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Two new species of monitor lizards (Squamata: *Varanus*) endemic to the Louisiade and Tanimbar Archipelagos with a key to the subgenus *Euprepiosaurus*

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ABSTRACT

We describe two new species of *Varanus*, one each endemic to the Louisiade and Tanimbar Archipelagos in Papua New Guinea and Indonesia, respectively. The new species belong to the subgenus *Euprepiosaurus* and, therein, to the widely distributed and relatively species-rich *Varanus indicus* group. They can be distinguished from all other recognised species by scalation, colour-pattern and genetic differences. The new species from Tanimbar is most closely related to *V. indicus* and *V. melinus*, from which it can be distinguished by its dark blue/grey tongue and higher middorsal and midventral scale counts. The new species from the Louisiades can be distinguished from its phylogenetically and geographically nearest relative, *V. chlorostigma*, by the presence of dorsal crossbands, the mostly pink tongue mottled with grey, and higher midbody scale count. The Louisiades constitute the easternmost archipelago of Milne Bay Province in eastern Papua New Guinea, and they host a diverse herpetofauna with a high degree of endemism; *Varanus louisiadensis* sp. nov. increases the known number of herpetofaunal endemics in that archipelago to 60. The Tanimbar Islands are situated in the southern part of Maluku Province (Moluccas), Indonesia, and are a minor centre of vertebrate endemism; *Varanus tanimbar* sp. nov. increases the number of known herpetofaunal endemics there to six.

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Introduction

Lizards of the genus *Varanus* Merrem, 1820 occurring in the south-western Pacific are largely confined to a clade comprising the monophyletic subgenus *Hapturosaurus* Bucklitsch, Böhme and Koch, 2016 plus three species groups within its monophyletic sister group, the subgenus *Euprepiosaurus* Fitzinger, 1843 (Ziegler *et al*. 2007; Weijola *et al*. 2019). *Hapturosaurus* consists of eight species found across New Guinea, several of its

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surrounding islands, and the northern tip of Australia. Within *Euprepiosaurus*, the *V. jobiensis* Ahl, 1932 group consists of a single nominal species restricted to New Guinea and the land-bridge island of Waigeo; the *V. doreanus* Meyer, 1874 group consists of four species ranging from New Britain to Mussau, New Guinea, Aru, Waigeo, Biak and Halmahera; and the *V. indicus* Daudin, 1802 group comprises 11 nominal species widely ranging from the Moluccas to the Solomon Islands and from northern Australia through western Micronesia (Weijola *et al*. 2019, 2020). The exact phylogenetic relations of *Varanus caerulivirens* Ziegler, Böhme and Philipp, 1999 and *V. zugorum* Böhme and Ziegler, 2005 – also within the subgenus *Euprepiosaurus* – are unknown, but neither appears to fit clearly into any of these three species groups. Phylogenetic results obtained using molecular data indicate that each of these clades requires further taxonomic investigation, but the *V. indicus* group is of greatest interest because it has the broadest range (Figure 1), greatest number of lineages, and most recent divergence times, having radiated across this vast region only since the Pleistocene (0.9–1.9 Mya).

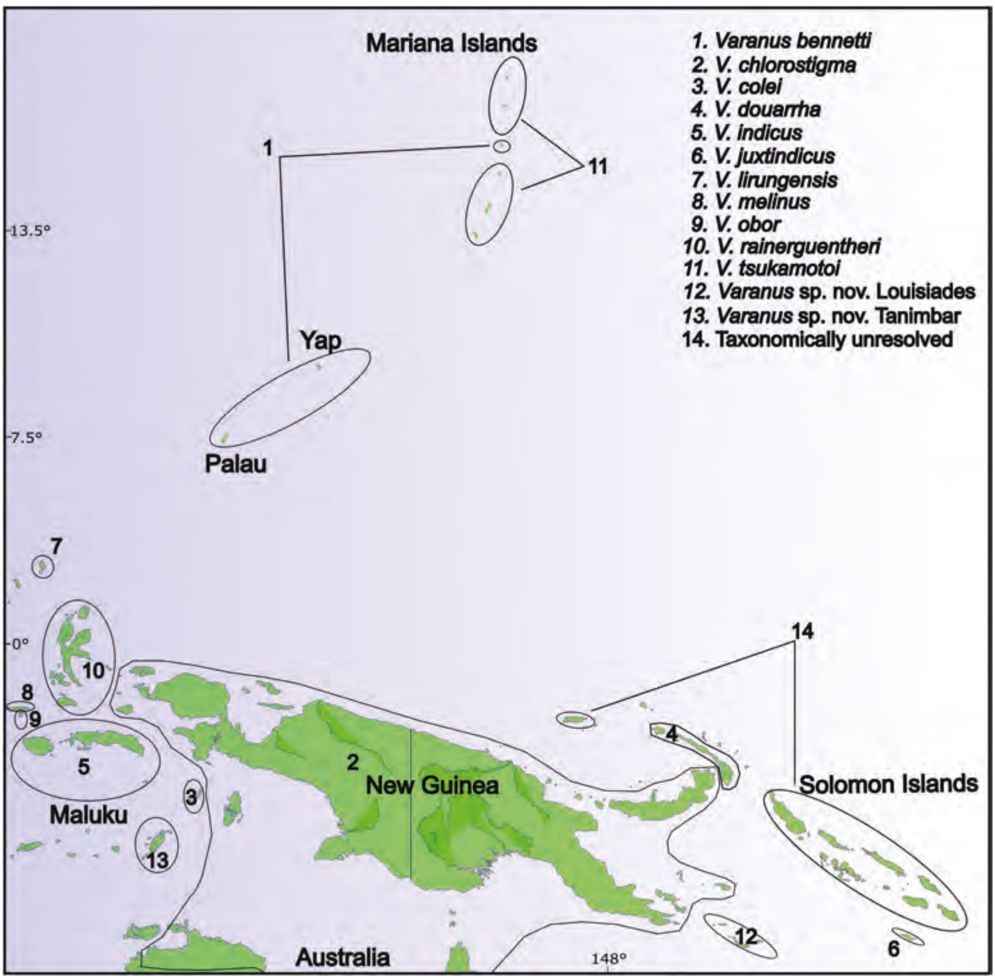

Figure 1. Map of the western Pacific region showing the geographic ranges of the species of the *Varanus indicus* group.

Within the *Varanus indicus* group, the molecular phylogeny published by Weijola *et al*. (2019) supported the status of the four then-recognised species for which genetic material was available but also identified several other distinct lineages as candidate species, although these have historically been subsumed under the name *V. indicus*. Subsequently, the taxonomic status of the Micronesian populations was revised, resulting in the recognition of *V. bennetti* Weijola, Vahtera, Koch, Schmitz and Kraus, 2020 and *V. tsukamotoi* Kishida, 1929 from Palau, the Federated States of Micronesia, and the Mariana Islands (Weijola *et al*. 2020). Böhme *et al*. (2019) described *V. colei* Böhme, Jacobs, Koppetsch and Schmitz, 2019 from the Kei Islands based mainly on morphological characters.

Here we continue to refine the taxonomy of *Euprepiosaurus* by describing two additional insular species of the *V. indicus* group (senso Weijola *et al*. 2019), of which one is endemic to the Louisiade Archipelago in easternmost Papua New Guinea and the other is endemic to the Tanimbar Islands in Maluku Province, Indonesia. Molecular data (Weijola *et al*. 2019) indicate that both species represent independent evolutionary lineages within the *V. indicus* group, and each is reliably distinguished from related species by external morphology. We also provide an updated key to the species belonging to the subgenus *Euprepiosaurus*, which has grown from 11 to 20 recognised species since the last key to the subgenus was published (Ziegler *et al*. 2007).

In this paper we follow the nomenclatural use for *V. indicus* Daudin, 1822, *V. cerambonensis* Philipp, Böhme and Ziegler, 1999, and *V. chlorostigma* Gray, 1831 proposed for the International Commission on Zoological Nomenclature (ICZN) in Case 3676 (Weijola 2015) and accepted in ICZN Opinion 2451 (ICZN 2020). Accordingly, *V. cerambonensis* is treated as a junior synonym of *V. indicus* and the name *V. chlorostigma* Gray, 1831 is used as the valid name for the species on New Guinea, many of its satellite islands, and parts of northern Australia (*V. indicus sensu* Philipp *et al*. 1999), while *V. indicus* is the valid name for the taxon endemic to Ambon, Seram, Buru, Saparua, Haruku and Banda islands. Because *V. indicus* is the oldest name for any species in this clade, we continue to refer to it as the '*Varanus indicus* group'.

