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Biol. Lett. 2010 **6**, 654-658 first published online 7 April 2010
doi: 10.1098/rsbl.2010.0119

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A spectacular new Philippine monitor lizard reveals a hidden biogeographic boundary and a novel flagship species for conservation

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As humans continue to explore the last uncharted regions of the planet, discoveries of previously unknown species of large vertebrates have become infrequent. Here, we report on the discovery of a spectacular new species of giant, secretive, frugivorous, forest monitor lizard (Genus: *Varanus*) from the forests of the northern Philippines. Using data from morphology and mitochondrial and nuclear DNA sequences, we demonstrate the taxonomic distinctiveness of this new 2 m long species and provide insight into its historical biogeography and systematic affinities. Our molecular phylogenetic analyses indicate that the new species is closely related to *Varanus olivaceus* (from southern Luzon and nearby islands), but it differs from this and other varanids with respect to characteristics of scalation, colour pattern, body size, anatomy of the reproductive organs and genetic divergence. The new species appears to be restricted to forests of the central and northern Sierra Madre mountain range; it is separated from the range of *V. olivaceus* by a more than 150 km stretch that includes at least three low-elevation river valley barriers to dispersal. This discovery identifies a seldom-perceived biogeographic boundary and emphasizes the need for continued biodiversity research in the megadiverse conservation hotspot of the Philippines. It is anticipated that the new species will serve as an important flagship species for conservation efforts aimed at preserving the remaining forests of northern Luzon.

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2010.0119> or via <http://rsbl.royalsocietypublishing.org>.

Received 7 February 2010
Accepted 15 March 2010

Keywords: biodiversity; conservation hotspots; flagship species; frugivory; Sierra Madre; *Varanus*

1. INTRODUCTION

Although the description of biodiversity is a continual process, discovery of previously undocumented, large-bodied and conspicuous new species of vertebrates is now a rare occurrence. As human populations increase, forested regions of the planet are charted, and large intact tracks of forest continue to shrink or become fragmented. With increasing exploration, fewer large-bodied vertebrates remain to be discovered. Exceptions to the asymptotic decline in the discovery of large new species of vertebrates include the discovery of the Vietnamese forest bovid *Pseudoryx nghetinhensis* (Dung *et al.* 1993) and the discovery of a new African primate (*Rungwecebus kipunji*; Davenport *et al.* 2006).

Monitor lizards occur throughout the Old World tropics (Bennett 1998; Pianka *et al.* 2004). They vary greatly in habitat (arid to tropical) and body size (*V. brevicauda*: less than 25 cm, 8–17 g versus *V. komodoensis*: greater than 3 m, 70–90 kg) and include the most massive lizards in the world (Komodo dragons). Fewer than 10 new species of monitor lizard have been described in recent years, and most have been small-bodied forms (Harvey & Barker 1998; Pianka *et al.* 2004; Ziegler *et al.* 2007). Philippine lizards of the family *Varanidae* include five species (Taylor 1922; Gaulke 1992): the water monitors (*Varanus cumingi*, *V. marmoratus*, and *V. nuchalis*), and the arboreal, frugivorous monitors (*Varanus olivaceus* and *V. mabitang*). *Varanus olivaceus* and *V. mabitang*, the world's only two frugivorous species, are rare and difficult to study (Auffenberg 1988; Gaulke *et al.* 2005). Shy and reclusive, *V. olivaceus* is known from lowland forests of southeastern Luzon and the smaller eastern islands of Polillo and Catanduanes (figure 1). *Varanus mabitang* is a poorly known species, endemic to Panay Island (Gaulke & Curio 2001). Both species are considered heavily threatened, primarily due to habitat destruction.

Because large species are conspicuous components of terrestrial faunas, they are usually well known to people. Here we describe a surprising finding from recent biodiversity studies: a giant (2 m body length), strikingly distinct, brightly coloured monitor lizard from the unexplored forests of northern Luzon Island.

2. MATERIAL AND METHODS

Data were scored from fluid-preserved specimens deposited in US and Philippine collections and measurements were taken following Auffenberg (1988) and Gaulke & Curio (2001). We sequenced the mitochondrial *16S-ND1* fragments and nuclear *PRLR*, *DNAH3*, *SNCAIP* genes and incorporated these data into a previously published *Varanus* phylogenetic dataset. We subjected the combined data to phylogenetic analyses using parsimony, maximum likelihood and Bayesian methods (figure 1). The description of the new species is based on diagnostic characters of morphology. Full details of analyses and results are included in the electronic supplementary material.

3. SYSTEMATICS

Varanus bitatawa sp. nov.

(a) Etymology

The specific epithet is derived from *bitatawa*, the Agta tribespeople's common name for the new species.

