

Refining the polytypic species concept of mangrove monitors (Squamata: *Varanus indicus* group): a new cryptic species from the Talaud Islands, Indonesia, reveals the underestimated diversity of Indo-Australian monitor lizards

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Abstract. The description of a new cryptic member of the mangrove monitor (*Varanus indicus*) (Daudin, 1802) group from Indonesia presents a refinement of the systematic concept for a polytypic complex of closely related species. The new species is recognised on the basis of morphological and molecular evidence. It is so far known only from the type locality, the remote Talaud Islands, located between Sulawesi, Halmahera and Mindanao at the outer boundary of the Wallacea transition zone between the Oriental and Australian faunal regions. While the descriptions of several sibling and mostly sympatric species within the last 15 years have not affected the range of *V. indicus*, here, we demonstrate that morphologically distinct island populations represent independent evolutionary lineages and warrant specific recognition as distinct species within an evolving superspecies complex. In addition, some basic natural history information is provided for the new species based on observations at the type locality. These systematic and zoogeographic investigations reveal shortcomings in the current knowledge concerning the diversity and endemism of Indo-Australian monitor lizards, particularly within the Wallacean region.

Introduction

The mangrove monitor lizard (*Varanus indicus*) is one of the most widespread varanid species. It ranges from the Moluccas through New Guinea, the Bismarck Archipelago and the Solomon Islands to the Marianas, Caroline and Marshall Islands in the north-west Pacific, finally reaching northern Australia (Dryden and Ziegler 2004; Ziegler *et al.* 2007b). For more than 120 years since its description in 1802, *V. indicus* was believed to be monotypic, that is, containing no subspecies, until Mertens (1926) recognised differences in colour pattern between distinct island populations and partitioned mangrove monitors into three subspecies: (1) *V. indicus* (Daudin, 1802) from the type locality Ambon and the surrounding Moluccan islands of Halmahera, Ternate, Buru and Ceram; (2) *V. indicus douarrha* (Lesson in Duperrey, 1830) from islands mainly east of New Guinea including New Ireland and the Admiralty, Duke of York, Solomon and Kai archipelagos; and (3) *V. indicus rouxi* Mertens, 1926 from the Aru Islands, southern New Guinea, and Australia. This partition into three subspecies was subsequently subject to taxonomic changes (Mertens 1942a, 1942b, 1942c, 1963) finally rendering *V. indicus* monotypic again (e.g. Böhme *et al.* 1994).

In 1994, a new era of systematic investigations in the mangrove monitor complex began with the revalidation of a first sibling species, *V. doreanus* Meyer, 1874, from New Guinea by Böhme *et al.* (1994) followed by the morphological redefinition of *V. indicus* by Philipp *et al.* (1999). Within the last 15 years, the discovery of further cryptic species demonstrated the previously unrecognised diversity of this species-rich monitor lizard group, leading to a growing number of members within the Indo-Australian region. Ernst Mayr (1942) coined the term 'superspecies' for such an assemblage of morphologically similar populations or species derived from a common ancestor. Currently, this species complex, which forms part of the subgenus *Euprepiosaurus* Fitzinger, 1843, comprises 11 species (Ziegler *et al.* 2007b): *V. indicus* (Daudin, 1802); *V. doreanus* (Meyer, 1874); *V. jobiensis* Ahl, 1932; *V. finschi* Böhme, Horn & Ziegler, 1994; *V. melinus* Böhme & Ziegler, 1997; *V. yuwonoi* Harvey & Barker, 1998; *V. caerulivirens* Ziegler, Böhme & Philipp, 1999; *V. cerambonensis* Philipp, Böhme & Ziegler, 1999; *V. juxtindicus* Böhme, Philipp & Ziegler, 2002; *V. zugorum* Böhme & Ziegler, 2005; and *V. rainerguentheri* Ziegler, Böhme & Schmitz, 2007a. A comprehensive taxonomic overview of these species has been documented in Ziegler *et al.* (2007b).

Despite the descriptions of these new species, the enormous range of *V. indicus* was not affected due to the confirmed sympatry of different members of the species group at most localities (Philipp 1999; Philipp *et al.* 1999; Ziegler *et al.* 1999a, 1999b, 2001). At present, all these geographically separated (allopatric) island populations of *V. indicus* are regarded as monotypic, although a wide range of phenetic variation in scalation and colour pattern is obvious (Brandenburg 1983; personal observation; see also Eidenmüller and Philippen 2008). As was recently shown in another widely distributed monitor species, the Asian water monitor (*V. salvator*), spatially isolated populations mainly at the outer border of the species' range tend to have experienced a particular evolutionary history, including (intra-)specific differentiation due to accumulation of unique morphological characteristics (Koch *et al.* 2007).

The Talaud Islands, an isolated archipelago of coral reef islands between north Sulawesi, Halmahera, and the southernmost Philippine island of Mindanao are inhabited by the most north-western population of a member of the *V. indicus* species group. The remote archipelago consists of three main islands: Karakelong, Salibabu and Kaburuang (Fig. 1). De Rooij (1915) was most probably the first to report mangrove monitors from the Talaud Archipelago based on material collected by Max Weber on Pulau (=Island) Salibabu during the Siboga Expedition in July 1899. De Jong (1928) provided another short account about a small collection by Herman J. Lam from the Talaud Archipelago containing one *Varanus* specimen (MZB Lac. 581).

During a one-week field expedition to Salibabu Island (3°93'N, 126°68'E) in July 2005, five specimens of a monitor species closely resembling *V. indicus* were collected by AK and EA with the help of a local villager. Subsequently, the specimens collected by M. Weber in 1899 were also reinvestigated. These

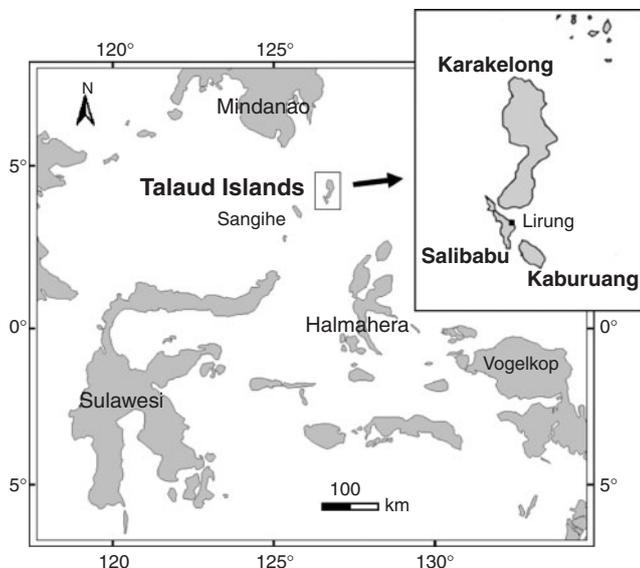


Fig. 1. Map of the Talaud Islands, the distribution range of *Varanus lirungensis*, located between the northern peninsula of Sulawesi, Halmahera (Moluccas) and Mindanao in the Philippines. Lirung, the type locality on Salibabu Island, is indicated by a dot.

historical vouchers had not been included in previous systematic studies by Böhme *et al.* (1994), Philipp *et al.* (1999), or Ziegler *et al.* (1999a). The taxonomic distinctness of the Talaud mangrove monitors has, therefore, remained unrecognised until the evaluation of the above-mentioned specimens. Preliminary investigations of the molecular phylogeny of the *V. indicus* species group strongly support these findings and demonstrate the need for a refinement of the polytypic species concept of Australo-Papuan mangrove monitors (Fig. 2) (Ziegler *et al.* 2007b).