Materials and methods

Morphology

Morphometrics, scale counts, mensural ratios and their abbreviations follow Brandenburg (1983) (Table 1). We took measurements with a tape (body, tail) or callipers (head) to nearest 1 mm (body, tail) or 0.5 mm. (head) and obtained comparative measurements and scale counts for *V. bennetti, V. caerulivirens, V. chlorostigma, V. colei, V. doreanus, V. douarrha* Lesson, 1830, *V. finschi* Böhme, Horn and Ziegler 1994, *V. indicus, V. juxtindicus* Böhme, Philipp and Ziegler, 2002, *V. lirungensis* Koch, Arida, Schmitz, Böhme and Ziegler, 2009, *V. melinus* Böhme and Ziegler, 1997, *V. obor* Weijola and Sweet, 2010, *V. rainerguentheri* Ziegler, Böhme and Schmitz 2009, *V. semotus* Weijola, Donnellan and Lindqvist 2016, *V. tsukamotoi, V. yuwonoi* Harvey and Barker, 1998 and *V. zugorum* from the literature (Brandenburg 1983; Böhme and Ziegler 1997, 2005; Harvey and Barker 1998; Böhme *et al*. 2002; Koch *et al*. 2009; Weijola and Sweet 2010; Weijola *et al*. 2017, 2020; Böhme *et al*. 2019). We also took novel scale counts for *V. jobiensis* (Supplemental Table S1). We conducted an *a posteriori* linear discriminant analysis in PAST v. 3.24 [33] on scalational characters P, Q, XY, m, S, T, N and R, including candidate

Table 1. Definitions of, and abbreviations used for, measurements, mensural ratios, and scale counts.

Symbol	Description
Measurements	
A	Head length from snout to anterior dorsal margin of tympanum
B	Head width at maximum span of postorbital arch
C	Head depth at midpoint of orbit
D	Head–neck length from tip of snout to gular fold
E	Body length from gular fold to cloaca
F	Tail length from cloaca to tip of tail
G	Facial length from centre of nostril to anterior margin of orbit
H	Snout length from tip of snout to centre of nostril
TL	Total length
SVL	Snout to vent length
Mensural ratios	
1	Relative tail to body length – F/SVL
10	Relative head length to head width – A/B
11	Relative head length to head height – A/C
Scale counts	
S	Midbody scale rows
XY	Dorsal scale rows from posterior margin of tympanic recess to anterior margin of hind limbs
T	Rows of ventral scales from gular fold to anterior margin of hind limbs
X	Rows of dorsal scales from posterior margin of tympanic recess to gular fold
m	Scales around neck at anterior margin of gular fold
N	Rows of ventral scales from tip of snout to gular fold
P	Scales from rictus to rictus across dorsum of head
Q	Scales around tail base
R	Scales around tail counted at 1/3 of tail length from the base
DOR	Number of dorsal scale rows from the last occipital scale to a point dorsal to the posterior margin of the cloaca
VEN	Ventral scales from the gular fold to the anterior margin of the cloaca

species 1 from the Louisiade Archipelago (n = 11) and candidate species 2 from Tanimbar (n = 4), *V. bennetti* (n = 11), *V. chlorostigma* (n = 53), *V. douarrha* (n = 14), *V. indicus* (n = 14), *V. lirungensis* (n = 11), *V. melinus* (n = 4) *V. rainerguentheri* (n = 7) and *V. tsukamotoi* (n = 38) (Supplemental Table S2). We excluded *V. colei*, *V. juxtindicus*, and *V. obor* from this analysis due to insufficient numbers of specimens or published scale count data. Morphological etymology in the descriptive sections follows Smith (1946).

Museum abbreviations are: American Museum of Natural History, New York (AMNH), Australian Museum, Sydney (AMS); Muséum national d'Histoire naturelle, Paris (MNHN); Museum Zoologicum Bogoriense, Cibinong (MZB); Naturalis Biodiversity Center, Leiden (RMNH); National Museum of Natural History, Washington, DC (USNM); University of Texas at Arlington, Arlington, Texas (UTA); Western Australian Museum, Perth (WAM); Zoological Museum Amsterdam (currently joined with Naturalis Biodiversity Center), Leiden (ZMA); Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK); Zoological Museum, University of Copenhagen (ZMUC); Zoological Museum, University of Turku, Finland (ZMUT).

Results

Morphology

The linear discriminant analysis retrieved a group structure that distinguished among several of the included species and candidate species (Figure 2). The candidate species from Tanimbar shows partial overlap in multivariate space with the candidate species

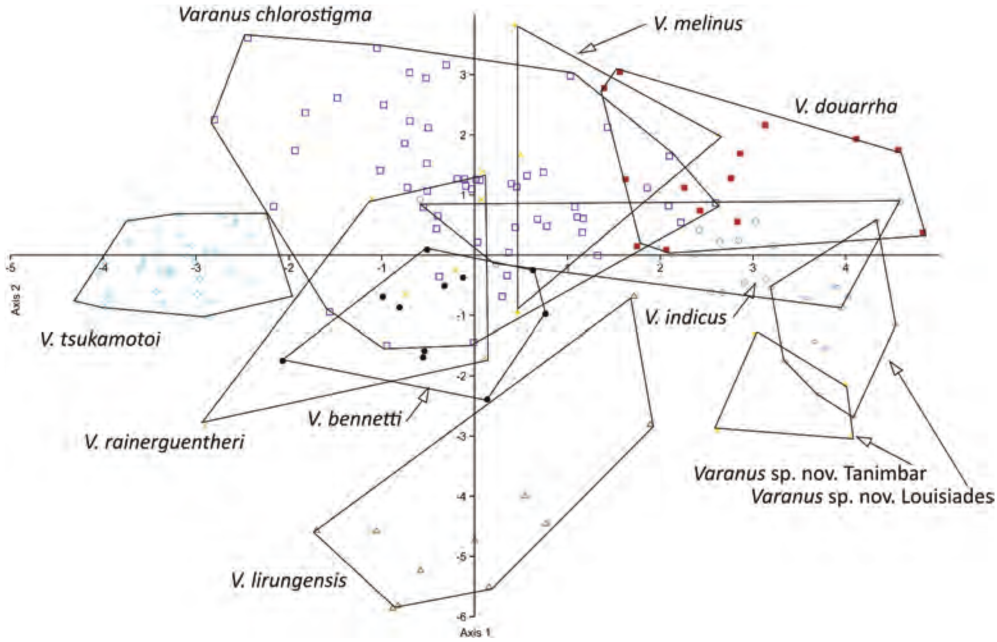

Figure 2. Linear discriminant analysis showing morphospaces for members of the *Varanus indicus* group based on scalation characters P, Q, R, S, T, N, XY and m.

Table 2. Factor loadings, proportion of variance and eigenvalues of the linear discriminant analysis. The amount of correctly assigned specimens is 79.3%.

	Axis 1	Axis 2	Axis 3
P	0.151	0.068	0.330
Q	0.045	0.124	0.013
R	−0.076	−0.009	0.021
S	0.092	−0.035	−0.075
T	0.161	−0.051	−0.080
N	−0.101	0.035	−0.057
XY	−0.059	−0.115	0.072
m	0.003	0.002	−0.038
Eigenvalue	5.065	2.323	1.257
Percentage	51.26	23.51	12.72

from the Louisiades but no overlap with any other species in the *V. indicus* group. The candidate species from the Louisiades also shows partial overlap with *V. indicus* and minor overlap with *V. douarrha*. Neither candidate species shows morphological overlap with their genetically and geographically nearest species, which is *V. chlorostigma* for the candidate species from the Louisiades, and *V. indicus* and *V. melinus* for the candidate species from Tanimbar (Weijola *et al*. 2019). Axes 1 and 2 account for almost 75% of morphometric variance in the samples; counts N, P, and T provided the greatest discrimination on Axis 1 and counts Q and XY on Axis 2 (Table 2).

Taxonomy

The morphological data presented here and the previously published molecular phylogenetic analyses (Weijola *et al*. 2019, 2020) both indicate that the *Varanus* populations from the Louisiades and Tanimbar islands comprise two independent taxonomic units distinguishable from all other described species in the *V. indicus* group by both genetic and morphological characters. This combination of evidence suggests that they are independently evolving lineages that fulfill the definition of species according to the unified species concept applicable to allopatric species (De Queiroz 2007), and we describe them as new species herein.

Species accounts

Varanus louisiadensis sp. nov.
(Figures 3–6)

Holotype
ZMUT Sa197 (Figures 3, 4) collected by Valter Weijola, 22 April 2013, at Bwagaoia, Misima Island, Milne Bay Province, Papua New Guinea.

