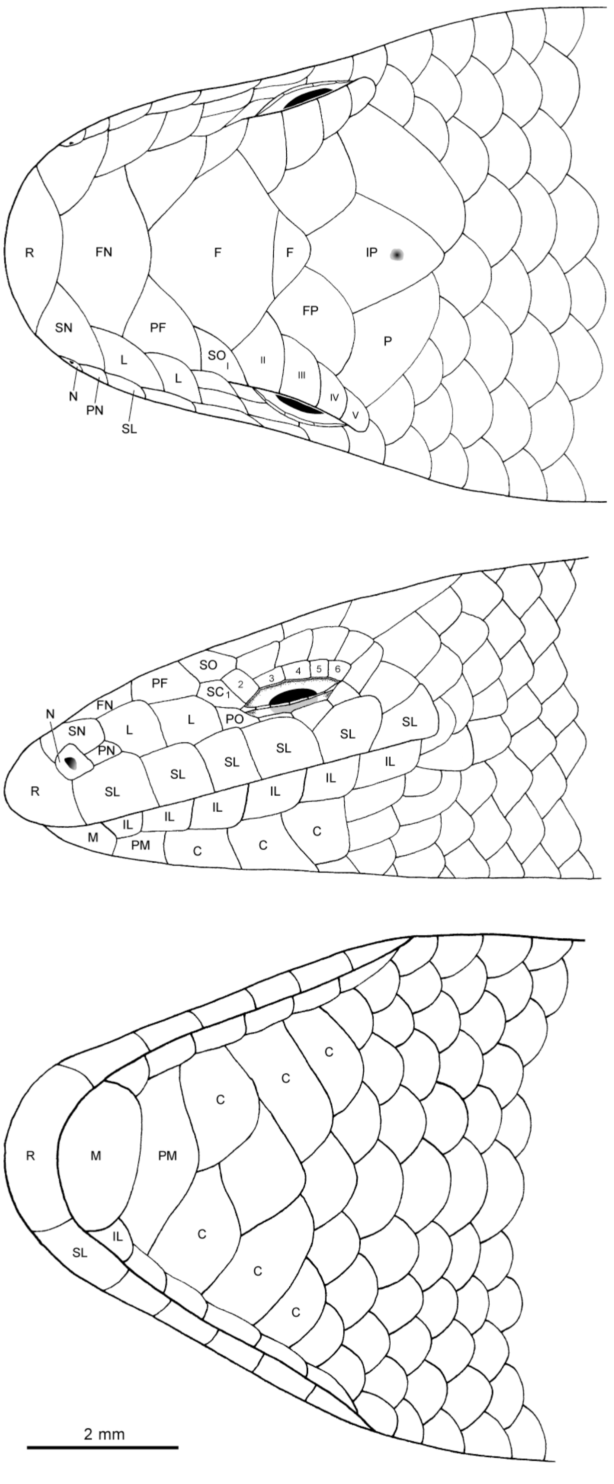
2 mm

Figure 5.5. Illustration of head of adult female neotype *Brachymeles sampu* (CAS 60366) and adult male holotype *Brachymeles anim* (PNM 9766; formerly KU 310359) in dorsal, lateral, and ventral views. Labels for taxonomically diagnostic head scales follow those shown in Figure 5.4. Illustrations by RMJ and CDS.

Brachymeles sampu



Brachymeles anim

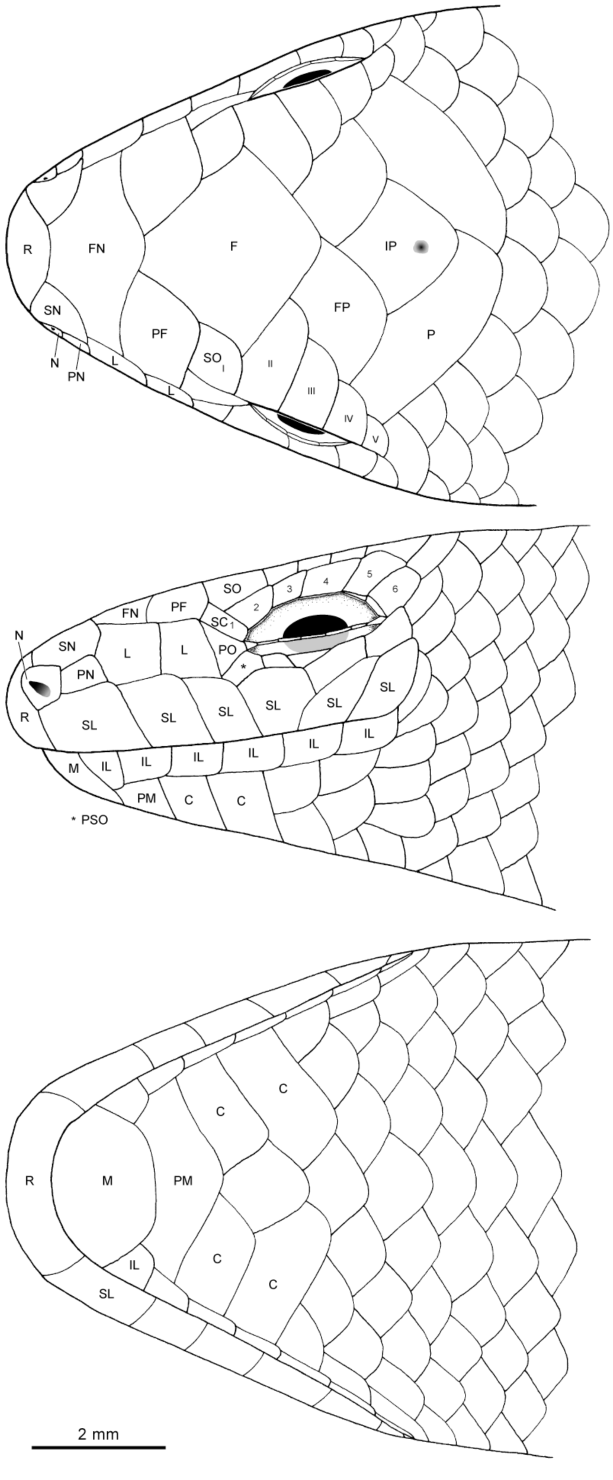
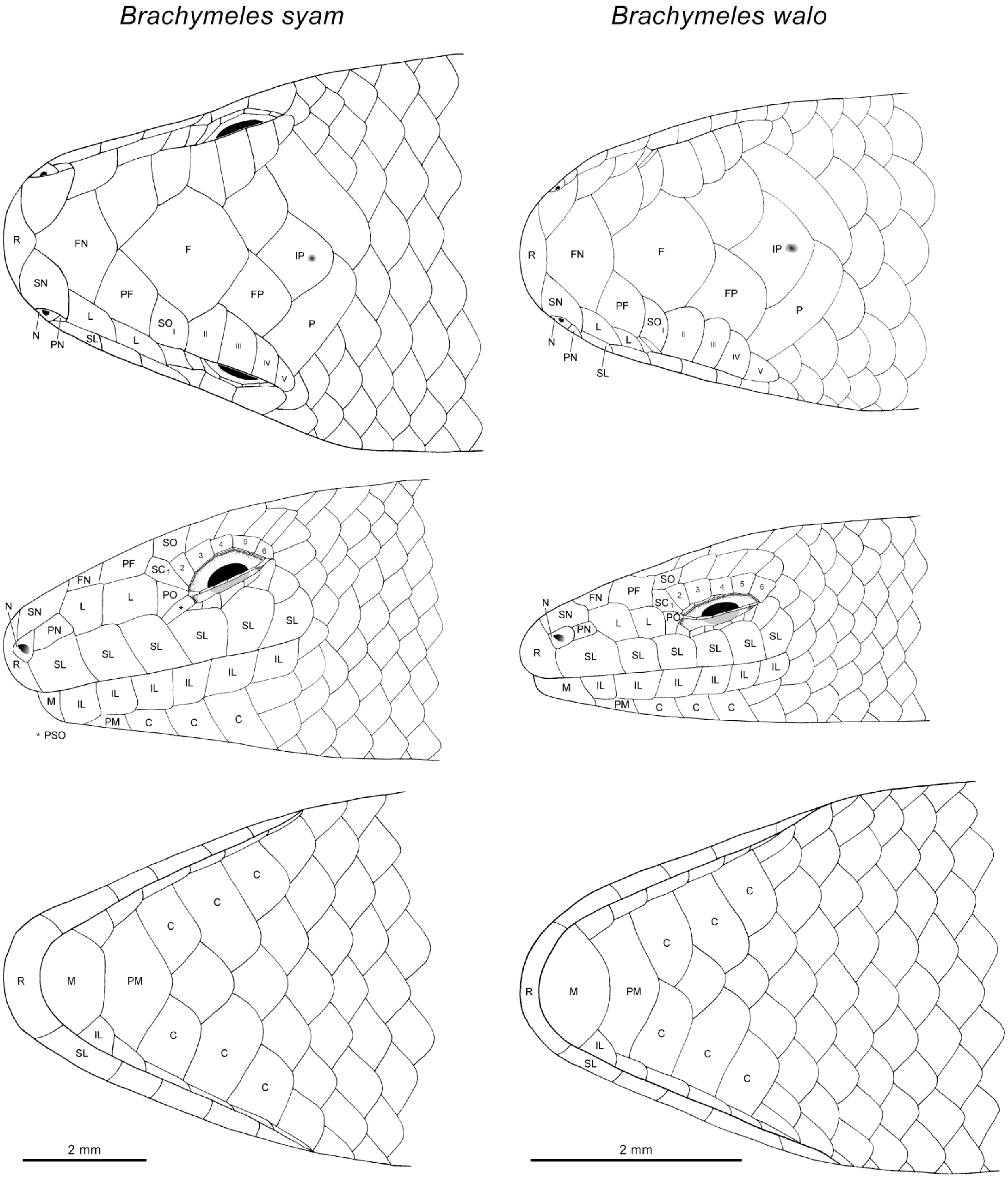


Figure 5.6. Illustration of head of adult male holotype *Brachymeles syam* (PNM 9767; formerly KU 310828) and adult female holotype *Brachymeles walo* (PNM 9777) in dorsal, lateral, and ventral views. Labels for taxonomically diagnostic head scales follow those shown in Figure 5.4. Illustrations by RMJ and CDS.


Brachymeles syam
Brachymeles walo
R
FN
F
IP
SN
PF
FP
L
SO
I
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III
IV
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PN
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4
5
6
PO
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M
IL
PM
C
* PSO
2 mm

Figure 5.7. Photograph in life of *Brachymeles syam* (KU 311223), SVL = 76.9 mm, from Leyte Island, Philippines. Photograph by CDS.

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Appendix I

Summary of specimens corresponding to genetic samples included in the study. PNM/CMNH = deposited in the Cincinnati Museum of Natural History; RMBR = David Bickford/Djoko Iskandar field number, deposited at the Raffles Museum of Biology; CUMZR = Chulalongkorn Museum of Zoology Reptile collection; SP = Sabah Parks Reference Collection; KU = University of Kansas Natural History Museum; LSUHC = La Sierra University Herpetological Collections; FMNH = Field Museum of Natural History Herpetological Collections; * = currently uncataloged specimen, deposited in the National Museum of the Philippines.