Materials and methods

Samples, selected characters and definitions

Morphometric and meristic data of 52 specimens from the north-western distribution range of the *V. indicus* complex were statistically analysed. Of these, 17 specimens, including nine of the new species from Talaud, were examined for the first time. Data for the remaining specimens were taken from literature sources (*V. indicus*: Brandenburg 1983; Philipp *et al.* 1999; *V. yuwonoi*: Harvey and Barker 1998; Böhme and Ziegler 2005; *V. rainerguentheri*: Ziegler *et al.* 2007a; *V. zugorum*: Böhme and Ziegler 2005; *V. caerulivirens*: Ziegler *et al.* 1999a; *V. melinus*: Böhme and Ziegler 1997). A list of all specimens examined is provided in Appendix 1.

In order to compare the Talaud population morphologically with other established Moluccan species of the *V. indicus* complex, 24 characters including body proportions and scalation were recorded for each specimen. Definitions of these characters are given in Table 1. Head measurements were made with a slide-calliper to the nearest 0.1 mm. Snout–vent length (SVL) and tail length (TaL) were measured using a measuring tape. In order to minimise observer-biased error, all measurements and scale counts were made by AK. Scale counts were taken according to Brandenburg (1983), Böhme *et al.* (1994) and Koch *et al.* (2007). For recording scalation character Q, the first continuously tail-spanning row of scales near the base of the tail was counted by excluding the first rows immediately after the cloaca, which form a non-continuous bow. Ventrally, the transverse scale rows from

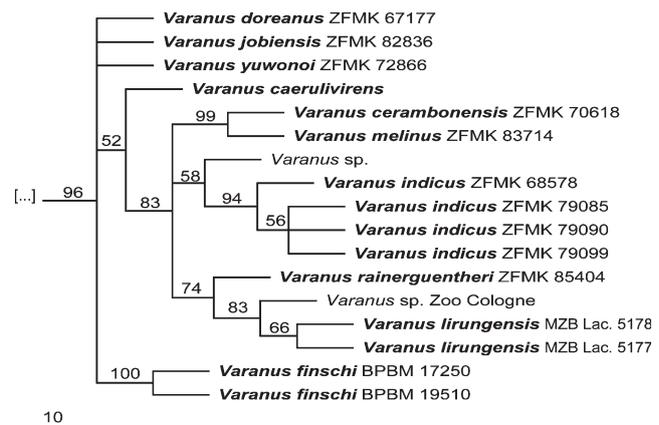


Fig. 2. Clade of the *Varanus indicus* species group modified from the 16S rRNA neighbour-joining phylogram by Ziegler *et al.* (2007b) containing all currently recognised species within the group except for *V. juxtindicus* and *V. zugorum*. Valid species names are shown in bold.

Table 1. List of morphometric and meristic characters and their codes used in this study

	Code	Definition of characters
Morphometry		
1	SVL	SVL from tip of snout to cloaca
2	TaL	Tail length from cloaca to tail tip
3	ToL	Total length from tip of snout to tip of tail
4	A	Head length from tip of snout to anterior margin of ear
5	B	Head width (= maximum width between eyes and ears)
6	C	Head height above the eyes
7	G	Distance from anterior eye margin to middle of nostril
8	H	Distance from middle of the nostril to tip of the snout
9	index 1 (=TaL/SVL)	Relative tail length
10	index 2 (=G/H)	Position of nostril between tip of snout and eye
11	index 10 (=A/B)	Relative head length in relation to head width
12	index 11 (=A/C)	Relative head length in relation to head height
Scalation		
13	P	Scales across head from rictus to rictus
14	Q	Scales around tail base
15	R	Scales around tail at approximately one-third from base
16	S	Scales around midbody
17	T	Transverse ventral scale rows from gular fold to insertion of the hind legs
18	N	Gular scales from tip of snout to gular fold
19	TN (=T+N)	Ventral scales from tip of snout to insertion of hindlegs
20	X	Transverse dorsal scale rows from hind margin of tympanum to gular fold
21	XY	Dorsal scales from hind margin of tympanum to insertion of hind legs
22	c	Supralabials exclusive the rostral scale
23	m	Scales around neck anterior to gular fold
24	U	Differentiated (=enlarged) supraocular scales

the tip of the snout to the insertion of the hind legs (character TN) were counted along throat and venter to the last continuous row before the scales become small and irregular in size towards the hind legs. Transverse scale rows on the dorsal side (character XY) were defined as the scales from an invisible line connecting the hind margins of tympana to another invisible line between the insertions of the hind legs. Supralabials (characters c) were counted on the left and right side except for the enlarged rostral scale. Description of genital morphology follows the terminology of Böhme (1988) and Ziegler and Böhme (1997).

Collection abbreviations used are: MZB, Museum Zoologicum Bogoriense, Cibinong, Indonesia; SMF, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M., Germany; RMNH, National Museum of Natural History, Leiden, the Netherlands; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA; UTA, University of Texas at Arlington, Arlington, TX, USA; UCM, University of Colorado Museum, Boulder, CO, USA; ZFMK, Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany; ZMA, Zoological Museum, University of Amsterdam, Netherlands.

Univariate and multivariate statistics

To test for taxonomic distinctness in the Talaud population, morphometric and meristic characters were analysed using Analysis of Variance (ANOVA) unless the assumptions underlying this statistical method were violated. The non-parametric Kolmogorov–Smirnov test was applied to confirm the assumption of normality, and homogeneity of variance was

tested using Levene's test. In addition to univariate methods, multivariate statistical techniques were used to examine the degree of separation between the different species. A Principal Components Analysis (PCA; e.g. McGarigal *et al.* 2000) included only those morphological characters that were significantly different ($P < 0.05$) in at least two pair-wise comparisons of the *post hoc* tests (characters Q, S, TN, XY, and m). Although not all scalation values were available for the type specimens of *V. yuwonoi*, both specimens were included in the PCA in order to enhance the sample size for this rare Halmahera monitor species ($n = 4$). All statistical analyses were calculated using the software packages PAST ver. 1.81 (Hammer *et al.* 2001) and SPSS ver. 11.5.2.1 (2003; SPSS Inc., Chicago).