Paratypes
Papua New Guinea: Milne Bay Province: AMNH 76828, ZMUT Sa196, Sa198 (Misima Island), ZMUT Sa199 (Figure 5)–200, AMNH 76755 (Rambuso, Sudest Island), ZMUT Sa201 (Figure 6), AMNH 76735–76737 (Saman [ZMUT], Jinian [AMNH], Rossell Island).

Etymology
The specific epithet refers to the Louisiade Archipelago of Milne Bay Province, Papua New Guinea, where this species is endemic.

Diagnosis
Varanus louisiadensis sp. nov. is a member of the subgenus *Euprepiosaurus*, which is defined by having the unique combination of an asymmetric sperm groove on the hemipenis and a laterally compressed tail (Ziegler *et al*. 2007). Molecular phylogenetic analyses place it within the *V. indicus* species group defined by the unilateral paryphasmata ornamentation of the hemipenis and lack of blue pigmentation on the tail (Ziegler *et al*. 2007; Weijola *et al*. 2019). It can be distinguished from all other species of *Euprepiosaurus* by its unique combination of: (1) dorsum black with more-or-less well-defined crossbands composed of yellow ocelli and/or dots, better defined in juveniles and subadults than adults; (2) tail black with distinct yellow bands, better defined in juveniles and subadults than adults; (3) tongue tines and a variable section of the mid-dorsal tongue surface dark grey, the remainder being pink; (4) pink-orange pigmentation usually present on cheeks and sides of neck; (5) venter pale yellow; (6) mid-body scale rows (S) 142–163; (7) mid-dorsal scale rows (XY) 139–169; (8) ventral scale rows (T) 101–113; (9) scales around neck (m) 101–118.

Comparisons. *Varanus louisiadensis* sp. nov. can be distinguished from *V. doreanus* and *V. jobiensis* (both present in Milne Bay Province but not in the Louisiade Archipelago) by the lack of blue pigmentation on the tail (vs present in *V. doreanus* and *V. jobiensis*); and from *V. chlorostigma* by the presence of yellow dorsal ocelli (vs absent in *V. chlorostigma*) and the bi-coloured pink/grey tongue (vs completely grey/blue in *V. chlorostigma*).

Figure 3. Dorsal, ventral and head profile of the holotype (ZMUT Sa197) of *Varanus louisiadensis* sp. nov.

Within the *V. indicus* group, *Varanus louisiadensis* sp. nov. is only likely to be confused with the remotely allopatric *V. colei*, *V. douarrha*, *V. finschi*, *V. indicus* or *V. lirungensis*, with which it shares a similar dorsal pattern composed of transverse bands of yellow ocelli. It is

Figure 4. The holotype (ZMUT Sa197) of *Varanus louisiadensis* sp. nov. on Misima Island (photo VW).

similar to *V. colei* in most scalational characters, but has slightly higher averages of S (153.5 vs 146) and m (109.6 vs 102.3) scale counts, and lacks the bright white gular region that characterises *V. colei*. It can be distinguished from *V. douarrha* by its uniformly yellow/orange throat (vs marbled with dark grey in *V. douarrha*) and its higher average S (153.5 vs 140.9), T (107.4 vs 96.9), XY (153.3 vs 136) and m (109.6 vs 100.7) scale counts. It can be distingushed from the more distantly related *V. finschi* by having a pink tongue with dark pigmentation on the distal part (vs a uniformly pink-white-yellow tongue in *V. finschi*), and from *V. indicus* by the lack of a distinct yellow temporal band (vs present in *V. indicus*). It can be distinguished from *V. lirungensis* by its average higher scale counts for characters Q (92.1 vs 83), S (153.5 vs 141.6), T (107.4 vs 97.5), XY (153.3 vs 139.8) and m (109.6 vs 97.8).

Description of the holotype. Well-preserved juvenile with a small incision on left thigh from where tissue was removed. Dorsal ground colour of body, tail, head and limbs black, covered by distinct crossbands of yellow rosettes and dots. Habitus slender; total length 585 mm (SVL = 240 mm, F = 345 mm); tail 1.44 times as long as body, 36.3 times as long as high (9.5 mm) at midlength, round at base, becoming laterally compressed distally, and with mid-dorsal ridge two scales wide starting at about 30 mm from base. Thirteen discernible cream-coloured crossbands on distal ¾ of the tail. Venter cream yellow, marmorated with brown, with incomplete crossbands between hind legs and gular fold that are one scale row wide. Throat cream with scattered brown scales laterally. Ventral surfaces of limbs cream with narrow, pale-brown bands and dots. Under tail cream with

Figure 5. Paratype (ZMUT Sa199) of *Varanus louisiadensis* sp. nov. on Sudest Island (photo VW).

interspersed brown scales at base of tail. Dorsal surfaces of limbs black with yellow dots, stripes, and ocelli composed of about 1–8 scales.

Head 1.82 times as long as wide, black with yellow dots and short stripes and with bright-yellow parietal scale. Well-defined temporal bands or postocular stripes lacking on both sides of head. Labial scales white at snout but each from below nostril to labial commissure with a brown dot. Nostrils oval, situated slightly nearer to snout than eye. Nasal capsules expanded, with shallow sagittal groove on rostrum.

Nuchal scales irregular in shape on anterior part of the neck, round on mid-neck, smaller and elongate on lower neck, all surrounded by granules. Dorsal scales somewhat irregular in size, elongate, keeled, each surrounded by few granules, most with single pit. Lateral caudal scales regular in size and shape, rectangular, flattened, usually with single posterior pit. Mid-ventral caudal scales twice as wide as mid-dorsal caudal scales, elongate, with sharp keel. Mid-ventral scales rectangular, flat, posterior margin rounded and bordered by row of granules. Scales on chest irregular in size, round to polygonal, each surrounded by few granules. Gular scales roundish to polygonal, each surrounded by granules. Mental scales elongate, rectangular to polygonal.

Infrafemorals and infratibials round, each surrounded by row of granules along lateral and posterior margins. Infracarpals and infratarsals round and highly domed, with brown traction pads on most scales. Subdigital scales domed, of irregular size and shape. Fourth toe with row of 11 (R) and 12 (L) enlarged scales along outer margin; third toe with four slightly enlarged scales along outer margin. Claws dark brown, sharp, and recurved.

Figure 6. Paratype (ZMUT Sa201) of *Varanus louisiadensis* sp. nov. on Rossell Island (photo VW).

Occipital scales flattened, relatively small, irregularly polygonal. Supraocular scales 8 (R) and 7 (L), enlarged, irregular in shape and size, each densely covered with pits. Scales of forehead and rostrum polygonal, flattened, larger than occipital scales. Supralabials pentagonal or rectangular, covered with pits. Infralabials of irregular size, pentagonal or polygonal. Tines of tongue blue, its trunk pink, except for thin, blue median line on both dorsal and ventral sides.

Scale counts. S: 157, XY: 155, DOR: 164, T: 103, VEN: 123, X: 43, m: 105, P: 42, Q: 93.

Measurements. SVL: 240 mm, F: 345 mm, TL: 585 mm, E: 135 mm, D: 84 mm, A: 40 mm, B: 22 mm, C: 15.5 mm, G: 10.5 mm, H: 8.5 mm, I: 21.5 mm.

Scale counts, measurements and proportion indices of the type series. See Table 3.

Variation and colouration in life. Variation is mostly seen in the dorsal crossbands which can be composed of either spots and ocelli or spots only (Figures 4–6). Judging from the material at hand these also tend to become less distinct as the animals age. The extent of grey pigmentation on the tongue varies considerably between individuals, varying from colouring only the tines to encompassing the whole dorso-distal half of the trunk.

Table 3. Scale counts, measurements (in mm), and mensural ratios for the type series of *V. louisiadensis* sp. nov. and *V. tanimbar* sp. nov.

