



Integrative taxonomy and phylogeny-based species delimitation of Philippine water monitor lizards (*Varanus salvator* Complex) with descriptions of two new cryptic species

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Abstract

We describe two new species of morphologically cryptic monitor lizards (genus *Varanus*) from the Philippine Archipelago: *Varanus dalubhasa* **sp. nov.** and *V. bangonorum* **sp. nov.** These two distinct evolutionary lineages are members of the *V. salvator* species complex, and historically have been considered conspecific with the widespread, northern Philippine *V. marmoratus*. However, the new species each share closer phylogenetic affinities with *V. nuchalis* (and potentially *V. palawanensis*), than either does to one another or to *V. marmoratus*. Divergent from other recognized species within the *V. salvator* Complex of water monitors by as much as 3.5% pairwise genetic distance, these lineages are also distinguished by unique gular coloration, metrics of body size and scalation, their non-monophyly with “true” *V. marmoratus*, and insular allopatric distributions, suggesting biogeographically distinct and unique evolutionary histories. We compare the new species with the most geographically proximate and phenotypically relevant lineages. Although we show that these new taxa are nearly indistinguishable morphologically from *V. marmoratus*, both species can be readily distinguished from their closest relatives (each’s respective sister taxon, *V. palawanensis* and *V. nuchalis*) by traditional morphological characters. Our findings underscore the high herpetological diversity and biogeographical complexity of vertebrates in the Philippines, and further emphasize the need for detailed study of species-level diversity, mechanisms of reproductive isolation, gene flow, and biologically relevant boundaries between taxa within the *V. salvator* Complex.

Key words: biogeography, cryptic diversity, Southeast Asia, Varanidae, within-island speciation

Introduction

The past decade has seen a paradigm shift in methods of species delimitation. The addition of multi-locus, molecular phylogenies and robust biogeographical reconstructions to the toolkits of systematists and taxonomists has led to rigorous pluralistic species delimitation approaches (derived from multiple sources of data). When coupled with the increased availability of specimen-based information due to continued survey efforts, we find ourselves in the midst of a new generation of biodiversity studies aimed at the identification and description of novel evolutionary lineages in Southeast Asia. A call for integrative approaches to taxonomy has been promoted across disciplines (Wilson 2003, 2004; Dayrat 2005; Vogler & Monaghan 2007; Knapp 2008). Proponents of this perspective suggest that the combined use of classic morphological characters with molecular data, environmental niche information, and biogeographic inference may inform researchers best about the origins and evolutionary trajectories of lineages (Padial *et al.* 2010; Welton *et al.* 2013a).

Many of these studies invoke the Evolutionary Species Concept of Simpson (1961), and Wiley (1978; see also Templeton 1989), and a recent extension of these ideas in the form of the General or “Unified” Species Concept of Mayden (1997, 2002) and de Queiroz (2005, 2007). These applications consider a species a distinctly evolving lineage (ancestor-descendant series of populations) whose members share a common evolutionary trajectory and

who are, for the most part, distinct from other such lineages (Frost & Hillis 1990). For the recognition of evolutionary lineage-based species, use of multiple lines of evidence releases the taxonomist from the pitfalls associated with sole reliance on one set of characters that may have been applied previously to diagnose a given taxon (Padial *et al.* 2010). Rather, integrative approaches to taxonomy may be better served by allowing the investigator to select the most appropriate (e.g., informative, diagnostic, robust) suite of data relevant to the specific organisms under study (Grismer *et al.* 2013; Welton *et al.* 2013a).

Although knowledge of biodiversity is a common motivation behind taxonomic study, conservation urgency and applied management issues add additional need for studies of species boundaries. A growing number of reptile and amphibian taxa are subject to intense anthropogenic pressures (Böhm *et al.* 2013; Wake 2013). Recent estimates indicate that nearly 19% of the world's reptiles (Böhm *et al.* 2013), and perhaps as much as 40% of the world's amphibians (Stuart *et al.* 2004; Wake 2013) are now at risk of extinction. Therefore it is vital that herpetologists assess the diversity within these groups in order to better understand conservation priorities, and more efficiently and effectively implement conservation actions. Recognizing genetically distinct lineages, through either taxonomic revision or their designation as evolutionarily significant units (ESUs), is vital to ensure persistence of these lineages, especially when they are found to represent populations facing intense harvest pressures (Evans *et al.* 2003; Spinks *et al.* 2012; Welton *et al.* 2013b).

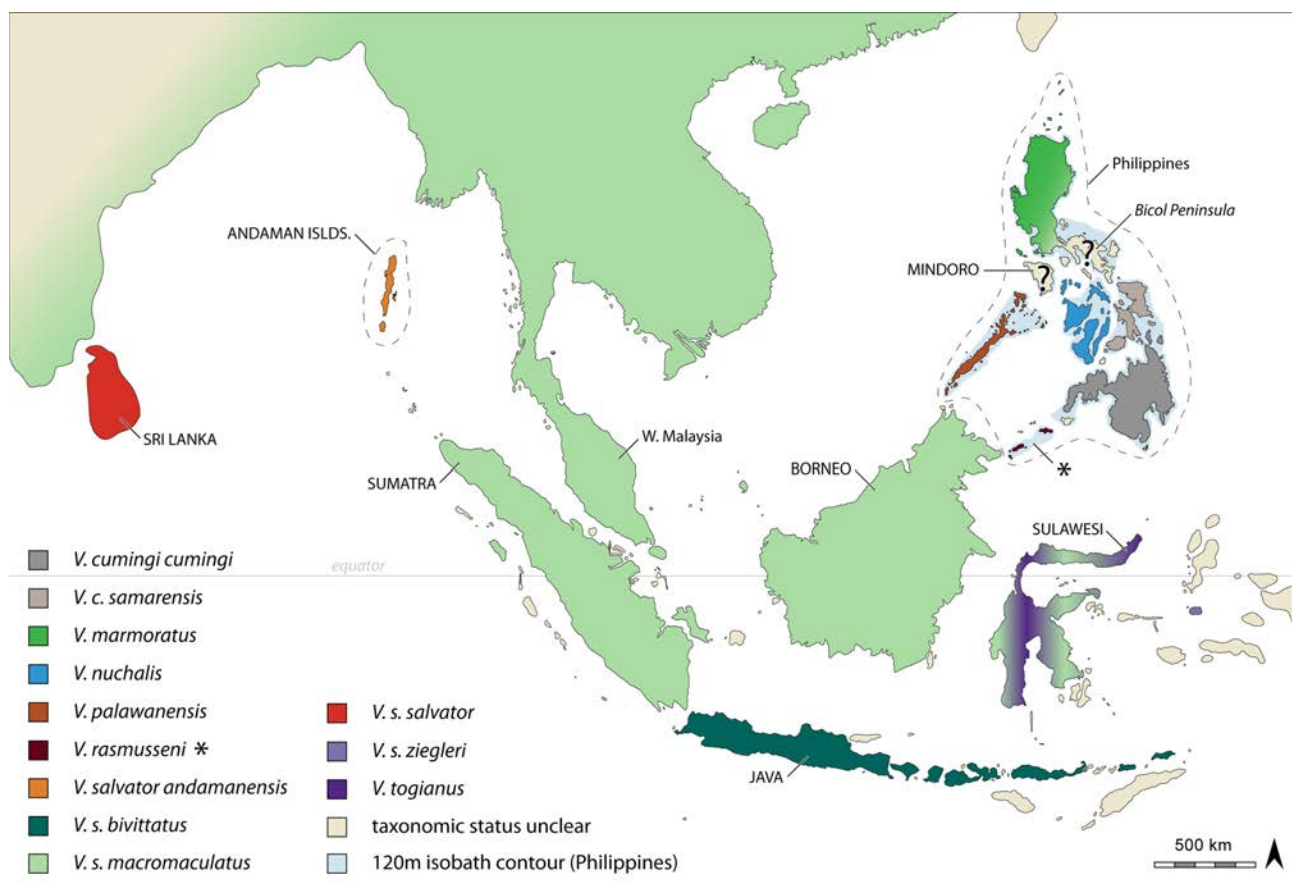


FIGURE 1. The distribution of the *Varanus salvator* Complex water monitor species. Pleistocene Aggregate Island Complex (PAIC) faunal regions in the Philippines (indicated by island group color differences) are delineated by the 120m underwater contour (Voris 2000; Brown & Diesmos 2009). Both *V. togianus* and *V. s. macromaculatus* are reported to occur on Sulawesi Island (Koch *et al.* 2010a). The distribution of *V. rasmusseni* is denoted with an asterisk, “*”, while the distributions of the two newly identified evolutionary lineages (Welton *et al.* 2013a,b) are denoted by question marks (?); see Figure 2.

The squamate genus *Varanus* (family Varanidae) is comprised of a charismatic and diverse assemblage of more than 100 named lineages (73 species, 30 subspecies; Koch *et al.* 2010a; Uetz & Hošek 2013) and is distributed throughout Africa, southern Asia, and the Indo-Australian regions. The past decade has seen an increase in the description of morphologically and genetically distinct taxa, many of which resulted from applying new data to the findings of previous authors who recognized the distinctiveness of insular populations, but either lacked the tools

or sufficient numbers of specimens to fully explore species boundaries on a fine geographic scale (Ziegler *et al.* 2007; Koch & Böhme 2010; Koch *et al.* 2010b).

The most taxonomically rich assemblage of monitor lizards is the *Varanus salvator* Complex, which consists of 12 taxa (seven species, five subspecies) and has a distribution stretching from the Indian subcontinent to western Wallacea (Fig. 1). More than half of these named taxa have only recently been described or elevated to their current taxonomic position (Koch & Böhme 2010; Koch *et al.* 2010b). The majority of these recent changes have followed the previous inferences of Mertens (1942a–c) and Koch *et al.* (2007), who identified morphologically distinct populations within the Asian water monitor, and named either subspecies or diagnosable island populations as new species, respectively.

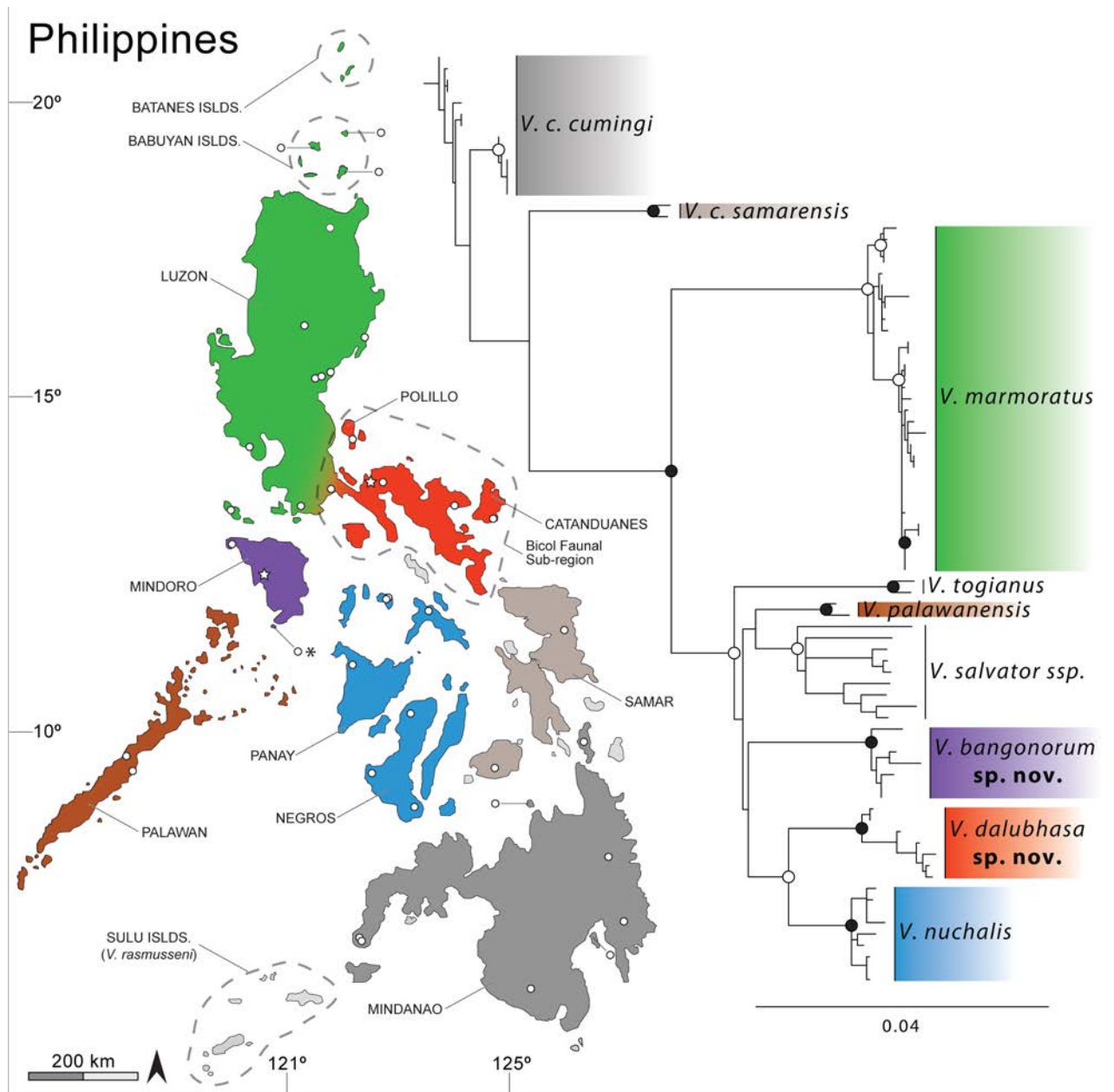


FIGURE 2. Distribution of Philippine species in the *Varanus salvator* Complex, and Maximum Likelihood phylogenetic inference (RAxML v7.5.4; Stamatakis, 2006) for the *V. salvator* Complex with Bayesian support values (MrBayes v3.2; Ronquist *et al.* 2011) mapped onto relevant nodes. Solid circles indicate posterior probabilities >95 and bootstrap support >75, open circles indicate bootstrap support >75 only. Asterisk “*” denotes sampling from Semirara Island. Open stars indicate type localities for *V. dalubhasa* **sp. nov.** (Bicol Peninsula, Luzon Island) and *V. bangonorum* **sp. nov.** (Mindoro Island). Scale bar represents number of changes.