Results

Statistical analyses

Standard univariate descriptive statistics for morphometric and meristic characters of *V. rainerguentheri*, *V. indicus* and the new monitor species are shown in Table 2. Significant results of the univariate analyses for the three focal species and two further Moluccan members of the *V. indicus* complex are summarised in Table 3. As in earlier studies by Böhme *et al.* (1994) and Philipp *et al.* (1999), ANOVA showed that the scales around the midbody (S) and those around the neck (m) provided the best means for discriminating between different mangrove monitor species. In contrast, morphometric characters showed only minor significant differences. ANOVA yielded no significant interspecific differences in pair-wise comparisons of means between the Talaud population and *V. rainerguentheri* from

Table 2. Descriptive statistics of *Varanus liruensis*, sp. nov., compared with those of its closest relatives *V. indicus* and *V. rainierguentheri*
Range and mean are shown

	<i>V. liruensis</i> , sp. nov. (n=9)	<i>V. indicus</i> ^A (n=36)	<i>V. rainierguentheri</i> ^B (n=3)
Index 1 ^C	1.43–1.75 (1.60)	1.42*	1.38–1.55 (1.46)
Index 2	1.11–1.31 (1.23)	1.33*	1.16–1.21 (1.19)
Index 10	1.71–2.18 (1.88)	1.76*	1.71–1.83 (1.76)
Index 11	2.25–2.69 (2.48)	2.59*	2.45–2.82 (2.61)
P	38–47 (42)	36–46 (41)	43–47 (46)
Q	79–88 (83)	58–85 (76)	79–85 (83)
R	55–65 (60)	–	53–68 (60)
S	135–151 (142)	106–137 (123)	138–141 (139)
T	92–102 (97)	74–107 (88)	94–97 (95)
N	81–88 (84)	67–92 (79)	92–97 (95)
TN	174–189 (181)	–	186–193 (190)
X	34–41 (38)	25–41 (34)	35–37 (36)
XY	131–144 (137)	105–140 (124)	130–136 (132)
c	53–59 (56)	49–56 (53)	51–52 (52)
m	94–106 (100)	70–94 (82)	95–107 (101)

^AData for *V. indicus* are taken from Philipp *et al.* (1999). Note that the specimens used in that study do not fully coincide with those of Brandenburg (1983). An asterisk (*) denotes values that refer to the juvenile neotype of *V. indicus* (ZFMK 70650).

^BData for *V. rainierguentheri* are mainly taken from Ziegler *et al.* (2007b); data of a third specimen (MZB Lac. 6145) from Halmahera Island are included.

^CData about proportion index 1 of *V. liruensis* are provided for seven specimens only because two specimens had incomplete tails.

Halmahera (Table 3). The reason may be the small sample size of the latter species ($n = 3$) and/or the close phylogenetic relationship between both species (Ziegler *et al.* 2007b; see Fig. 2). In contrast, *V. indicus*, which is phenetically closer to the Talaud monitors, shows significant differences in several scalation characters. The same is true for the remaining species (*V. yuwonoi*, *V. caerulivirens* and *V. melinus*), which show totally different colour patterns (see below).

A scatterplot of the first and second principal components (PC) is shown in Fig. 3. The first PC accounts for 84.1% of overall variation in the dataset. Factor loadings of the first, second, and third PC are given in Table 4. Two distinct groups of individual

scores are identifiable, representing six geographically correlated groups assorted in ordination space. Morphospaces of *V. indicus*, *V. melinus*, the Talaud specimens, and *V. rainierguentheri* only marginally overlap. On the other side, *V. caerulivirens* and *V. yuwonoi*, due to their high scale counts, form a distinct group separated from the other Moluccan and New Guinean monitor species with larger scales. The only available specimen of *V. zugorum* is situated close to *V. rainierguentheri*. For a better overview, specimens of *V. cerambonensis* were not included in multivariate analyses. When included, the morphospace of this species largely overlaps with *V. melinus*, *V. indicus*, and the Talaud monitors. The disjunct position of the type specimens of *V. yuwonoi* is due to missing data for scalation characters XY and m, which were not provided in the original description by Harvey and Barker (1998).

A specimen of *V. cf. indicus* without locality data, which appears to be most genetically similar to the Talaud monitors (see below), is placed directly between *V. indicus* and *V. melinus* (see open triangle in Fig. 3). Confirming the ANOVA results, the Talaud specimens are closely associated with three specimens of *V. rainierguentheri* from Halmahera.

Conclusions

Taxonomic interpretation

The application of advanced multivariate methods for taxonomic issues has greatly improved the possibilities for sophisticated discriminant analyses of cryptic species complexes (e.g. Rastegar-Pouyani 2005; Devitt *et al.* 2008; van Rooijen and Vogel 2008). The General Lineage Concept of de Queiroz (1998, 2005) was employed for a taxonomic interpretation of the observed differences between the Talaud population and the recognised members of the *V. indicus* species group. Diagnosibility and geographic isolation serve as the determining criteria for the recognition and definition of separate species (e.g. McGuire *et al.* 2007; Vogel and van Rooijen 2008).

Owing to their wide distribution, mangrove monitors have been renamed by several authors since the epithet *indicus* Daudin, 1802, was used for the first time more than 200 years ago. Most synonyms, however, such as *douarrha* Lesson, 1830, or *kalabeck* Lesson, 1830, were declared doubtful names by Böhme *et al.* (1994) when it became obvious that more than one monitor

Table 3. Significance levels of the differences in meristic characters between five established *Varanus* species from the Moluccas (*V. rainierguentheri*, *V. indicus*, *V. yuwonoi*, *V. caerulivirens*, and *V. melinus*) and the new species based on ANOVA
Characters examined that showed no significant differences are excluded

	<i>V. rainierguentheri</i>	<i>V. indicus</i>	<i>V. yuwonoi</i>	<i>V. caerulivirens</i>	<i>V. melinus</i>
Q	–	<0.000001	<0.000001	<0.000001	–
P	–	–	<0.00001	0.015	0.009
S	–	<0.000001	<0.000001	<0.000001	0.001
T	–	<0.000001	–	–	–
N	–	–	<0.00001	<0.001	–
TN	–	<0.00001	0.005	–	–
X	–	–	–	0.004	–
Y	–	–	<0.00001	<0.000001	–
XY	–	–	0.0002	<0.000001	–
c	0.051	0.051	–	0.006	–
m	–	<0.000001	<0.000001	<0.000001	0.008

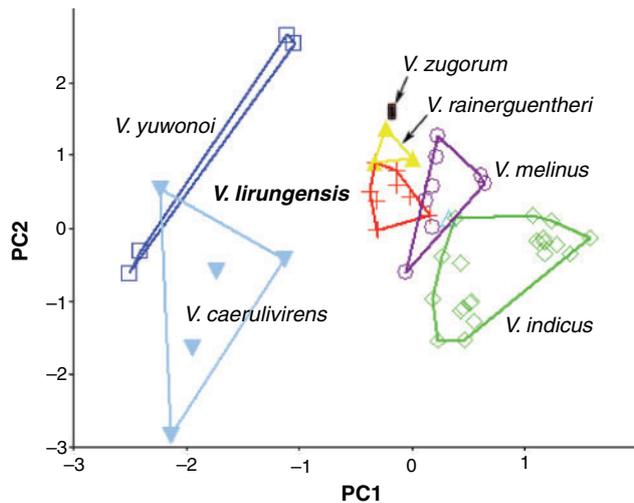


Fig. 3. Ordination of 52 *Varanus* specimens belonging to seven species of the *V. indicus* group (excluding the distantly related *V. cerambonensis*) along the first two principal components. PCA was calculated with scalation characters Q, S, TN, XY and m.