		P	Q	R	S	T	VEN	N	X	XY	DOR	C	M	SVL	F	TL	A	B	C	G	H	1	10	11
***Varanus louisiadensis* sp. nov.**																								
AMNH 76736	Rossell	41	91	61	157	112	132	94	42	148	163	28	114	125	165	290	24.5	13	9	6	6	1.32	1.88	2.72
AMNH 76737	Rossell	47	88	58	142	108	125	91	40	139	152	28	112	115	155	270	24	12	9	5.5	5.5	1.35	2.0	2.67
AMNH 76755	Sudest	47	100	66	163	107	128	101	43	158	170	25	110	145	205	350	29.5	16	11	7.5	6.5	1.41	1.84	2.68
AMNH 76828	Misima	47	86	53	152	103	119	93	45	148	160	25	118	205	300	505	36	19.5	14	11	8	1.46	1.85	2.57
AMNH 76735	Rossell	42	91	55	151	106	126	88	45	155	170	26	101	270	400	670	49	27	18	11	10.5	1.48	1.81	2.72
ZMUT Sa196	Misima	41	90	59	154	101	119	89	41	146	158	26	109	320	480	800	52	26	18	14	13	1.50	2.0	2.89
ZMUT Sa197	Misima	42	93	60	157	103	123	87	43	155	164	25	105	240	360	600	40	22	15	11.5	9	1.50	1.82	2.67
ZMUT Sa198	Misima	44	90	60	147	110	129	95	41	149	160	26	103	305	470	775	51	27	17	15	12	1.54	1.89	3.0
ZMUT Sa199	Sudest	43	100	62	161	106	123	90	47	169	184	26	107	460	630	1090	68	35	23	21	16		1.94	2.96
ZMUT Sa200	Sudest	44	97	66	161	112	134	94	42	168	180	25	118	460	710	1170	70	37	25	22	17	1.54	1.89	2.80
ZMUT Sa201	Rossell	40	87	60	144	113	132	91	42	151	163	25	109	400	540	940	62	33	23	18	16		1.88	2.70
***V. tanimbar* sp. nov.**																								
WAM112255	Yamdena	43	91	58	158	107	128	91	44	159	170	24	109	187	295	482	36.3	19.5	14.5	11.3	8.4	1.59	1.86	2.50
WAM109940	Yamdena	48	93	65	161	109	128	93	44	170	182	21	113	170	255	425	34.7	18	12.9	10.6	7.5	1.50	1.93	2.69
WAM112323	Selaru	46	95	60	145	107	125	92	48	162	173	21	119	305			61.7	34	24	20.5	14		1.81	2.57
WAM109896	Yamdena	42	89	63	152	107	126	90	45	164	175	22	109	390	680	1070	72	37	25.7	21.8	14.7	1.74	1.95	2.80

Range. *Varanus louisiadensis* sp. nov. has been recorded from coastal and lowland areas on all three major islands of the Louisiade Archipelago: Misima, Sudest, and Rossel (Figure 7). Considering the good dispersal abilities of monitors in the *V. indicus* group it can also be expected to occur on nearby smaller islands with suitable habitat, such as Paneati and Panatinane islands, but its presence on satellite islands of the Louisiade Archipelago has yet to be confirmed.

Natural history. *Varanus louisiadensis* sp. nov. does not appear to be particularly abundant on any of the larger islands in the Louisiades, and active searches on Misima, Sudest and Rossell by VW in 2013 resulted in a total of 16 sightings and five collected specimens over the course of three weeks. All of these observations were made around the coast in stands of mangrove or other coastal woodlands, often intermixed with coconut plantations.

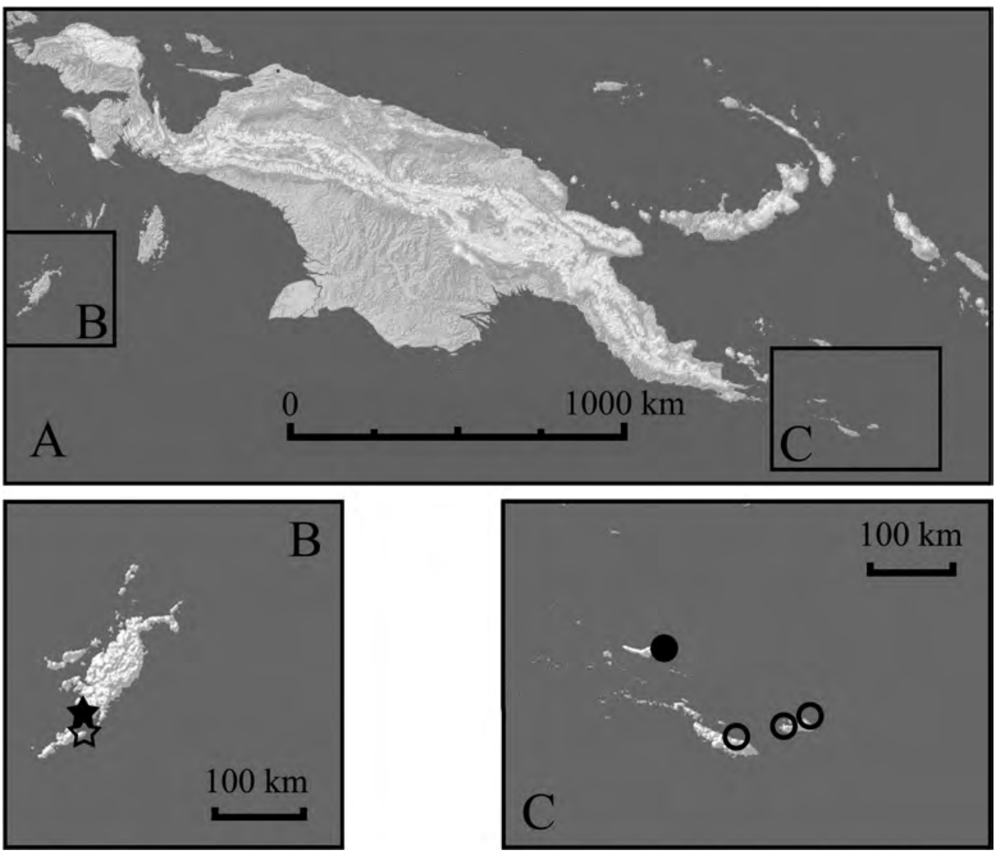

Figure 7. Map of the Papuan region (A) with the Tanimbar Islands (B) and Louisiade Archipelago (C) enlarged. The type locality of *Varanus louisiadensis* sp. nov. on Misima island is indicated with a filled circle, and additional collection localities for the paratypes on Sudest and Rossell are indicated by open circles. The type locality of *V. tanimbar* sp. nov., Latdalam, is indicated by a filled star, and the collection locality of one of the paratypes at Adaut, Selary Island, with an open star.

Remarks

The molecular phylogeny of *Euprepiosaurus* published by Weijola *et al*. (2019) retrieved monophyly of the samples of *V. louisiadensis* sp. nov. from Misima, Sudest, and Rossel with high support. The samples from Misima and Sudest were genetically most similar and formed a sister group to those from Rossel. *Varanus louisiadensis* sp. nov. formed a sister lineage to *V. chlorostigma*; that relationship was not well supported, but it is sensible on geographic grounds alone. The shortest ND4 (NADH dehydrogenase subunit 4) pairwise distances of *V. louisiadensis* sp. nov. are to *V. chlorostigma* (3.3%) and *Varanus sp*. from the Admiralty Islands (3.4%).

Varanus tanimbar sp. nov.
(Figures 8–12)

Holotype

WAM112255 (Figure 8) collected by Richard How (RH), Ronald Johnstone (RJ) and Darrell Kitchener (DK), 24 April 1993, at Latdalam, Yamdena Island, Tanimbar Islands, Indonesia.

Paratypes

WAM109940 (Figure 9) collected by RH, RJ and DK, 20 April 1993, at Latdalam, Yamdena Island, WAM109896 collected by RH, RJ and DK, 18 April 1993, at Lorulun, Yamdena Island, and WAM112323 collected by RJ and I. Maryanto, 27 April, at Adaut, Selaru Island, Tanimbar Islands, Indonesia.

Etymology

The specific epithet *tanimbar* is a noun in apposition and refers to the Tanimbar Archipelago of Maluku, Indonesia, to which this species is endemic.

Diagnosis

Varanus tanimbar sp. nov. is a member of the subgenus *Euprepiosaurus*, which is defined by having the unique combination of an asymmetric sperm groove and laterally compressed tail (Ziegler *et al*. 2007). Molecular phylogenetic analyses place it within the *V. indicus* species group defined by the unilateral paryphasmata ornamentation of the hemipenis and lack of blue pigmentation on the tail (Ziegler *et al*. 2007; Weijola *et al*. 2019). It can be distinguished from all other species of *Euprepiosaurus* by its unique combination of: (1) dorsum black with more or less well-defined crossbands composed of lemon-yellow ocelli and/or dots; (2) tail black with distinct yellow bands; (3) dorsal aspect of tongue blue-grey; (4) temporal region typically ornamented with a dark temporal band and a lemon-yellow postocular stripe; (5) venter pale yellow; (6) mid-body scale rows (S) 145–161; (7) mid-dorsal scale rows (XY) 159–170; (8) ventral scale rows (T) 107–109; (9) scales around neck (m) 109–119.