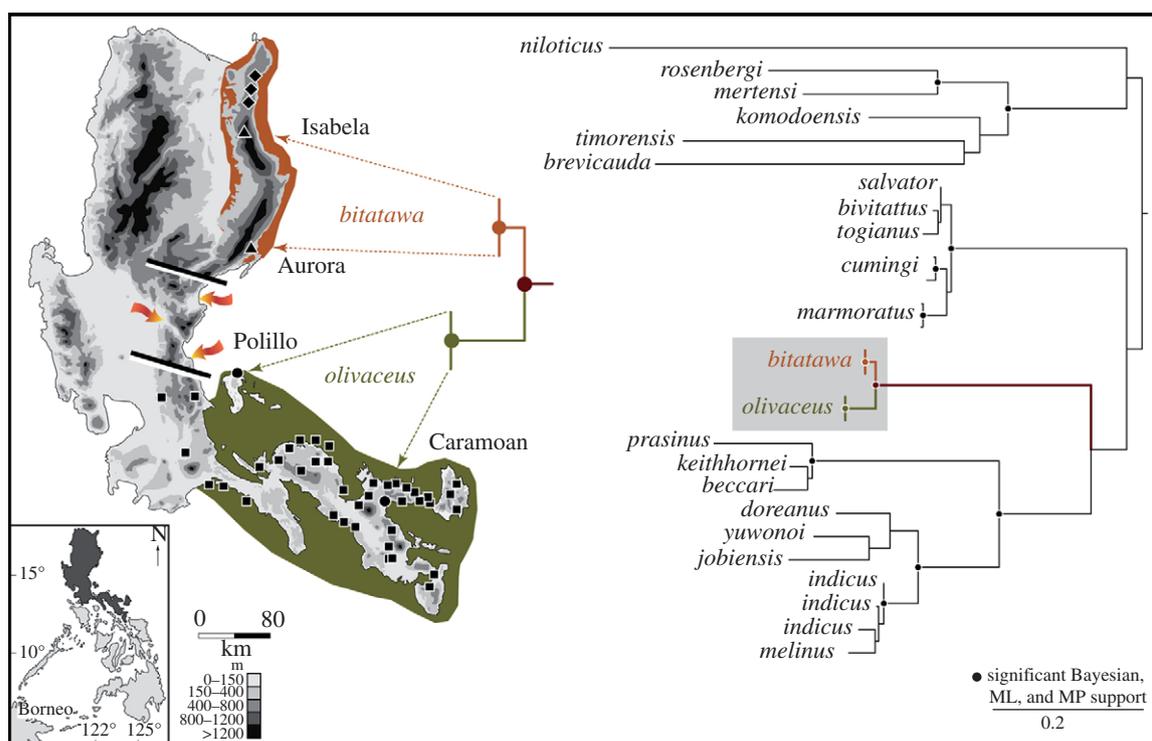


Figure 1. Distribution and phylogenetic relationships of *V. bitatawa*, n. sp. and its closest relative, *V. olivaceus*. Arrows indicate three river valleys constituting the Mid-Sierra Filter Zone (black lines bisecting the Sierra Madre). The phylogenetic tree is derived from a combined, partitioned, RAxML ML analysis of mitochondrial (*16S-ND1*) and nuclear (*PRLR*, *DNAH3*, *SNCAIP*) genes ($-\ln L$ 7336.421498). Filled triangles, *bitatawa*; filled diamonds, *bitatawa* (previous photographic records); filled circles, *olivaceus* (this study); filled squares, *olivaceus* (Affenberg 1988).

(b) Holotype and paratypes

Holotype: PNM 9719 (formerly KU 320000; LJW field number 071), adult male, salvaged from hunter at the base of the San Ildefonso Peninsula, Sitio Casapispan, Barangay Casiguran, Municipality of Casiguran, Aurora Province, Luzon Island, Philippines (16.286667° N, 122.185833° E, WGS-84; 1 m above sea level), 29 June 2009. Paratypes: KU 322188 (ACD 2796), juvenile male, from Sitio Dunoy, Barangay Dibuluan, Municipality of San Mariano, Isabela Province, Luzon Island, Philippines (200 m above sea level), April 2006; collected by A. C. Diesmos; PNM 9008, female, collected from the same locality on 16 July 2005 by R. Dugay.

(c) Diagnosis

Varanus bitatawa differs from congeners by the combination of (i) large, robust body (and related scalation differences: table 1), (ii) contrasting black and golden yellow dorsal coloration, (iii) dark gular coloration in juveniles, (iv) anteriorly directed, slit-like external nares, and (v) multiple characters of hemipeneal morphology (figure 2; electronic supplementary material). Additionally, the new species is distinguished from congeners by marked divergence in mitochondrial and nuclear gene sequences and differs from its closest relative, *V. olivaceus*, by genetic divergence in excess of the divergence between other Asian species (figure 1 and table 2; electronic supplementary material, figure S2 and table S3). Detailed comparisons are provided in the electronic supplementary material.

(d) Brief description of holotype

A large-bodied species of *Varanus*, holotype snout-vent length (SVL) 766 mm, tail 1036; head robust, length 124.9, width 73, maximum depth 66.8, depth at eye 45.4; snout length 65.7; snout rounded anteriorly; narial openings slit-like, surrounded by an elevated protuberance; cranial table squarish, wider than long, with hypertrophied adductor musculature; head scales heterogeneous; supralabials 58; infralabials 66, decreasing in size to rictus; nuchals large, polygonal, decreasing in size laterally; scales arranged in 56 semi-regular rows from the posterior margin of the cranial table to forelimb insertion; scales of the dorsal trunk smaller than those on the head, polygonal; scales in 94 rows in the axilla-groin region; paravertebrals from the gular fold to the anterior edge of hindlimb insertion 127; axilla-groin distance 272 mm; limb scales large, polygonal, slightly convex, decreasing in size distally; forelimb and hindlimb 164 and 198 mm respectively; digits terminating in robust, recurved claws; scales of manus and pes squarish, smaller than those of trunk; supradigitals ovalar; caudals rectangular, in semi-regular rows; scales around the base of the tail 101, around the tail one-third from the base, 59; double keel of paired, raised rectangular scales originating 110 mm from the base and extending posteriorly to tail terminus; ventrals less variable than dorsals; ventral nuchals small, increasing in size and becoming squarish through the mid-nuchal region, then decreasing in size anterior to the gular fold; scales around the neck anterior to the gular fold 145; gulars in 68 rows between the gular



Figure 2. Dorsal views of bodies, lateral views of heads and close-ups of hemipenes of (a) *V. bitatawa* (PNM 9719) and (b) *V. olivaceus* (KU 322187). Letters indicate: A, primary apical hemibaculum horn; B, secondary apical hemibaculum horn; and C, presence or absence of an evagination at the base of the primary hemibaculum.

Table 1. Characters distinguishing *V. bitatawa* from close relatives. Ranges for snout–vent and tail length of *V. olivaceus* represent our data combined with Auffenberg (1988; 90 specimens) and D. Bennett (2009, unpublished; 28 specimens); dashes, missing data. See electronic supplementary material for definitions and discussion.

	<i>bitatawa</i>	<i>olivaceus</i>	<i>mabintang</i>
vouchers	PNM 9719, 9008, KU 322188	KU 322186, 322187	PNM 7272, one released specimen
geographical range	central and northern Sierra Madre, Luzon	Polillo, Catanduanes, southern Luzon	Panay
snout–vent length	766, 490, 613	485–730	527, 640
tail length	1036, 694, 950	749–1025	741, 1110
hindlimb length	198, 112, 138	181, 124	227, —
forelimb length	164, 96, 115	127, 92	188, —
head length	124.9, 91.5, 122	127, 97.4	89.9, —
head width	73, 52.7, 64	76.9, 54.5	43.9, —
head depth at eye	45.4, 34.6, —	56.7, 40.7	32.9, —
maximum head depth	66.8, 41.4, 60	68.9, 49.9	35, —
eye–snout length	66.8, 47.7, 61	65.4, 49.6	49.1, —
eye–mid-nares length	39.7, 26.4, —	36.6, 25.6	27.2, —
Mid-nares–snout length	26.4, 18.5, —	27.9, 21.7	21.9, —
snout length/head length	0.54, 0.52, 0.50	0.52, 0.52	0.55, —
tympanum–eye length	37.8, 29.2, —	45.1, 30.5	42.3, —
rictus–rictus scales	69, 78, —	84, 69	70, —
scales around base of tail	101, 99, 103	109, 113	113, —
scales around tail one-third from base	59, 62, 49	74, 58	86, —
midbody scales	193, 185, 175	193, 193	212, —
ventrals (gular fold–hindlimb insertion)	107, 110, 106	117, 110	124, —
dorsals (paravertebrals)	127, 113, 116	108, 115	138, —
scales around neck	145, 151, 133	161, 148	160, —
gulars (chin–gular fold)	120, 109, 107	106, 106	117, —
supralabials	58, 54, 62	61, 64	—, —
infralabials	66, 59, 61	70, 62	68, —
mid-nares–snout tip/snout length	0.40, 0.39, —	0.43, 0.44	0.45, —
head length/depth	2.8, 2.6, —	2.2, 2.4	2.7, —

Table 2. Uncorrected mitochondrial DNA sequence divergence (%) in *V. bitatawa*, *V. olivaceus* and three clades of *Varanus* (figure 1). Percentages on the diagonal represent intraspecific (or within clade) genetic diversity. See electronic supplementary material for nuclear gene divergences.