By far, the highest taxonomic diversity within this group is endemic to the Philippines. This radiation, perhaps the initial ancestral lineage of the *Varanus salvator* Complex (Welton *et al.* 2013b, 2014), was re-evaluated by Koch *et al.* (2007) who elevated three taxa to full species status (*V. marmoratus*, *V. nuchalis*, and *V. cumingi*), and later described two new species and one subspecies (*V. palawanensis*, *V. rasmusseni*, and *V. c. samarensis*; Koch *et al.* 2010b). These studies resulted in the recognition of a total of six named endemic Philippine taxa (Figs. 1, 2). The phylogenetic placement of *V. rasmusseni* is unknown, due to the unavailability of genetic material.

Varanus marmoratus, the “widespread” species from the northern Philippines, had long been recognized as occurring throughout the Luzon, Mindoro, and Palawan faunal regions and the Sulu Archipelago (Figs. 1, 2; Mertens 1942a–c; Gaulke 1991, 1992, 1998; Koch *et al.* 2007). The work of Koch *et al.* (2010b) restricted this taxon’s range to Mindoro and Luzon islands, resulting in the recognition of the Palawan and Sulu faunal region populations as new species (*V. palawanensis* and *V. rasmusseni*, respectively). However, the population on Mindoro Island has recently been viewed as a putative distinct evolutionary lineage warranting additional taxonomic scrutiny (Gaulke & Koch 2010; Koch *et al.* 2010b; Welton *et al.* 2013a,b). Furthermore, recent phylogenetic analyses of the *V. salvator* Complex (Welton *et al.* 2013a,b) revealed that *V. marmoratus*, as currently recognized, is not a monophyletic lineage, and required further taxonomic scrutiny. In these studies, based either on mtDNA (Welton *et al.* 2013a) or a multilocus dataset (Welton *et al.* 2013b), *V. marmoratus* was shown to consist of three distinct, strongly supported evolutionary lineages. The first of these three lineages corresponds to “true” *V. marmoratus*, distributed throughout the majority of northern Luzon Island, as well as the Batanes and Babuyan island groups and Lubang Island (Fig. 2). The geographic distribution of this lineage contains the presumed type locality near the capital city, Manila (San Mateo [San Matheo]; Mertens 1942c). The second lineage was shown to have phylogenetic affinities to *V. palawanensis*, and occurs on the deep-water islands of Mindoro and Semirara (Fig. 2). Finally, and perhaps most surprising, was the recovery of a distinct lineage distributed in the Bicol faunal sub-region (the Bicol Peninsula of Luzon Island, Polillo Island, and Catanduanes Island; Fig. 2). This lineage, despite its geographic proximity to *V. marmoratus*, is most closely related to *V. nuchalis* of the Visayan faunal region in the central Philippines (Welton *et al.* 2013a,b).

In this study we take an additional step towards the taxonomic resolution of the *Varanus salvator* Complex by recognizing two additional evolutionary lineages from the biogeographically unique Mindoro faunal region and Bicol faunal sub-region (henceforth referred to as “Mindoro” and “Bicol” lineages) as distinct species. Although the new species are “cryptic” with respect to *V. marmoratus*, they are readily diagnosed from their actual closest relatives, *V. palawanensis* and *V. nuchalis*, respectively. Recognition of these distinct evolutionary lineages has the added benefits of imparting a classification that is consistent with evolutionary and biogeographic history as isolated allopatric lineages, further stabilizing water monitor taxonomy, and providing a taxonomic hypothesis for future genome-wide inquiries.

Materials and Methods

Morphological data. We scored morphological data from specimens preserved in 10% formalin and stored in 70% ethanol (see Specimens Examined section for specific specimen information). Morphological data were taken with digital calipers (to the nearest 0.1mm) by LJW only, in an effort eliminate inter-observer bias (Lee 1982; Hayek *et al.* 2001). Sex was determined by direct inspection of reproductive elements (hemipenes). When hemipenes were not everted, sex was determined by dissection to verify the presence/absence of hemipenes. Population Aggregation Analyses (Davis & Nixon 1992) were performed for all characters. The following morphological characters were scored for all specimens, and follow the character definitions of Koch *et al.* (2007): snout–vent length, head length, head width, head height at eye, eye–naris distance, naris–snout distance, rictus–rictus scale count, scale count around the base of the tail, scale count around the tail at 1/3 distance from the base, midbody scale row count, ventral scale count from gular fold to hind limb insertion, ventral scale count through gular region, dorsal scale count from tympanum to gular fold, dorsal scale counts from gular fold to hind limb insertion, supralabial scale count, scale count around the neck anterior to gular fold and enlarged supraocular scale count.

Principal Components Analyses. In an effort to more fully explore morphological variation, Principal Components Analyses were conducted on morphometric and meristic datasets. Both datasets were initially tested for normality using the Shapiro-Wilk Test (Shapiro & Wilk 1965; Royston 1995) implemented by the R stats

package in R (R Core Team 2013). We failed to reject normality, and proceeded directly with a log transformation of both datasets to standardize variances prior to Principal Component Analyses using the APE package (Paradis *et al.* 2004) in R. For both analyses, principal components were extracted until a cumulative 75% of the total variation was accounted for.

Sampling, DNA sequencing, phylogeny estimation and genetic distance. We supplemented the dataset of Welton *et al.* (2013a,b) with three additional samples from Mindoro Island (Table 1). The full dataset was trimmed to include only samples from the *Varanus salvator* Complex and *V. rudicollis* due to previous inferences of their sister relationship (Ast 2001; Vidal *et al.* 2012; Welton *et al.* 2013a,b). Extraction, PCR, and sequencing protocols followed those of Welton *et al.* (2013a,b). All novel sequences were submitted to Genbank (Table 1).

TABLE 1. Sample identity and data accession information (GenBank) for phylogenetic analyses. Institutional abbreviations are as follows: CAS, California Academy of Sciences; CMNH, Cincinnati Museum of Natural History; KU, University of Kansas Biodiversity Institute; LSUHC, La Sierra University; TNHC, Tennessee Natural History Collection, and UMMZ, University of Michigan Museum of Zoology. Uncatalogued/unvouchered samples are indicated by ACD, BSI, CDSGS, CDS, INA, LJW, and RMB field numbers. Due to alignment length, L74 data was deposited at Dryad (doi: 10.5061/dryad.m0n61).

Taxon	Institution	Locality	ND1/ND2	DGL-alpha	L52	PRLR
<i>V. bangonorum</i>	KU 305151	Semirara	JX677582/JX677699	KC795060	KC795105	KC795184
<i>V. bangonorum</i>	KU 305161	Semirara	JX677583/JX677700	KC795061	KC795106	KC795185
<i>V. bangonorum</i>	KU 305163	Semirara	JX677581/JX677698	KC795059	KC795104	KC795183
<i>V. bangonorum</i>	KU 308437	Mindoro	JX677584/JX677701	KC795062	KC795111	KC795188
<i>V. bangonorum</i>	KU 335742	Mindoro	KM888677/KM888678	KM888684	KM888682	–
<i>V. bangonorum</i>	KU 335743	Mindoro	KM888680/KM888681	–	–	–
<i>V. bangonorum</i>	KU 335744	Mindoro	KM888679	KM888683	–	–
<i>V. dalubhasa</i>	KU 306601	Bicol, Luzon	JX677589/JX677703	KC795034	KC795108	KC795186
<i>V. dalubhasa</i>	KU 306602	Bicol, Luzon	JX677590/JX677704	KC795035	KC795109	KC795187
<i>V. dalubhasa</i>	KU 306603	Bicol, Luzon	JX677591/JX677705	KC795036	KC795110	KC795188
<i>V. dalubhasa</i>	KU 308216	Catanduanes	JX677592/JX677706	KC795053	KC795095	KC795181
<i>V. dalubhasa</i>	KU 313880	Bicol, Luzon	JX677588/JX677702	KC795043	KC795150	KC795210
<i>V. dalubhasa</i>	KU 326702	Polillo	JX677614/JX677718	KC795040	KC795120	KC795195
<i>V. dalubhasa</i>	KU 326703	Polillo	JX677615/JX677719	KC795052	KC795121	KC795228
<i>V. cumingi</i>	CDSGS 08	Camiguin Sur	JX677619/JX677723	KC795016	KC795107	KC795219
<i>V. cumingi</i>	CMNH H1400	Talikud	JX677621/JX677725	KC795017	KC795112	KC795169
<i>V. cumingi</i>	CMNH H1627	E. Mindanao	JX677624/JX677728	KC795018	KC795113	KC795178
<i>V. cumingi</i>	CMNH H2627	E. Mindanao	JX677625/JX677729	KC795019	KC795114	KC795190
<i>V. cumingi</i>	KU 309898	Camiguin Sur	JX677620/JX677724	KC795014	KC795145	KC795208
<i>V. cumingi</i>	KU 314128	E. Mindanao	JX677622/JX677726	KC795015	KC795149	KC795209
<i>V. cumingi</i>	KU 315216	W. Mindanao	JX677626/JX677730	KC795025	KC795123	KC795170
<i>V. cumingi</i>	KU 315217	W. Mindanao	JX677631/JX677735	KC795023	KC795148	KC795217
<i>V. cumingi</i>	KU 315218	W. Mindanao	JX677627/JX677731	KC795021	KC795124	KC795168
<i>V. cumingi</i>	KU 315219	W. Mindanao	JX677629/JX677733	KC795024	–	KC795218
<i>V. cumingi</i>	KU 315220	W. Mindanao	JX677630/JX677734	KC795020	KC795147	–
<i>V. cumingi</i>	KU 321814	W. Mindanao	JX677628/JX677732	KC795022	–	–
<i>V. cumingi</i>	INA 0003	Dinagat	JX677623/JX677727	KC795074	–	KC795227
<i>V. c. samarensis</i>	KU 310870	Samar	JX677617/JX677721	KC795031	KC795097	–
<i>V. c. samarensis</i>	KU 335263	Bohol	JX677618/JX677722	KC795026	–	KC795224
<i>V. marmoratus</i>	ACD 2575	N. Luzon	JX677641/JX677745	KC795070	KC795086	KC795212

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TABLE 1. (Continued)

Taxon	Institution	Locale	ND1/ND2	DGL-alpha	L52	PRLR
<i>V. marmoratus</i>	ACD 5863	S. Luzon	JX677659/JX677763	–	KC795088	–
<i>V. marmoratus</i>	KU 336409	Lubang	JX677663/JX677767	KC795054	KC795100	KC795182
<i>V. marmoratus</i>	KU 304595	Calayan	JX677642/JX677746	KC795066	KC795140	KC795205
<i>V. marmoratus</i>	KU 304853	Babuyan Claro	JX677658/JX677762	KC795067	KC795141	KC795206
<i>V. marmoratus</i>	KU 304879	Calayan	JX677638/JX677742	KC795068	KC795142	KC795224
<i>V. marmoratus</i>	KU 304880	Calayan	JX677639/JX677743	KC795069	KC795143	KC795207
<i>V. marmoratus</i>	KU 305152	Lubang	JX677660/JX677764	KC795056	KC795093	KC795222
<i>V. marmoratus</i>	KU 305158	Lubang	JX677662/JX677766	KC795057	KC795094	KC795223
<i>V. marmoratus</i>	KU 305159	Lubang	JX677661/JX677765	KC795058	KC795095	KC795180
<i>V. marmoratus</i>	KU 314033	Batan	JX677637/JX677741	KC795073	KC795146	KC795216
<i>V. marmoratus</i>	KU 322191	Lubang	JX677664/JX677768	KC795055	KC795101	KC795179
<i>V. marmoratus</i>	KU 323362	E. Luzon	JX677650/JX677754	KC795045	KC795125	KC795198
<i>V. marmoratus</i>	KU 323432	E. Luzon	JX677648/JX677752	KC795033	–	KC795175
<i>V. marmoratus</i>	KU 323433	E. Luzon	JX677649/JX677753	KC795044	–	KC795197
<i>V. marmoratus</i>	KU 323434	E. Luzon	JX677646/JX677750	KC795039	KC795119	KC795194
<i>V. marmoratus</i>	KU 323435	E. Luzon	JX677644/JX677748	KC795037	KC795116	KC795215
<i>V. marmoratus</i>	KU 323436	E. Luzon	JX677647/JX677751	KC795032	KC795117	KC795192
<i>V. marmoratus</i>	KU 323437	E. Luzon	JX677651/JX677755	KC795046	KC795126	KC795213
<i>V. marmoratus</i>	KU 323438	E. Luzon	JX677653/JX677757	KC795048	KC795128	KC795200
<i>V. marmoratus</i>	KU 323439	E. Luzon	JX677645/JX677749	KC795038	KC795118	KC795193
<i>V. marmoratus</i>	KU 323440	E. Luzon	JX677652/JX677756	KC795047	KC795127	KC795199
<i>V. marmoratus</i>	KU 325842	C. Luzon	JX677654/JX677758	KC795049	–	KC795201
<i>V. marmoratus</i>	KU 326697	N. Luzon	JX677643/JX677747	KC795042	KC795087	KC795226
<i>V. marmoratus</i>	KU 327752	Calayan	JX677640/JX677744	–	KC795089	–
<i>V. marmoratus</i>	KU 329428	N. Luzon	–	–	KC795129	–
<i>V. marmoratus</i>	KU 330729	N. Luzon	–	KC795076	KC795132	KC795231
<i>V. marmoratus</i>	KU 330731	N. Luzon	–	–	KC795133	–
<i>V. marmoratus</i>	KU 330132	N. Luzon	–	KC795075	KC795130	KC795229
<i>V. marmoratus</i>	KU 330133	N. Luzon	–	KC795077	KC795131	KC795230
<i>V. marmoratus</i>	RMB 4290	W. Luzon	JX677655/JX677759	KC795041	KC795136	–
<i>V. marmoratus</i>	RMB 4519	S. Luzon	JX677657/JX677761	KC795050	KC795137	KC795211
<i>V. marmoratus</i>	TNHC 63000	S. Luzon	JX677656/JX677760	KC795051	KC795138	KC795203
<i>V. nuchalis</i>	CNMH H768	Panay	JX677603/JX677603	KC795071	KC795115	KC795191
<i>V. nuchalis</i>	KU 335262	Negros	JX677606/JX677713	KC795030	KC795102	KC795173
<i>V. nuchalis</i>	KU 305134	Sibuyan	JX677610/JX677610	KC795064	KC795139	KC795204
<i>V. nuchalis</i>	KU 305148	Sibuyan	JX677609/JX677609	KC795065	KC795092	KC795221
<i>V. nuchalis</i>	KU 305153	Negros	JX677604/JX677604	KC795027	KC795098	KC795171
<i>V. nuchalis</i>	KU 305157	Negros	JX677605/JX677605	KC795028	KC795099	KC795172
<i>V. nuchalis</i>	KU 305172	Sibuyan	JX677608/JX677715	KC795063	KC795134	–
<i>V. nuchalis</i>	KU 335261	Masbate	JX677607/JX677607	KC795072	KC795103	KC795214
<i>V. nuchalis</i>	RMB 3326	Negros	JX677600/JX677707	KC795029	KC795135	KC795174
<i>V. palawanensis</i>	KU 309607	Palawan	JX677580/JX677697	KC795013	KC795144	KC795176