Comparisons. *Varanus tanimbar* sp. nov. is the only species of *Varanus* known to occur in the Tanimbar Islands. It can be distinguished from other allopatric species of *Euprepiosaurus* present in the Moluccas by differences in scalation and colour pattern: from *V. caerulivirens* and *V. yuwonoi* by the lack of blue pigmentation on the tail (vs

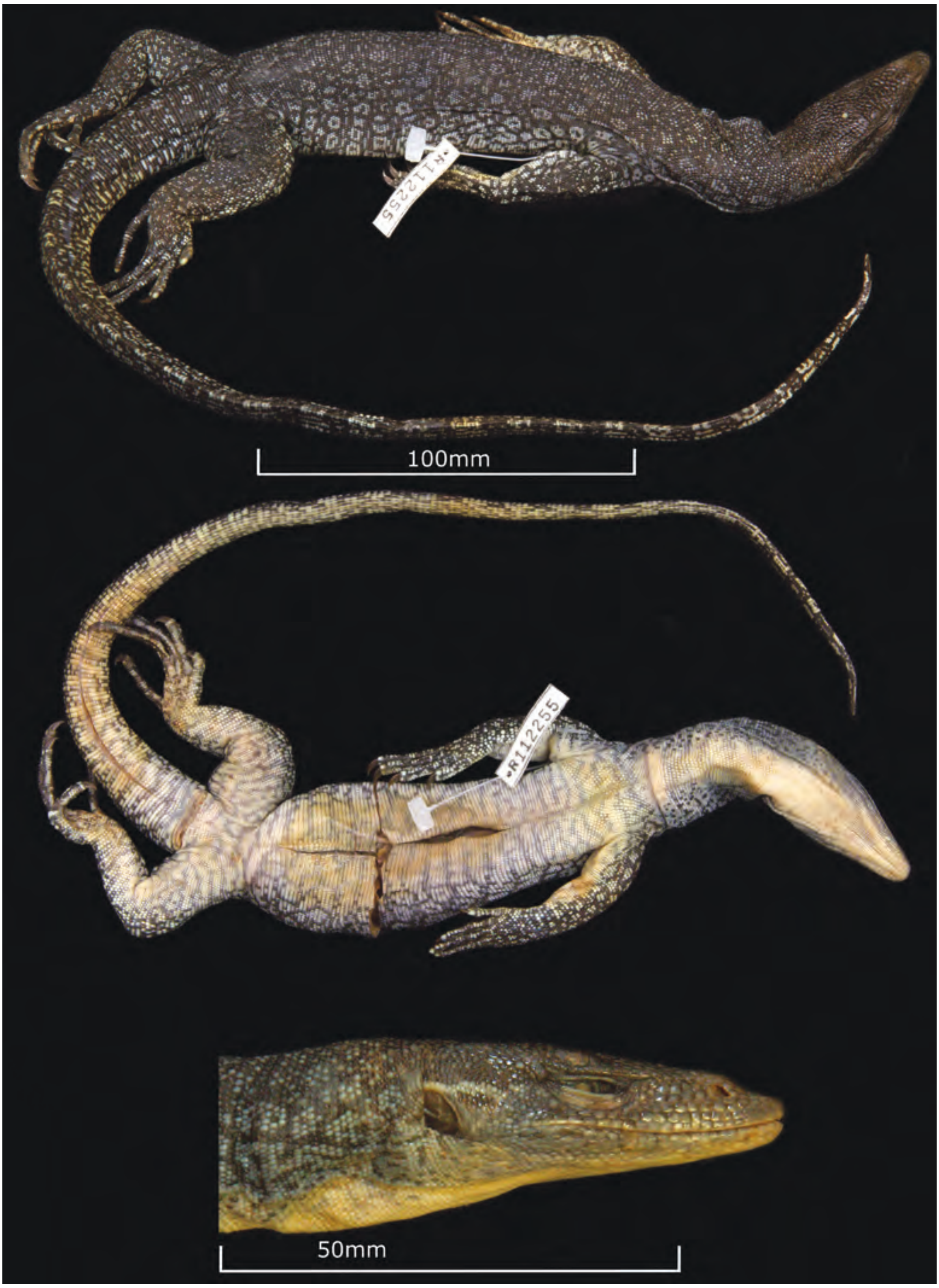

Figure 8. Dorsal, ventral and head profile of the holotype (WAM112255) of *Varanus tanimbar* sp. nov.

present in *V. caerulivirens* and *V. yuwonoi*), from *V. obor* and *V. zugorum* by its black dorsum with rows of yellow ocelli (vs solid black in *V. obor* and solid brown in *V. zugorum*), from *V. melinus* by its black (vs yellow in *V. melinus*) head and dark grey/ blue tongue (vs pink in *V. melinus*), and from *V. rainerguentheri* by having the dorsal

Figure 9. Dorsal and ventral aspect of paratype WAM 109940 of *Varanus tanimbar* sp. nov.

Figure 10. Adult *Varanus tanimbar* sp. nov. male killed by local hunters near Saumlaki, Yamdena (photo VW).

pattern of yellow ocelli arrayed more or less into crossbands (vs more irregularly scattered yellow spots in *V. rainerguentheri*) and the higher mid-body (S) scale counts (145–161 in *V. tanimbar* vs 120–139 in *V. rainerguentheri*).

Figure 11. Juvenile *Varanus tanimbar* sp. nov. caught by local hunters at Saumlaki, Yamdena (photo VW).

Figure 12. Adult *Varanus tanimbar* sp. nov. (WAM 109896) Lorulun, Yamdena Island (photo Richard How).

Within the *V. indicus* group, *Varanus tanimbar* sp. nov. is only likely to be confused with the allopatric *V. colei*, *V. douarrha*, *V. finschi*, *V. indicus*, *V. lirungensis* or *V. louisiadensis* sp. nov., with which it shares a similar dorsal pattern composed of transverse bands of yellow ocelli. It can be distinguished from *V. colei*, *V. douarrha*, *V. finschi*, *V. lirungensis*, and *V. louisiadensis* sp. nov. by the typical presence of a distinct yellow postocular stripe (vs absent in the other species). It can be distinguished from *V. indicus* by its completely blue-grey tongue (vs bicoloured pink and grey in *V. indicus*) and higher average scale counts in characters S (154 vs 141.4), T (107.5 vs 96.3) and m (112.5 vs 103.3).

Description of the holotype. Juvenile, abdomen opened with both single vertical and longitudinal slits; basal 1/3 of tail with longitudinal cut along ventral side. Habitus slender, total length 500 mm, SVL 200 mm, tail length 300 mm; head elongate. Ground colouration of dorsum, neck and head dark brown to black; densely scattered with pale grey/blue (yellow in life) scales; small blotches and rings/rosettes indistinctly arranged as crossbands over dorsum. These rings and spots are composed of grey/blue (yellow in life) scales; the skin surrounding the scales is grey/black. Tail black, banded on distal 2/3 of length by 17 indistinct bands, each 5–7 scale rows wide. Tail 1.5 times as long as body, relatively elongate (36.14 times as long as high at midlength). Dorsal keel formed by 1–4 enlarged mid-dorsal caudal scales starting at ~35 mm posterior to tail base. Tail round at base, becoming triangular where keel is formed and increasingly laterally compressed to around midlength. Ventral ground colour pale cream, intersected by numerous (23) grey crossbands between cloaca and gular fold.

Ventral sides of limbs cream coloured and intersected by mosaic of narrow grey bands. Pale cream stripe 10–12 mm (~18 scale rows) wide between snout and gular fold; throat rapidly turning marmorated lateral to this. Tail cream ventrally, densely covered by indistinct grey crossbands most clearly visible on basal and distal 1/3 of tail. Limbs black dorsally with white/grey (yellow in life) spots composed of about 1–7 scales.

Head 1.96 times as long as wide, dorsal aspect black with small amount of white on most scales, yellow parietal scale, dark temporal band ~5 scales wide, and white postocular stripe ~2 scales wide. Supralabials and infralabials paler than rostrum and dorsal aspect of head. Nostrils slightly elongate, pointed at anterior corner, closer to snout than to eye. Nasal capsules slightly expanded, with shallow sagittal groove on rostrum.