	<i>bitatawa</i>	<i>olivaceus</i>	clade 1 (<i>prasinus</i> clade)	clade 2 (<i>sakvator</i> clade)	clade 3 (<i>niloticus</i> clade)
<i>bitatawa</i>	0				
<i>olivaceus</i>	4.6	0			
clade 1	18.4–20.5	19.8–21.1	14.9–20.7		
clade 2	17.1–18.4	17.0–18.4	16.1–20.9	1.5–5	
clade 3	18.4–19.3	18.0–20.8	17.3–24.1	14.4–19.5	9.4–20

fold and the margin of the tympanum; ventrals posterior to the gular fold heterogeneous, larger than nuchals; scales in the scapular region polygonal, increasing in size posteriorly; midbody scales 193; ventrals from the gular fold to the anterior margin of hindlimb insertion 107; total ventrals 227; precloacals irregular, round to polygonal, decreasing in size distally through limbs; subcaudals small, heterogeneous, increasing in size posterior to the hemipenial bulge. Dorsal ground coloration black, accentuated with bright golden yellow in life; dorsum covered with golden yellow spots and flecks; head speckled yellow on black; forelimbs more yellow than black; trunk traversed by four distinct rows of yellow ocelli; hindlimbs

black with large, distinct, yellow spots; tail barred, contrasting black and yellow. Detailed description of the type series is provided in the electronic supplementary material.

4. DISCUSSION

Discovery of a highly distinctive new species of monitor lizard from heavily populated and highly deforested Luzon Island comes as an unprecedented surprise. How could such a large-bodied (2 m total length) monitor lizard have escaped the notice of the many biologists that have worked in the northern Philippines? We suspect a combination of factors

have contributed to this astonishing set of circumstances. Despite being identified as a conservation priority (Mallari & Jensen 1993; van Weerd *et al.* 2004), surprisingly few surveys have characterized the herpetological diversity of the forests of Sierra Madre (but see Brown *et al.* 2000a, 2007). Additionally, if the new species is similar in habitat preferences and behaviour to its closest relative (*V. olivaceus*), *V. bitatawa* is most likely a highly secretive species that may never leave forests to traverse open areas (D. Bennett 2009, unpublished data). Despite escaping recognition by biologists, the new species is well known to resident Agta and Ilongot tribespeople who rely on it as a major source of protein (M. R. Duya & E. L. B. Rico 2004, unpublished data).

(a) Biogeography

The geographical gap between the new species and its sister taxon *V. olivaceus*, together with our new phylogenetic data, is key to our interpretation of the biogeographic and evolutionary history of these taxa. In hindsight, it is not surprising that the forested Sierra Madre Range supports an evolutionarily distinct lineage of monitor lizard. The northern and southern portions of the mountain range are geologically isolated (Auffenberg 1988; Hall 2002; Yumul *et al.* 2009) and are now separated by at least three non-forested river valleys representing barriers to dispersal (figure 1). This series of topological, ecological and atmospheric barriers to dispersal has resulted in a more than 150 km gap, isolating the northern portions of the range of *V. olivaceus* from the southern portions of the range of *V. bitatawa* (figure 1). Our hypothesized history of isolation of these new species is entirely consistent with (i) the allopatric distributions of *V. bitatawa* and *V. olivaceus* on either side of these three low-elevation valleys (figure 1), (ii) the high levels of genetic divergence and sister relationship between the two taxa (figure 1 and table 2), and (iii) the concomitant morphological differentiation between the two species (figure 2; electronic supplementary material). The discovery of the new species identifies a disjunct distribution pattern that may embody a more general, and under appreciated, biogeographic phenomenon affecting other, unrelated lineages. If low-elevation valleys are barriers to gene flow in montane forest species endemic to the separate geological components of Luzon, we might expect to see additional north-south differentiation in other lineages, sister species pairs or closely related higher taxa. Although available data are few, recent findings suggest that the Mid-Sierra Filter Zone detected here may have similarly affected other lineages (Brown *et al.* 2000a,b, 2007) and may therefore have a more general biogeographic significance.

(b) Conservation

Our unexpected finding of a highly conspicuous new species of a large vertebrate that has escaped discovery in the forests of the northern Luzon emphasizes the unexplored nature of the Philippines. The discovery of a new *Varanus*, an anticipated flagship species for conservation, adds to the recognition of the Philippines

as a global conservation hotspot and a regional superpower of biodiversity (Brown & Diesmos 2009).

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Electronic Supplemental Material

There are five sections to the electronic supplemental material:

S1. Materials and Methods

S2. Supplemental Results and Discussion

- (a) *Field observations*
- (b) *Description of holotype*
- (c) *Morphological variation*
- (d) *Colouration*
- (e) *Comparisons*
- (f) *Hemipeneal Morphology*
- (g) *Ecology, natural history, and diet*
- (h) *Gastrointestinal morphology*
- (i) *Distribution*
- (j) *Molecular variation and phylogeny*
- (k) *Biogeography*

S3. Acknowledgements

S4. Supplemental References

S5. Supplemental Tables

- (a) *Supplemental Table 1*
- (b) *Supplemental Table 2*
- (c) *Supplemental Table 3*

S1. MATERIALS AND METHODS

Data were scored from specimens in U.S. and Philippine collections and from high-resolution photos when specimens were captured and released. Sex was determined by examination of reproductive organs and measurements (to the nearest 0.1 mm) follow character definitions by Auffenberg (1988), Böhme (1988, 1991, 1995), Harvey and Barker (1998), Gaulke and Curio (2001), and Koch et al. (2007). Hemipenes of *V. olivaceus* (KU 322187, Polillo Island) and the holotype of *V. bitatawa* (PNM 9719, Aurora Prov., Luzon Island) were removed, everted, cleaned, retractor muscles removed, stained for 24 hours in an alizarin red solution, and then inflated with blue paraffin; and descriptive morphology follows Branch (1982), Shea and Reddacliff (1986), Böhme (1988, 1991, 1995) and Ziegler *et al.* (2007).