Species	*Voucher*	Locality
Dasia grisea	KU 305573	Philippines, Luzon Island, Municipality of Tobaco
Davewakeum miriamae	KU 327693	Thailand
Davewakeum miriamae	KU 327692	Thailand
Emoia atrocostata	KU 04896	Philippines, Calayan Island, Municipality of Calayan
Eumeces quadrilineatus	KU 311490	China, Guangxi State, Shiwan Dashang Nature Reserve
Eutropis multifasciata	KU 302904	Philippines, Tablas Island, Municipality of San Agustin
Lamprolepis smaragdina	KU 326565	Philippines, Palawan Island, Municipality of Narra
Larutia seribuatensis	LSUHC 5168	West Malaysia
Lipinia pulchella pulchella	RMB 1079*	Philippines, Bohol Island, Municipality of

		Carmen
Lygosoma bowringii	LSUHC 6998	West Malaysia
Lygosoma sp.	LSUHC 6931	West Malaysia
Lygosoma quadrupes	LSUHC 8403	West Malaysia
Plestiodon fasciatus	KU 289462	United States, Texas, Smith County
Plestiodon anthracinus	KU 290718	United States, Kansas, Johnson County
Scincella lateralis	KU 289461	United States, Texas, Smith County
Scincella reevesii	FMNH 255540	Lao PDR, Khammouan Prov, Thakhek District
Sphenomorphus abdictus abdictus	KU 306538	Philippines, Dinagat Island, Municipality of Loreto
Tachydromus sexilineatus	KU 311512	China, Guangxi State, Shiwan Dashang Nature Reserve
Brachymeles apus	SP 06915	Malaysia, Borneo, Sabah, Mt. Kinabalu
Brachymeles cf. *apus*	RMBR 2040	Malaysia, Borneo, Kalimantan
Brachymeles bicolor	KU 323149	Philippines, Luzon Island, Municipality of Maria Aurora
Brachymeles bicolor	KU 323150	Philippines, Luzon Island, Municipality of Maria Aurora
Brachymeles bicolor	KU 323151	Philippines, Luzon Island, Municipality of Maria Aurora
Brachymeles boholensis	KU 323992	Philippines, Bohol Island, Municipality of

		Sierra Bullones
Brachymeles boholensis	KU 323939	Philippines, Bohol Island, Municipality of Bilar
Brachymeles boholensis	KU 323958	Philippines, Bohol Island, Municipality of Sierra Bullones
Brachymeles bonitae	KU 323086	Philippines, Luzon Island, Municipality of Baler
Brachymeles bonitae	KU 323085	Philippines, Luzon Island, Municipality of Baler
Brachymeles bonitae	KU 307748	Philippines, Mindoro Island, Municipality of Magsaysay
Brachymeles bonitae	KU 307749	Philippines, Mindoro Island, Municipality of Gloria
Brachymeles bonitae	KU 326089	Philippines, Luzon Island, Municipality of Tayabas, Mt. Banahao
Brachymeles bonitae	RMB 3681*	Philippines, Luzon Island, Municipality of Tayabas, Mt. Banahao
Brachymeles bonitae	KU 320471	Philippines, Lubang Island, Municipality of Lubang
Brachymeles bonitae	KU 320473	Philippines, Lubang Island, Municipality of Lubang
Brachymeles bonitae	KU 308004	Philippines, Calayan Island, Municipality of Calayan

Brachymeles bonitae	KU 307967	Philippines, Calayan Island, Municipality of Calayan
Brachymeles bonitae	KU 323937	Philippines, Masbate Island, Municipality of Masbate City
Brachymeles bonitae	KU 323938	Philippines, Masbate Island, Municipality of Masbate City
Brachymeles boulengeri	KU 323409	Philippines, Luzon Island, Municipality of Baler
Brachymeles boulengeri	KU 307752	Philippines, Polillo Island, Municipality of Polillo
Brachymeles boulengeri	KU 307753	Philippines, Polillo Island, Municipality of Polillo
Brachymeles cebuensis	KU 320419	Philippines, Cebu Island, Municipality of Carcar
Brachymeles cebuensis	KU 320421	Philippines, Cebu Island, Municipality of Carcar
Brachymeles cebuensis	KU 320420	Philippines, Cebu Island, Municipality of Carcar
Brachymeles gracilis hilong	KU 311216	Philippines, Leyte Island, Municipality of Baybay
Brachymeles gracilis hilong	KU 311220	Philippines, Leyte Island, Municipality of Baybay
Brachymeles gracilis hilong	KU 310825	Philippines, Samar Island, Municipality of

		Taft
Brachymeles gracilis hilong	KU 310731	Philippines, Samar Island, Municipality of Taft
Brachymeles elerae	KU 326566	Philippines, Luzon Island, Municipality of Balbalan
Brachymeles elerae	KU 326567	Philippines, Luzon Island, Municipality of Balbalan
Brachymeles gracilis gracilis	PNM/CMNH 1175	Philippines, Mindanao Island, Municipality of Toril, Mt. Apo
Brachymeles gracilis gracilis	PNM/CMNH 1176	Philippines, Mindanao Island, Municipality of Toril, Mt. Apo
Brachymeles gracilis gracilis	ACD 2695*	Philippines, Mindanao Island, Municipality of San Isidro, Mt. Hamiguitan
Brachymeles gracilis gracilis	KU 326099	Philippines, Mindanao Island, Municipality of Kiblawan
Brachymeles lukbani	KU 313602	Philippines, Luzon Island, Municipality of Labo
Brachymeles lukbani	KU 313596	Philippines, Luzon Island, Municipality of Labo
Brachymeles lukbani	KU 313597	Philippines, Luzon Island, Municipality of Labo
Brachymeles makusog	KU 313610	Philippines, Luzon Island, Municipality of Labo

Brachymeles makusog	KU 313611	Philippines, Luzon Island, Municipality of Labo
Brachymeles makusog	KU 308127	Philiippines, Catanduanes Island, Municipality of Gigmoto
Brachymeles makusog	KU 308128	Philiippines, Catanduanes Island, Municipality of Gigmoto
Brachymeles mindorensis	KU 304351	Philippines, Mindoro Island, Municipality of Calayan
Brachymeles mindorensis	KU 307740	Philippines, Mindoro Island, Municipality of Bongabong
Brachymeles mindorensis	KU 308447	Philippines, Mindoro Island, Municipality of Paluan
Brachymeles minimus	KU 308131	Philiippines, Catanduanes Island, Municipality of Gigmoto
Brachymeles minimus	KU 308129	Philiippines, Catanduanes Island, Municipality of Gigmoto
Brachymeles minimus	KU 308130	Philiippines, Catanduanes Island, Municipality of Gigmoto
Brachymeles muntingkamay	KU 308866	Philippines, Luzon Island, Municipality of Quezon, Mt. Palali
Brachymeles muntingkamay	KU 308923	Philippines, Luzon Island, Municipality of Quezon, Mt. Palali
Brachymeles muntingkamay	KU 308813	Philippines, Luzon Island, Municipality of

		Quezon, Mt. Palali
Brachymeles pathfinderi	KU 324057	Philippines, Mindanao Island, Municipality of Glan
Brachymeles pathfinderi	KU 324058	Philippines, Mindanao Island, Municipality of Glan
Brachymeles pathfinderi	KU 324096	Philippines, Mindanao Island, Municipality of Glan
Brachymeles samarensis	KU 324020	Philippines, Catanduanes Island, Municipality of Virac
Brachymeles samarensis	KU 324022	Philippines, Catanduanes Island, Municipality of Virac
Brachymeles samarensis	KU 310849	Philippines, Samar Island, Municipality of Taft
Brachymeles samarensis	KU 311225	Philippines, Leyte Island, Municipality of Baybay
Brachymeles samarensis	KU 310850	Philippines, Samar Island, Municipality of Taft
Brachymeles samarensis	KU 310851	Philippines, Samar Island, Municipality of Taft
Brachymeles samarensis	KU 311226	Philippines, Leyte Island, Municipality of Baybay
Brachymeles samarensis	KU 311227	Philippines, Leyte Island, Municipality of Baybay

Brachymeles orientalis	KU 314092	Philippines, Mindanao Island, Municipality of San Francisco
Brachymeles orientalis	KU 310942	Philippines, Samar Island, Municipality of San Jose de Buan
Brachymeles orientalis	KU 311232	Philippines, Leyte Island, Municipality of Baybay
Brachymeles orientalis	KU 324029	Philippines, Bohol Island, Municipality of Bilar
Brachymeles orientalis	KU 324027	Philippines, Bohol Island, Municipality of Bilar
Brachymeles schadenbergi	PNM/CMNH 1457	Philippines, Mindanao Island, Municipality of Kiamba, Mt. Busa
Brachymeles schadenbergi	KU 314973	Philippines, Mindanao Island, Municipality of Zamboanga City
Brachymeles schadenbergi	KU 314998	Philippines, Mindanao Island, Municipality of Zamboanga City
Brachymeles talinis	RMB 3283*	Philippines, Negros Island, Municipality of Valencia, Mt. Talinis
Brachymeles talinis	RMB 3305*	Philippines, Negros Island, Municipality of Valencia, Mt. Talinis
Brachymeles talinis	KU 303990	Philippines, Sibuyan Island, Mt. Guiting-Guiting Natural Park
Brachymeles talinis	KU 306756	Philippines, Panay Island, Municipality of

		San Remigio
Brachymeles talinis	KU 315355	Philippines, Tablas Island, Municipality of Calatrava
Brachymeles taylori	KU 320476	Philippines, Cebu Island, Municipality of Carcar
Brachymeles taylori	KU 320478	Philippines, Cebu Island, Municipality of Carcar
Brachymeles taylori	KU 307737	Philippines, Negros Island, Municipality of Valencia, Mt. Talinis
Brachymeles taylori	KU 320841	Philippines, Negros Island, Municipality of Valencia, Mt. Talinis
Brachymeles tridactylus	KU 320423	Philippines, Negros Island, Municipality of Hinoba-an
Brachymeles tridactylus	KU 324025	Philippines, Negros Island, Municipality of Hinoba-an
Brachymeles tridactylus	KU 320424	Philippines, Negros Island, Municipality of Hinoba-an
Brachymeles sp. A	KU 323936	Philippines, Masbate Island, Municipality of Mobo
Brachymeles sp. A	KU 323933	Philippines, Masbate Island, Municipality of Mobo
Brachymeles sp. A	KU 323934	Philippines, Masbate Island, Municipality of Mobo

Brachymeles sp. B	KU 324041	Philippines, Luzon Island, Municipality of Tobaco
Brachymeles sp. B	KU 324031	Philippines, Luzon Island, Municipality of Tobaco
Brachymeles sp. B	KU 304897	Philippines, Calayan Island, Municipality of Calayan
Brachymeles sp. B	KU 304558	Philippines, Camiguin Norte Island, Municipality of Tobaco

Appendix II

Summary of Genbank voucher numbers corresponding to genetic samples included in the study.