Nuchal scales of irregular shape on upper neck, round at mid-neck, and increasingly elongate towards shoulders; nuchals domed, with one to several scale pits, surrounded by one or two rows of granules. Dorsal scales oval, slightly irregular in size, domed or keeled (towards abdominal region), most with single pit posteriorly and surrounded by single row of granules. Lateral caudal scales rectangular, elongate, with a single pit centrally or posteriorly. Ventral caudal scales rectangular, elongate, strongly keeled, twice length of mid-dorsal caudals, occurring in row of 10 at midlength of tail. Ventral scales of pubic region polygonal to round, bordered posteriorly by row of granules. Abdominal scales rectangular with rounded corners, bordered posteriorly by row of granules. Ventral scales become increasingly less elongate and round towards chest and finally quadrate or polygonal and irregular in shape near gular fold; ventrals polished, often equipped with single pit and with few granules posteriorly. Gular scales rounded with few granules along posterior edge but become oval to rectangular and elongate towards mental region; mental scales larger laterally, rectangular or polygonal and densely covered in pits.

Infrafemorals and infratibials round or polygonal, often with a few granules along posterior margin. Infracarpals and infratarsals round, of irregular size, highly domed. Subdigital scales irregular in size and shape, highly domed to almost flat. Twelve rows of enlarged scales along outer margin of fourth toe; four slightly enlarged scales along outer margin of third toe. Claws brown/translucent, sharp, recurved.

Occipital scales relatively small, irregular, polygonal. Five enlarged, irregularly shaped supraocular scales, elongate rectangular to pentagonal, densely covered with pits. Scales on forehead and rostrum larger than occipital scales, polygonal, flattened. Supralabials rectangular or pentagonal, covered with pits. Infralabials of irregular size, triangular or polygonal. Tines and dorsal aspect of distal half of tongue grey. Lateral sides of tongue white with only a small amount of grey pigment; distal half of ventral aspect pale blue with a grey central groove.

Scale counts. S: 158, XY: 159, DOR: 170, T: 107, VEN: 128, X: 44, m: 109, P: 43, Q: 91.

Measurements. SVL: 200 mm, F: 300 mm, TL: 500 mm, E: 125 mm, D: 75 mm, A: 35.3 mm, B: 18 mm, C: 12.5 mm, G: 10.8 mm, H: 7.0 mm, I: 18.0 mm.

Scale counts, measurements and proportion indices of the type series. See Table 3.

Variation and colouration in life. The paratypes are similar to the holotype although there is some variation in the amount of dark pigmentation on the gular region, venter and ventral surfaces of limbs (Figures 8, 9). While most individuals have a well-defined yellow temporal band, this was absent in one of seven individuals seen by us (Figure 12). In life, dorsal ground colour black; throat, dorsal spots, and ocelli greenish lemon-yellow (Figures 8–12). Tongue pink basally with grey blue on tines and dorsodistal half.

Range. *Varanus tanimbar* sp. nov. is known from Yamdena and Selaru – the two largest islands in the Tanimbar Archipelago. The species is also likely to occur on surrounding islands such as Larat, Fordate, Wotap, Wuliaru, Selu and Sera, but its presence on those islands needs confirmation.

Natural history. There are no specific details about the biology of this species, but it is likely similar in diet and habitat preferences to other closely related species of the *V. indicus* group, which are habitat generalists of mangroves, coastal, and lowland forests (Weijola and Sweet 2015). During a brief visit to Yamdena in 2009, VW found the species being hunted for food by local residents, and this might well suppress populations in the vicinity of human settlements.

Remarks

Varanus tanimbar sp. nov. formed a well-supported clade together with the Moluccan species *V. indicus* and *V. melinus* in the BEAST analysis based on the 16S and ND4 markers used by Weijola *et al*. (2019). Within this Moluccan clade, *V. tanimbar* sp. nov. formed a basal sister lineage to the closely related *V. indicus* and *V. melinus*. ND4 pairwise distances between *V. tanimbar* sp. nov. and these two species are 3.4% and 3.9%, respectively, and 2.3% between *V. indicus* and *V. melinus* (Weijola *et al*. 2019).

Discussion

The molecular phylogeny of Weijola *et al*. (2019) identified four named species as well as eight candidate species within the *Varanus indicus* group, with the candidate species each having a similar degree of genetic divergence to the already recognised species, hence pointing to the need for further partitioning of this species complex. Beyond mere molecular distinctiveness among these widely scattered insular populations, several also had consistent morphological differences that were immediately obvious in the field. Among the eight candidate species, two from Micronesia were geographically distinct and treated in a separate paper that resurrected the name *V. tsukamotoi* for the species in the Mariana Islands and described *V. bennetti* from Palau, Yap, and Sarigan Island (Weijola *et al*. 2020). The remaining six lineages are all from Melanesia (n = 5) and the Moluccas (n = 1), and herein we have treated two of those. The last four lineages – from the Solomon Islands and Admiralty Islands – are more difficult to diagnose, and we defer taxonomic action on those until more detailed molecular phylogenetic and morphological studies have been completed. Many of the islands in the Solomons also require further sampling to obtain a complete understanding of the species diversity and biogeographical patterns of that region.

The biogeographic history of the *Varanus indicus* group remains poorly settled at present. Weijola *et al*. (2019) noted that the most divergent lineages in that group were on islands peripheral to New Guinea, with the more recently derived *V. chlorostigma* occuring on New Guinea and nearby islands. They interpreted that pattern as consistent with the taxon cycle of island species turnover (Wilson 1961; Ricklefs and Bermingham 2002), though noting that it was only a preliminary hypothesis, given the data at hand. This was because the phylogeny presented by them was based on only two mitochondrial genes, and a more robust resolution of relationships based on nuclear markers is to be desired. Nonetheless, using their phylogeny as the best information currently available, we note that *V. louisiadensis* sp. nov. clustered in their tree with *V. chlorostigma* from western Melanesia and Australia, that *V. tanimbar* sp. nov. was a member of a clade of three southern Moluccan species, and that those Moluccan species were sister to a clade of populations from eastern Melanesia. Thus, *V. louisiadensis* sp. nov. and *V. tanimbar* sp. nov. have evolutionary and biogeographic origins that are distinctly independent of each other, occupying archipelagos isolated on the south-eastern and south-western peripheries of the distribution of the *Varanus indicus* group, respectively, yet each is most closely related to geographically proximate congeners.

Both archipelagos are centres of endemism for reptiles and amphibians, as well as other organisms. *Varanus tanimbar* sp. nov. is the sixth known endemic reptile taxon from the Tanimbar Islands (Uetz *et al*. 2022). These islands are a minor centre of endemism in the Indo-Australian Archipelago, with nine endemic species and 11 endemic subspecies of bird (Haryoko *et al*. 2021), three endemic mammals (Suyanto *et al*. 2002), and at least seven endemic beetles (Narakusumo *et al*. 2019). The known endemic reptile fauna encompasses four species and one subspecies in addition to *V. tanimbar* sp. nov.: *Cylindrophis yamdena* Smith and Sidik 1998, *Simalia nauta* (Harvey et al. 2000), *Oligodon unicolour* (Kopstein, 1926), *Lophognathus maculilabris* Boulenger 1883 and *Tiliqua scincoides chimaerea* Shea 2000. Another three species are shared with one or several of the surrounding Banda-, Damar- and Babar islands: *Carlia babarensis* (Kopstein, 1926), *Lepidodactylus oorti* (Kopstein, 1926), and *Oligodon forbesi* (Boulenger, 1883).

For most biota the islands have not been well surveyed, so rates of endemism are likely to eventually prove higher than this. The Tanimbar Islands were formed from the collision of the oceanic Banda Arc with the Australian Plate, with the main phase of deformation occurring during the Pliocene (Charlton *et al*. 1991). This archipelago is bounded all around by deep water – including troughs to the east and west – so it has never been connected to other land masses. Consequently, the ancestors of species endemic to those islands arrived via trans-marine dispersal. *Varanus tanimbar* sp. nov. is estimated to have diverged from its closest relatives *V. indicus* and *V. melinus* approximately 900,000 years ago (Weijola *et al*. 2019), at a time well into the deformation creating the Tanimbar Islands.

Varanus louisiadensis sp. nov. occupies an archipelago of far greater importance for endemic biota, holding at least 221 endemic species of reptiles, amphibians, birds, land snails, heteropterans, odonata and plants (Polhemus and Allen 2007; Johns *et al*. 2009; Polhemus 2011; Pratt and Beehler 2015; Kraus 2021; J. Slapcinsky unpubl. data), the only taxa yet surveyed there. The Louisiade Islands comprise the three major islands of Misima, Sudest and Rossel, along with several smaller satellite islands. Only the major islands have been surveyed for reptiles and amphibians, though occasional specimens from the small islands have made their way into museum collections. The Louisiade Islands contain 59 endemic species of reptiles and amphibians, with Misima having 12, Sudest 20, and Rossel 20, and seven species being shared between Sudest and Rossel (Kraus 2021). Several of those 59 species remained to be described, and *V. louisiadensis* sp. nov. was one of them. It is the only endemic reptile or amphibian from this archipelago to be found across all three main islands, which may reflect the talent for trans-marine dispersal found in many *Varanus* species.