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TABLE 1. (Continued)

Taxon	Institution	Locale	ND1/ND2	DGL-alpha	L52	PRLR
<i>V. palawanensis</i>	KU 327843	Palawan	JX677601/JX677708	KC795012	–	KC795177
<i>V. rudicollis</i>	LJW 0088	Trade sample	JX677685/JX677774	KC795078	KC795166	–
<i>V. salvator bivittatus</i>	UMMZ 227121	Java	JX677575/JX677692	–	KC795151	–
<i>V. s. bivittatus</i>	UMMZ 227122	Java	JX677576/JX677693	–	KC795152	–
<i>V. s. bivittatus</i>	UMMZ 227129	Java	JX677577/JX677694	–	KC795155	–
<i>V. s. macromaculatus</i>	ACD 3585	Singapore	JX677570/JX677688	–	–	–
<i>V. s. macromaculatus</i>	CAS 212011	Myanmar	JX677572/JX677690	–	KC795091	–
<i>V. s. macromaculatus</i>	LSUHC	W. Malaysia	JX677571/JX677689	KC795009	KC795156	KC795167
<i>V. s. macromaculatus</i>	UMMZ 225562	Sumatra	JX677678/JX677695	–	–	–
<i>V. s. macromaculatus</i>	UMMZ 227119	Sumatra	JX677574	–	–	–
<i>V. s. macromaculatus</i>	UMMZ 227128	Sumatra	JX677573/JX677691	–	KC795154	–
<i>V. togianus</i>	RMB	Sulawesi	JX677579/JX677696	KC795010	KC795122	KC795196
<i>V. togianus</i>	BSI 1565	Sulawesi	JX677602/JX677709	KC795011	KC795090	KC795220

Sequences were initially aligned with the program Muscle (v3.831; Edgar 2004) as implemented in Geneious (v5.5.6; Drummond *et al.* 2011), with manual adjustments made in Mesquite (v2.75; Maddison & Maddison 2011) to ensure proper reading frame when coding regions were translated into amino acids. We conducted partitioned Maximum Likelihood (RAxML v7.5.5; Stamatakis 2006) and Bayesian (MrBayes v3.2; Ronquist *et al.* 2011) phylogenetic analyses. Partitioning schemes for ML and Bayesian analyses and applied models of evolution follow those of Welton *et al.* (2013a). Likelihood analyses were performed with a random starting tree under the GTR + I + Γ model, employing 100 replicate ML inferences, and with nodal support estimated by 1000 bootstrap pseudoreplicates. Bayesian analyses were run with four independent Metropolis-coupled MCMC analyses, each with four chains and default heating schemes. Analyses were run for 20 million generations, sampling every 1000 generations, and with the initial 20% discarded as a conservative burn-in. Stationarity and convergence were assessed using Tracer (v1.4; Rambaut & Drummond 2007). We considered nodes strongly supported if they were recovered with ≥ 70 bootstrap and ≥ 95 posterior probability support across analyses (Ronquist & Huelsenback 2003; Rambaut & Drummond 2007).

Our alignment of ND1 and ND2 sequences was analysed with MEGA5 (v5.2.2; Tamura *et al.* 2011) to estimate mean pairwise genetic distances between groups, with uniform rates applied among sites and sequences with gaps or missing data removed. Groups were defined on the basis of recognized taxonomy and geography, with ten total groups comprised of all sampled taxa of the *Varanus salvator* Complex plus representatives from the Mindoro and Bicol populations (Figs. 1, 2).

Topological hypotheses. We tested the following taxonomy-based hypotheses to address monophyly of the three focal species in this study: (1) Monophyly of *Varanus bangonorum* **sp. nov.** (all samples of Philippine *V. marmoratus* Complex populations from the Mindoro faunal region); (2) Monophyly of *V. dalubhasa* **sp. nov.** (all samples of Philippine *V. marmoratus* Complex populations from the Bicol Peninsula of Luzon Island, and Catanduanes and Polillo islands); and (3) Monophyly of *V. marmoratus* (all samples of Philippine *V. marmoratus* Complex populations from Lubang Island, Luzon Island Proper, and the Babuyan and Batanes island groups). To do so, we estimated the probability of each hypothesis within a Bayesian framework by using the proportion of 4,786 post burn-in trees from the posterior distribution of our Bayesian analyses consistent with each null hypothesis of monophyly to arrive at a posterior probability for rejecting the hypothesis.

Species concept. We apply the Unified Species Concept of de Queiroz (2005, 2007; see also Mayden 1997, 2002) as a general extension of the Evolutionary Species Concept of Simpson (1961) and Wiley (1978), wherein a species is defined as a distinctly evolving ancestor–descendant metapopulation series, constituting an evolutionary lineage, with a unique evolutionary history and trajectory (Wiley 1978; Frost & Hillis 1990). Application of lineage-based evolutionary species concepts are noncontroversial and have been commonly applied in island archipelagos like the Philippines where the geological history of the archipelago is reasonably well understood (Hall 1998, 2002; Yumul *et al.* 2009), and species boundaries often coincide with geologically cohesive

landmasses. For the purpose of diagnosing evolutionary species in the Philippines, we consider as distinct species those populations that are isolated as allopatric insular endemics on separate island banks or geological platforms (i.e., isolated on separate Pleistocene Aggregate Island Complexes, PAICs; Voris 2000; Brown & Diesmos 2009; Brown *et al.* 2013), and diagnosable as cohesive lineages, with supporting evidence from multiple sources of data, including diagnostic differences in morphology, ecology, genetic information, and/or biogeographical inference.

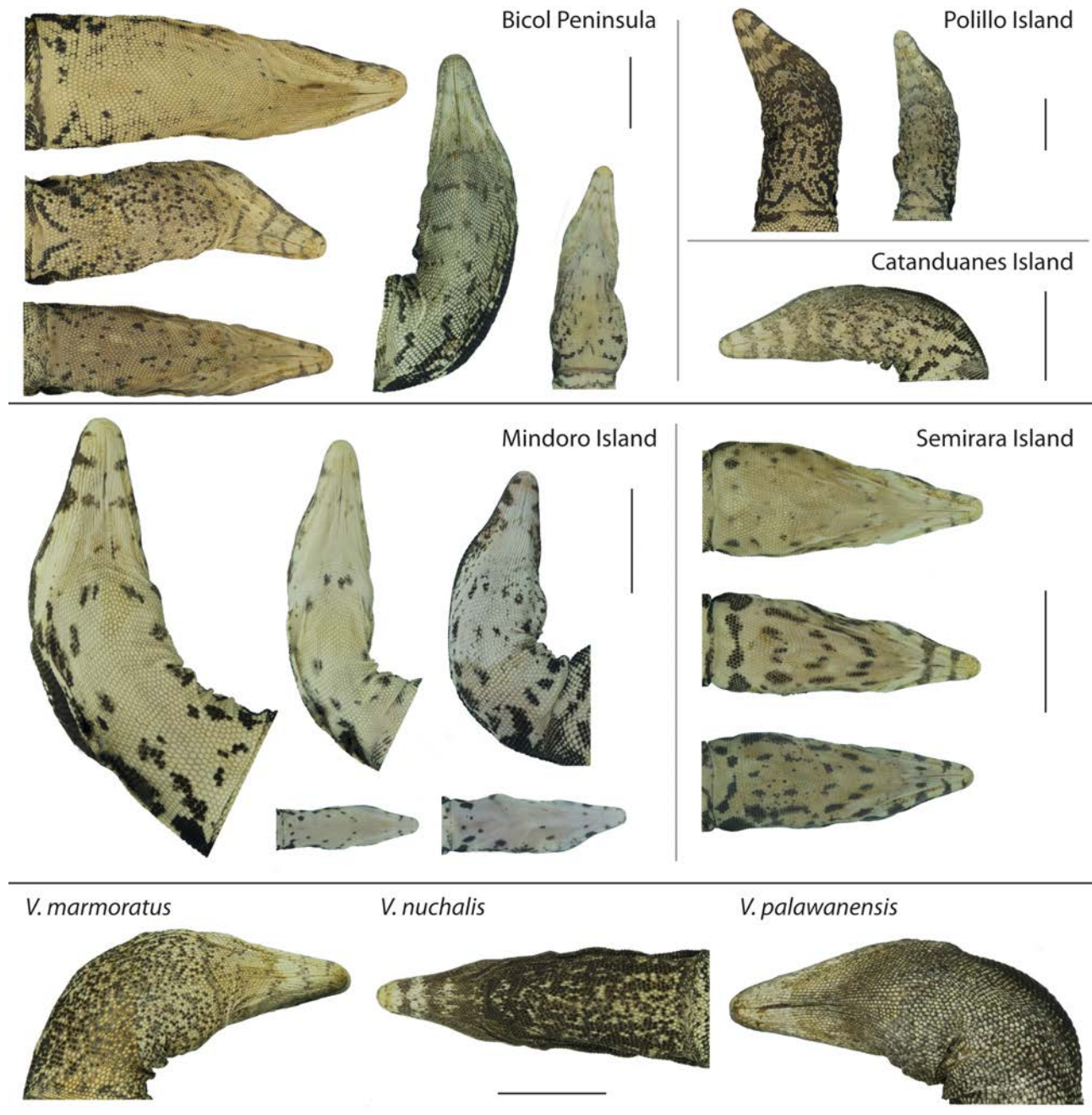


FIGURE 3. Comparison of gular coloration and patterning among *Varanus dalubhasa* **sp. nov.** (Bicol, Polillo, Catanduanes), *V. bangonorum* **sp. nov.** (Mindoro, Semirara), *V. marmoratus*, *V. nuchalis*, and *V. palawanensis*. Scale = 50mm.

Results

Morphology. Our analyses of meristic and mensural data support the recognition of two morphologically cryptic species, reinforcing the difficulty faced by previous researchers to identify these lineages. These two, unique

lineages have historically been assigned to *Varanus marmoratus* due to their similar morphological features. Despite the lack of diagnostic morphological characters delimiting the new species from *V. marmoratus*, there are characters present that distinguish each new species from its closest relative (Fig. 3). Dorsal scales and those around the neck anterior to the gular fold (Table 2) distinguish the Mindoro lineage from its presumed closest relative, *V. palawanensis* (based on Welton *et al.* 2013a; see below). Similarly, scale counts around the tail at one-third the distance from the base of the tail, and gular and dorsal scale counts (Table 2) distinguish the Bicol lineage from its closest relative, *V. nuchalis*. Additionally, we identified consistent diagnostic differences in gular color pattern among all taxa, with the Mindoro lineage exhibiting distinct clusters of moderately sized, dark spots and the Bicol lineage exhibiting smaller, more variable dark speckling and occasional anterior bands. By comparison, the related taxa, *V. palawanensis*, *V. marmoratus*, and *V. nuchalis*, generally exhibit variable speckling with anterior transverse bands (*V. palawanensis* and *V. marmoratus* *sensu stricto*) or a solid dark coloration with no discernable pattern (*V. nuchalis*; Fig 3). We did not find any consistent differences in dorsal coloration or numbers of lighter, transverse dorsal bands. A summary of morphological and gular coloration data can be found in Table 2.

TABLE 2. Morphological data for the geographically proximate and relevant lineages of water monitors in the *Varanus salvator* Complex. All meristic characters taken in millimeters, and numbers in parentheses represent standard deviations. Characters follow Koch *et al.* (2007, 2010b). Naris position measured as eye–naris distance/naris–snout distance.