Species	Gene	Genbank Voucher Number
Brachymeles.apus.RMBR2040	ATP 8,6	HQ907142
	BDNF	HQ907234
	NADH 1	HQ907332
	NADH 2	HQ907434
	PTGER	HQ907534
	R35	HQ907641
Brachymeles.apus.SP06915	ATP 8,6	HQ907141
	BDNF	HQ907233
	NADH 1	HQ907331
	NADH 2	HQ907433
	PTGER	HQ907533
	R35	HQ907640
Brachymeles.bicolor.KU323149	ATP 8,6	HQ907181
	BDNF	HQ907279
	NADH 1	HQ907377
	NADH 2	HQ907479
	PTGER	HQ907579
	R35	HQ907687
Brachymeles.bicolor.KU323150	ATP 8,6	HQ907182
	BDNF	HQ907280

	NADH 1	HQ907378
	NADH 2	HQ907480
	PTGER	HQ907580
	R35	HQ907688
Brachymeles.bicolor.KU323151	ATP 8,6	HQ907183
	BDNF	HQ907281
	NADH 1	HQ907379
	NADH 2	HQ907481
	PTGER	HQ907581
	R35	HQ907689
Brachymeles.bonitae.KU307748	ATP 8,6	HQ907149
	BDNF	HQ907241
	NADH 1	HQ907339
	NADH 2	HQ907441
	PTGER	HQ907541
	R35	HQ907648
Brachymeles.bonitae.KU307749	ATP 8,6	HQ907150
	BDNF	HQ907242
	NADH 1	HQ907340
	NADH 2	HQ907442
	PTGER	HQ907542
	R35	HQ907649
Brachymeles.bonitae.KU307967	ATP 8,6	HQ907156

	BDNF	HQ907248
	NADH 1	HQ907346
	R35	HQ907655
Brachymeles.bonitae.KU308004	ATP 8,6	HQ907155
	BDNF	HQ907247
	NADH 1	HQ907345
	NADH 2	HQ907447
	PTGER	HQ907547
	R35	HQ907654
Brachymeles.bonitae.KU320471	ATP 8,6	HQ907153
	BDNF	HQ907245
	NADH 1	HQ907343
	NADH 2	HQ907445
	PTGER	HQ907545
	R35	HQ907652
Brachymeles.bonitae.KU320473	ATP 8,6	HQ907154
	BDNF	HQ907246
	NADH 1	HQ907344
	NADH 2	HQ907446
	PTGER	HQ907546
	R35	HQ907653
Brachymeles.bonitae.KU323085	BDNF	HQ907319
	NADH 1	HQ907415

	NADH 2	HQ907519
	PTGER	HQ907619
	R35	HQ907727
Brachymeles.bonitae.KU323086	ATP 8,6	HQ907148
	BDNF	HQ907240
	NADH 1	HQ907338
	NADH 2	HQ907440
	PTGER	HQ907540
	R35	HQ907647
Brachymeles.bonitae.KU323937	ATP 8,6	HQ907157
	BDNF	HQ907249
	NADH 1	HQ907347
	NADH 2	HQ907448
	PTGER	HQ907548
	R35	HQ907656
Brachymeles.bonitae.KU323938	ATP 8,6	HQ907158
	BDNF	HQ907250
	NADH 1	HQ907348
	NADH 2	HQ907449
	PTGER	HQ907549
	R35	HQ907657
Brachymeles.bonitae.KU326089	ATP 8,6	HQ907151
	BDNF	HQ907243

	NADH 1	HQ907341
	NADH 2	HQ907443
	PTGER	HQ907543
	R35	HQ907650
Brachymeles.bonitae.RMB3681	ATP 8,6	HQ907152
	BDNF	HQ907244
	NADH 1	HQ907342
	NADH 2	HQ907444
	PTGER	HQ907544
	R35	HQ907651
Brachymeles.boulengeri.boholensis.KU323939	ATP 8,6	HQ907185
	BDNF	HQ907283
	NADH 1	HQ907381
	NADH 2	HQ907483
	PTGER	HQ907583
	R35	HQ907691
Brachymeles.boulengeri.boholensis.KU323958	ATP 8,6	HQ907186
	BDNF	HQ907284
	NADH 1	HQ907382
	NADH 2	HQ907484
	PTGER	HQ907584
	R35	HQ907692
Brachymeles.boulengeri.boholensis.KU323995	ATP 8,6	HQ907184

	BDNF	HQ907282
	NADH 1	HQ907380
	NADH 2	HQ907482
	PTGER	HQ907582
	R35	HQ907690
Brachymeles.boulengeri.boulengeri.KU307752	ATP 8,6	HQ907164
	BDNF	HQ907256
	NADH 1	HQ907354
	NADH 2	HQ907456
	PTGER	HQ907556
	R35	HQ907664
Brachymeles.boulengeri.boulengeri.KU307753	ATP 8,6	HQ239375
	BDNF	HQ907257
	NADH 1	HQ907355
	NADH 2	HQ907457
	PTGER	HQ907557
	R35	HQ907665
Brachymeles.boulengeri.boulengeri.KU323409	ATP 8,6	HQ907163
	NADH 1	HQ907353
	NADH 2	HQ907455
	PTGER	HQ907555
	R35	HQ907663
Brachymeles.boulengeri.mindorensis.KU304351	ATP 8,6	HQ907161

	BDNF	HQ907253
	NADH 1	HQ907351
	NADH 2	HQ907452
	PTGER	HQ907552
	R35	HQ907660
Brachymeles.boulengeri.mindorensis.KU307740	ATP 8,6	HQ239372
	BDNF	HQ907254
	NADH 1	HQ907352
	NADH 2	HQ907453
	PTGER	HQ907553
	R35	HQ907661
Brachymeles.boulengeri.mindorensis.KU308447	ATP 8,6	HQ907162
	BDNF	HQ907255
	NADH 2	HQ907454
	PTGER	HQ907554
	R35	HQ907662
Brachymeles.boulengeri.taylori.KU307737	ATP 8,6	HQ907167
	BDNF	HQ907260
	NADH 1	HQ907358
	NADH 2	HQ907460
	PTGER	HQ907560
	R35	HQ907668
Brachymeles.boulengeri.taylori.KU320476	ATP 8,6	HQ907165

	BDNF	HQ907258
	NADH 1	HQ907356
	NADH 2	HQ907458
	PTGER	HQ907558
	R35	HQ907666
Brachymeles.boulengeri.taylori.KU320478	ATP 8,6	HQ907166
	BDNF	HQ907259
	NADH 1	HQ907357
	NADH 2	HQ907459
	PTGER	HQ907559
	R35	HQ907667
Brachymeles.boulengeri.taylori.KU320481	ATP 8,6	HQ907168
	BDNF	HQ907261
	NADH 1	HQ907359
	NADH 2	HQ907461
	PTGER	HQ907561
	R35	HQ907669
Brachymeles.cebuensis.KU320419	ATP 8,6	HQ907214
	BDNF	HQ907314
	NADH 1	HQ907410
	NADH 2	HQ907514
	PTGER	HQ907614
	R35	HQ907722

Brachymeles.cebuensis.KU320420	ATP 8,6	HQ907216
	BDNF	HQ907316
	NADH 1	HQ907412
	NADH 2	HQ907516
	PTGER	HQ907616
	R35	HQ907724
Brachymeles.cebuensis.KU320421	ATP 8,6	HQ907215
	BDNF	HQ907315
	NADH 1	HQ907411
	NADH 2	HQ907515
	PTGER	HQ907615
	R35	HQ907723
Brachymeles.elerae.KU326566	ATP 8,6	HQ907176
	BDNF	HQ907274
	NADH 1	HQ907372
	NADH 2	HQ907474
	PTGER	HQ907574
	R35	HQ907682
Brachymeles.elerae.KU326567	ATP 8,6	HQ907177
	BDNF	HQ907275
	NADH 1	HQ907373
	NADH 2	HQ907475
	PTGER	HQ907575

	R35	HQ907683
Brachymeles.gracilis.gracilis.KU326098	ATP 8,6	HQ907196
	BDNF	HQ907294
	NADH 1	HQ907391
	NADH 2	HQ907494
	PTGER	HQ907594
	R35	HQ907702
Brachymeles.gracilis.gracilis.KU326099	ATP 8,6	HQ907197
	BDNF	HQ907295
	NADH 1	HQ907392
	NADH 2	HQ907495
	PTGER	HQ907595
	R35	HQ907703
Brachymeles.gracilis.gracilis.PNMCMNHH1175	ATP 8,6	HQ907194
	BDNF	HQ907292
	NADH 2	HQ907492
	PTGER	HQ907592
	R35	HQ907700
Brachymeles.gracilis.gracilis.PNMCMNHH1176	ATP 8,6	HQ907195
	BDNF	HQ907293
	NADH 1	HQ907390
	NADH 2	HQ907493
	PTGER	HQ907593

	R35	HQ907701
Brachymeles.gracilis.hilong.KU310731	ATP 8,6	HQ907190
	BDNF	HQ907288
	NADH 1	HQ907386
	NADH 2	HQ907488
	PTGER	HQ907588
	R35	HQ907696
Brachymeles.gracilis.hilong.KU310825	ATP 8,6	HQ907189
	BDNF	HQ907287
	NADH 1	HQ907385
	NADH 2	HQ907487
	PTGER	HQ907587
	R35	HQ907695
Brachymeles.gracilis.hilong.KU311216	ATP 8,6	HQ907187
	BDNF	HQ907285
	NADH 1	HQ907383
	NADH 2	HQ907485
	PTGER	HQ907585
	R35	HQ907693
Brachymeles.gracilis.hilong.KU311220	ATP 8,6	HQ907188
	BDNF	HQ907286
	NADH 1	HQ907384
	NADH 2	HQ907486

	PTGER	HQ907586
	R35	HQ907694
Brachymeles.lukbani.KU313596	ATP 8,6	HQ907212
	BDNF	HQ907312
	NADH 1	HQ907408
	NADH 2	HQ907512
	PTGER	HQ907612
	R35	HQ907720
Brachymeles.lukbani.KU313597	ATP 8,6	HQ907213
	BDNF	HQ907313
	NADH 1	HQ907409
	NADH 2	HQ907513
	PTGER	HQ907613
	R35	HQ907721
Brachymeles.lukbani.KU313602	ATP 8,6	HQ907211
	BDNF	HQ907311
	NADH 1	HQ907407
	NADH 2	HQ907511
	PTGER	HQ907611
	R35	HQ907719
Brachymeles.makusog.KU308127	ATP 8,6	HQ907200
	BDNF	HQ907298
	NADH 1	HQ907394

	NADH 2	HQ907498
	PTGER	HQ907598
	R35	HQ907706
Brachymeles.makusog.KU308128	ATP 8,6	HQ907201
	BDNF	HQ907299
	NADH 1	HQ907395
	NADH 2	HQ907499
	PTGER	HQ907599
	R35	HQ907707
Brachymeles.makusog.KU313610	ATP 8,6	HQ907198
	BDNF	HQ907296
	NADH 2	HQ907496
	PTGER	HQ907596
	R35	HQ907704
Brachymeles.makusog.KU313611	ATP 8,6	HQ907199
	BDNF	HQ907297
	NADH 1	HQ907393
	NADH 2	HQ907497
	PTGER	HQ907597
	R35	HQ907705
Brachymeles.minimus.KU308129	ATP 8,6	HQ907209
	BDNF	HQ907309
	NADH 1	HQ907405

	NADH 2	HQ907509
	PTGER	HQ907609
	R35	HQ907717
Brachymeles.minimus.KU308130	ATP 8,6	HQ907210
	BDNF	HQ907310
	NADH 1	HQ907406
	NADH 2	HQ907510
	PTGER	HQ907610
	R35	HQ907718
Brachymeles.minimus.KU308131	ATP 8,6	HQ907208
	BDNF	HQ907308
	NADH 1	HQ907404
	NADH 2	HQ907508
	PTGER	HQ907608
	R35	HQ907716
Brachymeles.muntingkamay.KU308813	ATP 8,6	HQ907180
	BDNF	HQ907278
	NADH 1	HQ907376
	NADH 2	HQ907478
	PTGER	HQ907578
	R35	HQ907686
Brachymeles.muntingkamay.KU308866	ATP 8,6	HQ907178
	BDNF	HQ907276

	NADH 1	HQ907374
	NADH 2	HQ907476
	PTGER	HQ907576
	R35	HQ907684
Brachymeles.muntingkamay.KU308923	ATP 8,6	HQ907179
	BDNF	HQ907277
	NADH 1	HQ907375
	NADH 2	HQ907477
	PTGER	HQ907577
	R35	HQ907685
Brachymeles.pathfinderi.KU324057	ATP 8,6	HQ907191
	BDNF	HQ907289
	NADH 1	HQ907387
	NADH 2	HQ907489
	PTGER	HQ907589
	R35	HQ907697
Brachymeles.pathfinderi.KU324058	ATP 8,6	HQ907192
	BDNF	HQ907290
	NADH 1	HQ907388
	NADH 2	HQ907490
	PTGER	HQ907590
	R35	HQ907698
Brachymeles.pathfinderi.KU324096	ATP 8,6	HQ907193