Table 4. Factor loadings for the first, second and third principal components

Values greater than 0.50 in absolute value are considered significant. See Table 1 for character definitions

	PC1	PC2	PC3
Q	-0.260	0.156	0.133
S	-0.582	0.288	0.312
TN	-0.366	0.530	0.691
XY	-0.516	-0.782	-0.342
m	-0.422	-0.022	0.539
Eigenvalue	4.180	0.349	0.237
% of total variance	84.100	6.974	4.750

species was involved. Because their type specimens are unequivocally now lost, a precise taxonomic allocation is impossible. In turn, other names, like *chlorostigma* Gray, 1831, are identical with *indicus* Daudin, 1802, or were revalidated from synonymy, such as in the case of *doreanus* Meyer, 1874 (Böhme *et al.* 1994). The names *tsukamotoi* Kishida, 1929, and *rouxi* Mertens, 1926, are still available, but given the knowledge of extreme morphological variation even on a fine geographic scale, their type localities (Saipan, Caroline Islands, and Wamer, Aru Islands, respectively) are too distant from the Talaud Islands. Thus, in the absence of available names the population of the Talaud Islands are here described as a new cryptic member of the *V. indicus* species complex.

Taxonomic account

Family **VARANIDAE** Hardwicke & Gray, 1827

***Varanus lirungensis*, sp. nov.**

(Figs 4–7)



Fig. 4. The holotype of *Varanus lirungensis*, MZB Lac. 5178.

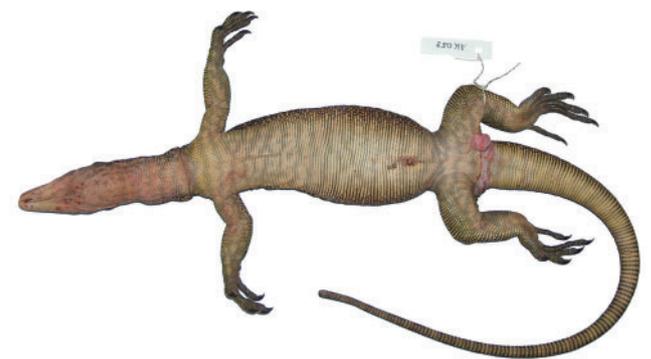


Fig. 5. Ventral view of the holotype of *Varanus lirungensis* showing the characteristic pattern of faded cross-bands at the venter.

Material examined

Holotype. MZB Lac. 5178 (field number AK059), adult male (Figs 4–6), collected by A. Koch and E. Arida near Lirung, Pulau Salibabu, Talaud Islands, Indonesia, on 18.vii.2005.

Paratypes. MZB Lac. 5177 (AK064), adult female, collected by A. Koch and E. Arida on 19.vii.2005, same locality data as holotype; MZB Lac. 5179 (AK066) and MZB Lac. 5180 (AK065), two adult males; MZB Lac. 5176 (AK067), subadult, same data as previous specimens; ZMA 15411b, juvenile, Lirung, Pulau (=Island) Salibabu, Kepulauan (=Archipelago) Talaud, collected by the Siboga Expedition of M. Weber, 25–27.vii.1899; ZFMK 87587 (formerly ZMA 15411a), adult female, same collection data as the previous specimen.

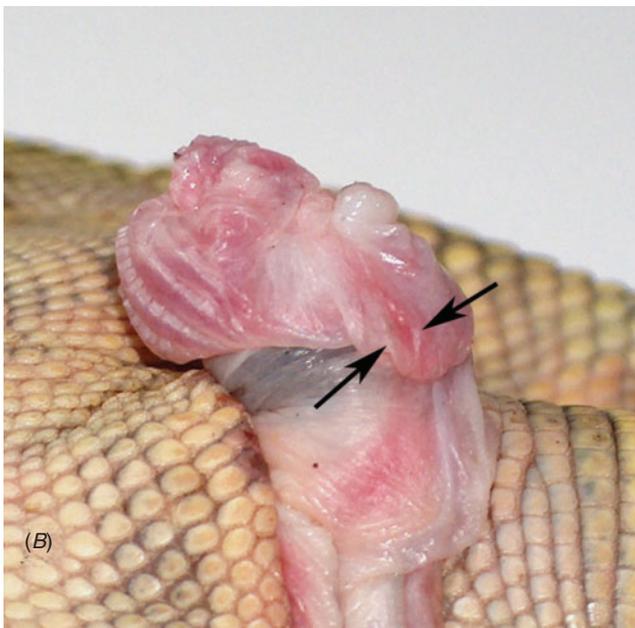
Referred material. MZB Lac. 581 (954), 'Karakelang' (=Karakelong), Talaud Islands, subadult, collected by H. J. Lam, 21.iv.–16.v. or 29.v.–9.vi.1926 (according to van Steenis-Kruseman 1950: 308), respectively (but see details in the Introduction). The collecting date is erroneously stated as '1920' on the specimen tag; MZB Lac. 4195, subadult, collected by World Conservation Society (Jon Riley), Beo, Karakelong, 9.vi.1999.

Diagnosis

The newly described monitor lizard species from the Talaud Islands is characterised by the following combination of characters: (1) dorsal background colour black, irregularly



(A)



(B)

Fig. 6. Sulcal (A) and asulcal (B) view of the left hemipenis of the holotype of *Varanus lurungensis* (MZB Lac. 5178). Arrows show paryphasman rows on the inner hemipenis lobe.

scattered with numerous yellow scales that form indistinct blotches or short transverse lines consisting of 3–8 scales on the dorsum; (2) limbs also irregularly spotted with yellow scales; (3) tail of adults without distinct light and dark crossbands but mottled with yellow scales; (4) lack of blue pigmentation; (5) head dark grey to blackish, each scale with yellow markings mainly consisting of a light margin or a small central spot; (6) a light temporal streak is missing; (7) a pinkish throat; (8) tongue of adults only dorsally pigmented dark grey, flesh-coloured at base

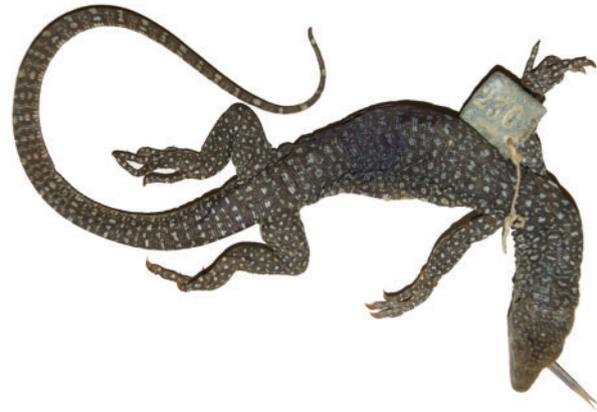


Fig. 7. A juvenile specimen of *Varanus lurungensis* (ZMA 15411b). Note the lighter-coloured tongue in contrast to the adult holotype.

and ventrally; (9) 16–21 faded dark crossbands on the ventral side, and a light, pinkish throat at least on adult specimens with faded dark blotches on the sides; (10) tail laterally compressed with a well defined double keel on the dorsal ridge; (11) hemipenis with paryphasman rows ('frills') on both sides of the sulcus; (12) 135–151 scales around midbody; (13) 131–143 transverse rows of dorsal scales from the hind margin of tympanum to the beginning of the hind legs; (14) 79–88 scales around base of tail; (15) 94–106 scales around neck before the gular fold.