	<i>bangonorum</i> sp. nov. (n=17)	<i>dalubhasa</i> sp. nov. (n=10)	<i>marmoratus</i> (n=11)	<i>nuchalis</i> (n=7)	<i>palawanensis</i> (n=9)
max. snout–vent length	390	505	454	442	576
head length	60.17 (± 18.95)	67.13 (±14.81)	78.68 (± 11.14)	58.31 (± 17.51)	82.26 (± 20.64)
head width	30.42 (± 7.59)	37.67 (± 8.33)	41.39 (± 6.69)	30.85 (± 8.99)	42.23 (±11.16)
head depth at eye	20.82 (± 5.50)	25.62 (± 5.67)	28.61 (± 3.06)	20.56 (± 5.75)	27.08 (± 7.84)
eye–naris distance	20.57 (± 7.18)	23.51 (± 5.73)	27.64 (± 4.24)	19.46 (± 6.70)	27.89 (± 7.84)
naris–snout distance	9.94 (± 3.04)	11.27 (± 2.71)	13.26 (± 1.81)	9.83 (± 3.11)	14.61 (±3.72)
naris position	2.05 (± 0.15)	2.09 (± 0.13)	2.08 (± 0.11)	1.96 (± 0.13)	1.90 (± 0.11)
head/snout–vent length	0.066 (± 0.004)	0.068 (± 0.003)	0.071 (± 0.005)	0.067 (± 0.005)	0.067 (± 0.004)
naris–snout/ snout–vent length	0.032 (± 0.003)	0.032 (± 0.002)	0.034 (± 0.002)	0.034 (± 0.004)	0.035 (± 0.003)
head length/head width	1.86 (± 0.17)	1.85 (± 0.08)	1.90 (± 0.05)	1.89 (± 0.07)	1.95 (± 0.08)
head length/head depth at eye	2.61 (± 0.17)	2.73 (± 0.17)	2.75 (± 0.22)	2.82 (± 0.16)	2.63 (± 0.12)
scales from rictus to rictus	56 (± 4)	55 (± 5)	54 (± 3)	52 (± 4)	62 (±4)
scales around the base of the tail	98 (± 6)	98 (± 5)	91 (± 7)	97 (± 6)	102 (± 6)
scales around the tail a 1/3 distance from the base	51 (± 4)	53 (± 4)	53 (± 5)	46 (± 3)	55 (± 5)
mid-body scales	136 (± 9)	138 (± 7)	132 (± 7)	150 (± 7)	142 (± 7)
ventral scales from gular fold to hind-limb insertion	82 (± 3)	83 (± 5)	80 (± 4)	85 (± 3)	84 (± 4)
gular scales count	78 (± 5)	80 (± 3)	72 (± 5)	73 (± 3)	78 (±2)
total ventral scales	160 (± 6)	162 (± 7)	152 (± 9)	158 (± 6)	161 (± 4)
dorsal scales from tympanum to gular fold	26 (± 2)	27 (± 2)	28 (± 3)	23 (± 2)	32 (± 3)
dorsal scales from gular fold to hind-limb insertion	80 (± 9)	84 (± 5)	81 (± 4)	83 (± 6)	96 (± 3)
total dorsal scales	106 (± 10)	111 (± 5)	109 (±5)	106 (±5)	128 (± 3)

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TABLE 2. (Continued)

	<i>bangonorum</i> nov. (n=17)	sp. <i>dalubhasa</i> sp. nov. (n=10)	<i>marmoratus</i> (n=11)	<i>nuchalis</i> (n=7)	<i>palawanensis</i> (n=9)
supralabials	59 (± 5)	58 (± 3)	59 (±3)	59 (±4)	59 (± 2)
scales around the neck anterior to the gular fold	76 (± 6)	78 (± 3)	71 (± 3)	73 (± 4)	87 (± 4)
enlarged supraoculars	4–8L, 5–8R	5 or 6L, R	3–6L, R	4–7L, 5–7R	4–7L, 5–8R
gular coloration	distinct spotting	variable speckling and bands	variable speckling and bands	dark, no pattern	variable speckling and bands

Principal Components Analysis. Principal Components Analyses of our mensural data failed to identify group structure between recognized or proposed taxa (Fig. 4A), however analysis of the meristic data clearly delimits *Varanus marmoratus* from *V. palawanensis* and *V. nuchalis*, and *V. nuchalis* from both the Bicol and Mindoro lineages (Fig. 4B). The first three principal components in the analysis of meristic data account for 74.3% of the total variance, with eigenvalues of 5.115, 1.914, and 1.260 for PC1, PC2, and PC3, respectively. Loadings for PC1 were all negative, except for scales around the base of the tail, midbody scales, gular scales, and total ventrals. All loadings for PC2 were positive, and the dispersion among taxa along this axis is driven by relatively high loading values from: (1) the number of rictus–rictus scales (0.347); (2) dorsals from the gular fold to hindlimb insertion (0.382); (3) total dorsals (0.347); and (4) scales around the neck anterior to the gular fold (0.390). Not surprisingly, the numbers of dorsals and scales around the neck anterior to the gular fold are diagnostic for the new taxa described herein. A summary of PCA metrics can be found in Table 3.

TABLE 3. Loading values, eigenvalues, and proportion of variance for Principal Components Analysis of meristic data. Disproportionately heavily-loading variables are bolded for emphasis.

	Comp. 1	Comp. 2	Comp. 3
rictus–rictus scales	-0.001	0.347	0.198
scales around the base of the tail	0.006	0.271	0.042
scales around the tail 1/3 distance from base	-0.050	0.293	-0.143
midbody scales	0.011	0.208	0.001
vertrals from gular fold to hindlimb insertion	-0.003	0.109	-0.014
gular scales	0.004	0.220	0.076
total ventrals	0.001	0.162	0.028
dorsals from tympanum to gular fold	-0.062	0.238	0.129
dorsals from gular fold to hindlimb insertion	-0.038	0.382	0.065
total dorsals	-0.043	0.347	0.079
supralabials	-0.013	0.125	0.054
scales around the neck anterior to the gular fold	-0.012	0.390	0.206
proportion of variance	0.427	0.196	0.120
cummulative proportion of variance	0.427	0.622	0.743
eigenvalue	5.115	1.914	1.260

Phylogenetic and Topological hypotheses. Maximum Likelihood and Bayesian inferences yielded similar topologies, with no well-supported conflicts. Phylogenetic relationships recovered in this study, while differing slightly from those of Welton *et al.* (2013a,b), recover a paraphyletic *Varanus marmoratus* (Fig. 2). *Varanus cumingi* + *V. c. samarensis* is consistently recovered as the most basal, divergent lineage within the *V. salvator* Complex, with *V. marmoratus* recovered as a successively diverging lineage. Remaining members of the *V.*

salvator Complex (*V. nuchalis*, *V. palawanensis*, *V. togianus*, *V. salvator* ssp., and the Mindoro and Bicol lineages) are recovered as a moderately supported clade (BS >75), sister to *V. marmoratus*. Each of these taxa are supported as distinct, divergent, monophyletic lineages, though the inter-relationships among them largely remain unresolved (similar to Welton *et al.* 2013a,b). The phylogenetic placement of *V. palawanensis* and the Mindoro lineage could not be resolved (but see Welton *et al.* 2013b), while the sister relationship between the Bicol lineage and *V. nuchalis* has been recovered as either well-supported (Welton *et al.* 2013b) or moderately supported (Fig. 2; Welton *et al.* 2013a). Topology tests failed to reject the monophyly of the Mindoro and Bicol lineages, with Bayesian posterior probabilities supporting the monophyly of each lineage recovered as 0.96 and 0.81, respectively. For *V. marmoratus* the posterior probability recovered was 0.43, which may be indicative of remaining paraphyly within this group, possible gene flow, or a lack of phylogenetic signal in the loci analyzed. Despite the variable support for most inter-lineage relationships, all analyses (here and Welton *et al.* 2013a,b) failed to recover a monophyletic *V. marmoratus* as is currently recognized.

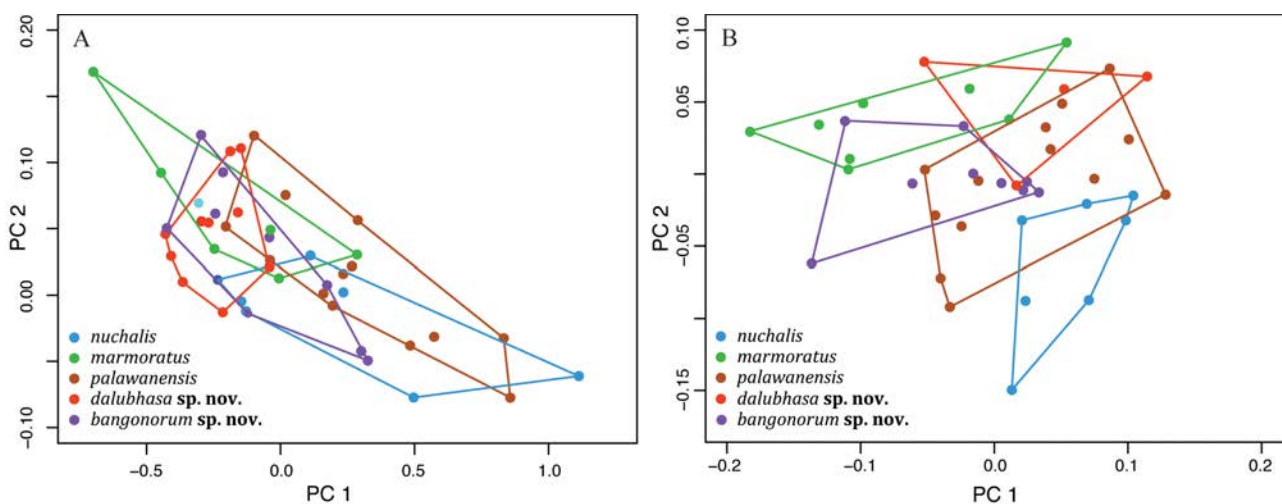


FIGURE 4. Principal Components Analyses for A) mensural, and B) meristic characters for *Varanus nuchalis*, *V. marmoratus*, *V. palawanensis*, *V. dalubhasa* sp. nov., and *V. bangonorum* sp. nov..

Genetic Distinctiveness. Estimates of pairwise genetic distance between taxa indicate levels of divergence similar to those found between currently recognized species. Currently recognized taxa are recovered as 1.0 % to 3.5% divergent from other such taxa within the *Varanus salvator* Complex (Table 4). The Mindoro lineage is divergent from recognized taxa by 2.0–3.5% uncorrected sequence divergence, while the Bicol lineage is 0.8–3.2% divergent (Table 4).

Although we do not use genetic distances to diagnose or define the taxa we describe here, we are confident in their use as proxies to guide our examination of morphology and biogeography and to refute or bolster taxonomic hypotheses. In the case of the taxa we describe here, we emphasize that genetic distances between our new taxa (the lineages of the Bicol and Mindoro faunal regions) are compatible with genetic distances between other, non-controversial, previously described and morphologically highly distinctive lineages (Koch *et al.* 2007, 2010b; Ziegler *et al.* 2007; Welton *et al.* 2013a,b). More importantly, our newly defined species are more genetically distant from the phenotypically similar *Varanus marmoratus* than either are to their own sister species, the traditionally recognized (and morphologically distinct) *V. nuchalis* and/or *V. palawanensis*.

Taxonomic hypotheses. We recognize two additional species in the *Varanus salvator* Complex based on (1) their positions in multilocus phylogenetic estimates (Welton *et al.* 2013a,b; and data presented here), (2) the lack of statistical or character support rejecting the monophyly of these lineages, (3) subtle but consistent differences in coloration, and (4) the inference of distinctive biogeographical ranges on separate islands or geological components (suggesting barriers to gene flow and a history of geographic isolation in allopatry). Additionally, to impart stable taxonomy and in the name of consistency of application of species recognition criteria (de Queiroz 1999), we elevate the morphologically diagnosable, genetically distinct, and biogeographically circumscribed *V. cumingi samarensis* (Koch *et al.* 2010b) to the level of full species (*V. samarensis*), below.

TABLE 4. Percent pairwise genetic distance between taxa in the *Varanus salvator* Complex for the mitochondrial data (ND1 + ND2).

	<i>bangonorum</i> sp. nov.	<i>dalubhasa</i> sp. nov.	<i>cumingi</i>	<i>marmoratus</i>	<i>nuchalis</i>	<i>palawanensis</i>	<i>salvator</i> <i>macromaculatus</i>	<i>salvator</i> <i>bivittatus</i>	<i>togianus</i>
<i>bangonorum</i> sp. nov.	—								
<i>dalubhasa</i> sp. nov.	3.1	—							
<i>cumingi</i>	3.4	3.1	—						
<i>marmoratus</i>	3.5	3.0	2.3	—					
<i>nuchalis</i>	2.4	0.8	2.5	2.6	—				
<i>palawanensis</i>	2.1	1.5	2.3	2.4	1.0	—			
<i>samarensis</i>	3.2	3.2	1.6	2.6	2.4	2.1	—		
<i>salvator</i> <i>macromaculatus</i>	2.4	2.4	2.7	2.7	1.7	1.4	2.6	—	
<i>salvator</i> <i>bivittatus</i>	2.0	3.0	3.1	3.5	2.3	2.0	3.2	2.2	—
<i>togianus</i>	2.8	1.9	2.7	3.1	1.5	1.4	2.8	1.9	1.8

Species Descriptions

Varanus dalubhasa sp. nov.

Figs. 3, 5–8

Holotype. PNM 9796 (formerly University of Kansas Biodiversity Institute [KU] 306603; Field No. CWL 521), adult male, collected by Charles W. Linkem and CDS, 08 July 2006, 18 m above sea level (14.03202, 122.34143; WGS-84), Barangay Madlangdungan, Municipality of Calauag, Quezon Province, Luzon Island, Philippines.

Paratopotypes. KU 305155 (CDS Field No. 2202), adult male; PNM 9797 (formerly KU 306601; CWL Field No. 440), juvenile; KU 306602 (CWL Field No. 520), adult male.

Paratypes. KU 308216 (CDS Field No. 2298), juvenile, collected 22 February 2007, Barangay Buenavista, Municipality of Bato, Catanduanes Province, Catanduanes Island, Philippines; KU 313880 (RMB Field No. 9910), adult male, collected 01 July 2008, Barangay Tulay Na Lupa, Municipality of Labo, Camarines Norte Province, Luzon Island; KU 326702 and 326703 (LJW Field No. 0075, 0077), adult males, salvaged 3 August 2009, Polillo Island (exact locality information unknown).