Molecular data were derived from all available genetic samples, including two sites at the extremes of the distribution of *Varanus olivaceus* and two geographically distant sites within the presumed range of the new species (Fig. 1). *Varanus mabitang* was not included because tissues for this species are unavailable. Outgroup sampling was selected from species-level molecular phylogenetic estimates (Ast, 2001), and includes new samples of *V. marmoratus* (Luzon island, Philippines) and *V. cumingi* (Mindanao Island, Philippines). For all samples, fragments of the 16S ribosomal RNA (16S) and NADH Dehydrogenase Subunit 1 (ND1) were sequenced, including the interverning transfer RNA (tRNA^{leu}), following the methods of Ast (2001). Additionally we sequenced the PRLR, DNAH3, and SNCAIP nuclear protein-coding loci (Townsend et al., 2008) for four samples including exemplars of the new species, *V. olivaceus*, *V. marmoratus*, and *V. cumingi*. Genomic DNA was extracted from tissues

following the guanidine thiocyanate method of Esselstyn *et al.* (2008). All sequences were deposited in GenBank under accession numbers provided in Supplemental Table 1. Primers used for amplifying mitochondrial gene sequences include: 16S–ND1 (L3827, 5'–GCAATCCAGGTCGGTTTCTATC–3' and H4644vs2, 5'–AATGGGGCTCGGTTGGTTTC–3'); PRLR (PRLR.f1, 5'–GACARYGARGACCAGCAACTRATGCC–3' and PRLR.r3, 5'–GACYTTGTGRACCTCYACRTAATCCAT–3'); DNAH3 (DNAH3.f1, 5'–GGTAAAATGATAGAAGAYTACTG–3' and DNAH3.r6, 5'–CTKGAGTTRGAHACAATKATGCCAT–3'); and SNCAIP (SNCAIP.f10, 5'–CGCCAGYTGYTGGGRAARGAWAT–3' and SNCAIP.r13, 5'–GGWGAYTTGAGDGCCTTTRGGRCT–3'). We used the following thermal profiles for the 16S–ND1 region: 4 min at 94°, followed by 35 cycles of 94° for 30 sec, 58° for 30 sec, and 72° for 1 min 30 sec, and a final extension phase at 72° for 7 min. For the nuclear loci, the thermal profile was identical to the profile for 16S–ND1, with the exception of having an annealing temperature of 55°. Amplified products were visualized on 1.5% agarose gels. PCR products were purified with 1 μ L of a 20% dilution of ExoSAP-IT (US78201, Amersham Biosciences, Piscataway, NJ) 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 Medium (NC9406038, Amersham Biosciences, Piscataway, NJ) in Centri-Sep 96 spin plates (CS-961, Princeton Separations, Princeton, NJ). Purified product was analyzed with an ABI Prism 3130xl Genetic Analyzer (Applied Biosystems). Gene sequence contigs were assembled and edited using Sequencher 4.8 (Gene Codes Corp., Ann Arbor, MI).

Initial sequence alignments were produced in Muscle (Edgar, 2004), and manual adjustments were made in MacClade 4.08 (Maddison and Maddison, 2005). To assess for possible phylogenetic incongruence between the mitochondrial and nuclear data, we inferred the phylogeny for each subset independently using likelihood and Bayesian analyses. Following no observation of statistically significant incongruence between datasets, we decided to conduct separate analyses on each locus, as well as the combined data. Exploratory analyses of the combined dataset of 27 individuals (including 23 lacking nuclear sequences) and the mitochondrial dataset (no missing data) supported identical relationships for the individuals we sequenced for nuclear loci, and we therefore chose to include all available data for subsequent analyses of the concatenated 16S–ND1 + PRLR + DNAH3 + SNCAIP dataset.

Parsimony analyses were conducted in PAUP* 4.0b 10 (Swofford, 1999) for the combined dataset, 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 confidence, 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) for the combined dataset. The dataset was partitioned by 16S fragment, codon position for the protein-coding region of ND1, intervening tRNA (tRNA^{leu}), and by nuclear loci. The Akaike Information Criterion (AIC) as implemented in Modeltest v3.7 (Posada and Crandall, 1998) was used to select the model of nucleotide substitution for each subset (Supplemental Table 2). We ran four independent Metropolis-coupled MCMC analyses, each with four chains and the default heating scheme (temp = 0.2). All analyses

were run for 20 million generations, sampling every 1000 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). All samples showed patterns consistent with stationarity after 4 million generations, hence the first 20% of samples were discarded as burn-in.

Partitioned maximum likelihood (ML) analyses were conducted in RAxMLHPC v7.0 (Stamatakis, 2006) for the combined dataset under the same partitioning strategy as for Bayesian analysis. The more complex model (GTR + I + 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 1000 bootstrap pseudoreplicates employing the rapid bootstrapping algorithm (Stamatakis et al., 2008).