The Louisiade Islands were formerly connected to New Guinea as the outlying portion of the Owen Stanley Range, which forms the mountainous spine of the Papuan Peninsula. These islands became isolated from New Guinea in the past 6 million years as the opening of the Woodlark Rift led to crustal relaxation and submergence beneath sea level of the Pocklington Rise, the intervening land that connects the Louisiade Islands to the remainder of the Owen Stanleys (Taylor *et al*. 1999; Miller *et al*. 2012). The exact time at which the Pocklington Rise became totally submerged is unknown to us, but the molecular tree provided by Weijola *et al*. (2019) suggests that *V. louisiadensis* sp. nov. became isolated from *V. chlorostigma* approximately 900,000 years ago. Whether that isolation reflected loss of the land connection or trans-marine dispersal remains unknown, however.

Since the key and identification guides of Ziegler *et al*. (2007), Koch *et al*. (2013) and Auliya and Koch (2020) were published, five additional species of *Euprepiosaurus* have been described (*V. semotus*, *V. colei*, *V. bennetti*, *V. louisiadensis* and *V. tanimbar*; Weijola *et al*. 2016; Böhme *et al*. 2019; Weijola *et al*. 2020; this study), three species have been resurrected from synonymy (*V. chlorostigma*, *V. douarrha* and *V. tsukamotoi*; Weijola 2015; Weijola *et al*. 2017, 2020; ICZN 2020), and *V. cerambonensis* has been designated as a junior synonym of *V. indicus* (Weijola 2015; ICZN 2020). Hence, we find it advisable to provide updated identification charts and a diagnostic key to all currently recognised members of this subgenus. Species identification is generally uncomplicated for specimens with known geographical origin. Wherever two or more species of *Euprepiosaurus* occur in sympatry they belong to different species groups and are easily distinguished from each other based on characteristics such as colour pattern and scale counts. Below we provide two tables with scale-count characters (Table 4) and colouration and range (Table 5).

Table 4. Scale counts for the members of *Euprepiosaurus*.

Varanus indicus group	P	Q	R	S	T	N	X	XY	M
V. bennetti (n = 16)	39–49 (43.3)	74–96 (87.1)	55–68 (62.1)	131–145 (136.9)	92–100 (95.7)	87–98 (91.8)	41–48 (45.9)	148–160 (153.8)	85–117 (101.6)
V. colei (n = 11)		87–105 (96.4)		139–155 (146)			39–43 (41.4)	150–162 (154.5)	95–108 (102.3)
V. chlorostigma (n = 40)	36–47 (42)	60–99 (78.4)	46–69 (60.8)	100–145 (124)	74–96 (88)	71–94 (78.9)	28–42 (36.4)	109–158 (127.8)	73–103 (87.3)
V. douarrha (n = 14)	39–50 (43.5)	83–104 (90.2)	49–64 (57.5)	129–153 (140.9)	90–108 (96.9)	82–92 (85.7)	35–44 (39.9)	125–147 (136)	91–115 (100.7)
V. indicus (n = 11)	46–54 (50.1)	79–91 (85.5)	49–60 (53.5)	131–150 (141.4)	93–100 (96.3)	79–91 (85.5)	35–43 (39.9)	138–154 (147.7)	96–110 (103.3)
V. juxtindicus (n = 7)	39–43 (41)	72–87 (78)	47–52	128–140 (135.2)	104–111 (106.6)	83–96 (87.6)	34–43 (38.2)	132–149 (140.2)	92–104 (97.4)
V. lirungensis (n = 11)	38–47 (42.4)	79–88 (83)	55–65 (59.5)	134–151 (141.6)	92–102 (97.5)	81–88 (84.1)	34–48 (39)	131–159 (139.8)	87–106 (97.8)
V. louisiadensis (n = 11)	40–47 (43.5)	87–100 (92.1)	53–66 (60)	142–163 (153.5)	101–113 (107.4)	87–101 (92.1)	40–45 (42.8)	139–169 (153.3)	101–118 (109.6)
V. melinus (n = 4)	46–55 (49.3)	81–85 (83)	58–68 (63.3)	124–133 (128.3)	87–99 (93)	83–89 (86.5)	29–45 (37.8)	119–151 (134.3)	83–91 (86.8)
V. obor (n = 1/7*)	47	80		119–134 (125.4*)	88–94 (92.4*)	80	35	119–127 (123.4*)	85
V. rainerguentheri (n = 7)	38–44 (42.1)	76–82 (79.1)	57–61 (58.3)	120–139 (128.9)	90–94 (91.9)	85–92 (87.6)	38–47 (41.7)	133–163 (144)	85–94 (89.4)
V. tanimbar (n = 4)	42–48 (44.8)	89–95 (92)	58–65 (61.5)	145–161 (154)	107–109 (107.5)	90–93 (91.5)	44–48 (45.3)	159–170 (163.7)	109–119 (112.5)
V. tsukamotoi (n = 41)	31–40 (34.8)	54–74 (67)	48–59 (54)	101–126 (113.5)	78–88 (84)	74–90 (79.9)	33–45 (39.2)	117–140 (131)	76–103 (86.4)
***V. doreanus* group**									
V. doreanus (n = 9)	43–56 (52.1)	96–114 (104.4)	56–73 (60.7)	158–180 (167.6)	82–97 (89.2)	87–100 (90.8)	38–57 (43.4)	153–180 (165.2)	95–120 (110)
V. finschi (n = 5)	45–50 (48)	103–121 (109.2)	45–58 (53.6)	172–188 (179.8)	94–105 (98.8)	92–100 (97.6)	46–54 (49.4)	165–188 (180.8)	125–131 (128.4)
V. semotus (n = 5)	47–52 (48.2)	97–103 (100.4)	66–74 (68.4)	152–167 (160.4)	87–89 (88.2)	85–93 (90)	38–43 (39.8)	147–153 (150.2)	108–119 (115)
V. yuwonoi (n = 2)	47–53 (50)	98–108 (103)		174–188 (181)	100–101 (100.5)	103	45	184	137
Other									
V. caerulivirens (n = 3)	44–51 (47.6)	97–102 (100)	53–56 (54.7)	175–178 (176.7)	91–97 (93.6)	91–94 (93)	44–56 (50.4)	169–202 (185.7)	128–134 (131)
V. jobiensis (n = 13)	47–64 (55.1)	90–114 (105.2)	51–65 (58.9)	156–197 (180.7)	92–110 (98.5)	91–110 (100.8)	43–54 (46)	160–189 (171)	117–150 (132.5)
V. zugorum (n = 1)	45	82	56	134	97	101	35	128	105

Table 5. Type specimen, geographic distribution and colour-pattern characteristics of the members of *Euprepiosaurus*.

Varanus indicus group	Holotype	Type locality	Distribution	Dorsum	Blue pigmentation on tail	Throat	Tongue	Temporal band
V. bennetti Weijola, Vahtera, Koch, Schmitz and Kraus, 2020	USNM 507504	Ngaramasch, Ngeaur island	Palau archipelago, Yap, Losiep and Sarigan islands	Black with yellow dots	No	Yellow, typically with some orange on the sides	Distal part grey, axial part pink	Present
V. chlorostigma Gray, 1831	MNHN 2202	Rawack island, Raja Ampat	New Guinea, New Britain and islands of the Bismarck volcanic arc, D'Entrecasteaux Archipelago, Cape York, Northern Territory, Raja Ampat Islands, Biak and Yapen	Black with yellow dots	No	White/cream and unpatterned in most populations	Dark grey	Absent
V. colei Böhme, Jacobs, Koppetsch and Schmitz, 2019	MZB 14729	Ohoitel, Kei Kecil	Kei Archipelago	Black with yellow ocelli	No	Bright white	Pink with grey tines	Absent
V. douarrha Lesson, 1830	ZMUT Sa185 (neotype)	Port Praslin, New Ireland	New Ireland, Lavongai, Djaul	Black with crossbands of yellow dots and ocelli	No	Yellow and often marbled with black markings	Tines and often distal half grey, axial part pink	Absent
V. indicus Daudin, 1802	RMNH 40846 (neotype)	Ambon, Maluku	Ambon, Seram, Saparua, Buru	Black with crossbands composed of yellow dots or dots and ocelli	No	Cream/yellow, unpatterned	Distal part grey, axial part pink	Present
V. juxtindicus Böhme, Philipp and Ziegler, 2002	ZMUC R E 605	Lake Tenggano, Rennell island	Rennell Island	Black with yellow dots	No	White, unpatterned	Pink with grey tines	Absent
V. lirungensis Koch, Arida, Schmitz, Böhme and Ziegler, 2009	MZB Lac. 5178	Near Lirung, Salibabu island	Talaud Islands	Black with yellow dots and rosettes	No	Pinkish	Distal dorsal half grey	Absent

(*Continued*)

Table 5. (Continued).