Description of the holotype

Habitus relatively stoutly built. SVL 355 mm, tail length 445 mm, tip of tail missing (tail >1.25 times as longer as SVL), total length 800 mm. Head length 54.8 mm, head width 32.0 mm, head height 23.0 mm. Head 1.71 times as long as wide, and 2.38 times as long as high. Nostrils oval, 1.26 times nearer the tip of snout than the eye. Distance from anterior margin of eye to middle of nostril 14.5 mm, distance from middle of nostril to tip of snout 11.5 mm. Nasal regions slightly swollen. Tail after base laterally compressed with a well defined double keel on dorsal ridge. The teeth are slender, relatively pointed, and slightly recurved.

Scalation: Scalation of the body is heterogeneous. Head scales are smooth, irregularly pentagonal or hexagonal, 44 in number from rictus to rictus. Five supraoculars, distinctly broader than long, are found above the eyes. Pileus scales between the supraoculars enlarged. Pineal organ visible as a light roundish blotch through a slightly enlarged scale. 58 supralabials (30 right/28 left) plus one enlarged rostral scale. Dorsal neck scales are domed, oval to roundish in shape, not keeled, and surrounded by numerous granules. The head scales exhibit several small grooves or pits which are distinctly darker coloured on light spotted scales. 105 scales around the neck anterior to gular fold. Dorsal scales oval and slightly keeled with one pit at the distal end, arranged in 143 transverse rows from the hind margin of tympanum to insertion of the hind legs. Limbs are covered with smooth, oval scales. Digits with strong curved claws; fourth toe longest, laterally a row with 11 enlarged scales on the first half. Scales of tail keeled, rectangular, and arranged in 86 regular

transverse rows around base of tail and 62 after approximately one-third of its length; they exhibit one pit posteriorly. The two median rows of caudal scales form a distinct longitudinal double crest from the first sixth onwards. Ventral scales with a prominent keel except at the basal part, twice as large as dorsals. Gular scales smooth, square under head, roundish to oval in the medial part and increasing in size towards the gular fold; in total, 83 scales from tip of snout to gular fold. Chest scales similar in shape. Belly covered with longish oval to rectangular scales in regular transverse rows, slightly keeled, with one apical pit posteriorly; 100 scales from the gular fold to insertion of the hind legs, 138 scales around midbody. Three ticks present in the nape region which shows considerable damage caused by persistent parasitic infection.

Genital morphology: In the male holotype specimen the left hemipenis is partly everted. It is flesh-coloured and ~30 mm long (Fig. 6). The following description is based on detailed photographs of the organ. The hemipenis passes apically into two asymmetrically shaped lobes. Sulcus spermaticus basally oblique; mesially running straight but apically crooked towards the outer lobe, bearing the outer and smaller hemibaculum. The inner sulcal lip is slightly notched towards the inner hemibaculum at the distal branching point of the apical lobes. The outer sulcal lip is somewhat more developed, the sulcus being largely open in the truncus area. The apical platform is asymmetrically prolonged towards the outer lobe and markedly distorted towards the sulcal side. Only the inner hemibaculum is protruding, the outer hemibaculum is not everted due to a preparation artefact. The inner hemibaculum is apically directed, concavely bent towards the sulcus and somewhat shovel shaped. On the asulcal side of the hemipenis, there exist numerous well discernible paryphasman rows ('frills'). Most of the paryphasman rows are stretching towards the outer lobe, where they nearly encircle the region where the outer hemibaculum normally protrudes, but there are also a few paryphasman rows stretching to the inner lobe, which bears the shovel shaped hemibaculum. Pedicel and truncus are unornamented and smooth.

Colouration in life: Dorsal background colour of head, neck, dorsum, limbs and tail black irregularly scattered with numerous light scales. First scales on the digits after claws have a large light spot. Neck dotted with single yellow scales. Dorsum is black with a pattern of indistinct blotches or short transverse lines consisting of 3–8 yellow scales. Tail is without distinct light and dark crossbands but mottled with many yellow scales. Blue pigmentation is lacking. Head scales have cream-yellow spots. Eyes lightly encircled with granular scales below a whitish eyelid. Lateral head scales including supralabials posteriorly blackish with light greyish margins towards the mouth. No indication of a light temporal streak. The tympanum is not surrounded by a light margin. Tongue is only dorsally dark grey, flesh-coloured at the base and ventral side. Ground colour of venter and limbs is cream to yellow-greyish with a pattern of faded darker cross lines. Throat is pinkish with faded dark blotches.

Intraspecific variation

The six paratype specimens largely correspond with the description of the holotype. A summary of measurements, morphometrics and scalation data for the new species is provided

in Table 2. There are some minor differences in the proportion index 10 (= head length/head width) between the populations of Salibabu and Karakelong. While both specimens from Karakelong show significantly higher values (2.04 and 2.18, respectively; mean = 2.11, $P=0.001$), values for the Salibabu population ($n=7$) range between 1.71 and 1.90 (mean 1.81). Correspondingly, values for proportion index 11 (= head length/head height) are higher, though above the significance level ($P=0.053$), for both Karakelong specimens (2.66 and 2.67, respectively, mean 2.67 v. 2.25–2.50, mean 2.43). These individual values are just surpassed by specimen ZMA 15411b (index 11 = 2.69) from Salibabu Island, the only juvenile voucher of the type series. This deviation, however, may be explained by ontogenetic differences in head proportions of the juvenile monitor lizard which probably hatched the year it was collected. In sum, specimens from Karakelong Island exhibit generally more slender and flatter heads compared with specimens from Salibabu Island.

The colour pattern of the subadult and adult voucher specimens largely corresponds with that shown by the holotype. However, some differences are obvious in the only juvenile specimen of the type series, ZMA 15411b (Fig. 7). The dorsum is covered with more distinct light blotches or clear ocelli which are arranged in ~20 indistinct transverse rows. The tail is covered with a narrow pattern of light-centred dark ocelli arranged in pairs on a dark grey background. The ventral colour pattern is more distinct than in the mature voucher specimens. It consists of clear dark cross bands on the belly towards a reticulate pattern on the limbs. The underside of the tail shows a narrow pattern of distinct white and dark cross bands. In contrast to the adult specimens, the tongue is light with blue-greyish pigmentation only dorsally along an ill-defined longitudinal stripe slightly broadened around the bifurcation. The tips of the juvenile's tongue are light. This observation indicates an ontogenetic shift in tongue colouration for *V. liringensis* similar to that reported for *V. cerambonensis* (Philipp *et al.* 1999).