Other Material. See Specimens Examined Section.

Etymology. The specific epithet, *dalubhasa*, is derived from the Tagalog word “dalubhasa” meaning a person who has authoritative and comprehensive knowledge of a particular area, or a skilled expert in a particular subject. We choose this term in honor of Vicente “Enteng” Yngente of Polillo Island, whose extensive knowledge of natural history and ecology of Philippine reptiles (particularly monitor lizards) has been instrumental to our research and conservation work. Suggested common name: Enteng’s Monitor Lizard.

Diagnosis. *Varanus dalubhasa* can be distinguished from congeners by (1) small, dark speckling and variable transverse banding through the gular region (Fig. 3); (2) number of scales around the tail at 1/3 distance from the base; (3) number of gular scales; (4) number of dorsal scales in nuchal region; (5) total number of dorsal scales; (6) number of scales around the neck anterior to the gular fold; and (7) phylogenetic placement sister to *V. nuchalis*. Additionally, this distinct lineage is biogeographically circumscribed in the Bicol Peninsula faunal sub-region, a distinct geological component of greater Luzon Island which remained insular until 3 Ma (Hall 2002).

Comparisons. The new species is phenotypically nearly indistinguishable from *Varanus marmoratus*, but can generally be diagnosed by the presence of small, dark speckling in the gular region and faint anterior transverse bands (versus speckling and distinct anterior transverse bands; Fig. 3), and its allopatric distribution in the Bicol faunal sub-region (versus the remaining portions of Luzon and Lubang islands, and the Batanes and Babuyan

island groups). Additionally, although *V. dalubhasa* is phenotypically similar to *V. marmoratus*, available data suggest that it is not most closely related to this species (Fig. 2).

Varanus dalubhasa can be conveniently distinguished from its allopatric sister taxon, *V. nuchalis* (distributed in the West Visayan islands of Negros, Panay, Guimaras, Masbate, and the Romblon Province islands of Sibuyan, Tablas, and Romblon; Fig. 1, 2), by the presence of more scales around the tail at 1/3 distance from the base (mean = 53 ± 4 , versus 46 ± 3), fewer gular scales (mean = 80 ± 3 , versus 73 ± 3), and more dorsal scales from the tympanum to the gular fold (mean = 27 ± 2 , versus 23 ± 2). Of the remaining, geographically proximate species of the *V. salvator* Complex, this new species can be distinguished from *V. palawanensis* by having fewer dorsal scales from the tympanum to the gular fold (mean = 27 ± 2 , versus 32 ± 3), fewer dorsal scales from the gular fold to the hind limb insertion (mean = 84 ± 5 , versus 96 ± 3), fewer total dorsals scales longitudinally (mean = 111 ± 5 , versus 128 ± 3), and fewer scales around the neck anterior to the gular fold (mean = 78 ± 3 , versus 87 ± 4). Additionally, *V. dalubhasa* can be distinguished from the allopatric Mindoro lineage by having variable dark speckling and transverse bands in the gular region (versus distinct spotting; Fig. 3). Lastly, *V. dalubhasa* is comprised of entirely distinct haplotypes or haplotype networks, relative to all other members of the *V. salvator* Complex (see Welton *et al.*, 2010a). We have constrained our morphological analyses to the geographically most proximate taxa due to previous studies (Koch *et al.* 2007, 2010b) demonstrating their distinctiveness relative to the remaining diversity withing the *V. salvator* Complex.

Description of holotype. An adult male (Fig. 5), hemipenes everted; SVL 505.0 mm; tail 657 mm; head relatively slender, length 89.1 mm, width 51.0 mm, and depth at eye 32.0 mm; snout length 47.6 mm, 53.4% head length; snout rounded anteriorly; narial openings 5.4 mm, ovular, posteriorly elevated, encircled by 9L/9R small polygonal scales; snout elevated sharply just anterior to narial region, then continuing gradually to ocular region; narial region not distinctly elevated above horizon of snout; cranial table squarish, only slightly wider than long.

Head scales ovular to polygonal (Fig. 5), heterogeneous in size with the smallest occurring dorso-laterally between ocular opening and tympanum, and largest occurring dorso-medially from tip of snout to conspicuous parietal; supraoculars 6L/6R, subrectangular and elongated transversely; supralabials 59, slightly larger than lateral head scales; infralabials 61, smaller than both supralabials and nearest rows of gular scales; both supra- and infralabials increasing in size anteriorly; nuchals large, circular, increasing in size to forelimb insertion along both dorsal and lateral surfaces; lateral nuchals less than half the size of dorsals; scales immediately posterior to cranial table quite small, granular; sutures between scales slightly larger in nuchal region than on head; nuchals 31, in semi-regular transverse rows from posterior margin of tympanum to forelimb insertion; dorsal trunk scales arranged in 88 semi-regular transverse rows from fore- to hindlimb insertions, ovular, slightly smaller than nuchals, gradually decreasing in size to hindlimb insertion as well as laterally, with smallest scales occurring laterally adjacent to limb insertions; midbody scales 138; axilla–groin distance 245 mm; dorsal limb scales ovular, decreasing in size distally to digits; fore- and hindlimbs 92 and 107 mm, respectively, 18.2% and 21.2% snout–vent length, 32.6 and 53.9 mm diameter at insertions; limb scales present in semiregular rows; scales of manus and pes smaller and more irregular in shape, ranging from circular to nearly rectangular dorsally; supradigitals rectangular dorsally, ovular laterally, with terminal scale nearly twice as large as others; digits terminate in long, slender recurved claws; caudals ovular and granular at insertion, becoming rectangular posteriorly; dorsal keel composed of paired, posteriorly elevated scales commences 65 mm posterior to hindlimb insertion, and continues to tail terminus with paired scales gradually decreasing in size; caudal scales moderately keeled, in regular transverse and longitudinal rows laterally, decreasing in size posteriorly.

Ventrals less variable than dorsals; gular scales generally rectangular anteriorly, becoming more ovular towards gular fold; smallest scales medially in anterior third of gular region, with largest scales just anterior to gular fold but followed posteriorly by three transverse rows of smaller, more granular gulars; scales around the neck anterior to the gular fold 78, mid-gular 87; gular scales in 85 irregular rows from tip of snout to gular fold; ventrals of fore- and hindlimbs circular to polygonal, with those of forelimbs slightly smaller than those of hindlimbs; precloacals homogenous in size and shape with those of hindlimbs; ventral trunk scales from gular fold to hindlimb insertion 85, ovular anteriorly, becoming rectangular posteriorly, and present in semi-regular rows; scales decreasing in size laterally and at hindlimb insertions; ventral caudal scales rectangular, smallest just posterior to cloacal opening; scale surface slightly rounded anteriorly, becoming sharply keeled and more longitudinally elongate posteriorly.

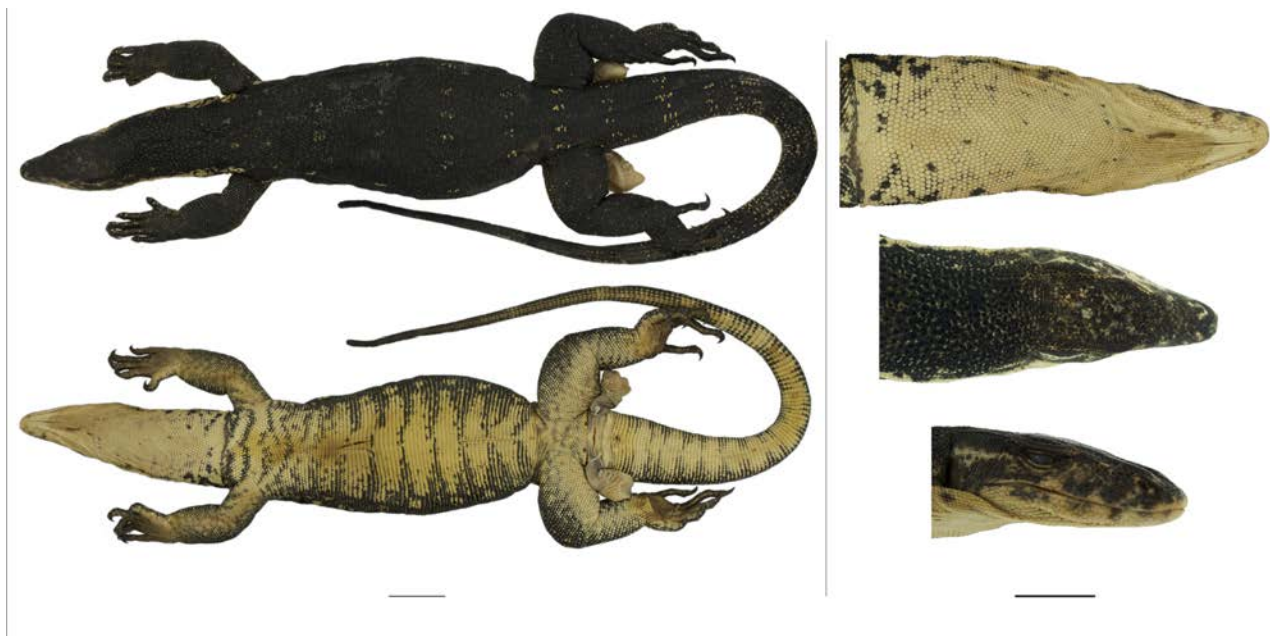


FIGURE 5. Holotype of *Varanus dalubhasa* sp. nov. (PNM 9796), with body shown in dorsal and ventral aspects; and head shown in dorsal, ventral, and profile aspects. Scale = 50 mm.

Right and left hemipenes partially everted; maximum length 56.2 mm, with proximal cylindrical section extending 26.2 mm; bifurcation resulting in primary cylindrical apical portion with external flounces, and more diminutive portion resembling an “ear” or reduced fold; flounces present in irregular rows, totalling 15 anterior to sulcus spermaticus, 6 posteriorly; lacking notable external appearance of ossified hemibaculum.

Measurements of holotype (in mm). SVL 505; tail length 657; head length 89.1, width 51.0, depth at eye 32.0; eye–naris distance 33.7; naris–snout distance 14.9; rictus–rictus scales 60; scales around tail base 103; scales around tail 1/3 distance from base 59; mid-body scales 138; gular scales 85; ventrals from gular fold to hind limb insertion 85; total ventral scales 170; dorsals from tympanum to gular fold 31; dorsals from gular fold to hind limb insertion 88; total dorsals 119; supralabials 59; scales around the neck anterior to gular fold 78; and enlarged supraoculars 6L/6R.

Coloration of holotype in preservative. Dorsal surfaces of head, body, and limbs black; aggregation of yellow-gold scales present dorsoanteriorly to narial openings, along canthal ridge just anterior to oculars, and irregularly dispersed throughout cranial table; trunk with seven transverse rows comprised of yellow-gold, indistinct ocelli; tail with nine, slightly more distinct yellow-gold bands, becoming more diffuse or speckled laterally; forelimbs with irregularly distributed yellow-gold scales, density increasing distally and along lateral surfaces; hindlimbs with irregular aggregations of ocelli consisting of only two or three yellow-gold scales (Fig. 5).

Lateral coloration of head consisting of partial, near vertical yellow-gold bands at the tip of snout, posterior margin of narial opening, and two between the narial opening and the ocular; posterior band with ventral widening oriented more posteriorly; post-orbitally, a yellow-gold stipe extends to tympanum, and a yellow-gold spot consisting of four or five scales appears ventral to the anterior margin of the stripe; lateral coloration of the nuchal region consists of 2L/3R faint spots directly posterior to the tympanum; ventral margins of nuchal region with yellow-gold variable demarcation, extending more dorsally along the posterior margin and appearing to wrap around the dorsal margin of the fore-limb insertions; trunk with variable yellow-gold spotting directly posterior to forelimbs, fading to solid black posteriorly (Fig. 5).

Ventral coloration predominately yellow-gold throughout; gular region with irregular spots, faint anteriorly but becoming prominent and dark along lateral margins just anterior to gular fold; scapular region with two irregular black bands; trunk with irregular black bands and spots anteriorly, becoming more broken medially and posteriorly, appearing as laterally elongated yellow-gold ovals; forelimbs with faint, irregular dark mottling; hindlimbs with near uniform venter medially, with dark mottling along lateral margins; manus and pes dark yellow-gray; venter of tail appearing anteriorly much like that of the trunk, with yellow-gold laterally elongated ovals; posterior portions of tail with more regular alternation of dark and yellow-gold bands (Fig. 5).

Variation. Our small type series exhibits some color variation, but specimens are generally phenotypically similar. The holotype (KU 306603) and three paratypes (KU 305155, 306602, and 308126) have lighter interstitial coloration between the dorsal scales, yielding an overall lighter appearance than other specimens. These three specimens also exhibit much more diffuse yellow gold coloration on limbs and tail, while two specimens (KU 313880, 326702) exhibit much more distinct yellow-gold spots or ocelli throughout. Additionally, the yellow-gold coloration in the lateral portions of the nuchal region, among all specimens, and on either side of a single specimen, are present as either a single longitudinal stripe extending posteriorly from the posterior margin of the tympanum or as a series of two or three longitudinally elongated spots or blotches. Two specimens (KU 305155, 306602) exhibit two relatively well-defined yellow crossbands on the snout, with the former's being even more pronounced than the latter, and with this specimen (KU 305155) also exhibiting a much larger proportion of yellow coloration in the supraocular and temporal regions. In contrast, two specimens (KU 308216, 313880) exhibit nearly uniform, dark dorsal head coloration, with the former being completely devoid of yellow-gold accents with the exception of the pineal scale.