S2. SUPPLEMENTAL RESULTS AND DISCUSSION

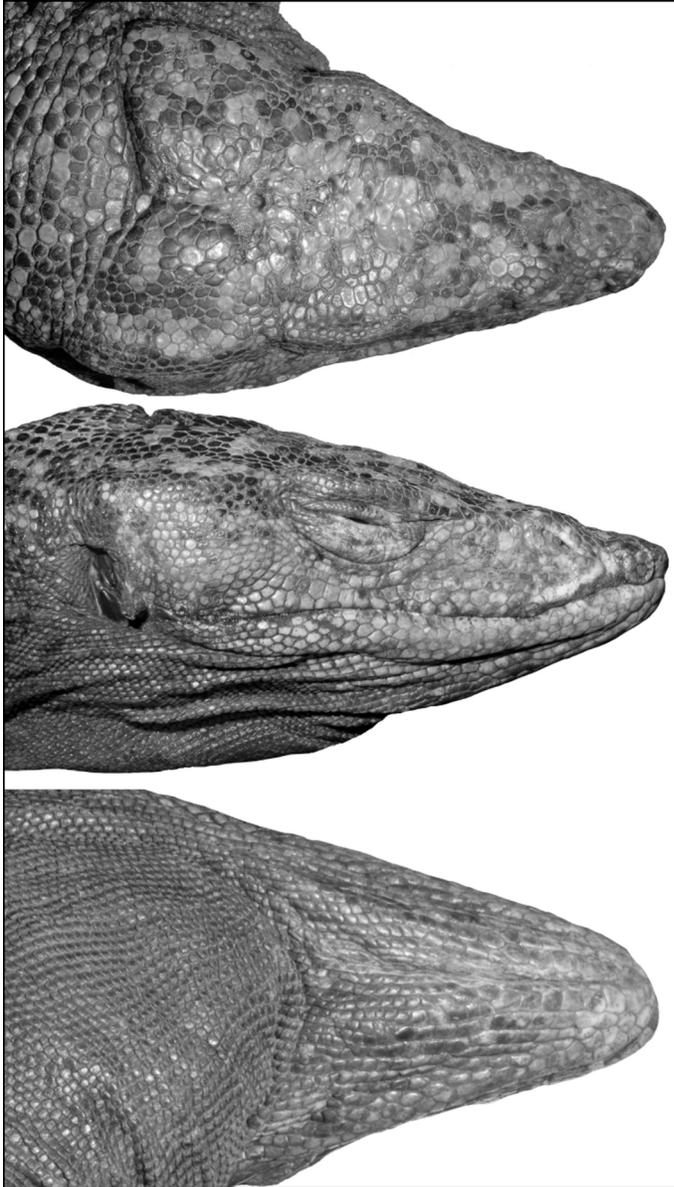
(a) *Field observations*

As early as 2001, evidence of a phenotypically distinct, arboreal, large-bodied, monitor lizard appeared in the form of photographed specimens circulated throughout the Philippine conservation community. The first photograph that we are aware of featured a single specimen, trapped by a local hunter and subsequently consumed by residents. Agta hunters interviewed by us in Isabela Province indicated that the local name for the species is "*bitatawa*;" in Aurora Province, Ilongot tribes' peoples refer to the new species as "*butikaw*." Subsequent surveys along the Sierra Madre range along the east coast of Luzon Island confirmed the presence of the species at numerous localities (E. L. Rico, R. Duya, L. Duya, N. A. Bartolome, U. Carestia, T. Minter, and J. Guerrero, RD, MVW, and ACD, unpublished data, 2004). In July 2005 RD collected a specimen at Sitio Dunoy, Barangay Dibulan, San Mariano, Isabela Province that was deposited at the National Museum of the Philippines (PNM 8009). Based on information from local hunters he concluded that the animal was very rarely seen. In interviews of Agta hunters, more than 50% of respondents claimed the "*bitatawa*" was better tasting than the "*biawak*" (*V. marmoratus*).

(b) *Description of holotype*

Adult male, SVL 766.0 (all measurements in mm); tail 1036.0; head robust, head length 124.9, width 73.0, and maximum depth 66.8 (depth at eye 38.8); snout length 66.8, 55.5% head length; snout rounded anteriorly; narial openings 9.0, slit-like, posteriorly elevated, encircled by 11L/12R small polygonal scales; area surrounding narial opening elevated, forming distinct protuberance along canthal ridge; cranial table squarish, wider than long, with hypertrophied masseter muscle complexes enlarged and triangular in dorsal aspect.

Head scales polygonal (Supplemental Fig. 1), large, and generally homogenous in size; ocular in four semi-regular rows anterior to eye, extending posteriorly to margin of orbit; lateral head scales slightly smaller than those of dorsum, polygonal, less homogenous dorsals; dorsal and lateral head scales smooth, with shallow sutures between; supralabials 58, slightly



Supplemental Figure 1.—Details of head scalation in the adult male holotype of *Varanus bitatawa* (PNM 9719) in dorsal (above), lateral (middle) and ventral (below) views.

smaller than lateral head scales; infralabials 66, similar in size and shape, both series decreasing in size to rictus; nuchals large, polygonal, decreasing in size and becoming suboval to squarish laterally, and posteriorly in nuchal region; sutures between scales wider in nuchal region than on head; scales arranged in 56 semi-regular rows from posterior margin of cranial table to forelimb insertion; dorsal trunk scales slightly smaller than those of head, polygonal, becoming smaller, squarish, and more convex laterally; scales in 94 semi-regular rows through axilla–groin region; longitudinal dorsal scales (paravertebrals) 127; axilla–groin distance 272; limb scales large, polygonal, slightly convex, and decreasing in size distally; fore- and hindlimb 164 and 198 mm respectively, 21.4% and 25.8% snout–vent length, 68.8 and 81.0 diameter at insertion; digits terminating in robust, recurved claws; scales on limbs in semi-regular rows; scales of manus and pes smaller, squarish dorsally; supradigitals ovular; caudals rectangular, in semi-regular rows;

smaller than lateral head scales; infralabials 66, similar in size and shape, both series decreasing in size to rictus; nuchals large, polygonal, decreasing in size and becoming suboval to squarish laterally, and posteriorly in nuchal region; sutures between scales wider in nuchal region than on head; scales arranged in 56 semi-regular rows from posterior margin of cranial table to forelimb insertion; dorsal trunk scales slightly smaller than those of head, polygonal, becoming smaller, squarish, and more convex laterally; scales in 94 semi-regular rows through axilla–groin region; longitudinal dorsal scales (paravertebrals) 127; axilla–groin distance 272; limb scales large, polygonal, slightly convex, and decreasing in size distally; fore- and hindlimb 164 and 198 mm respectively, 21.4% and 25.8% snout–vent length, 68.8 and 81.0 diameter at insertion; digits terminating in robust, recurved claws; scales on limbs in semi-regular rows; scales of manus and pes smaller, squarish dorsally; supradigitals ovular; caudals rectangular, in semi-regular rows;

Ventrals less variable than dorsals; ventral head and nuchal scales

heterogenous; scales small and granular anteriorly, increasing in size and becoming squarish through mid-nuchal region, then decreasing in size anterior to gular fold; scales around

neck anterior to gular fold 145, mid-gular 142; gular scales in 68 semi-regular transverse rows between gular fold and margin of tympanum; total gulars from tip of chin to gular fold, 120; trunk scales posterior to gular fold heterogenous, larger than those of nuchal region; scales in scapular region polygonal, in irregular rows, size increasing posteriorly; midbody scales in 193 semiregular rows around trunk; ventrals from gular fold to anterior margin of hindlimb

insertion 107; total ventrals from snout to hind limb insertion 227; precloacals irregular, round to polygonal slightly convex, decreasing in size distally through limbs; subcaudals heterogenous, small and granular anteriorly, increasing in size and present in semi-regular transverse rows of rectangular scales posterior to hemipeneal bulge; scales around the base of the tail 101, at one third distance from the base 59; two rows of enlarged keels (raised rectangular scales) originating 110 mm from tail base and extending posteriorly to tail terminus; terminus of tail detached.

(c) Morphological variation

Summaries of univariate morphological variation between the holotype and paratypes are presented in Table 1.

(d) Colouration

Information on variation in color pattern (Fig. 2) is limited but our description is based on the adult holotype (PNM 9719), a juvenile paratype (KU 322188), a small adult male (PNM 9008), and photographic vouchers of three additional specimens (captured and released). In general, dorsal surfaces of the new species consist of a brightly contrasting pattern of black and bright yellow or golden yellow. Most specimens are covered with round golden yellow spots and a fine speckling of contrasting gold flecks on a black background. The head is speckled yellow and black, the forelimbs have a noticeably greater concentration of golden yellow pigment, the body is traversed by 3 or 4 bold golden yellow, round, spot rows, the hindlimbs are black with large, distinct, round yellow spots, and the tail is barred with contrasting colors of black and yellow.

Dorsal ground coloration black; head and neck with bright gold blotches enclosing 1–8 scales; density of gold scales increases on anterolateral portions of head; trunk with series of transverse bands of variably-sized yellow to gold ocelli; at mid-body ocelli rows interspersed with smaller irregular blotches between rows (Fig. 2); proximal forelimbs black with transverse ocelli bands, becoming near uniform golden yellow distally; manus and digits primarily golden yellow, with irregular aggregations of black scales; hind-limbs similar to forelimbs, but with more regular arrangement of six transverse gold ocelli bands; digits with 1–4 golden yellow bands; digits with single enlarged yellow terminal scale sheathing claw; tail with 11 regular golden yellow bands from insertion to terminus, with alternating black bands containing small irregular yellow blotches; ventral coloration less variable, bright yellow; gular and nuchal region with darker melanin, resulting in an overall darker appearance (Fig. 2); ventral surfaces of forelimbs yellow; palmar surface of manus black; hind-limbs similar to forelimbs; plantar surface of pes black, except for a 1–5 terminal rows of yellow; ventral surface of tail uniform yellow. Tongue pinkish gray; iris brick red.