The longest known specimen of *V. liringensis*, ZFMK 87587, has a total length of 912 mm. Photographic evidence (not shown) suggests that this species may reach a total length of more than 1500 mm and may exceed the total length of the closely related *V. indicus* (see Dryden and Ziegler 2004 and citations therein).

Etymology

The specific epithet, *liringensis*, is derived from the name of the small town of Lirung on Salibabu Island in the Talaud Archipelago, from where the type series originates. We propose the vernacular name 'Talaud mangrove monitor' for the new monitor species.

Comparisons with other species

The new species is compared below with all currently recognised members of the *V. indicus* complex although not all species have been included in the statistical analyses due either to the paucity of available data or because their distribution ranges do not fall within the Wallacea region of central Indonesia.

In contrast to *V. liringensis*, *V. caerulivirens* Ziegler, Böhme & Philipp, 1999 has a characteristic light blue to turquoise tinge on

the head and dorsal body parts, as well as a pink-coloured light tongue that may have dark pigmentation on the tips and/or at their bifurcation. On average, the nostrils are nearer the tip of the snout than the eye (index 2: 1.29–1.5, mean 1.41) compared with *V. lirungensis* (1.11–1.31, mean 1.23), and *V. caerulivirens* has smaller scales than the new species. This is obvious, for instance, for the scales around the base of the tail (97–102 v. 79–88, mean 83.11), the scale row count around the midbody (170–185, mean 177 v. 135–151, mean 142.11), and the dorsal scales from the hind margin of the tympanum to the insertion of the hind legs (169–202, mean 186 v. 131–144, mean 137). *V. caerulivirens* exhibits fewer supralabials (49–52, mean 50 v. 53–59, mean 56). In contrast to the new species, *V. caerulivirens* bears differentiated paryphasman rows on only one side of the sperm groove (Ziegler *et al.* 1999a).

V. cerambonensis Philipp, Böhme & Ziegler, 1999 from the central Moluccas shows a dorsal colour pattern with indistinct crossbands in adults, a well defined yellow temporal streak, and a light tongue in juveniles. The head is, on average, longer than high (index 11: 2.43–3.06, mean 2.74) compared with *V. lirungensis* (2.25–2.69, mean 2.48). It possesses, on average, more scales across the head from rictus to rictus (41–54, mean 48 v. 38–47, mean 42 in *V. lirungensis*). In contrast to the new species, *V. cerambonensis* bears differentiated paryphasman rows on only one side of the sperm groove (Philipp *et al.* 1999).

V. doreanus (Meyer, 1874) from New Guinea, its smaller offshore islands and northern Australia, has a light tongue, a black to marbled throat and a blue banded tail. The nostrils are, on average, nearer the tip of the snout than the eye (1.25–1.58, mean 1.49 v. 1.11–1.31, mean 1.23 in *V. lirungensis*) and the head is longer than high (index 11: 2.5–3.06, mean 2.78) compared with *V. lirungensis* (2.25–2.69, mean 2.48). On average, *V. doreanus* has more scales across the head from rictus to rictus (42–57, mean 50.6 v. 38–47, mean 42), around the tail base (94–114, mean 103.4 v. 79–88, mean 83.11), around the midbody (154–180, mean 168.3 v. 135–151, mean 142.11), and from the hind margin of the tympanum to the insertion of the hind legs (152–182, mean 162.1 v. 131–144, mean 136.8) (Böhme *et al.* 1994).

V. finschi Böhme, Horn & Ziegler, 1994 from New Guinea, the Bismarck Archipelago and northern Australia, has a dorsal colour pattern of dark-centred ocelli, a dark-bordered temporal band, and a light tongue. In general, *V. finschi* possesses smaller scales than *V. lirungensis* and therefore has more scales around the tail base (95–110, mean 102.2 v. 79–88, mean 83.11), around the midbody (158–196, mean 180 v. 135–151, mean 142.11), from the tip of the snout to the gular fold (94–123, mean 104.8 v. 81–88, mean 84.22), and around the neck (86–145, mean 123.7 v. 94–106, mean 100.0), but fewer scales around the tail at approximately one-third from base (43–59, mean 51.4 v. 55–65, mean 60) (Böhme *et al.* 1994).

V. indicus (Daudin, 1802) as defined by Philipp *et al.* (1999) can be distinguished from *V. lirungensis* by the following characters: an unpatterned throat and belly without pale dark spots or crossbands; a dorsal colour pattern mostly consisting of single light scales in adult specimens; lower scale counts around the midbody (106–137, mean 123 v. 135–151, mean 142.11, in *V. lirungensis*) and around the neck anterior to the gular fold (70–94, mean 82 v. 94–106, mean 100.0, in the new species),

and, on average, fewer scales from the hind margin of the tympanum to the beginning of the hind legs (105–140, mean 124 v. 131–144, mean 136.78). In contrast to the new species, *V. indicus* bears differentiated paryphasman rows on only one side of the sperm groove (Philipp *et al.* 1999).

V. jobiensis Ahl, 1932 from New Guinea, has a pink tongue, large eyes, a dark olive dorsum with indistinct light and dark transverse stripes, and a blue-banded tail. The nostrils are, on average, nearer the tip of the snout than the eye (1.17–1.9, mean 1.56 v. 1.11–1.31, mean 1.23) and the head is, on average, longer than high (index 11: 2.22–3.13, mean 2.81) compared with *V. lirungensis* (2.25–2.69, mean 2.48). In general, *V. jobiensis* exhibits smaller, and therefore more, scales than *V. lirungensis*, around the tail base (96–121, mean 105 v. 79–88, mean 83.11), around the midbody (164–201, mean 182.7 v. 135–151, mean 142.11), and dorsally from the hind margin of the tympanum to the insertion of the hind legs (163–196, mean 176.4 v. 131–144, mean 136.78) (Böhme *et al.* 1994).

V. juxtindicus Böhme, Philipp & Ziegler, 2002, an endemic of the Solomon Islands, has a roundish tail in its first third lacking a differentiated double keel along the dorsal ridge, an extremely swollen parietal region in adult males, and the tongue is light with an ill-defined dark pigmentation on its anteriormost part. The head is relatively shorter than is the case in *V. lirungensis* (index 10: 1.4–1.8, mean 1.7 v. 1.71–2.18, mean 1.88), and *V. juxtindicus* possesses more transverse ventral scale rows from the gular fold to the insertion of the hind legs (104–111, mean 106.6 v. 92–102, mean 97.11). Contrasting with the new species, *V. juxtindicus* bears differentiated paryphasman rows on only one side of the sperm groove (Böhme *et al.* 2002).

V. melinus Böhme & Ziegler, 1997 from the Moluccas has a distinct yellow background colouration and a light pinkish tongue. The nostrils are much closer to the tip of the snout than to the eye (1.67–1.86, mean 1.78 v. 1.11–1.31, mean 1.23, in *V. lirungensis*). The head is longer than in *V. lirungensis* both in relation to head width (index 10: 2.23–2.39, mean 2.33 v. 1.71–2.18, mean 1.88) and head height (index 11: 2.75–3.06, mean 2.95 v. 2.25–2.69, mean 2.48). On average, *V. melinus* has more scales across the head from rictus to rictus (46–55, mean 49 v. 38–47, mean 42), but fewer scales around the midbody (124–133, mean 128 v. 135–151, mean 142.11) and around the neck (83–91, mean 87 v. 94–106, mean 100.0). Again, in contrast with the new species, *V. melinus* bears differentiated paryphasman rows on only one side of the sperm groove (Böhme and Ziegler 1997; Ziegler and Böhme 1999).