Ventral coloration is only slightly more variable than that of the dorsum. All specimens exhibit variable speckling in the gular region, generally consisting of 1–4 black scales. In the holotype (KU 306603), this speckling is much more reduced. In one specimen (KU 305155) anterior speckling in the gular region gives way to 2 broken transverse bands, and somewhat reduced speckling through the remainder of the gular region. Three specimens (KU 306602, 308216, and 326702) exhibit four, more well-defined dark transverse bands in the anterior portion of the gular regions, with speckling throughout the remainder of the gular region being relatively dense. A single specimen (KU 313880) exhibits nearly complete dark transverse bands throughout the gular region, with less prominent bands present anteriorly. Ventral trunk coloration is nearly uniform among specimens, with the only notable variation present in two individuals (KU 305155, 326702), the first of which exhibits reduced dark coloration extending medially onto the abdomen, and the second of which with darker, more distinct coloration extending medially onto the abdomen. Ventral tail coloration lacks any notable variation among specimens (see Figures 6 and 7 for further information on color pattern variation).

Coloration in life. Based on the only available image, PNM 9797 (formerly KU 306601; Fig. 8A), and field notes of the authors. Dorsal ground coloration black to dark gray, with conspicuous transverse cross bands of yellow-gold ocelli from the posterior margin of the nuchal region through the anterior third of the tail. Trunk ocelli larger with a darkened, ground-colored center. Additionally, dorsal trunk with faded reticulate pattern, owing to light brown interstitial coloration. Lateral margins of head and nuchal region with conspicuous yellow-gold stripe, extending from the the posterior margin of the ocular, through the tympanum, and midway into the nuchal region. Yellow-gold ocelli brightest at lateral margins of trunk and adjacent to hindlimb and tail insertions.

Dorsal limb surfaces colored similarly to body, but with ocelli irregularly arranged and significantly smaller, lacking any dark-colored center. Dorsal ground color of limbs bright yellow, with irregular dark pigmentation.

Ventral coloration bright yellow-gold, with scattered black pigmentation and with ocelli of ventro-lateral surfaces irregularly arranged and significantly smaller, lacking any dark-colored center (Fig. 8A).

Ecology, Distribution, and Natural History. As with all members of the *Varanus salvator* Complex, *V. dalubhasa* should be considered a habitat generalist, often thriving in a range of habitats from primary forest to more urbanized areas. While no detailed studies have been undertaken on this taxon specifically, the findings of Gaulke (in Luxmoore & Groombridge 1989, 1992) are likely relevant. This taxon is most likely to be found in mangrove and riparian habitats (as their common name might suggest). Additionally, most water monitors seek out shelters in the form of rock crevices or even trees, most often near water sources. In more urban areas, human habitation may be used in lieu of more “natural” shelters (Gaulke 1992).

Not surprisingly, *Varanus dalubhasa* has been found throughout the Bicol Peninsula and faunal sub-region, including genetically confirmed specimen identifications from Polillo and Catanduanes islands (Figs. 1, 2). This is an area with significant agricultural (rice fields) and coastal environments, and is additionally subdivided by a number of moderately sized river drainages. The northern extent of distribution for this taxon, and potential contact zone with *V. marmoratus* requires further study.

Although no dietary preferences have been observed for this taxon, one can reasonably assume that its diet consists primarily of invertebrates and smaller vertebrates (fish, rodents, frogs, snakes). Additionally, this species is attracted to a number of carion items, with a particular affinity for fish (LJW pers. obs.).

***Varanus bangonorum* sp. nov.**

Figs. 3, 6–9

Holotype. PNM 9798 (formerly University of Kansas Natural Biodiversity Institute [KU] 335744; Field no. RMB 17757), sub-adult male, collected by SLT and RMB, 16 July 2013, 230 m above sea level (12.787806, 120.915972; WGS-84), Sitio Aruyan, Barangay Malisbong, Municipality of Sablayan, Occidental Mindoro Province, Mindoro Island, Philippines.

Paratopotypes. KU 335742 (RMB Field No. 17720), juvenile, collected 11 July 2013.

Paratypes. KU 335743 (RMB Field No. 17824), juvenile, Lake Libuao, Barangay Malisbong, Municipality of Sablayan, Occidental Mindoro Province, Mindoro Island, Philippines; PNM 9799 (formerly KU 308403), 308437 (ELR Field Nos. 843, 877), juvenile and adult female, Sitio Ulasan, Barangay Harrison, Municipality of Paluan, Occidental Mindoro Province, Mindoro Island, Philippines; KU 305151, 305161, 305163 (CDS Field Nos. 714, 715, 648), juveniles, Barangay Tinogboc, Municipality of Caluya, Antique Province, Semirara Island, Philippines.

Other Material. See Specimens Examined Section

Etymology. The specific epithet, *bangonorum*, is a plural noun derived from the name of the indigenous Bangon peoples of Mindoro Island, who reside along the rivers and central Cordillera mountain system in Oriental Mindoro Province. Anthropologists have shown the Bangon tribal group to be culturally distinct from other tribal groups inhabiting Mindoro (Tweddell 1970; Mangyan Heritage Center). Suggested common name: Bangon Monitor Lizard.

Diagnosis. *Varanus bangonorum* can be distinguished from congeners by (1) distinct, relatively large dark spots or blotches in the gular region; (2) low counts of dorsal gular scales; (3) low counts of dorsal trunk scales; and (4) low counts of scales around the neck anterior to the gular fold. Additionally, this distinct lineage is biogeographically circumscribed on the deepwater islands of Mindoro and Semirara.

Comparisons. This new species is phenotypically most similar to *Varanus marmoratus*, from which it can be distinguished by the presence of distinct, dark and irregularly-shaped spots or blotches in the gular region (versus speckling and transverse bands; Fig. 3), and an allopatric distribution on the islands of Mindoro and Semirara (versus Luzon and Lubang islands, and the Batanes and Babuyan island groups; Figs. 1, 2). Additionally, although the new species is phenotypically similar to *V. marmoratus*, it is not closely related to this species (Fig. 2, phylogeny). *Varanus bangonorum* can be distinguished from its closest but allopatric relative, *V. palawanensis*, by having generally fewer rictus–rictus scales (mean = 56 ± 4 , versus 62 ± 4), fewer dorsal scales from the tympanum to the gular fold (mean = 26 ± 2 , versus 32 ± 3), fewer dorsal scales from the nuchal fold to the hind limb insertion (mean = 80 ± 9 , versus 96 ± 3), fewer total dorsal scales (mean = 106 ± 10 , versus 128 ± 3), fewer scales around the neck anterior to the gular fold (mean = 76 ± 6 , versus 87 ± 4), and by having distinct, dark irregular spots or blotches in the gular region (versus irregular speckling with anterior transverse bands). Of the remaining geographically proximate species of the *V. salvator* Complex, this new species can be distinguished from *V. nuchalis* by a distribution on Mindoro and Semirara islands (versus Visayan islands), generally fewer midbody scales (mean = 136 ± 9 , versus 150 ± 7), generally more dorsal scales from the tympanum to the gular fold (mean = 26 ± 2 , versus 23 ± 2), and the presence of distinct dark spots or blotches in the gular region (versus a uniform dark gular coloration). Additionally, this new species can be distinguished from the allopatric Bicol species *V. dalubhasa* by having distinct, irregularly shaped spots or blotches (versus variable speckling and faint anterior transverse bands) in the gular region. Lastly, *V. bangonorum* exhibits entirely unique haplotypes or haplotype networks, relative to all other members of the *V. salvator* Complex (see Welton *et al.* 2010a,b). We have constrained our morphological analyses to the geographically most proximate taxa due to previous studies (Koch *et al.* 2007, 2010b) demonstrating their distinctiveness relative to the remaining diversity within the *V. salvator* Complex.

Description of holotype. A sub-adult male, hemipenes not everted; snout–vent length 343 mm; tail 601 mm; head relatively slender, length 65.9 mm, width 38.2 mm, and depth at eye 28.5 mm; snout length 34.0 mm, 51.6% head length; snout rounded anteriorly; narial openings 4.3 mm, ovular, posteriorly elevated, encircled by 9L/9R small polygonal scales; snout elevated sharply just anterior to narial region, then continuing gradually to ocular region; narial region only moderately elevated above horizon of snout; cranial table squarish, slightly wider than long.

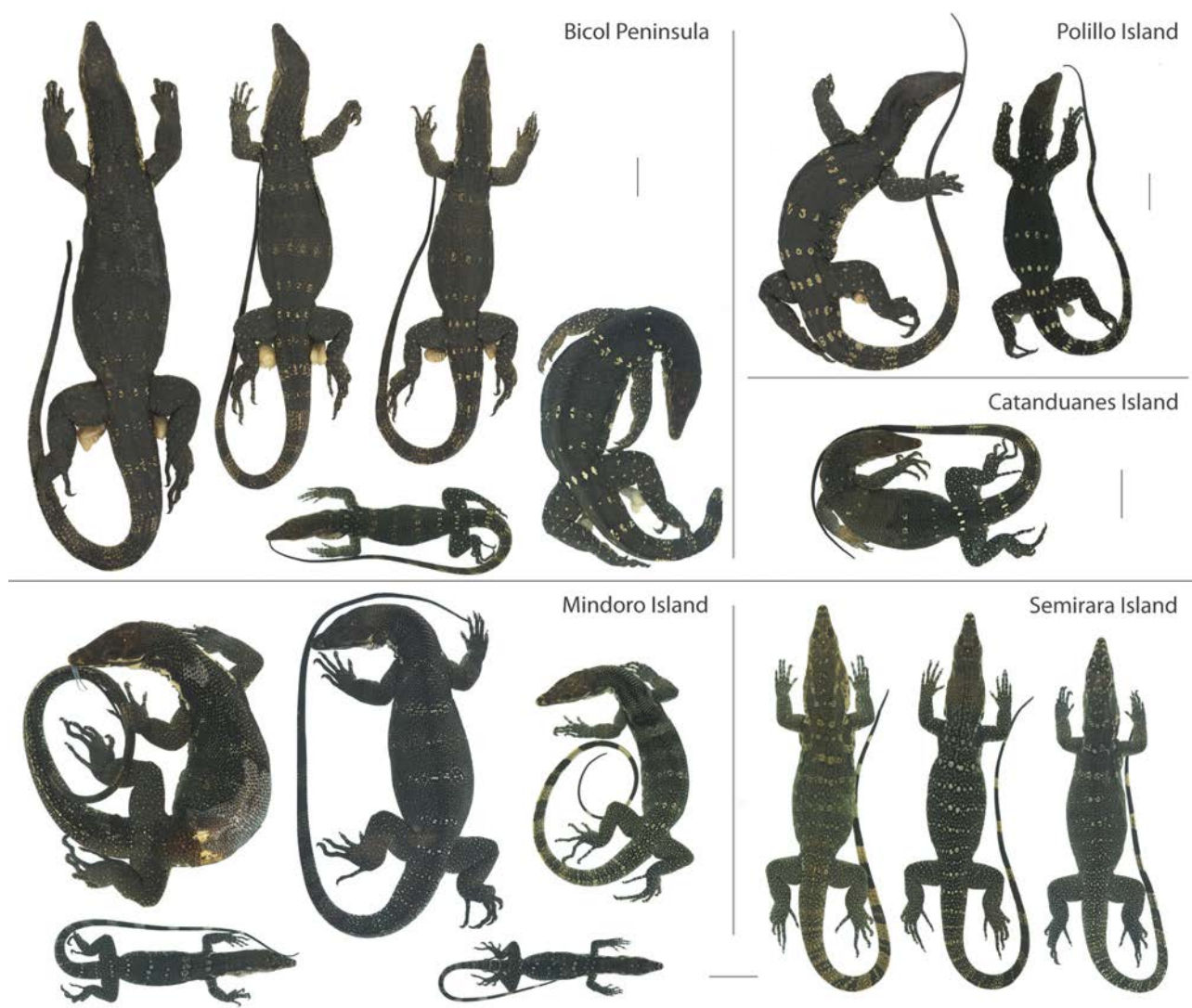


FIGURE 6. Dorsal color variation in the type series for both *Varanus dalubhasa* **sp. nov.** (top) and *V. bangonorum* **sp. nov.** (bottom). Scale = 50mm.

Head scales ovular to polygonal (Fig. 9), heterogenous in size with the smallest occurring on lateral margins of cranial table and directly surrounding pinneal scale, and largest occurring dorso-medially from tip of snout to pineal region; supraoculars 7L/6R, subrectangular and elongated transversely; supralabials 52, slightly larger than head scales; infralabials 52, smaller than supralabials; both supra- and infralabials increasing in size anteriorly; nuchals large, circular, generally homogenous in size throughout nuchal region except for directly posterior to cranial table; lateral nuchals small and granular, approximately $\frac{1}{4}$ the size of dorsals; sutures between scales larger than those on head; nuchals 25, in semi-regular transverse rows from posterior margin of tympanum to forelimb insertion; dorsal trunk scales arranged in 77 semi-regular transverse rows from fore- to hindlimb insertions, ovular, generally smaller than nuchals, and decreasing in size posteriorly to hindlimb insertion as well as laterally, with smallest scales occurring adjacent to limb insertions; midbody scales 131; axilla-groin distance 157 mm; dorsal limb scales ovular, decreasing in size distally and ventrally; fore- and hindlimbs 55 and 82 mm, respectively, 16.0% and 23.9% snout-vent length, respectively, 24.2 and 36.8 mm diameter at insertions, respectively; limb scales present in semiregular rows; scales of manus and pes smaller and more irregular in shape, ranging from circular to nearly square dorsally; supradigitals rectangular dorsally, ovular laterally, with terminal scale nearly twice as large as others; digits terminate in long, slender recurved claws; caudals ovular, small and granular anteriorly, becoming rectangular posteriorly; dorsal keel composed of paired, posteriorly elevated scales commences 37.7 mm from hindlimb insertion, continuing to tail terminus with scales gradually decreasing in size; caudal scales moderately keeled, in regular transverse and longitudinal rows laterally, decreasing in size posteriorly.