The paratypes exhibit the same general color pattern as the holotype but differ by slight color differences. The juvenile paratype (KU 322188) has a nearly black gular region with 3 gray chevrons. Additionally, this specimen differs from the holotype by a reduction in the small aggregations of golden yellow spots overlaying the black portions of the dorsal pattern. The adult paratype (PNM 9008) has anterior regions of the body, neck and head, almost completely black.

In preservative, golden yellow coloration fades to pale olive. Color pattern (comparing the type series to photographs of captured and released specimens) is fairly consistent, with some specimens exhibiting greater of lesser amounts of yellow. Color of the juvenile

paratype and photographs of some released specimens indicate that juveniles can have a greater amount of yellow body coloration than black. There is little or no ontogenetic variation in pattern in the new species which, unlike *V. olivaceus*, does not appear to fade in color pattern with age.

(e) Comparisons

The holotype of *V. bitatawa* is distinguished from the largest specimens of *V. olivaceus* by a more robust body, with thicker, more robust limbs (Fig. 2); maximum adult snout–vent length 766.0 mm, and tail length 1,036.5 mm (vs. 730.0, 1,025.0, respectively); maximum fore- and hindlimb lengths 164.1 mm and 198.7 mm (vs. 127.0 and 181.3, respectively). Additional distinguishing characteristics include a less robust head: maximum length to depth ratio 2.8 (vs. 2.4 in *V. olivaceus*); maximum nares–snout distance/snout length 0.39 (vs. 0.45); a shorter maximum tympanum–eye distance (37.8 vs. 45.1 mm); lower maximum scale count around the base of the tail (101 vs. 113); and a higher maximum number of ventrals anterior to gular fold (120 vs. 106). Distinguishing color characteristics include dorsal ground color black, with bright gold rows of transverse ocelli (vs. gray ground color with brown to black transverse bands); limbs black with gold ocelli (vs. gray to black dorsum overlain with lighter random spots); juvenile gular color gray with black chevrons (vs. chevrons absent); and brightly colored, highly contrasting color pattern in juveniles and adults (vs. bright, contrasting color pattern faded in adults of *V. olivaceus*). Hemipeneal characters distinguishing *V. bitatawa* from *V. olivaceus* include an arcing, broad, primary apical hemibaculum horn (vs. hemibaculum horn flat, squarish); the presence of a short, blunt, secondary apical hemibaculum horn (vs. secondary horn sharp and pointed); and the presence (vs. absence) of a distinct evagination at the base of the primary hemibaculum (Fig. 2).

The holotype of new species is distinguished from the only adult specimens of *V. mabitang* (PNM 7272) by a considerably larger body size: mass 9 kg, SVL 766.0 mm (vs. 5.8 kg, 640 respectively); a shorter tail (1,036.5 mm vs. 1,110); shorter fore- and hindlimbs (164.1 and 198.7 mm, vs. 188.0 and 227.0 respectively); a more robust head, length to depth ratio 2.8 (vs. 2.7); narial position closer to the eye (vs. further from eye): nares–snout distance/snout length 0.39 (vs. 0.45); shorter tympanum–eye distance (37.8 vs. 42.3); fewer scales around the base of the tail (101 vs. 113); fewer midbody scale rows (193 vs. 212); fewer ventrals from gular fold to hindlimb insertion (107 vs. 124), fewer scales around the neck (120 vs 117), fewer gulars from the chin to the gular fold (145 vs. 160); dorsal trunk and limb coloration patterned black and yellow (vs. nearly uniform black); gular region patterned (vs. uniform dark gray to black).

For brevity, we do not exhaustively compare the new species to all remaining 69 species of *Varanus*. Rather, we emphasize that the new species can be distinguished from the non-frugivorous species by the same diagnostic characters used for more than a century and a half to distinguish *V. olivaceus* from other species of *Varanus* (Hallowell, 1857; Mertens, 1942; Auffenber, 1988; Bennett, 1998; Gaulke and Curio, 2002; Pianka et al., 2004).

(f) Hemipeneal Morphology

The everted hemipenis lengths of *Varanus bitatawa* and *V. olivaceus* are 63.9 and 68.1 mm respectively. Both organs (Fig. 2) are robust, differentiated into a cylindrical proximal section and a lobed, distal portion that consists of a larger primary lobe, and a smaller secondary lobe. Each lobe terminates in an ossified apical hemibaculum horn. The sulcal surface (Fig. 2) has

two distinct structures in both species: the apical hemibaculum horn, at the terminus of each lobe, and a secondary out-pocketing present proximally on the primary lobe. The sulcus spermaticus of both species is basally oblique, extending distally along the sulcal surface and terminating at the bifurcation of lobes. The sulcus spermaticus is generally straight in both species, although that of *V. bitatawa* curves away from the primary hemibaculum and that of *V. olivaceus* curves towards the primary hemibaculum. The larger, primary hemibaculum of *V. olivaceus* is terminally square, while that of *V. bitatawa* is arced, slightly concave, and nearly twice the thickness (Fig. 2). The secondary hemibaculum of *V. olivaceus* is long and conical, while that of *V. bitatawa* is significantly shorter, and cylindrical. The proximal evagination of the primary lobe has a slightly rounded protrusion in *V. olivaceus*, but a distinct, elongate, near-conical structure in *V. bitatawa*. The sulcus of *V. bitatawa* is deeper, and completely enclosed distally by the inflated lobes of the hemipenis, while that of *V. olivaceus* is shallow and barely enclosed distally, although this may be an artifact of preservation (Fig. 2). In both species, the entire hemipenis is ornamented with transverse paraphasma, or flounces, on the asulcal surface. The primary lobes of both species are adorned with eight paraphasman rows, while the secondary lobes have ten (Fig. 2). The lobes share four rows of paraphasma on the distal portion of the base, before the bifurcation of the lobes. The distal paraphasma are separated by a shallow sulcus spermaticus in *V. olivaceus*, versus a deep groove in *V. bitatawa*. The *V. bitatawa* hemipeneal structures described above are evident in both the paraffin-prepared holotype hemipenes and in the ethanol preserved everted hemipenes of the juvenile paratype (KU 322188), suggesting that the diagnostic character differences discussed here are shared by members of the new species and are not artifacts of preservation.

Due to a lack of adult female specimens, we are unable to comment on the morphology of reproductive structures in female *Varanus bitatawa*. Given the similarity between hemipeneal morphology of *V. bitatawa* and *V. olivaceus*, it is likely that the homologous structures found in females will share the same level of similarity (and perhaps difference).