V. rainerguentheri Ziegler, Böhme & Schmitz, 2007 from the island of Halmahera has a grey dorsum with more or less distinct blackish ocelli with yellow centers, a light and black temporal streak, and a pink-coloured tongue with greyish tips and in the area of the bifurcation. This species has fewer supralabial scales (51–52 v. 53–59, mean 55.89 in *V. lirungensis*), but more ventral scales from the tip of the snout to the gular fold (92–97, mean 94.5 v. 81–88, mean 84.22). *V. rainerguentheri* bears differentiated paryphasman rows on only one side of the sperm groove (Ziegler *et al.* 2007a).

In contrast to *V. lirungensis*, *V. yuwonoi* Harvey & Barker, 1998 from Halmahera Island has a blackish body with a few wide bands on the anterior part, while the caudal half of the

body is finely speckled with green, blue and black. The tail is blue. *V. yuwonoi* generally has smaller scales across the body expressed by higher scale counts around the tail base (98–108, mean 103.7 v. 79–88, mean 83.11), around the midbody (174–196, mean 186.17 v. 135–151, mean 142.11), from the hind margin of the tympanum to the insertion of the hind legs (184 v. 131–144, mean 137), and around the neck (137 v. 94–106, mean 100.0) (Harvey and Barker 1998; Ziegler and Böhme 1999).

V. zugorum Böhme & Ziegler, 2005 from Halmahera, which is known from only one specimen, the holotype, has a uniformly greyish to greenish-olive dorsum without any pattern of yellow spots but with single bluish scales interspersed on the neck and body. Its habitus is very slender, with an elongated neck. *V. zugorum* has more gular scales from the tip of the snout to the gular fold (101 v. 81–88, mean 84.22 in *V. lirungensis*) (Böhme and Ziegler 2005).

Discussion

Systematic position of *V. lirungensis*

V. lirungensis unequivocally belongs to the subgenus *Euprepiosaurus* Fitzinger, 1843 of *Varanus* Merrem, 1820 (*sensu* Ziegler and Böhme 1997) due to specific characteristics of the genital morphology, such as the asymmetric sulcus spermaticus. With regard to the colour pattern, the newly described species from the Talaud Islands seems closely related to *V. indicus*. However, the ventral pattern of dark crossbands, as typical for *V. lirungensis*, is also present in *V. rainierguentheri* but missing in adult *V. indicus*. Likewise, but only in the juvenile voucher of *V. lirungensis*, the tail shows a colour pattern of light-centred dark ocelli on a dark grey background, as is diagnostic for *V. rainierguentheri*. Morphological comparisons show that *V. lirungensis* is nearly indistinguishable from *V. rainierguentheri* in scalation characters. Scalation values for both species largely overlap (see Table 2).

In contrast, the preliminary molecular data by Ziegler *et al.* (2007b) demonstrate that *V. lirungensis* (there still listed as '*V. indicus* Talaud') seems to be most closely genetically related to a live specimen (uncorrected p-distance: 0.2%) of unknown provenance formerly kept in the Cologne Zoo, Germany (Fig. 2). This specimen, however, shows only marginal morphological similarities with *V. lirungensis*. Genetically, the next most closely related species is *V. rainierguentheri* (uncorrected pair-wise sequence distance: 0.5%) from the neighbouring island of Halmahera (Ziegler *et al.* 2007a), lying at about the same level of genetic differentiation for the mitochondrial 16S gene as, for example, the phenetically distinct *V. cerambonensis* and *V. melinus* (Ziegler *et al.* 2007b). The p-distance values with respect to the *V. indicus* specimens analysed vary between 0.7% and 1.1%. The sequence distances of *V. lirungensis* with respect to the remaining members of the *V. indicus* group included in Ziegler *et al.* (2007b) are as follows: *V. caerulevirens* 1.3%; *V. cerambonensis* 0.9%; *V. doreanus* 2.4%; *V. finschi* 2.2%; *V. jobiensis* 2.0%; *V. melinus* 0.9%; and *V. yuwonoi* 1.4%. However, one of the most distinctive characters clearly separating the new species from *V. indicus* and *V. rainierguentheri* are the paryphasman rows, which stretch to both lobes of the hemipenis as is clearly observable from Fig. 6. In *V. indicus* and

V. rainierguentheri, the paryphasman rows stretch only along the outer lobe side.

Distribution and general biology

V. lirungensis is known only from the type locality, the Talaud Islands, in the Celebes Sea between North Sulawesi, Mindanao in the southern Philippines, and Halmahera in the northern Moluccas (Fig. 1). Thus, *V. lirungensis* has one of the smallest known distribution ranges amongst all varanids, comprising an island area of less than 30 × 90 km (~1400 km²). The Talaud mangrove monitor populations must therefore be treated as 'vulnerable' according to criterion B (and possibly C) of the International Union for Conservation of Nature (IUCN 2001).

Our observations suggest that *V. lirungensis* is abundant on the Talaud Islands. At least on Salibabu these monitors were frequently encountered even in disturbed and cultivated areas such as coconut plantations near the coastline (Koch *et al.* 2009). The Talaud mangrove monitors almost exclusively used palm trunks for basking, hunting and mating. On one occasion a juvenile specimen was flushed out from near a creek but escaped in the dense vegetation. Although limited, these observations suggest an ecological separation of different age groups in the Talaud mangrove monitors. Juveniles appear to hide in thickets on the ground, while adults prefer a semi-arboreal life. An analysis of the stomach contents (see below) of adult *V. lirungensis* specimens supports this observation. Avoidance behaviour by juvenile specimens seems reasonable since cannibalism, common in many monitor species, cannot be excluded for *V. lirungensis*.

Investigations of defaecated prey items and stomach contents support preliminary conclusions about the natural diet of *V. lirungensis*. Specimen MZB Lac. 5178 defaecated the undigested remains of a small intertidal crab and a large green orthopteran (*Sexava* sp., Tettigoniidae). The stomach of ZFMK 87587 contained a well preserved specimen of a large spider ('*Olios*' *coccineiventris* group, Deleninae), and a fragmented crab. However, no reptilian, mammalian or molluscan items were found, as reported by Dryden (1965) and McCoid and Wittman (1993) for mangrove monitors on Guam and Rota.

Observation of active mating behaviour during the field survey, and the presence of two and three eggs for two of the voucher specimens, suggests that the reproductive period for *V. lirungensis* occurs throughout May, June and July. Wikramanayake and Dryden (1988) similarly noted that reproduction of *V. indicus* on Guam occurs during the dry season.