Ventrals less variable than dorsals; gular scales generally rectangular anteriorly, becoming more ovular towards gular fold; smallest scales medially in anterior third of gular region, with largest scales just anterior to gular fold but followed posteriorly by three transverse rows of smaller, more granular gulars; scales around the neck anterior to the gular fold 67, mid-gular 76; gular scales in 70 irregular rows from tip of snout to gular fold; ventrals of fore- and hindlimbs circular to polygonal, with those of forelimbs slightly smaller than those of hindlimbs; precloacals similar to those of hindlimbs; ventral trunk scales from gular fold to hind limb insertion 83, ovular anteriorly, becoming rectangular posteriorly, present in semi-regular rows; scales decreasing in size laterally and at hindlimb insertions; ventral caudal scales rectangular, smallest just posterior to cloacal opening; scale surface slightly rounded anteriorly, becoming sharply keeled and more longitudinally elongate posteriorly.

Measurements of holotype (in mm). SVL 343; tail length 601; head length 65.9, width 38.2, depth at eye 28.5; eye–naris distance 22.2; naris–snout distance 11.6; rictus–rictus scales 52; scales around tail base 91; scales around tail 1/3 distance from base 47; mid-body scales 131; gular scales 70; ventrals from gular fold to hind limb insertion 83; total ventral scales 153; dorsals from tympanum to gular fold 25; dorsals from gular fold to hind limb insertion 77; total dorsals 102; supralabials 52; scales around the neck anterior to gular fold 67; and enlarged supraoculars 7L/6R.

Coloration of holotype in preservative. Dorsal surfaces of body, head and limbs black; head nearly uniform black, with dark brown accents dorsal to narial openings and with white pineal scale; trunk with five transverse rows of white blotches; tail with nine irregular bands comprised of diffuse white speckling; forelimbs with sparse white speckling, becoming more regular ventrally; hindlimbs more speckled than forelimbs, and with more speckling ventrally; dorsal surfaces of manus and pes with few white speckles, but surface of pes with slightly more; terminal scale on digits with conspicuous white spot.

Lateral coloration of head consisting of vague, anterior dark brown band extending ventrally from dark brown dorsal markings to narial openings; post-orbitally, lateral surface with longitudinal white stripe extending from the posterior margin of ocular to tympanum (Fig. 9); lateral coloration of the nuchal region consists of bright white mottling, gradually increasing in dorsal extent posteriorly, and terminating at forelimb insertion; lateral portions of trunk with variable white blotches and speckling, with greatest concentration directly posterior to forelimbs, the distribution of which does not correspond to dorsal banding; terminal half of tail solid black dorsally.

Ventral coloration predominately yellow-white throughout; gular region with characteristic dark blotches, becoming more prominent posteriorly; anterior portions of gular region with three triangular projections extending medially; scapular region with irregular dark blotches; trunk with irregular dark triangular projections extending medially from margins, and generally not connecting with projections from opposite side; forelimbs and hindlimbs almost uniform white at insertions, but with increasing dark mottling laterally and in distal portions; manus and pes dark gray; venter of tail similar to that of trunk, but with triangular projections connecting and forming vague bands posteriorly; terminal third of tail solid black ventrally.

Variation. Our small type series exhibits some color variation but specimens are generally phenotypically similar to one another. Four specimens from Mindoro, including the holotype (KU 308437, 335742–44) generally appear darker dorsally, owing to a combination of darker interstitial skin between the scales and fewer white-colored scales. The holotype (KU 335744) and an additional specimen from Mindoro (KU 308437) were the largest intact specimens examined, and both exhibit a reduction in the size and vibrancy of dorsal banding, with the latter individual having bands that are only faintly discernable. Juvenile specimens from both Mindoro (KU 335742, 335743) and Semirara (KU 305151, 305161, 305163) exhibit much more distinct dorsal bands comprised of series of yellowish to white spots or ocelli. One juvenile from Mindoro (PNM 9799; formerly KU 308403) appears to be an intermediate, with dorsal bands discernable posteriorly on the trunk and becoming less defined anteriorly. One specimen from Semirara (KU 305161) exhibits a faded reticulate pattern interspersed among the more well-defined dorsal bands, owing to clusters of grayish spots comprised of lightly colored scales and interstitial space. Specimens from Semirara (KU 305151, 305161, 305163) and one from Mindoro (KU 335742) exhibit a more well-defined light-colored longitudinal stripe laterally in the nuchal region, which extends from the ventral margin of the tympanum dorso-posteriorly over the forelimb insertions, joining with the first dorsal trunk band to form a vague “U” shape when viewed from dorsal perspective. Dorsal nuchal coloration varies from uniform black in the holotype (KU 335774) and three paratypes (PNM 9799, KU 308437, 335772), the presence of 4–10 variable spots or blotches (KU 305151, 308161, 335743), to a more mottled and irregular combination of stipes and blotches posteriorly (KU 305163). One specimen (KU 308437) exhibits a reduction in white speckling on the dorsal surfaces of the limbs.

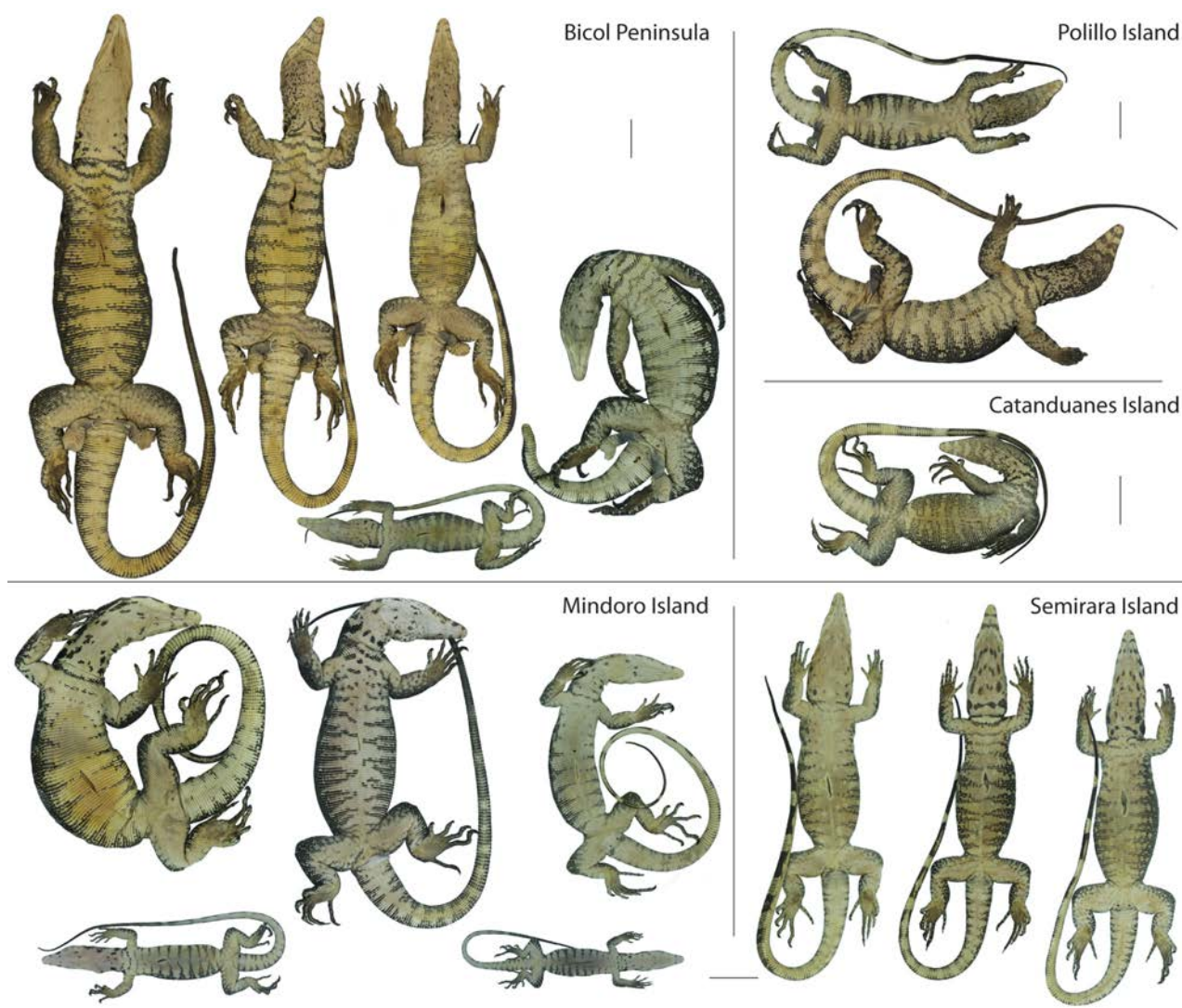


FIGURE 7. Ventral color variation in the type series for both *Varanus dalubhasa* **sp. nov.** (top) and *V. bangonorum* **sp. nov.** (bottom). Scale = 50mm.



FIGURE 8. Photos in life of *Varanus dalubhasa* **sp. nov.** (A; KU 306601) and *V. bangonorum* **sp. nov.** (B; KU 335742).

Ventral coloration is moderately variable. The characteristic gular blotches or spots are present in all specimens, though the number and relative size of blotches is somewhat reduced in four specimens (KU 305161, 308403, 335742, 335743). Two specimens (KU 305151, 305163) exhibit much larger and more conspicuous gular

spots. Ventral trunk coloration is less variable, with only three specimens (KU 305161, 308403, 308437) exhibiting reduced transverse dark bands, which generally fail to converge medially. Ventral coloration of the limbs is nearly identical among specimens, with only slight variation in the appearance of black color encroaching on the lateral margins of both fore- and hindlimbs, but generally appearing as partial transverse bands. The holotype (KU 335774) and three paratypes (KU 308437, 305151, 305161) exhibit a more irregular pattern on the margins of the ventral limb surfaces, with dark coloration appearing as an almost reticulate pattern. Ventral coloration of the tail is nearly uniform across specimens, with only minor variation in the extent of medial extension of dark bands. In all specimens, dark bands fail to coalesce anteriorly, but posteriorly to the terminus form a distinct alternating black and white pattern (see Figures 6 and 7 for additional information on color pattern variation).

Coloration in life. Based on the only available image, KU 335742 (Fig. 8B), and field notes of the authors. Dorsal ground coloration black, with transverse crossbands of irregularly shaped creamy white to light yellow ocelli from the posterior margin of the nuchal region through the hind limb insertion. Trunk with few, larger ocelli with darkened, ground-colored centers. Additionally, dorso-lateral margins of trunk with smaller, variably distributed light yellow spots or blotches. Lateral margins of head and nuchal region with conspicuous light yellow stripe, extending from the the posterior margin of the ocular, through the tympanum, and midway into the anterior portion of the nuchal region. An additional light yellow stripe extends dorsally and posteriorly from the ventro-lateral margin of the nuchal region, and extends to the dorsal region above the forelimb insertion. Snout with distinct and conspicuous bands extending ventrally from dorsal surface.

Dorsal limb surfaces colored similarly to body, but with ocelli irregularly arranged and significantly smaller, lacking any dark-colored center. Forelimbs with larger ocelli dorso-medially.

Ventral coloration creamy white to light yellow, with scattered black pigmentation and with ocelli of ventro-lateral surfaces irregularly arranged and significantly smaller, lacking any dark-colored center (Fig. 8b).



FIGURE 9. Holotype of *Varanus bangonorum* sp. nov. (PNM 9798), with body shown in dorsal and ventral aspects; and head shown in dorsal, ventral and profile aspects. Scale = 50 mm.

Ecology, Distribution, and Natural History.—As with all members of the *Varanus salvator* Complex, *V. bangonorum* should be considered a habitat generalist, often thriving in a range of habitats from primary forest to more urbanized areas. Like *V. dalubhasa*, no detailed studies have been undertaken on this taxon specifically, but the findings of Gaulke (in Luxmoore & Groombridge 1989, 1992) are likely relevant. This taxon is most likely to be found in mangrove and riparian habitats (as their common name might suggest). Additionally, most water monitors seek shelter in rock crevices or even trees, often near water sources.

Not surprisingly, *Varanus bangonorum* has been found on the islands of Mindoro and Semirara (Figs. 1, 2), both of which are separated by deep water channels that likely have facilitated the isolation of this species and its

evolution as a distinct lineage, even during inter-glacial cycles and lowered sea levels (Voris 2000; Brown & Diesmos 2009).

Again, the findings of Gaulke (1992) are relevant as far as dietary preferences are concerned, and it can reasonably be assumed that the diet of *Varanus bangonorum* consists primarily of invertebrates and smaller vertebrates (fish, rodents, frogs, snakes). Additionally, as with any species of water monitor, this species is attracted to a number of carion items, with a particular affinity for fish (LJW pers. obs.).

***Varanus samarensis* Koch *et al.* 2010**

Synonymy. *Varanus cumingi samarensis* Koch *et al.*, 2010. Zootaxa 2446, 19–23.

Holotype.—ZFMK 64713, subadult male, collected by M. Gaulke 1989, San Augustin near Gandara, Samar Island, Philippines.

New material examined.—Samar (1 specimen): KU 310870 (CDS Field No. 2654), adult male, collected by Cameron D. Siler, 13 October 2007, Barangay San Rafael, Municipality of Taft, Eastern Samar Province, Samar Island, Philippines; Bohol (1 specimen): KU 335263 (CDS Field No. 4768), adult male, collected by Cameron D. Siler, 04 August 2009, Barangay Danicop, Municipality of Sierra Bullones, Bohol Province, Bohol Island, Philippines.

Other material.—Refer to Koch *et al.* (2010b).

Diagnosis.—Following the findings of Koch *et al.* (2010b), *Varanus samarensis* can be distinguished from other members of the *V. salvator* Complex by a combination of (1) distinctive dorsal color pattern of 5–8 transverse bands of yellow ocelli or spots through the trunk; (2) a dark (black) head dorsally, with symmetrical yellow markings; (3) a variable black stripe in the temporal region, occasionally bordered by a bright (yellow-white) stripe ventrally; (4) the absence of a medio-dorsal stripe on the lateral surfaces of the nuchal region and trunk; (5) narial openings positioned approximately 2.5 times closer to the tip of the snout than to the ocular.