	BDNF	HQ907291
	NADH 1	HQ907389
	NADH 2	HQ907491
	PTGER	HQ907591
	R35	HQ907699
Brachymeles.samarensis.KU310849	ATP 8,6	HQ907217
	BDNF	HQ907317
	NADH 1	HQ907413
	NADH 2	HQ907517
	PTGER	HQ907617
	R35	HQ907725
Brachymeles.samarensis.KU310850	BDNF	HQ907320
	NADH 1	HQ907416
	NADH 2	HQ907520
	PTGER	HQ907620
	R35	HQ907728
Brachymeles.samarensis.KU310851	BDNF	HQ907321
	NADH 1	HQ907417
	NADH 2	HQ907521
	PTGER	HQ907621
	R35	HQ907729
Brachymeles.samarensis.KU311225	ATP 8,6	HQ907218
	BDNF	HQ907318

	NADH 1	HQ907414
	NADH 2	HQ907518
	PTGER	HQ907618
	R35	HQ907726
Brachymeles.samarensis.KU311226	BDNF	HQ907322
	NADH 1	HQ907418
	NADH 2	HQ907522
	PTGER	HQ907622
	R35	HQ907730
Brachymeles.samarensis.KU311227	BDNF	HQ907323
	NADH 1	HQ907419
	NADH 2	HQ907523
	PTGER	HQ907623
	R35	HQ907731
Brachymeles.samarensis.KU324020	ATP 8,6	HQ907159
	BDNF	HQ907251
	NADH 1	HQ907349
	NADH 2	HQ907450
	PTGER	HQ907550
	R35	HQ907658
Brachymeles.samarensis.KU324022	ATP 8,6	HQ907160
	BDNF	HQ907252
	NADH 1	HQ907350

	NADH 2	HQ907451
	PTGER	HQ907551
	R35	HQ907659
Brachymeles.schadenbergi.orientalis.KU310942	ATP 8,6	HQ907202
	BDNF	HQ907301
	NADH 1	HQ907397
	NADH 2	HQ907501
	PTGER	HQ907601
	R35	HQ907709
Brachymeles.schadenbergi.orientalis.KU311232	ATP 8,6	HQ907203
	BDNF	HQ907302
	NADH 1	HQ907398
	NADH 2	HQ907502
	PTGER	HQ907602
	R35	HQ907710
Brachymeles.schadenbergi.orientalis.KU314092	BDNF	HQ907300
	ATP 8,6	HQ239400
	NADH 1	HQ907396
	NADH 2	HQ907500
	PTGER	HQ907600
	R35	HQ907708
Brachymeles.schadenbergi.orientalis.KU324027	ATP 8,6	HQ907205
	BDNF	HQ907304

	NADH 1	HQ907400
	NADH 2	HQ907504
	PTGER	HQ907604
	R35	HQ907712
Brachymeles.schadenbergi.orientalis.KU324029	ATP 8,6	HQ907204
	BDNF	HQ907303
	NADH 1	HQ907399
	NADH 2	HQ907503
	PTGER	HQ907603
	R35	HQ907711
Brachymeles.schadenbergi.schadenbergi.KU314973	ATP 8,6	HQ907206
	BDNF	HQ907306
	NADH 1	HQ907402
	NADH 2	HQ907506
	PTGER	HQ907606
	R35	HQ907714
Brachymeles.schadenbergi.schadenbergi.KU314998	ATP 8,6	HQ907207
	BDNF	HQ907307
	NADH 1	HQ907403
	NADH 2	HQ907507
	PTGER	HQ907607
	R35	HQ907715
Brachymeles.schadenbergi.schadenbergi.PNMCMN	ATP 8,6	HQ239397

HH1457		
	BDNF	HQ907305
	NADH 1	HQ907401
	NADH 2	HQ907505
	PTGER	HQ907605
	R35	HQ907713
Brachymeles.speciesA.KU323933	ATP 8,6	HQ239395
	BDNF	HQ907268
	NADH 1	HQ907366
	NADH 2	HQ907468
	PTGER	HQ907568
	R35	HQ907676
Brachymeles.speciesA.KU323934	BDNF	HQ907267
	ATP 8,6	HQ239396
	NADH 1	HQ907365
	NADH 2	HQ907467
	PTGER	HQ907567
	R35	HQ907675
Brachymeles.speciesA.KU323936	ATP 8,6	HQ239394
	BDNF	HQ907269
	NADH 1	HQ907367
	NADH 2	HQ907469
	PTGER	HQ907569

	R35	HQ907677
Brachymeles.speciesB.KU304558	ATP 8,6	HQ907175
	BDNF	HQ907273
	NADH 1	HQ907371
	NADH 2	HQ907473
	PTGER	HQ907573
	R35	HQ907681
Brachymeles.speciesB.KU304897	ATP 8,6	HQ907174
	BDNF	HQ907272
	NADH 1	HQ907370
	NADH 2	HQ907472
	PTGER	HQ907572
	R35	HQ907680
Brachymeles.speciesB.KU324031	ATP 8,6	HQ907173
	BDNF	HQ907271
	NADH 1	HQ907369
	NADH 2	HQ907471
	PTGER	HQ907571
	R35	HQ907679
Brachymeles.speciesB.KU324041	ATP 8,6	HQ907172
	BDNF	HQ907270
	NADH 1	HQ907368
	NADH 2	HQ907470

	PTGER	HQ907570
	R35	HQ907678
Brachymeles.talinis.KU303990	ATP 8,6	HQ239388
	BDNF	HQ907264
	NADH 1	HQ907362
	NADH 2	HQ907464
	PTGER	HQ907564
	R35	HQ907672
Brachymeles.talinis.KU306756	ATP 8,6	HQ907170
	BDNF	HQ907265
	NADH 1	HQ907363
	NADH 2	HQ907465
	PTGER	HQ907565
	R35	HQ907673
Brachymeles.talinis.KU315355	ATP 8,6	HQ907171
	BDNF	HQ907266
	NADH 1	HQ907364
	NADH 2	HQ907466
	PTGER	HQ907566
	R35	HQ907674
Brachymeles.talinis.RMB3283	ATP 8,6	HQ907169
	BDNF	HQ907262
	NADH 1	HQ907360

	NADH 2	HQ907462
	PTGER	HQ907562
	R35	HQ907670
Brachymeles.talinis.RMB3305	ATP 8,6	HQ239387
	BDNF	HQ907263
	NADH 1	HQ907361
	NADH 2	HQ907463
	PTGER	HQ907563
	R35	HQ907671
Brachymeles.tridactylus.KU320423	ATP 8,6	HQ907145
	BDNF	HQ907237
	NADH 1	HQ907335
	NADH 2	HQ907437
	PTGER	HQ907537
	R35	HQ907644
Brachymeles.tridactylus.KU320424	ATP 8,6	HQ907146
	BDNF	HQ907238
	NADH 1	HQ907336
	NADH 2	HQ907438
	PTGER	HQ907538
	R35	HQ907645
Brachymeles.tridactylus.KU320425	ATP 8,6	HQ907147
	BDNF	HQ907239

	NADH 1	HQ907337
	NADH 2	HQ907439
	PTGER	HQ907539
	R35	HQ907646
Dasia.grisea.KU305573	BDNF	HQ907226
	NADH 2	HQ907425
	PTGER	HQ907528
	R35	HQ907631
Davewakium.miriamae.KU327692	ATP 8,6	HQ907143
	BDNF	HQ907235
	NADH 1	HQ907333
	NADH 2	HQ907435
	PTGER	HQ907535
	R35	HQ907642
Davewakium.miriamae.KU327693	ATP 8,6	HQ907144
	BDNF	HQ907236
	NADH 1	HQ907334
	NADH 2	HQ907436
	PTGER	HQ907536
	R35	HQ907643
Emoia.atrocostata.KU304896	BDNF	HQ907222
	NADH 1	HQ907326
	NADH 2	HQ907421

	R35	HQ907627
Eumeces.quadrilineaturs.KU311490	BDNF	HQ907223
	NADH 2	HQ907422
	PTGER	HQ907525
	R35	HQ907628
Eutropis.multifasciata.KU302904	NADH 2	HQ907427
	R35	HQ907633
Lamprolepis.smaragdina.KU326565	BDNF	HQ907221
	NADH 1	HQ907325
	R35	HQ907626
Larutia.seribuatensis.LSUHC5168	ATP 8,6	HQ907137
	BDNF	HQ907229
	NADH 1	HQ907327
	NADH 2	HQ907429
	PTGER	HQ907530
	R35	HQ907636
Lipinia.pulchella.pulchella.RMB1079	BDNF	HQ907220
	NADH 1	HQ907324
	R35	HQ907625
Lygosoma.bowringii.LSUHC6998	ATP 8,6	HQ907138
	BDNF	HQ907230
	NADH 1	HQ907328
	NADH 2	HQ907430

	R35	HQ907637
Lygosoma.LSUHC9321	ATP 8,6	HQ907139
	BDNF	HQ907231
	NADH 1	HQ907329
	NADH 2	HQ907431
	PTGER	HQ907531
	R35	HQ907638
Lygosoma.quadrupes.LSUHC8403	ATP 8,6	HQ907140
	BDNF	HQ907232
	NADH 1	HQ907330
	NADH 2	HQ907432
	PTGER	HQ907532
	R35	HQ907639
Plestiodon.anthracinus.CAS325	BDNF	HQ907225
	NADH 2	HQ907424
	PTGER	HQ907527
	R35	HQ907630
Plestiodon.fasciatus.KU289462	BDNF	HQ907224
	NADH 2	HQ907423
	PTGER	HQ907526
	R35	HQ907629
Scincella.lateralis.KU289461	BDNF	HQ907228
	R35	HQ907635

Scincella.reevesii.FMNH255540	BDNF	HQ907227
	NADH 2	HQ907428
	PTGER	HQ907529
	R35	HQ907634
Sphenomorphus.abdictus.abdictus.KU306539	NADH 2	HQ907426
	R35	HQ907632
Tachydromus.sexilineatus.KU311512	BDNF	HQ907219
	NADH 2	HQ907420
	PTGER	HQ907524
	R35	HQ907624

Appendix III

Supporting Information—Materials and Methods

VARIABLE CHOICE FOR MORPHOMETRIC SIZE CORRECTION

In order to explore whether head length is an appropriate measure with which to standardize morphometric variables, and in doing so account for body size allometry, we first conducted a multivariate correlation analysis of all variables to determine which morphometric variable was most highly correlated with all measures of body size. We then conducted three sets of analyses using three different variables to correct for size. Following the methods of Lande (1978), Wiens and Slingluff (2001), and Brandley et al. (2008), we calculated measurements of relative limb and body sizes by regressing independent contrasts of limb and body-length measurements against contrasts in head length, snout–vent length, and midbody width. Each regression line was forced through the origin following Felsenstein (1985) and the standardized residuals were saved as variables. Relative measurements in each of the three sets of size-corrected morphometric variables (head-length-corrected, snout–vent-length-corrected, midbody-width-corrected) were subsequently used in bivariate and multivariate analyses. For all sets of analyses, the Benjamini and Hochberg (1995) method for controlling the false discovery rate (FDR) was applied to determine significant *P*-values (Verhoeven et al. 2005). SPSS 18.0 was used for all statistical analyses and JMP 8 was used for graphical output.