(g) Ecology, natural history, and diet

Little is known about the specific habits and ecology of *Varanus bitatawa*. All specimens of the new species were collected or observed deep within or on the edges of large, forested regions of the Sierra Madre Mountain Range of northeast Luzon. We strongly suspect that the new species is a forest-obligate species (like its relatives *V. olivaceus* and *V. mabitang*) and that it is heavily dependent upon unfragmented forests with sufficient stands of *Pandanus* (apparently a dominant dietary component of all frugivorous monitors). When collected at the end of June 2009 (the end of the east Luzon dry season) the holotype had *Pandanus* drupes and snail shells in its stomach; another specimen (PNM 9008) collected in July 2005 contained 11 *Pandanus* drupes. Dissections of other specimens and scat from animals held temporarily in captivity indicate a diet of *Pandanus*, *Canarium*, and *Ficus* fruits, and snails (E. L. Rico, M. R. Duya, unpublished data, 2004). These findings confirm an ecological affinity with *V. olivaceus*, a species whose diet consists almost entirely of fruit and snails (Auffenberg, 1988 Bennett, 2000). The lower digestive tract of the holotype at the time of preservation was heavily parasitized with nematodes.

(h) *Gastrointestinal morphology*

Our examination of the holotype's stomach and intestine confirm reports by resident hunters on dietary preferences of *Varanus bitatawa*. The digestive tract is anatomically regionalized, with the striations and out-pocketings of the stomach, the intestine anterior to the caecum, the caecum, and the intestine posterior to the caecum. The presence of a caecum and elaborate internal morphology support a conclusion of generally non-carnivorous dietary habits for this species.

(i) *Distribution*

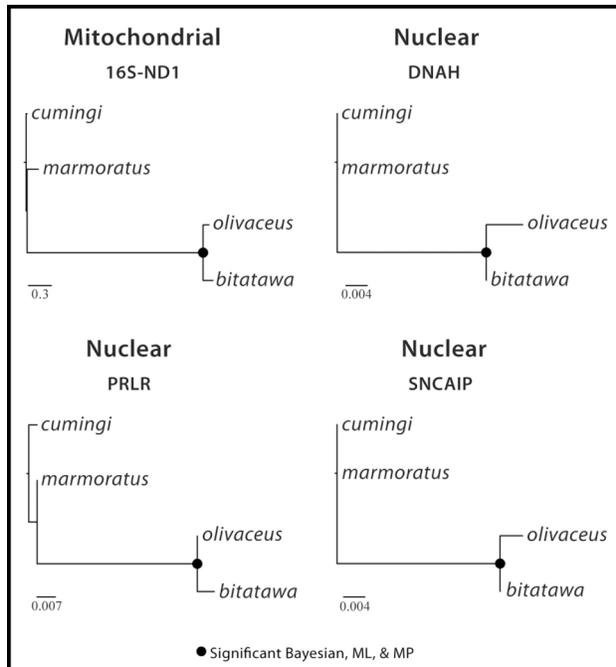
The new species is only known from central and northern portions of the Sierra Madre range, Luzon Island, in pristine to moderately disturbed lowland and mid-elevation forests. Currently, confirmed specimens are known from the type locality of San Ildefonso Peninsula, Sitio Casapsipan, Barangay Casiguran, Municipality of Casiguran, Aurora Province, Luzon Island. The paratypes, were collected in the Lake Dunoy area, Barangay Dibuluan, Municipality of San Mariano, Isabela Province. Sight and/or photographic records include released specimens from (1) Sitio Baguio Point and Sitio Bayan, Barangay Lapi, Municipality of Peñablanca and (2) Sitio Tabugan, Barangay Santa Margarita, Municipality of Baggao (E. L. Rico and M. R. Duya, unpublished data). The forests spanning these localities (Fig. 1) can be assumed to harbor populations of *V. bitatawa*, given the presence of suitable habitat and sufficient densities of fruiting fig, *Pandanus* and *Canarium* trees.

(j) *Molecular variation and phylogeny*

The complete, aligned matrices contain 27 and 4 *Varanus* samples for the mitochondrial and nuclear datasets, respectively. Following initial unrooted analyses, we polarized the tree using samples of *V. niloticus*. Within each dataset, variable and parsimony-informative characters were observed as follows: 69/282 out of 720 for the mitochondrial data, 2/9 out of 387 for PRLR, 1/4 out of 637 for DNAH3, and 1/7 out of 480 for SNCAIP.

In mitochondrial DNA, the new species is 4.6% divergent from its closest relative, *V. olivaceus* (Table 2). Although this variation does not indicate extremely high levels of divergence between the two species, it is as great or greater than most members of the uncontroversial, morphologically distinct (Koch et al., 2007), widely allopatric species of the *V. salvator* group (Fig. 1; Table 2). Thus, we interpret this divergence as lending support to the hypothesis that each lineage represents a separate species. Additionally we found no intraspecific molecular divergence between the two geographically distant samples of the new species (Aurora vs. Isabela Province; Fig. 1) and no intraspecific divergence between *V. olivaceus* separated by > 200 km and the ocean channel between Luzon and Polillo Islands (Fig. 1). Thus, we take the reciprocally monophyletic gene lineages and absence of divergence within putative species (Fig. 1) as additional evidence for the hypothesized coalescence of gene lineages, consistent with the hypothesis of speciation.

All three nuclear genes sequenced by us, although substantially less variable and informative than mitochondrial gene sequences, demonstrated identical patterns of divergence: detectable and consistent divergence between putatively distinct species. Thus each separate nuclear gene, when analyzed alone (Supplemental Fig. 2) lends support from independent gene loci to the observation of molecular divergence between *V. olivaceus* and the new species (Supplemental Table 3).



Supplemental Figure 2—Four-taxon trees pared from separate phylogenetic analyses of each locus: mitochondrial (16S, ND1) and nuclear (PRLR, DNAH3, SNCAIP) genes.

side of the Lingayen-Dingalan fault zone (Defant et al., 1989; Yumul et al., 2003). The coincidence between *Varanus* species distributions and the boundaries of the geological components of Luzon lends support to the hypothesis that the divergence of the two species may be related to geological processes that bisected today's apparently contiguous Sierra Madre Range (Auffenberg, 1988; Hall, 2002; Yumul et al., 2009).

Aside from ancient geological events (Yumul et al., 2003, 2009), purely ecological factors may drive species divergence. As we conceive of it, the Mid-Sierra Filter Zone hypothesis predicts that if low elevation, arid non-forested valleys serve as barriers to dispersal for obligate montane forest species, then patterns of genetic divergence and geographical structure should geographically coincide in unrelated taxa across the proposed barriers subdividing the Sierra Madre Mountain Range (Fig. 1). This hypothesis provides fertile ground for future phylogeographic and conservation genetic studies. If supported with data from other taxa, recognition of the Mid-Sierra Filter Zone may require revision of prevailing conservation and management strategies that currently treat the Sierra Madre as a single, contiguous corridor of relatively uninterrupted habitat. Thus, the “Sierra Madre Corridor” may actually represent two or more sub-centers of endemism, each of which might best be managed separately.