Comment and justification.—Although within the same PAIC (Brown & Diesmos 2009), the Samar–Leyte versus Mindanao Island biogeographical boundary (informally referred to as the “Dinagat–Caraga Filter Zone”) has been evoked in several previous studies to explain the existence of deep phylogenetic splits between the northern and southern reaches of the Mindanao faunal region (Steppan *et al.* 2003; Hosner *et al.* 2013, 2014; Brown *et al.* 2013, 2014). We therefore do not find it surprising that Samar, Leyte, Bohol (and, presumably, smaller associated landmasses) have a distinctive species of monitor lizard that apparently is isolated from Mindanao’s *Varanus cumingi* (Welton *et al.* 2013a,b).

Distribution.—See Koch *et al.* (2010b) for additional data about variation, ecology, and distribution.

Discussion

Our description of two new taxa and the recognition of *Varanus samarensis* as a full species draw on a growing body evidence (Koch *et al.* 2007, 2010a,b; Welton *et al.* 2013a,b) supporting the recognition of no fewer than seven distinct evolutionary lineages of water monitors in the Philippines. Although these taxa show varying degrees of morphological distinctiveness, with some being morphologically cryptic, they all represent reciprocally monophyletic metapopulations with distributions confined to distinct geological components of the Philippine Archipelago (Brown *et al.* 2013). As such, these lineages warrant recognition under a Unified Species Concept. The recognition of these lineages rectifies the problematic status of *V. marmoratus*, which has been shown to represent a taxonomically invalid, polyphyletic assemblage of three unrelated lineages, with two groups (Bicol and Mindoro) demonstrated to be more closely related to two other, traditionally diagnosed and morphologically distinctive species (*V. nuchalis* and *V. palawanensis*, respectively). Although the recognition of *V. bangonorum* and *V. dalubhasa* fails to fulfill the classic operational criteria for species recognition established in the previous studies of Mertens (1942a,b,c) and Koch *et al.* (2007, 2010a,b), the methods of delimitation employed here (those not relying solely on morphological characters) in conjunction with those of Welton *et al.* (2013a,b) provide a more robust and comprehensive assessment of diversity in an evolutionary context. Similarly, the use of genetic data as a means for delimiting distinct, divergent evolutionary lineages (species) has become an increasingly useful practice,

especially for widespread taxa distributed over a geologically complex area (Wiens & Penkrot 2002; Fritz *et al.* 2004; Bergman & Russell 2007).

Although the polyphyletic pattern observed in phylogenetic analyses of the *Varanus salvator* Complex seems to indicate an inability of previous studies to identify the full diversity of this group, there remains the possibility that this pattern may instead be the result of additional factors. Given that taxa comprising the *V. salvator* Complex are the products of relatively recent speciation events (<5Ma, Welton *et al.* 2014), the conserved morphology and phylogenetic patterns observed may be due to incomplete lineage sorting and/or ancestral gene polymorphisms (Funk & Omland 2003). Additionally, and consistent with these lineages being relatively young and having relatively high dispersal potentials, there remains the possibility of contemporary gene flow and introgression, even among widely accepted and morphologically distinct species (Funk & Omland 2003). Distinguishing between these alternatives, however, may be difficult given the allopatric nature of these lineages (Masta *et al.* 2002; Redenbach & Taylor 2002) and the the potential for historic or sporadic episodes of hybridization (Patton & Smith 1994; Freeland & Boag 1999; Funk 1999; Sota & Vogler 2001; Shaw 2002; Funk & Omland 2003). Finally, there remains the possibility that both *V. dalubhasa* and *V. bangonorum* exhibit an ancestral morphology also seen in *V. marmoratus*, and simply, that speciation in some members of this group has not been accompanied by morphological change (e.g., Barley *et al.* 2013). This seems plausible given the more basal phylogenetic position of *V. marmoratus*, and is a pattern that has been inferred for other taxa (Jarman & Elliot 2000). Unfortunately, convincing inferences that might distinguish between these competing hypotheses cannot be made with the data currently available, although future studies employing the use of genome-wide data, anonymous fragment length polymorphisms (AFLPs), microsatellite loci, or single-nucleotide polymorphisms (SNPs), may find these processes to be prevalent and even responsible for the phylogenetic patterns observed in this group. Until this time, however, we treat the recognition of these divergent mitochondrial-based lineages as reasonable, evolutionarily and biogeographically sensible, and conservative hypotheses for the diversity in the *V. salvator* Complex.

The recognition of *Varanus dalubhasa* and *V. bangonorum* brings the total number of named taxa in the *V. salvator* Complex to 14, and the Philippine compliment to 7 (Fig. 2). However, a number of these taxa are currently considered subspecies—a status that in some cases should be reevaluated. For example, here we elevate *V. cumingi samarensis* (Samar, Leyte, and Bohol islands, Philippines; Fig. 2) to full species status and it remains a possibility that the same action may be warranted for *V. salvator ziegleri* (Obi Island, Indonesia) should the necessary support for validation become available. Their recognition is nonproblematic under the criteria of the Unified and Evolutionary species concepts. Both of these taxa are morphologically distinct, endemic to unique biogeographic areas, and clearly constitute independent evolutionary lineages. In the case of *V. c. samarensis* (for which genetic data are available [Welton *et al.* 2013a,b]), this taxon represents a divergent, monophyletic lineage, with levels of pairwise genetic distance from recognized members of the complex ranging from 1.6–3.2% (levels greater than those seen between currently recognized species; Table 4). Although comprehensive data are lacking for the remaining subspecies within *Varanus salvator*, insular lineages (i.e., *V. s. andamanensis*) should be prioritized for scrutiny and possible elevation to full species status, if additional, corroborating lines of evidence come to light. At this time, however, we only take action with respect to *V. c. samarensis* and elevate this named taxon to full species, based on the work of Koch *et al.* (2010b), Welton *et al.* (2013a,b), and additional data presented here.

Within the Philippines, the deep-water islands of Burias and Siquijor remain to be sampled for many vertebrate taxa, including *Varanus*. The faunal affinities of these islands with the West Visayan region make the presence of *V. nuchalis* a reasonable assumption. Similarly, many of the major islands throughout the Greater and Lesser Sundas have yet to be thoroughly surveyed for *Varanus* (but see Kaiser *et al.* 2013), and thus represent ideal and necessary targets for future study. Clearly large, deep water islands, separate PAICS (Brown & Diesmos 2009), isolated geological components of large islands, and small isolated islands deserve further scrutiny of water monitor species diversity, especially throughout western Wallacea and the Lesser Sunda islands of Indonesia. Additionally, the taxonomic status of water monitors throughout Borneo, Indochina, and the Indian subcontinent warrant further taxonomic and phylogenetic scrutiny, owing to a lack of both available specimens and genetic resources from these regions. Finally, transect studies are required along the boundary of the Bicol Peninsula and southeastern Luzon in order to accurately delimit the species boundaries between *V. marmoratus* and *V. dalubhasa*, and to assess the ecological or biogeographical factors maintaining the distinctiveness of these lineages.

The Philippine assemblage of water monitors offers an interesting case study in the diversification patterns in the archipelago (review: Brown *et al.* 2013). Surprisingly, these highly mobile species show patterns of diversity in

line with the classic Pleistocene Aggregate Island Complex (PAIC) paradigm (Heaney 1985; Brown & Diesmos 2002, 2009; Roberts 2006; Siler *et al.* 2010, 2012), wherein complexes of islands that were joined together as single land masses during interglacial cycles (and lowered sea levels) share faunal affinities and evolutionary histories. Although there is a growing body of literature highlighting cases that apparently contradict or deviate in various ways from this paradigm (Brown & Diesmos 2009; Linkem *et al.* 2010; Siler *et al.* 2010; Brown *et al.* 2013), it is surprising to find that the habitat generalist monitor lizards with high capacities for dispersal over marine channels (Hoogerworf 1954; Gaulke 1991; Rawlinson *et al.* 1992) in large part conform to the PAIC paradigm's predictions regarding species distributions and patterns of endemism (Brown & Diesmos 2009).

The commercial trade (both legal and illegal) in reptiles and amphibians is a direct source of decline for natural populations, however the actual effect of commercial harvest on populations is often difficult to measure given the parameters involved (Sutherland 2001). Regardless, identifying lineages that may be at risk of overexploitation based on sheer numbers can be easily accomplished when reference data from natural populations are available (Stuart & Parham 2007; Fong *et al.* 2007; Li *et al.* 2011; Spinks *et al.* 2012; Welton *et al.* 2013a). When genetically divergent lineages, masquerading under a single taxon and facing unbalanced harvest pressures are identified, those lineages must be recognized in order to warrant the application of relevant conservation resources. For example, the Bicol Peninsula should be considered an important target of future conservation efforts. Our findings, coupled with those of Welton *et al.* (2013a) and Siler *et al.* (2013), support the presence of unique evolutionary lineages of large vertebrate taxa that are endemic to the Bicol faunal region. Both water monitors (Welton *et al.* 2013a) and sailfin lizards (*Hydrosaurus* sp.; Siler *et al.* 2014) are being targeted by the illicit pet trade in vital habitat necessary for the persistence of these lineages (Bicol Peninsula, Luzon). Additionally, the findings of Welton *et al.* (2013a,b) likewise support the recognition of Mindoro and Semirara islands representing a unique faunal region in the Philippines, containing floral and faunal components with distinct evolutionary histories.

The findings of Welton *et al.* (2013b), and the descriptions provided here, underscore the need for comprehensive phylogenetic analyses when attempting to fully enumerate the biodiversity of a given region. The point is made clearly by the case of Philippine water monitor lizards where an inadequate understanding of species diversity would have persisted if not for both morphological (Koch *et al.* 2010; data presented here) and genetic data that have recently come to light (Welton *et al.* 2013a,b). Morphologically conserved, cryptic, or phenotypically similar taxa do not always represent single, cohesive, clades but rather can comprise multiple, distinct evolutionary lineages that are recovered in unexpected positions in phylogenies, suggesting unanticipated evolutionary and biogeographic relationships (Welton *et al.* 2013a,b; Barley *et al.* 2013). Necessarily, extensive genetic sampling of biogeographically unique components from throughout the distribution of widespread taxa are warranted in order to fully understand the evolutionary history of a given taxon, and test both historical and contemporary taxonomic hypotheses (Linkem *et al.* 2010; Welton *et al.* 2013a,b; Brown *et al.* 2014).

Specimens examined

Varanus bangonorum **sp. nov.** (17 specimens): Philippines, Mindoro Island: CAS 15766–70; Occidental Mindoro Province, Municipality of Paluan, Barangay Harrison, Sitio Ulasan, locality *Matingaram*: KU 308403, 308437; Municipality of Sablayan, Barangay Malisbong, Sitio Aruyan: KU 335742–44; Municipality of San Jose: CAS 85674, 85675; Oriental Mindoro Province, Municipality of Naujan: CAS-SUR 28130; Mt. Halcon: USNM 37869; Semirara Island, Antique Province, Municipality of Caluya, Barangay Tinogboc: KU 305151, 305161, 305163.

Varanus dalubhasa **sp. nov.** (10 specimens): Philippines, Catanduanes Island, Catanduanes Province, Municipality of Bato, Barangay Buenavista: KU 308216; Luzon Island, Camarines del Sur Province, Municipality of Presentacion, Barangay Maangas: KU 306601; Camarines Norte Province, Municipality of Labo, Barangay Tulay Na Lupa: KU 313880; Quezon Province, Municipality of Calauag: KU 305155; Barangay Madlangdungan: KU 306602, 306603; Municipality of Real: USNM 163985; Polillo Island: KU 326702, 326703; Quezon Province, Municipality of Burdeos: USNM 512318.

Varanus marmoratus (11 specimens): Philippines, Batan Island, Batanes Province, Municipality of Basco, Barangay Kayvalugangn, Sitio Masupit: KU 314033; Calayan Island, Cagayan Province, Municipality of Calayan, Barangay Balatbat, locality *Limandok*: KU 304595; Barangay Magsidel, locality *Macarra*: KU 304879, 304880; Lubang Island, Occidental Mindoro Province, Municipality of Lubang, Barangay Vigo, Sitio Dangay: KU 322191;

Luzon Island, Aurora Province, Municipality of Casiguran, Barangay Casapsipan: KU 323434, 323439; Municipality of Maria Aurora, Barangay Villa Aurora, Sitio Dimani, Aurora Memorial National Park: KU 323435; Municipality of San Luis, Barangay Real, Sitio Minoli: KU 323440; Batanes Province, Municipality of Basco, Barangay Kayvalugangn, Sitio Masupit: KU 314033; Bulacan Province, Municipality of Doña Remedios Trinidad, Barangay Kabayunan, Sitio Langud: KU 329428; Ilocos Norte Province, Municipality of Adams, Barangay Adams: KU 330133.

Varanus nuchalis (7 specimens): Philippines, Masbate Island, Masbate Province, Municipality of Masbate City: KU 335261; Negros Island, Negros Occidental Province, Municipality of Cauayan, Barangay Camalanda-an: KU 305153, 305157; Municipality of Silay City, Barangay Patag: KU 335262; Sibuyan Island, Romblon Province, Municipality of Magdiwang, Barangay Talaba, Mt. Guiting-Guiting Natural Park: KU 305134, 305148; Barangay Tampayan: KU 305172.

Varanus palawanensis (9 specimens): Philippines, Candaraman Island, Palawan Province, Municipality of Balabac: USNM 39928; Malapina Island, Palawan Province, Municipality of Coron: USNM 39929; Palawan Island, Palawan Province, Municipality of Puerto Princessa: KU 79146–50; Puerto Princessa City: KU 327843; Municipality of Brooke's Point, Barangay Mainit, Mainit Falls: KU 309607.

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