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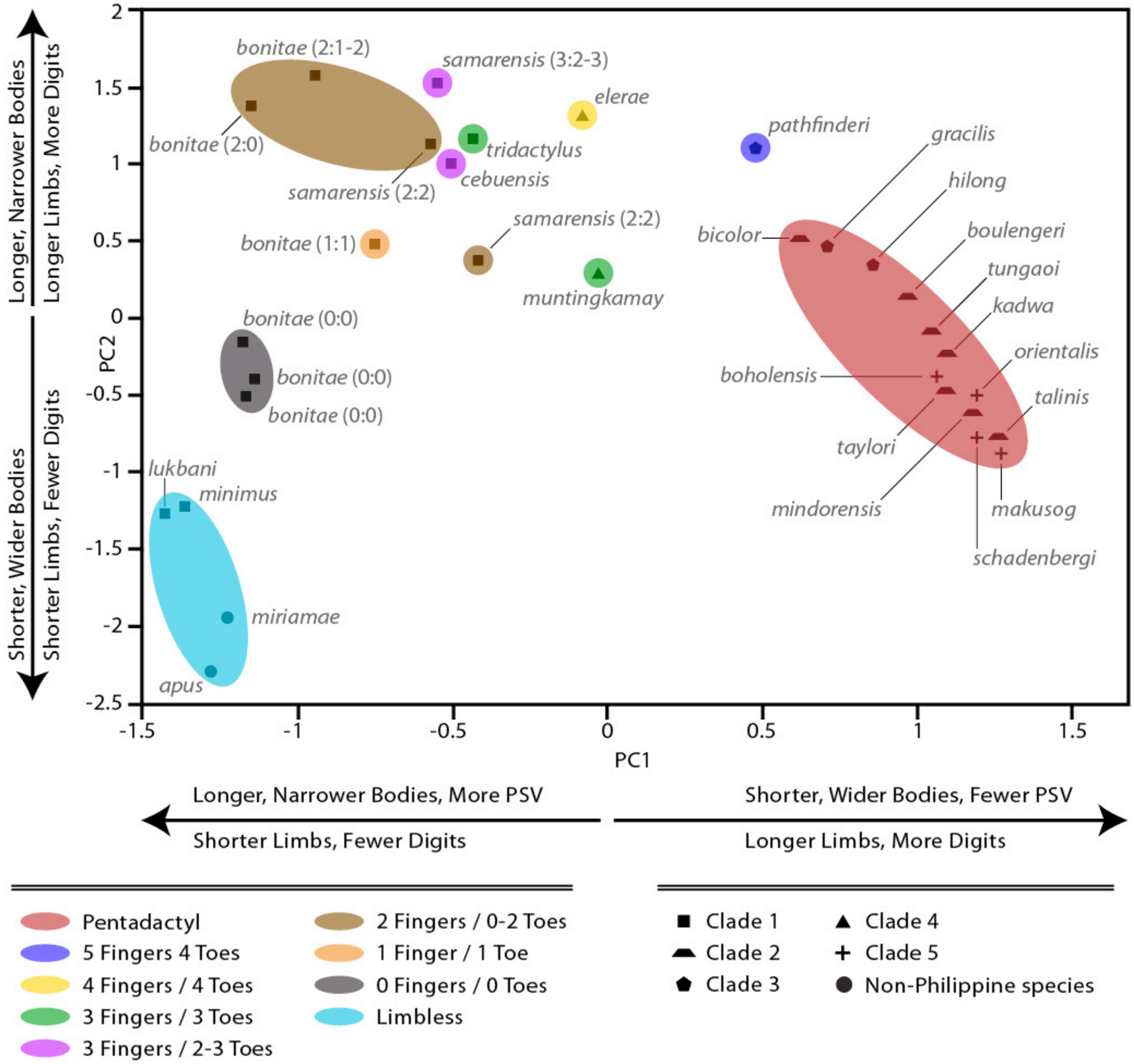

Supplementary Figure 1. Multivariate plot of morphometric and meristic data showing variable loadings for the first and second components for a non-phylogenetic PCA. Colored spheres indicate body form groups among *Brachymeles*, with shapes referring to labeled phylogenetic clades in Figure 2.1.

Appendix IV

Additional Specimens Examined

Numbers in parentheses indicate the number of specimens examined. With the exception of *Brachymeles apus*, all specimens examined are from the Philippines. Numbers in parentheses indicate the number of specimens examined for each species. Several sample sizes are greater than those observed in the description due to the examination of sub-adult specimens which were excluded from morphometric analyses.

Brachymeles apus (1)

BORNEO: MALAYSIA: *Sabah*: Mt. Kinabalu National Park, Sayap Sub-Station: SP 06915.

Brachymeles bicolor (24)

LUZON ISLAND: Aurora Province: *Municipality of Maria Aurora*: Barangay Villa Aurora, Sitio Dimani, Aurora Memorial National Park: KU 323149–52; CAGAYAN PROVINCE: *Municipality of Baggao*: Sitio Hot Springs: CAS 186111, USNM 140847, 498829–30, 498833; Isabela Province, Sierra Madres Mountain Range: KU 324097–99, PNM 5785, 9568–77; KALINGA PROVINCE: Balbalasang-Balbalan National Park: FMNH 259438.

Brachymeles boholensis (19)

BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Sierra Bullones,* Barangay Danicop: KU 323944, 323948–9, 323952–6, 323960, 323962–3, 323966, 323970, 323972, 323975–6, 323981–2, 323990, 324001; BOHOL ISLAND: BOHOL PROVINCE: *6 km S of Municipality of Sierra Bullones*: Teachers Park: CAS-SU (Holotype) 24528; *13 km SE Municipality of Sierra Bullones*:

Dusita Barrio: CAS-SU (Paratypes) 24502–04, 24518, 24520–25, 24541, 24543, CAS-SU 25443–44, 25447; 1 km E Dusita Barrio: Abacjanan: CAS-SU 24867; *Municipality of Sierra Bullones*: Sandayong: CAS-SU 18709, 18717.

Brachymeles bonitae (13)

MASBATE ISLAND: MASBATE PROVINCE: *Municipality of Mobo*: Tugbo Barrio: CAS 144223; Mapuyo Barrio: Palangkahoy: CAS 144270; MINDORO ISLAND: MINDORO ORIENTAL PROVINCE: Mt Halcon: SE slope Barawanan Peak: CAS-SU 25713, 25793, 25886–88, 25904; Sumagui: CAS 62064 (Paratype); POLILLO ISLAND: QUEZON PROVINCE: *Municipality of Polillo*: Barangay Pinaglubayan: KU 307747–49, 307755.

Brachymeles boulengeri (26)

LUZON ISLAND: AURORA PROVINCE: *Municipality of BAler*: KU 322314–20; LUZON ISLAND: LAGUNA PROVINCE: *Municipality of Los Banos,* Barangay Batong Malake: KU 32058–60; *Municipality of Los Banos*: CAS 61096; Mt. Maquiling: CAS 61297; POLILLO ISLAND: QUEZON PROVINCE: *Municipality of Polillo*: CAS (Paratypes) 62272–73, 62276–77; Barangay Pinaglubayan: KU 307438–9, 307750–54, 307756 (Neotype), 307757–58.

Brachymeles cebuensis (8)

CEBU ISLAND: *40 km SW of Cebu City*: Tapal Barrio, Sitio Mantalungon: CAS-SU (Holotype) 24400, (Paratypes) 24396–97, 24399, 24401, 24403; *Municipality of Carcar*: Tapal Barrio: CAS 102405 (Paratype); *3 km NW Cebu City*, Buhisan Barrio, Buhisan Reforestation Project: CAS-SU 27537.

Brachymeles elerae (4)

LUZON ISLAND: Kalinga Province: *Municipality of Balbalan*: CAS 61499–500, PNM 9563–4.

Brachymeles gracilis gracilis (18)

MINDANAO ISLAND: Davao del Sur Province: *Municipality of Malalag*: Sitio Kibawalan: CAS-SU 24163, 24165, CAS 124811, 139307–09; *Davao City*: Buhangin, Kabanti-an: CAS 124803–04, 139293–95, 139303–05; *Digos City*: Tres de Mayo Barrio: CAS 124806–08, 139300.

Brachymeles gracilis hilong (20)

MINDANAO ISLAND: Agusan del Norte Province: *Municipality of Cabadbaran*: Diuata Mountain Range: Mt. Hilonghilong: Balangbalang : CAS-SU (Holotype) 24407, (Paratype) 102406, 133578, CAS-SU 24411, 133577, 133581–82, 133609, 133612, 133692–93, 133703–06, 133743, 133745–47; Surigao del Sur Province: *Municipality of Lanuza*: Diuata Mountain Range: Sibuhay Barrio: CAS-SU (Paratype) 24315.

Brachymeles lukbani (14)

LUZON ISLAND: Camarines Norte Province: *Municipality of Labo*: Barangay Tulay Na Lupa, Mt. Labo: PNM (Holotype) 9567, (Paratopotypes) 9589–92, KU (Paratopotypes) 313597–99, 313601, 313603–04, 313606, 313608, FMNH (Paratopotype) 270191.

Brachymeles makusog (17)

CATANDUANES ISLAND: CATANDUANES PROVINCE: *Municipality of Gigmoto*: Barangay San Pedro, Sitio Tungaw: PNM (Holotype) 9565, (Paratopotypes) 9583–9584, KU (Paratopotypes) 308126, 308128, 308136, 308208; LUZON ISLAND: CAMARINES NORTE PROVINCE: *Municipality of Labo*, Barangay Tulay Na Lupa, Mt. Labo: KU (Paratypes) 313612–313614, 313616, 313617, PNM (Paratypes) 9585–9588, FMNH (Paratype) 270200.

Brachymeles mindorensis (34)

MINDORO ISLAND: MINDORO OCCIDENTAL PROVINCE: KU 304351–5, 304412–3, 304488, 307739–42, 308404, 308447–8, 308534; MINDORO ISLAND: MINDORO ORIENTAL PROVINCE: *30 km SE Municipality of Calapan*: Bank of Tarogin River: CAS-SU (Holotype) 24487; SE slope Mt Halcon, Tarogin Barrio: CAS-SU (Paratypes) 24549–54, 24561–62, 24564; 24566, 24568, 24573–74, 24577–79; Mt Halcon, SE slope Barawanan Peak: CAS-SU (Paratype) 24570.

Brachymeles minimus (6)

CATANDUANES ISLAND: CATANDUANES PROVINCE: *Municipality of Gigmoto*: Barangay San Pedro: KU 308129–31, 308210–12.

Brachymeles muntingkamay (17)

LUZON ISLAND: NUEVA VIZCAYA PROVINCE: *Municipality of Quezon*: Barangay Maddiangat, Mt. Palali: PNM (Holotype) 9566, (Paratopotypes) 9578–82, KU (Paratopotypes) 308865–66, 308900–06, 308908, 308953.

Brachymeles pathfinderi (40)

MINDANAO ISLAND: SARANGANI PROVINCE: *Municipality of Glan*: Barangay Taluya: CDS 5235–42; Barangay Tanibulad, Sitio Padido: CDS 5192–5206, 5210–20, 5222–27.

Brachymeles samarensis (7)

SAMAR ISLAND: EASTERN SAMAR PROVINCE: *Municipality of Taft*: Barangay San Rafael: KU 310849–50, 310852, 311294–6; LEYTE ISLAND: LEYTE PROVINCE: *Municipality of Baybay*: Barangay Pilim: Sitio San Vicente: KU 311225.

Brachymeles orientalis (53)

BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Sierra Bullones*: Dusita Barrio: CAS-SU (Holotype) 24436, CAS-SU (Paratypes) 24428, 24434, 24437, CAS (Paratype) 102404, CAS-SU 25452; Dusita Barrio: Abacjanan: CAS-SU (Paratypes) 24446–51, CAS-SU 25460; Cantaub Barrio: CAS-SU (Paratypes) 18702, 24442, 24458; CAMIGUIN SUR ISLAND: CAMIGUIN PROVINCE: *Municipality of Catarman*: Mt. Mambajao: Sitio Sangsangan: CAS 110976–83; LEYTE ISLAND: Leyte PROVINCE: *Municipality of Baybay*: KU 311231–5, 311241; MINDANAO ISLAND: AGUSAN DEL NORTE PROVINCE: *Municipality of Cabadbaran*: Diuata Mountain Range: Mt. Hilonghilong: Kasinganan: CAS-SU 133301, 133616, 133749, 133752, 133754; SAMAR ISLAND: Eastern Samar PROVINCE: *Municipality of Taft*: KU 305470, 310734–6, 310739, 310942–6, 310949, 310951, 310955.