S3. ACKNOWLEDGEMENTS

Support for fieldwork was provided by the University of Kansas, National Museum of the Philippines, National University of Singapore, Rufford Small Grants Foundation (171/07/04 to ACD), North of England Zoological Society, Dallas Zoo, Conservation International, the

Analyses of the combined data (16S-ND1 + PRLR + DNAH3 + SNCAIP) resulted in topologies with mixed bootstrap support (MP and ML) and posterior probabilities (Supplemental Fig. 2). Topologies were congruent across these analyses, and parsimony and likelihood bootstrapping analyses and posterior probability in Bayesian analyses all consistently showed high support for the sister relationship between *Varanus olivaceus* and *V. bitatawa* (Figure 1).

(k) Biogeography

The new species appears to be separated from its closest relative, *V. olivaceus*, by a distributional gap of greater than 150 km. This gap in the known ranges of two species is crossed by no fewer than three proposed barriers to dispersal (Fig. 1: low elevation, arid, nonforested valleys) and also coincides with division of the two main geological components of the Sierra Madre on either

Cagayan Valley Program on Environment and Development, and the U.S. National Science Foundation (DEB 0743491 to RMB). We thank the Philippines' Department of Environment and Natural Resource for facilitating research and export permits and the Local Government Units of Peñablanca, Baggao, Cagayan, Maconacon, and San Mariano for their cooperation. We thank J. Siler, J. Brown, N. Antoque, D. Afan, M. Quilala, H. Garcia, E. Jose, and M. and Adonis Diesmos, and V. and M. Yngente for assistance in the field and D. Blackburn and an anonymous reviewer for critical review. Thanks to L. Trueb for assistance with figures. Liza Duya, N. Bartolome, T. Headland, U. Carestia, S. Telan, W. Oliver, R. Sison, T. Minter, J. Guerrero graciously shared observations and data.

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S5. SUPPLEMENTAL TABLES

(a) *Supplemental Table 1*.—Summary of specimens corresponding to genetic samples included in the study, general locality, and GenBank accession numbers.

Species	Voucher	Locality	Genbank Accession Numbers			
			16S–ND1	PRLR	DNAH3	SNCAIP
<i>Varanus timorensis</i>	WAM R107008	Timor, Semau, Savu	AF407532	–	–	–
<i>Varanus rosenbergi</i>	No voucher	Southern Australia	AY264941	–	–	–
<i>Varanus mertensi</i>	AM R123877	Northern Australia	AF407512	–	–	–
<i>Varanus komodoensis</i>	Zoo specimen	Komodo Island, Indonesia	AF407510	–	–	–
<i>Varanus keithhornei</i>	QM 70792	Northeast Australia	AF407508	–	–	–
<i>Varanus beccari</i>	UMFS 10371	Aru islands, Indonesia	AF407490	–	–	–
<i>Varanus salvator togianus</i>	UMFS 10298	No locality data	AF407524	–	–	–
<i>Varanus salvator bivitatus</i>	UMFS 10670	Java Island, Indonesia	AF407525	–	–	–
<i>Varanus salvator salvator</i>	No voucher	No locality data	AF407526	–	–	–
<i>Varanus prasinus</i>	UMFS 10684	Papua New Guinea	AF407519	–	–	–
<i>Varanus jobiensis</i>	UMMZ 211713	Papua New Guinea	AF407507	–	–	–
<i>Varanus indicus</i>	AM 36431	Northern Australia or New Guinea	AF407506	–	–	–
<i>Varanus indicus</i>	AM 51525	New Guinea	AF407504	–	–	–
<i>Varanus indicus</i>	AM R137997	Indonesia	AF407505	–	–	–
<i>Varanus doreanus</i>	UMFS 10296	Papua New Guinea	AF407493	–	–	–
<i>Varanus melinus</i>	UMFS 10164	Indonesia	AF407511	–	–	–
<i>Varanus yuwonoi</i>	UMMZ 225545	Halmaherra island, Indonesia	AF407535	–	–	–
<i>Varanus niloticus</i>	UMMZ 221377	South Africa or Central Africa	AF407514	–	–	–
<i>Varanus brevicauda</i>	No voucher	Australia	AY264940	–	–	–
<i>Varanus bitatawa</i>	KU 322188	Philippines, Luzon Island, Isabela Province, Municipality of San Mariano, Barangay Dibuluan, Sitio Dunoy	HM017191, HM017196	–	–	–
<i>Varanus bitatawa</i>	PNM 9719	Philippines, Luzon Island, Aurora Province, Municipality of Casiguran, Barangay Casiguran, Sitio Casapsipan,	HM017192, HM017197	HM017205	HM017201	HM017209
<i>Varanus olivaceus</i>	KU 322187	Philippines, Polillo Island, Quezon Province, “East Polillo”	HM017193, HM017198	HM017206	HM017202	HM017210
<i>Varanus olivaceus</i>	KU 322186	Philippines, Luzon Island, Camarines Sur Province, Caramoan Peninsula	AF407515	–	–	–
<i>Varanus marmoratus</i>	KU 322191	Philippines, Occidental Mindoro Province, Lubang Island, Municipality	HM017194, HM017199	HM017207	HM017203	HM017211
<i>Varanus cumingi</i>	KU 321814	Philippines, Zamboanga City Province, Pasonanca Natural Park	HM017195, HM017200	HM017208	HM017204	HM017212

(b) **Supplemental Table 2.**—Models of evolution selected by AIC and applied for partitioned, Bayesian phylogenetic analyses¹.

Partition	AIC Model	Number of Characters
16S	HKY + G	59
tRNA ^{Leu}	GTR + G	74
ND1, 1 st codon position	GTR + G	196
ND1, 2 nd codon position	GTR + I + G	196
ND1, 3 rd codon position	GTR + I + G	195
PRLR	HKY	387
DNAH	GTR	637
SNCAIP	GTR	480

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

(c) **Supplemental Table 3.**—Uncorrected pairwise sequence divergence (%) for nuclear data for *Varanus bitatawa*, *V. olivaceus*, *V. marmoratus*, and *V. cumingi*. In each cell, sequence divergences are shown for PRLR, DNAH3, SNCAIP (top to bottom, respectively), and total nuclear sequence divergence (bolded for emphasis).

	<i>bitatawa</i>	<i>olivaceus</i>	<i>marmoratus</i>	<i>cumingi</i>
<i>bitatawa</i>	—			
	0.3			
<i>olivaceus</i>	0.2	—		
	0.2			
	(0.2)			
	2.8	2.3		
<i>marmoratus</i>	0.6	0.8	—	
	1.5	1.7		
	(1.4)	(1.5)		
	2.8	2.6	0.3	
<i>cumingi</i>	0.6	0.8	0.0	—
	1.5	1.7	0.0	
	(1.5)	(1.5)	(0.1)	