Varanus indicus group	Holotype	Type locality	Distribution	Dorsum	Blue pigmentation on tail	Throat	Tongue	Temporal band
V. louisiadensis Weijola and Kraus, 2022	ZMUT Sa197	Bwagoia, Misima island	Misima, Sudest and Rossell	Black with crossbands of yellow rosettes and/or dots	No	White with a variable amount of black markings	Pink with grey tines and variable amount of grey on trunk	Usually absent
V. melinus Böhme and Ziegler, 1997	ZFMK 65737	Obi (in error)	Mangole and possibly Taliabu	Black with yellow rosettes to almost completely yellow	No	Yellow	Pink	Variable
V. obor Weijola and Sweet, 2010	RMNH 7225	Sanana, Sula Islands	Sanana	Black	No	Black, often with some white markings	Pink	Absent
V. rainerguentheri Ziegler, Böhme and Schmitz, 2009	ZFMK 85404	Jailolo, Halmahera	Halmahera, Morotai, Ternate, Bacan, Obi and Gebe	Black with yellow dots and sometimes small ocelli	No	Cream	Dark grey	Usually present
V. tanimbar Weijola and Kraus, 2022	WAM 112255	Latdalam, Yamdena island	Yamdena and Selaru islands, Tanimbar Archipelago	Black with yellow rosettes	No	Greenish yellow	Dark grey	Present
V. tsukamotoi Kishida, 1929	USNM 576258 (neotype)	Saipan, Marianas	Most of the Mariana Islands except Sarigan; Enewetak Atoll in the Marshall islands	Black with yellow dots	No	Yellow, usually with black markings	Dark grey	Absent
***Varanus doreanus* group**								
V. doreanus Meyer 1874	ZFMK 52922 (neotype)	Doreh bay, Vogelkop peninsula	New Guinea, Aru, Biak, Salawati, Waigeo, Karkar, Cape York	Black with yellow dots or ocelli	Yes	Black/white marbled	Yellow	Absent
V. finschi Böhme, Horn and Ziegler 1994	ZFMK 26347	Blanche bay, New Britain	New Britain, Duke of York	Black with yellow rosettes	No	White with black-brown spots	White to yellow	Present

(*Continued*)

Table 5. (Continued).

Varanus indicus group	Holotype	Type locality	Distribution	Dorsum	Blue pigmentation on tail	Throat	Tongue	Temporal band
V. semotus Weijola, Donnellan and Lindqvist 2016	ZMUT Sa176	Near Nai, Mussau island	Mussau, Crown Island	Black with yellow dots and markings	Yes	Black/white marbled	Pink with white and yellow pigment	Absent
V. yuwonoi Harvey and Barker 1998	UTA R41281	Near Jailolo, Halmahera	Halmahera	Predominantly black on anterior half and covered with dense yellow spotting on posterior half	Yes	White with few spots	Purple with yellow tines	Present
Other species								
V. caerulivirens Ziegler, Böhme and Philipp 1999	ZFMK 68874	Halmahera	Halmahera, Morotai, Bacan and Obi	Black with bands of blue-yellow dots and ocelli	Yes	White/grey with few spots	Pink with grey tines	Variable
V. jobiensis Ahl 1932	ZMB 34106	Yapen Island	New Guinea, Waigeo, Biak, Japen, D'Entrecasteaux Islands	Dark brown to black with yellow spots and ocelli and narrow brown-black crossbands	Yes	Peach	Pink	Present
V. zugorum Böhme and Ziegler 2005	USNM 237439	Pasir Putih, Halmahera	Halmahera	Uniform grey/brown	No	Pale, patternless	Blue-grey	Absent

A dichotomous key to the subgenus *Euprepiosaurus*

Most monitors go through some form of ontogenetic colour change from hatchling to maturity, making it difficult to produce a key that accommodates all life stages. The colour-pattern characteristics used in the key provided below are adapted to animals that have passed the juvenile stage. It should also be taken into account that some characters – in particular yellow or white pigmentation of the tongue – are often lost in preserved specimens. For comparative purposes, photographs of most of these species in life may be found in Auliya and Koch (2020).

1. a. No blue pigmentation present on tail **2**

   b. Blue pigmentation present on tail **16**

2. a. Head black or brown with or without yellow markings **3**

   b. Head completely yellow or yellow with some black markings .... ***V. melinus***

3. a. Dorsum charcoal grey to black with distinct yellow spots or spots and ocelli **4**

   b. Dorsum uniform black or brown **15**

4. a. Yellow temporal band typically present **5**

   b. Yellow temporal band typically absent **8**

5. a. Dorsum black with yellow spots or incomplete ocelli typically not partially arranged in distinct crossbands **6**

   b. Dorsum black with distinct crossbands composed of yellow spots or spots and ocelli **7**

6. a. Tail relatively long (1.6–1.9 as long as SVL), cheeks typically with some orange pigmentation .... ***V. bennetti***

   b. Tail relatively short (1.35–1.55 as long as SVL), throat cream ... ***V. rainerguentheri***

7. a. XY = 159–170, T = 107–109 .... ***V. tanimbar***

   b. XY = 138–154, T = 93–100 .... ***V. indicus***

8. a. Tongue white-yellow or pink with grey on tines or only on dorsodistal half **9**

   b. Dorsal aspect of tongue completely blue-grey **14**

9. a. Tongue pink with grey on tines or only half of dorsodistal aspect **10**

   b. Tongue white-yellow, sometimes with small grey markings, black temporal band present .... ***V. finschi***

10. a. Pink or orange pigmentation typically present on cheeks, gular region or lateral aspect of neck **11**

    b. Pink or orange pigmentation typically absent on cheeks, gular region or lateral aspect of neck **12**

11. a. Orange colouration typically present on cheeks and lateral aspects of neck Q = 87–100, T = 101–113 .... ***V. louisiadensis***

    b. Pink colouration typically present on gular region, Q: 79–88, T. 92–102 .... ***V. lirungensis***

12. a. Throat distinctly bright white, dorsum with yellow ocelli .... ***V. colei***

    b. Throat cream coloured to yellow with or without black markings **13**

13. a. Basal 1/3 of tail rounded without double scale ridge; dorsum black with small yellow spots, throat cream .... ***V. juxtindicus***

    b. Basal 1/6 of tail rounded without double scale ridge; dorsum black with crossbands of yellow dots and ocelli, throat cream to yellow, often with black spots ***V. douarrha***

14. a. Throat typically uniformly cream white to pale yellow, S = 100–145. .... ***V. chlorostigma***

    b. Throat typically yellow with grey or black markings, Marianas, S = 101–126 .... ***V. tsukamotoi***

15. a. Dorsum and head uniformly black, sometimes with small faint yellow spots, cheeks typically orange, throat black with or without white markings .... ***V. obor***

    b. Dorsum, tail and head uniformly olive-brown .... ***V. zugorum***

16 a) Throat peach; tongue uniformly pink; dorsum with narrow brown-black crossbands .... ***V. jobiensis***

   b) Throat white or black and white; tongue other than uniformly pink; posterior dorsum without narrow black crossbands **17**

17 a) Throat light grey or white with few dark spots **18**

   b) Throat marbled black and white **19**

18 a) Dorsum black or with black bands anteriorly, heavily spotted with yellow posteriorly, imparting a two-toned appearance to dorsum; tongue purple with yellow tines .... ***V. yuwonoi***

   b) Dorsum black with turquoise and yellow spots or spots and ocelli; tongue pink with grey tines .... ***V. caerulivirens***

19 a) Tongue yellow; dorsal scales (XY) = 153–180, Cape York and New Guinea region except Mussau and Crown .... ***V. doreanus***

   b) Tongue pink mottled with white and yellow; dorsal scales (XY) = 147–153, Mussau .... ***V. semotus***

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