Brachymeles schadenbergi (45)

BASILAN ISLAND: BASILAN PROVINCE: Port Holland: Sawmill: CAS 60493; MINDANAO ISLAND: MISAMIS OCCIDENTAL PROVINCE: 2 km NW of Masawan: CAS 23468–69; 4 km NW of Masawan: CAS 23471; 3 km NW Masawan: south bank of Dapitan River: CAS 23479–81, 23484–85; COTABATO PROVINCE: *Municipality of Tatayan*: MCZ 26553, 26555–8, 26561, 26566, 26568, 26571–2, 26574; ZAMBOANGA DEL NORTE PROVINCE: Dapitan River: CAS-SU 23494–96; ZAMBOANGA CITY PROVINCE: *Municipality of Pasonanca*: Barangay Baluno: Pasonanca Natural Park: KU 314967, 314969, 314970–8, 314980, 314984–85, 314988–92, 314994, 314996–7.

Brachymeles talinis (31)

NEGROS ISLAND: NEGROS ORIENTAL PROVINCE: *6 km W Municipality of Valencia*: Cuernos de Negros Mountain Range: ridge on north side of Maite River: CAS-SU (Holotype) 18358, (Paratype) 89813; Cuernos de Negros Mountain Range: Dayungan Ridge: CAS 133871; *Dumaguete City*: CAS-SU (Paratype) 12225; *Municipality of Siaton*: 20 km N Bondo Barrio: CAS-SU 22311–12; 22317, 22323; INAMPULAGAN ISLAND: GUIMARAS PROVINCE: *Municipality of Sibunag*: 8 km W Pulupandan Town: CAS-SU 27972, 27996–97; PANAY ISLAND: ANTIQUE PROVINCE: *Municipality of San Remigio*: KU 306756–60, 306762–7, 306769, 306770–6, 306786.

Brachymeles taylori (34)

NEGROS ISLAND: NEGROS OCCIDENTAL PROVINCE: *Municipality of Silay City*, Barangay Patag: KU 324044–56; NEGROS ISLAND: NEGROS ORIENTAL PROVINCE: *3 km W Municipality of Valencia*: Cuernos de Negros Mountain Range: Sitio Lunga: ridge on north side of Maiti River: CAS-SU (Holotype) 18615, CAS-SU 21873; ridge on south side of Maiti River: CAS-SU (Paratype) 18641, 18656–57, 18748; Cuernos de Negros Mountain Range: CAS-SU

(Paratype) 18649; top of Dayungan Ridge: CAS-SU 21877, 21880, 21883–84; 24 km NW Bondo Barrio: Bantolinao: CAS-SU 22355–56; CEBU ISLAND: CEBU PROVINCE: *Municipality of Carcar*: Tapal Barrio: Sitio Mantalongon: CAS 154671, 154673, 154678–82, 154686.

Brachymeles tridactylus (20)

NEGROS ISLAND: NEGROS OCCIDENTAL PROVINCE: *16 km E Municipality of La Castellana*: Barrio Cabagna-an: Southern Slope of Mt. Canlaon: CAS-SU 19424, 19426–27, 19429, 19452, 19458; *20 km E Municipality of La Castellana*: Sitio Kalapnagan: CAS-SU 27082–83; NEGROS ORIENTAL PROVINCE: Hills North and Northwest of Mayaposi: CAS-SU (Holotype) 18354; PANAY ISLAND: ANTIQUE PROVINCE: *Municipality of Culasi*: Barangay Alojipan: KU 307726–36.

Brachymeles vermis (5)

JOLO ISLAND: SULU PROVINCE: CAS-SU (Paratype) 62489, CAS-SU 60720–22, 60857.

Appendix V

Additional Specimens Examined

Numbers in parentheses indicate the number of specimens examined. With the exception of *Brachymeles apus* and *B. miriamae*, all specimens examined are from the Philippines. Numbers in parentheses indicate the number of specimens examined for each species. Several sample sizes are greater than those observed in the description due to the examination of sub-adult specimens which were excluded from morphometric analyses.

Brachymeles apus (1)

BORNEO: MALAYSIA: *Sabah*: Mt. Kinabalu National Park, Sayap Sub-Station: SP 06915.

Brachymeles lima (20)

See type description.

Brachymeles bicolor (24)

LUZON ISLAND: Aurora Province: *Municipality of Maria Aurora*: Barangay Villa Aurora, Sitio Dimani, Aurora Memorial National Park: KU 323149–52; CAGAYAN PROVINCE: *Municipality of Baggao*: Sitio Hot Springs: CAS 186111, USNM 140847, 498829–30, 498833; Isabela Province, Sierra Madres Mountain Range: KU 324097–99, PNM 5785, 9568–77; KALINGA PROVINCE: Balbalasang-Balbalan National Park: FMNH 259438.

Brachymeles boholensis (19)

BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Sierra Bullones,* Barangay Danicop: KU 323944, 323948–9, 323952–6, 323960, 323962–3, 323966, 323970, 323972, 323975–6, 323981–2, 323990, 324001; BOHOL ISLAND: BOHOL PROVINCE: *6 km S of Municipality of Sierra Bullones*: Teachers Park: CAS-SU (Holotype) 24528; *13 km SE Municipality of Sierra Bullones*: Dusita Barrio: CAS-SU (Paratypes) 24502–04, 24518, 24520–25, 24541, 24543, CAS-SU 25443–44, 25447; 1 km E Dusita Barrio: Abacjanan: CAS-SU 24867; *Municipality of Sierra Bullones*: Sandayong: CAS-SU 18709, 18717.

Brachymeles bonitae (13)

MASBATE ISLAND: MASBATE PROVINCE: *Municipality of Mobo*: Tugbo Barrio: CAS 144223; Mapuyo Barrio: Palangkahoy: CAS 144270; MINDORO ISLAND: MINDORO ORIENTAL PROVINCE: Mt Halcon: SE slope Barawanan Peak: CAS-SU 25713, 25793, 25886–88, 25904; Sumagui: CAS 62064 (Paratype); POLILLO ISLAND: QUEZON PROVINCE: *Municipality of Polillo*: Barangay Pinaglubayan: KU 307747–49, 307755.

Brachymeles boulengeri (26)

LUZON ISLAND: AURORA PROVINCE: *Municipality of BAler*: KU 322314–20; LUZON ISLAND: LAGUNA PROVINCE: *Municipality of Los Banos,* Barangay Batong Malake: KU 32058–60; *Municipality of Los Banos*: CAS 61096; Mt. Maquiling: CAS 61297; POLILLO ISLAND: QUEZON PROVINCE: *Municipality of Polillo*: CAS (Paratypes) 62272–73, 62276–77; Barangay Pinaglubayan: KU 307438–9, 307750–54, 307756 (Neotype), 307757–58.

Brachymeles tatlo (3)

See type description.

Brachymeles cebuensis (8)

CEBU ISLAND: *40 km SW of Cebu City*: Tapal Barrio, Sitio Mantalungon: CAS-SU (Holotype) 24400, (Paratypes) 24396–97, 24399, 24401, 24403; *Municipality of Carcar*: Tapal Barrio: CAS 102405 (Paratype); *3 km NW Cebu City*, Buhisan Barrio, Buhisan Reforestation Project: CAS-SU 27537.

Brachymeles apat (10)

See type description.

Brachymeles elerae (5)

LUZON ISLAND: KALINGA PROVINCE: *Municipality of Balbalan*: CAS 61499–500, CM (Paratype) 1717, PNM 9563–4.

Brachymeles gracilis gracilis (18)

MINDANAO ISLAND: DAVAO DEL SUR PROVINCE: *Municipality of Malalag*: Sitio Kibawalan: CAS-SU 24163, 24165, CAS 124811, 139307–09; *Davao City*: Buhangin, Kabanti-an: CAS 124803–04, 139293–95, 139303–05; *Digos City*: Tres de Mayo Barrio: CAS 124806–08, 139300.

Brachymeles gracilis hilong (20)

MINDANAO ISLAND: AGUSAN DEL NORTE PROVINCE: *Municipality of Cabadbaran*: Diuata Mountain Range: Mt. Hilonghilong: Balangbalang : CAS-SU (Holotype) 24407, (Paratype)

102406, 133578, CAS-SU 24411, 133577, 133581–82, 133609, 133612, 133692–93, 133703–06, 133743, 133745–47; SURIGAO DEL SUR PROVINCE: *Municipality of Lanuza*: Diuata Mountain Range: Sibuhay Barrio: CAS-SU (Paratype) 24315.

Brachymeles kadwa (101)

LUZON ISLAND: AURORA PROVINCE: *Municipality of Baler*: Barangay Zabali, Aurora State College of Technology campus: PNM (Holotype) 9721, KU (Paratopotypes) 232092, 323094–96, 323100, 323104, 323106, KU 323090–91, 323093, 323097–99, 323101–03, 323105, 323107; *Municipality of Casiguran*, IDC property: KU 323108–48; *Municipality of San Luis*, Barangay Real, Sitio Minoli: KU 322320; CALAYAN ISLAND: CAGAYAN PROVINCE: *Municipality of Calayan*: Barangay Magsidel: KU (Paratypes) 304875, 304897, 304900, 304902–3, 304905–6, 304915, 304929, 304941, KU 304908, , 304899, 304907, 304909, 304921, 304941; CAMIGUIN NORTE ISLAND: CAGAYAN PROVINCE: *Municipality of Calayan*: Barangay Balatubat: KU (Paratypes) 304559, 304575, 304593, 304708, 304754, 307984, 307996, 307998, 308011, KU 304558, 304562–65, 304569, 304571–74, 304627–30, 304643, 304647, 304696–99, 304704–07, 304709–12, 304714, 304753, 304755–59, 307965–66, 307985–86, 307997, 307999–8003, 308006–10, 308012–15, 308017–18.

Brachymeles dalawa (46)

See type description.

Brachymeles lukbani (14)

LUZON ISLAND: CAMARINES NORTE PROVINCE: *Municipality of Labo*: Barangay Tulay Na Lupa, Mt. Labo: PNM (Holotype) 9567, (Paratopotypes) 9589–92, KU (Paratopotypes) 313597–99, 313601, 313603–04, 313606, 313608, FMNH (Paratopotype) 270191.

Brachymeles makusog (17)

CATANDUANES ISLAND: CATANDUANES PROVINCE: *Municipality of Gigmoto*: Barangay San Pedro, Sitio Tungaw: PNM (Holotype) 9565, (Paratopotypes) 9583–9584, KU (Paratopotypes) 308126, 308128, 308136, 308208; LUZON ISLAND: CAMARINES NORTE PROVINCE: *Municipality of Labo*, Barangay Tulay Na Lupa, Mt. Labo: KU (Paratypes) 313612–313614, 313616, 313617, PNM (Paratypes) 9585–9588, FMNH (Paratype) 270200.

Brachymeles mindorensis (34)

MINDORO ISLAND: MINDORO OCCIDENTAL PROVINCE: KU 304351–5, 304412–3, 304488, 307739–42, 308404, 308447–8, 308534; MINDORO ISLAND: MINDORO ORIENTAL PROVINCE: *30 km SE Municipality of Calapan*: Bank of Tarogin River: CAS-SU (Holotype) 24487; SE slope Mt Halcon, Tarogin Barrio: CAS-SU (Paratypes) 24549–54, 24561–62, 24564; 24566, 24568, 24573–74, 24577–79; Mt Halcon, SE slope Barawanan Peak: CAS-SU (Paratype) 24570.

Brachymeles minimus (6)

CATANDUANES ISLAND: CATANDUANES PROVINCE: *Municipality of Gigmoto*: Barangay San Pedro: KU 308129–31, 308210–12.

Brachymeles miriamae (2)

THAILAND: NAKHON RATCHASIMA PROVINCE: *Wang Nam Khieo District*: Sakaerat Environmental Research Station: DSM 1293, 1363 (Currently uncataloged specimens housed at KU).

Brachymeles muntingkamay (17)

LUZON ISLAND: NUEVA VIZCAYA PROVINCE: *Municipality of Quezon*: Barangay Maddiangat, Mt. Palali: PNM (Holotype) 9566, (Paratopotypes) 9578–82, KU (Paratopotypes) 308865–66, 308900–06, 308908, 308953.

Brachymeles orientalis (53)

BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Sierra Bullones*: Dusita Barrio: CAS-SU (Holotype) 24436, CAS-SU (Paratypes) 24428, 24434, 24437, CAS (Paratype) 102404, CAS-SU 25452; Dusita Barrio: Abacjanan: CAS-SU (Paratypes) 24446–51, CAS-SU 25460; Cantaub Barrio: CAS-SU (Paratypes) 18702, 24442, 24458; CAMIGUIN SUR ISLAND: CAMIGUIN PROVINCE: *Municipality of Catarman*: Mt. Mambajao: Sitio Sangsangan: CAS 110976–83; LEYTE ISLAND: Leyte PROVINCE: *Municipality of Baybay*: KU 311231–5, 311241; MINDANAO ISLAND: AGUSAN DEL NORTE PROVINCE: *Municipality of Cabadbaran*: Diuata Mountain Range: Mt. Hilonghilong: Kasinganan: CAS-SU 133301, 133616, 133749, 133752, 133754; SAMAR ISLAND: Eastern Samar PROVINCE: *Municipality of Taft*: KU 305470, 310734–6, 310739, 310942–6, 310949, 310951, 310955.

Brachymeles isa (17)

See type description.

Brachymeles pathfinderi (40)

MINDANAO ISLAND: SARANGANI PROVINCE: *Municipality of Glan*: Barangay Taluya: KU 324089–96; Barangay Tanibulad, Sitio Padido: KU 324057–88.

Brachymeles samarensis (7)

SAMAR ISLAND: EASTERN SAMAR PROVINCE: *Municipality of Taft*: Barangay San Rafael: KU 310849–52, 311294–6.

Brachymeles schadenbergi (34)

BASILAN ISLAND: BASILAN PROVINCE: Port Holland: Sawmill: CAS 60493; MINDANAO ISLAND: MISAMIS OCCIDENTAL PROVINCE: 2 km NW of Masawan: CAS 23468–69; 4 km NW of Masawan: CAS 23471; 3 km NW Masawan: south bank of Dapitan River: CAS 23479–81, 23484–85; ZAMBOANGA DEL NORTE PROVINCE: Dapitan River: CAS-SU 23494–96; ZAMBOANGA CITY PROVINCE: *Municipality of Pasonanca*: Barangay Baluno: Pasonanca Natural Park: KU 314967, 314969, 314970–8, 314980, 314984–85, 314988–92, 314994, 314996–7.

Brachymeles talinis (31)

NEGROS ISLAND: NEGROS ORIENTAL PROVINCE: *6 km W Municipality of Valencia*: Cuernos de Negros Mountain Range: ridge on north side of Maite River: CAS-SU (Holotype) 18358, (Paratype) 89813; Cuernos de Negros Mountain Range: Dayungan Ridge: CAS 133871; *Dumaguete City*: CAS-SU (Paratype) 12225; *Municipality of Siaton*: 20 km N Bondo Barrio: CAS-SU 22311–12; 22317, 22323; INAMPULAGAN ISLAND: GUIMARAS PROVINCE:

Municipality of Sibunag: 8 km W Pulupandan Town: CAS-SU 27972, 27996–97; PANAY ISLAND: ANTIQUE PROVINCE: *Municipality of San Remigio*: KU 306756–60, 306762–7, 306769, 306770–6, 306786.

Brachymeles taylori (34)

NEGROS ISLAND: NEGROS OCCIDENTAL PROVINCE: *Municipality of Silay City*, Barangay Patag: KU 324044–56; NEGROS ISLAND: NEGROS ORIENTAL PROVINCE: *3 km W Municipality of Valencia*: Cuernos de Negros Mountain Range: Sitio Lunga: ridge on north side of Maiti River: CAS-SU (Holotype) 18615, CAS-SU 21873; ridge on south side of Maiti River: CAS-SU (Paratype) 18641, 18656–57, 18748; Cuernos de Negros Mountain Range: CAS-SU (Paratype) 18649; top of Dayungan Ridge: CAS-SU 21877, 21880, 21883–84; 24 km NW Bondo Barrio: Bantolinao: CAS-SU 22355–56; CEBU ISLAND: CEBU PROVINCE: *Municipality of Carcar*: Tapal Barrio: Sitio Mantalongon: CAS 154671, 154673, 154678–82, 154686.

Brachymeles tridactylus (20)

NEGROS ISLAND: NEGROS OCCIDENTAL PROVINCE: *16 km E Municipality of La Castellana*: Barrio Cabagna-an: Southern Slope of Mt. Canlaon: CAS-SU 19424, 19426–27, 19429, 19452, 19458; *20 km E Municipality of La Castellana*: Sitio Kalapnagan: CAS-SU 27082–83; NEGROS ORIENTAL PROVINCE: Hills North and Northwest of Mayaposi: CAS-SU (Holotype) 18354; PANAY ISLAND: ANTIQUE PROVINCE: *Municipality of Culasi*: Barangay Alojipan: KU 307726–36.

Brachymeles tungaoi (12)

MASBATE ISLAND: MASBATE PROVINCE: *Municipality of Masbate City*: PNM (Holotype) 9722, KU (Paratopotypes) 323934–36; *Municipality of Mobo*, Barangay Tugbo: CAS (Paratypes) 144229–30, 144290, 144306–7, 144313, 144341–2.

Brachymeles vermis (5)

JOLO ISLAND: SULU PROVINCE: CAS-SU (Paratype) 62489, CAS-SU 60720–22, 60857.

Brachymeles vindumi (4)

JOLO ISLAND: SULU PROVINCE: CAS (Holotype) 60724, CAS (Paratypes) 60723, 60725, MCZ (Paratype) 26577).

Brachymeles wrighti (2)

LUZON ISLAND: BENGUET PROVINCE: *Municipality of La Trinidad*: MCZ (Holotype) 26589, USNM 140756.

Appendix VI

Additional Specimens Examined

Numbers in parentheses indicate the number of specimens examined. With the exception of *Brachymeles apus* and *B. miriamae*, all specimens examined are from the Philippines. Numbers in parentheses indicate the number of specimens examined for each species. Several sample sizes are greater than those observed in the description due to the examination of sub-adult specimens which were excluded from morphometric analyses.

Brachymeles apus (1)

BORNEO: MALAYSIA: *Sabah*: Mt. Kinabalu National Park, Sayap Sub-Station: SP 06915.

Brachymeles bicolor (24)

LUZON ISLAND: Aurora Province: *Municipality of Maria Aurora*: Barangay Villa Aurora, Sitio Dimani, Aurora Memorial National Park: KU 323149–52; CAGAYAN PROVINCE: *Municipality of Baggao*: Sitio Hot Springs: CAS 186111, USNM 140847, 498829–30, 498833; Isabela Province, Sierra Madres Mountain Range: KU 324097–99, PNM 5785, 9568–77; KALINGA PROVINCE: Balbalasang-Balbalan National Park: FMNH 259438.

Brachymeles boholensis (19)

BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Sierra Bullones,* Barangay Danicop: KU 323944, 323948–9, 323952–6, 323960, 323962–3, 323966, 323970, 323972, 323975–6, 323981–2, 323990, 324001; BOHOL ISLAND: BOHOL PROVINCE: *6 km S of Municipality of Sierra Bullones*: Teachers Park: CAS-SU (Holotype) 24528; *13 km SE Municipality of Sierra Bullones*:

Dusita Barrio: CAS-SU (Paratypes) 24502–04, 24518, 24520–25, 24541, 24543, CAS-SU 25443–44, 25447; 1 km E Dusita Barrio: Abacjanan: CAS-SU 24867; *Municipality of Sierra Bullones*: Sandayong: CAS-SU 18709, 18717.

Brachymeles bonitae (13)

MASBATE ISLAND: MASBATE PROVINCE: *Municipality of Mobo*: Tugbo Barrio: CAS 144223; Mapuyo Barrio: Palangkahoy: CAS 144270; MINDORO ISLAND: MINDORO ORIENTAL PROVINCE: Mt Halcon: SE slope Barawanan Peak: CAS-SU 25713, 25793, 25886–88, 25904; Sumagui: CAS 62064 (Paratype); POLILLO ISLAND: QUEZON PROVINCE: *Municipality of Polillo*: Barangay Pinaglubayan: KU 307747–49, 307755.

Brachymeles boulengeri (26)

LUZON ISLAND: AURORA PROVINCE: *Municipality of BAler*: KU 322314–20; LUZON ISLAND: LAGUNA PROVINCE: *Municipality of Los Banos,* Barangay Batong Malake: KU 32058–60; *Municipality of Los Banos*: CAS 61096; Mt. Maquiling: CAS 61297; POLILLO ISLAND: QUEZON PROVINCE: *Municipality of Polillo*: CAS (Paratypes) 62272–73, 62276–77; Barangay Pinaglubayan: KU 307438–9, 307750–54, 307756 (Neotype), 307757–58.

Brachymeles cebuensis (8)

CEBU ISLAND: *40 km SW of Cebu City*: Tapal Barrio, Sitio Mantalungon: CAS-SU (Holotype) 24400, (Paratypes) 24396–97, 24399, 24401, 24403; *Municipality of Carcar*: Tapal Barrio: CAS 102405 (Paratype); *3 km NW Cebu City*, Buhisan Barrio, Buhisan Reforestation Project: CAS-SU 27537.

Brachymeles elerae (5)

LUZON ISLAND: Kalinga Province: *Municipality of Balbalan*: CAS 61499–500, CM (Paratype) 1717, PNM 9563–4.

Brachymeles gracilis (69)

MINDANAO ISLAND: Davao del Sur Province: FMNH 52642–44, 52646–47, 52662, 52669–70; *Davao City*: Buhangin, Kabanti-an: CAS 124803–04, 139293–95, 139301–05; *Digos City*: Tres de Mayo Barrio: CAS 124806–08, 139296–300; *Municipality of Kiblawan*: Barangay Kimlawis: KU 326096, 326098–108, 326298–99; *Municipality of Malalag*: Sitio Kibawalan: CAS-SU 24158–65, 24171, CAS 124809–12, 139306–11; *Municipality of Toril*: Barangay Baracatan, Mt. Apo, Old Eagle Station: CMC 12170–71; South Cotabato Province: MCZ 26539, 26541, 26543–44, 26546, 26548–50.

Brachymeles pito (28)

MINDANAO ISLAND: Agusan del Norte Province: *Municipality of Cabadbaran*: Diuata Mountain Range: Mt. Hilonghilong: Balangbalang: CAS-SU (Holotype) 24407, (Paratypes) 102406, 133578, CAS-SU 24411, 133577, 133579, 133581–82, 133609, 133612, 133692–93, 133703–06, 133743, 133745–47; Agusan del Sur Province: *Municipality of San Francisco*: Barangay Bagusan II: Mt. Magdiwata: KU 319934–40; Surigao del Sur Province: *Municipality of Lanuza*: Diuata Mountain Range: Sibuhay Barrio: CAS-SU (Paratype) 24315.

Brachymeles kadwa (101)

LUZON ISLAND: AURORA PROVINCE: *Municipality of Baler*: Barangay Zabali, Aurora State College of Technology campus: PNM (Holotype) 9721, KU (Paratopotypes) 232092, 323094–96, 323100, 323104, 323106, KU 323090–91, 323093, 323097–99, 323101–03, 323105, 323107; *Municipality of Casiguran*, IDC property: KU 323108–48; *Municipality of San Luis*, Barangay Real, Sitio Minoli: KU 322320; CALAYAN ISLAND: CAGAYAN PROVINCE: *Municipality of Calayan*: Barangay Magsidel: KU (Paratypes) 304875, 304897, 304900, 304902–3, 304905–6, 304915, 304929, 304941, KU 304908, , 304899, 304907, 304909, 304921, 304941; CAMIGUIN NORTE ISLAND: CAGAYAN PROVINCE: *Municipality of Calayan*: Barangay Balatubat: KU (Paratypes) 304559, 304575, 304593, 304708, 304754, 307984, 307996, 307998, 308011, KU 304558, 304562–65, 304569, 304571–74, 304627–30, 304643, 304647, 304696–99, 304704–07, 304709–12, 304714, 304753, 304755–59, 307965–66, 307985–86, 307997, 307999–8003, 308006–10, 308012–15, 308017–18.

Brachymeles lukbani (14)

LUZON ISLAND: CAMARINES NORTE PROVINCE: *Municipality of Labo*: Barangay Tulay Na Lupa, Mt. Labo: PNM (Holotype) 9567, (Paratopotypes) 9589–92, KU (Paratopotypes) 313597–99, 313601, 313603–04, 313606, 313608, FMNH (Paratopotype) 270191.

Brachymeles makusog (17)

CATANDUANES ISLAND: CATANDUANES PROVINCE: *Municipality of Gigmoto*: Barangay San Pedro, Sitio Tungaw: PNM (Holotype) 9565, (Paratopotypes) 9583–9584, KU (Paratopotypes) 308126, 308128, 308136, 308208; LUZON ISLAND: CAMARINES NORTE PROVINCE:

Municipality of Labo, Barangay Tulay Na Lupa, Mt. Labo: KU (Paratypes) 313612–313614, 313616, 313617, PNM (Paratypes) 9585–9588, FMNH (Paratype) 270200.

Brachymeles mindorensis (34)

MINDORO ISLAND: MINDORO OCCIDENTAL PROVINCE: KU 304351–5, 304412–3, 304488, 307739–42, 308404, 308447–8, 308534; MINDORO ISLAND: MINDORO ORIENTAL PROVINCE: *30 km SE Municipality of Calapan*: Bank of Tarogin River: CAS-SU (Holotype) 24487; SE slope Mt Halcon, Tarogin Barrio: CAS-SU (Paratypes) 24549–54, 24561–62, 24564; 24566, 24568, 24573–74, 24577–79; Mt Halcon, SE slope Barawanan Peak: CAS-SU (Paratype) 24570.

Brachymeles minimus (6)

CATANDUANES ISLAND: CATANDUANES PROVINCE: *Municipality of Gigmoto*: Barangay San Pedro: KU 308129–31, 308210–12.

Brachymeles miriamae (2)

THAILAND: NAKHON RATCHASIMA PROVINCE: *Wang Nam Khieo District*: Sakaerat Environmental Research Station: DSM 1293, 1363 (Currently uncataloged specimens housed at KU).

Brachymeles muntingkamay (17)

LUZON ISLAND: NUEVA VIZCAYA PROVINCE: *Municipality of Quezon*: Barangay Maddiangat, Mt. Palali: PNM (Holotype) 9566, (Paratopotypes) 9578–82, KU (Paratopotypes) 308865–66, 308900–06, 308908, 308953.

Brachymeles orientalis (53)

BOHOL ISLAND: BOHOL PROVINCE: *Municipality of Sierra Bullones*: Dusita Barrio: CAS-SU (Holotype) 24436, CAS-SU (Paratypes) 24428, 24434, 24437, CAS (Paratype) 102404, CAS-SU 25452; Dusita Barrio: Abacjanan: CAS-SU (Paratypes) 24446–51, CAS-SU 25460; Cantaub Barrio: CAS-SU (Paratypes) 18702, 24442, 24458; CAMIGUIN SUR ISLAND: CAMIGUIN PROVINCE: *Municipality of Catarman*: Mt. Mambajao: Sitio Sangsangan: CAS 110976–83; LEYTE ISLAND: Leyte PROVINCE: *Municipality of Baybay*: KU 311231–5, 311241; MINDANAO ISLAND: AGUSAN DEL NORTE PROVINCE: *Municipality of Cabadbaran*: Diuata Mountain Range: Mt. Hilonghilong: Kasinganan: CAS-SU 133301, 133616, 133749, 133752, 133754; SAMAR ISLAND: Eastern Samar PROVINCE: *Municipality of Taft*: KU 305470, 310734–6, 310739, 310942–6, 310949, 310951, 310955.

Brachymeles pathfinderi (40)

MINDANAO ISLAND: SARANGANI PROVINCE: *Municipality of Glan*: Barangay Taluya: KU 324089–96; Barangay Tanibulad, Sitio Padido: KU 324057–88.

Brachymeles syam (45)

See type description.

Brachymeles samarensis (7)

SAMAR ISLAND: EASTERN SAMAR PROVINCE: *Municipality of Taft*: Barangay San Rafael: KU 310849–52, 311294–6.

Brachymeles schadenbergi (34)

BASILAN ISLAND: BASILAN PROVINCE: Port Holland: Sawmill: CAS 60493; MINDANAO ISLAND: MISAMIS OCCIDENTAL PROVINCE: 2 km NW of Masawan: CAS 23468–69; 4 km NW of Masawan: CAS 23471; 3 km NW Masawan: south bank of Dapitan River: CAS 23479–81, 23484–85; ZAMBOANGA DEL NORTE PROVINCE: Dapitan River: CAS-SU 23494–96; ZAMBOANGA CITY PROVINCE: *Municipality of Pasonanca*: Barangay Baluno: Pasonanca Natural Park: KU 314967, 314969, 314970–8, 314980, 314984–85, 314988–92, 314994, 314996–7.

Brachymeles sampu (2)

See neotype description.

Brachymeles talinis (31)

NEGROS ISLAND: NEGROS ORIENTAL PROVINCE: *6 km W Municipality of Valencia*: Cuernos de Negros Mountain Range: ridge on north side of Maite River: CAS-SU (Holotype) 18358, (Paratype) 89813; Cuernos de Negros Mountain Range: Dayungan Ridge: CAS 133871; *Dumaguete City*: CAS-SU (Paratype) 12225; *Municipality of Siaton*: 20 km N Bondo Barrio: CAS-SU 22311–12; 22317, 22323; INAMPULAGAN ISLAND: GUIMARAS PROVINCE: *Municipality of Sibunag*: 8 km W Pulupandan Town: CAS-SU 27972, 27996–97; PANAY ISLAND: ANTIQUE PROVINCE: *Municipality of San Remigio*: KU 306756–60, 306762–7, 306769, 306770–6, 306786.

Brachymeles taylori (34)

NEGROS ISLAND: NEGROS OCCIDENTAL PROVINCE: *Municipality of Silay City*, Barangay Patag: KU 324044–56; NEGROS ISLAND: NEGROS ORIENTAL PROVINCE: *3 km W Municipality of Valencia*: Cuernos de Negros Mountain Range: Sitio Lunga: ridge on north side of Maiti River: CAS-SU (Holotype) 18615, CAS-SU 21873; ridge on south side of Maiti River: CAS-SU (Paratype) 18641, 18656–57, 18748; Cuernos de Negros Mountain Range: CAS-SU (Paratype) 18649; top of Dayungan Ridge: CAS-SU 21877, 21880, 21883–84; 24 km NW Bondo Barrio: Bantolinao: CAS-SU 22355–56; CEBU ISLAND: CEBU PROVINCE: *Municipality of Carcar*: Tapal Barrio: Sitio Mantalongon: CAS 154671, 154673, 154678–82, 154686.

Brachymeles walo (3)

See type description.

Brachymeles tridactylus (20)

NEGROS ISLAND: NEGROS OCCIDENTAL PROVINCE: *16 km E Municipality of La Castellana*: Barrio Cabagna-an: Southern Slope of Mt. Canlaon: CAS-SU 19424, 19426–27, 19429, 19452, 19458; *20 km E Municipality of La Castellana*: Sitio Kalapnagan: CAS-SU 27082–83; NEGROS ORIENTAL PROVINCE: Hills North and Northwest of Mayaposi: CAS-SU (Holotype) 18354; PANAY ISLAND: ANTIQUE PROVINCE: *Municipality of Culasi*: Barangay Alojipan: KU 307726–36.

Brachymeles tungaoi (12)

MASBATE ISLAND: MASBATE PROVINCE: *Municipality of Masbate City*: PNM (Holotype) 9722, KU (Paratopotypes) 323934–36; *Municipality of Mobo*, Barangay Tugbo: CAS (Paratypes) 144229–30, 144290, 144306–7, 144313, 144341–2.

Brachymeles vermis (5)

JOLO ISLAND: SULU PROVINCE: CAS-SU (Paratype) 62489, CAS-SU 60720–22, 60857.

Brachymeles vindumi (4)

JOLO ISLAND: SULU PROVINCE: CAS (Holotype) 60724, CAS (Paratypes) 60723, 60725, MCZ (Paratype) 26577).

Brachymeles anim (20)

See type description.

Brachymeles wrighti (2)

LUZON ISLAND: BENGUET PROVINCE: *Municipality of La Trinidad*: MCZ (Holotype) 26589, USNM 140756.

Brachymeles apat [Catanduanes Island; Siler et al., in press c] (10)

CATANDUANES ISLAND: CATANDUANES PROVINCE: *Municipality of Virac*: Barangay Palta Small: KU (Paratopotypes) 306311, 308077, 324019–21, 324025–26, PNM (Holotype) 9761, (Paratopotypes) 9562–63.

Brachymeles lima [Central Bicol Peninsula, Luzon Island; Siler et al., in press c] (20)

LUZON ISLAND: ALBAY PROVINCE: *Municipality of Malinao*: Barangay Labnig: CAS (Paratypes) 140065, 152025–26; *Municipality of Tabaco City*: Barangay Common: KU (Paratopotypes) 324005–11, 324015–16, 323087, PNM (Holotype) 9756, (Paratopotypes) 9757–60; CAMARINES SUR PROVINCE: *Municipality of Pili*: Barrio Curry, Mt. Isarog: CAS-SU (Paratypes) 24173, 24413.

Brachymeles dalawa [Lapinig Group islands; Siler et al., in press c] (46)

LAPINIG CHICO ISLAND: BOHOL PROVINCE: *Municipality of President Carlos P. Garcia*: CAS-SU (Paratypes) 27556, 28454–55; LAPINIG GRANDE ISLAND: BOHOL PROVINCE: *Municipality of President Carlos P. Garcia*: Barangay Villa Milagrosa: KU (Paratopotypes) 320428–30, 320435–63, 320466–67, PNM (Holotype) 9749 (Paratopotypes) 9750–55; 0.5 km SW of Barrio Pitogo: CAS-SU (Paratype) 28453; POLONG DAKO ISLAND: BOHOL PROVINCE: *Municipality of President Carlos P. Garcia*: CAS-SU (Paratype) 27554.

Brachymeles isa [Leyte Island; Siler et al., in press c] (13)

LEYTE ISLAND: LEYTE PROVINCE: *Municipality of Burauen*: Barrio Tambis: CAS-SU (Paratypes) 26110, 26112, 26115, 26120–23; *Baybay City*: Barangay Pilim, Siotio San Vicente Tree Nursery: KU (Paratopotypes) 311224–25, 311224, PNM (Holotype) 9746, (Paratopotypes) 9747–48.

Brachymeles tatlo [Southern Bicol Peninsula, Luzon Island; Siler et al., in press c] (3)

LUZON ISLAND: SORSOGON PROVINCE: *Municipality of Irosin*: PNM (Holotype) 9764; Barangay San Roque, Mt. Bulusan National Park: TNHC (Paratype) 62469, PNM (Paratype) 4856.