Sexual maturity in female *V. lirungensis* is attested by the two egg-bearing voucher specimens with SVLs of 350 mm and 340 mm, respectively. *V. indicus* on Guam reached sexual maturity at 275 mm SVL in the wild (Wikramanayake and Dryden 1988), and at 300–400 mm in captivity (McCoid 1993). The two small eggs of ZFMK 87587 measure 8 × 17 mm, while the three well developed eggs of MZB Lac. 5177 measure 29 × 63 mm, 28 × 63 mm, and 27 × 61 mm.

Additional field studies on the ecology and biology of the locally endemic Talaud monitor lizard are desirable.

Varanus indicus: a superspecies in action

'True' Mangrove monitors, *V. indicus sensu stricto*, are extremely widespread throughout the eastern part of the chain of partly

oceanic islands stretching between Asia, Australia and the Pacific. Some authors have asserted that isolated populations of *V. indicus* on remote island groups like the Marianas were introduced by man (e.g. Brown 1956; Lever 2003). Evidence from the Talaud Archipelago, however, demonstrates that such islands may harbour morphologically and genetically distinct populations that undoubtedly represent independent evolutionary lineages. In light of this finding, introduction by man as a universal phenomenon for the wide distribution of *V. indicus* appears untenable and some allopatric island populations may warrant specific recognition within the concept of a polytypic superspecies, *V. indicus sensu lato* (unpubl. data). The application of multivariate statistical techniques will considerably refine the taxonomic concept of the *V. indicus* complex. In addition, the application of new species concepts that, more than the biological species concept, reflect evolutionary history (e.g. de Queiroz 1998) will have a substantial impact on the systematics of this closely related monitor species group, especially with regard to the numerous allopatric populations of *V. indicus sensu stricto*. Under these circumstances, even the outdated intraspecific dissection by Mertens (1926) may prove to have, at least in part, a systematic basis.

Two groups have to be distinguished for a systematic concept of the mangrove monitor complex: one group of evolutionarily older species distantly related to *V. indicus*, such as *V. jobiensis*, *V. finschi*, or *V. doreanus*; and a second group that is in *statu nascendi* (i.e. incipient speciation), or 'already beyond' (see Fig. 2). Remarkably, the three former species occur in (secondary) sympatry with *V. indicus* in New Guinea, while other evolutionarily younger species such as *V. rainerguentheri* and *V. lirungensis*, are found on geographically isolated islands within the former range of *V. indicus sensu stricto*.

Because of the young age of the *V. indicus* complex, according to Jennings and Pianka (2004), the species group experienced a recent diversification in the Indo-Australian region and exhibits a low level of interspecific genetic differentiation, at least when only a portion of the mitochondrial 16S rRNA gene is analysed (Fig. 2) (Ziegler et al. 2007b). However, claims of only modest genetic divergence are inconsistent with the high degree of morphological differentiation seen in genital morphology, scalation, and colour pattern between the monitor species reviewed by Ziegler et al. (2007b). In contrast, the phylogeny of varanid lizards published by Ast (2001) showed a much finer resolution for the *V. indicus* species group, although only five species of this complex were included in the study. Three samples of *V. indicus* from New Guinea, northern Australia and the Solomon Islands showed genetic differentiation between populations, confirming cryptic diversity within this group. The huge land mass of New Guinea, for instance, is home to a considerable diversity of monitors with, among others, four known species of the mangrove monitor complex (*V. indicus*, *V. jobiensis*, *V. doreanus*, and *V. finschi*). Potentially, additional unknown species or even additional polytypic species may be involved (Ziegler et al. 2007b).

Current knowledge about the diversity and degree of endemism of Indo-Australian monitor lizards, particularly within the Wallacea region, is far from complete. This paper presents some initial steps towards a refinement of the concept of a

polytypic species in these varanids, and highlights directions for future systematic investigations and research.

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References

- Ast, J. C. (2001). Mitochondrial DNA evidence and evolution in Varanoidea (Squamata). *Cladistics* **17**, 211–226. doi: 10.1006/clad.2001.0169
- Böhme, W. (1988). Zur Genitalmorphologie der Sauria: Funktionelle und stammesgeschichtliche Aspekte. *Bonner Zoologische Monographien* **27**, 3–176.
- Böhme, W., and Ziegler, T. (1997). *Varanus melinus* sp. n., ein neuer Waran aus der *V. indicus* Gruppe von den Molukken, Indonesien. *Herpetofauna* **19**, 26–34.
- Böhme, W., and Ziegler, T. (2005). A new monitor lizard from Halmahera, Moluccas, Indonesia (Reptilia: Squamata: Varanidae). *Salamandra (Rheinbach)* **41**, 51–59.
- Böhme, W., Horn, H.-G., and Ziegler, T. (1994). Zur Taxonomie der Pazifikwarane (*Varanus indicus*-Komplex): Revalidierung von *Varanus doreanus* (A.B. Meyer, 1874) mit Beschreibung einer neuen Unterart. *Salamandra (Rheinbach)* **30**, 119–142.
- Böhme, W., Philipp, K. M., and Ziegler, T. (2002). Another new member of the *Varanus (Euprepiosaurus) indicus* group (Sauria, Varanidae): an undescribed species from Rennell Island, Solomon Islands. *Salamandra (Rheinbach)* **38**, 15–26.
- Brandenburg, T. (1983). Monitors of the Indo-Australian Archipelago. M.Sc. Thesis, University of Leyden, The Netherlands.
- Brown, W. C. (1956). The distribution of terrestrial reptiles in the islands of the Pacific Basin. *Proceedings of the 8th Pacific Science Congress* **3A**, 1479–1491.
- De Jong, J. K. (1928). Beiträge zur Kenntnis der Reptilienfauna von Niederländisch-Ost Indien. *Treubia* **10**, 145–151.
- De Queiroz, K. (1998). The general lineage concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. In 'Endless Forms: Species and Speciation'. (Eds D. J. Howard and S. H. Berlocher.) pp. 57–75. (Oxford University Press: Oxford.)

- De Queiroz, K. (2005). A unified concept of species and its consequences for the future of taxonomy. *Proceedings of the California Academy of Sciences* **56**(Suppl. 1), 196–215.
- De Rooij, N. (1915). 'The Reptiles of the Indo-Australian Archipelago.' (E. J. Brill Ltd.: Leiden.)
- Devitt, T. J., LaDuc, T. J., and McGuire, J. A. (2008). The *Trimorphodon biscutatus* (Squamata: Colubridae) species complex revisited: a multivariate statistical analysis of geographic variation. *Copeia* **2008**, 370–387. doi: 10.1643/CH-07-045
- Dryden, G. L. (1965). The food and feeding habits of *Varanus indicus* on Guam. *Micronesia* **2**, 73–76.
- Dryden, G., and Ziegler, T. (2004). *Varanus indicus*. In 'Varanoid Lizards of the World'. (Eds E. R. Pianka and D. R. King.) pp. 184–188. (Indiana University Press: Bloomington, IN.)
- Eidenmüller, B., and Philippen, H.-D. (2008). 'Varanoid Lizards – Warane und Krustenechsen. Terralog 6.' (Chimaira: Frankfurt a. M.)
- Hammer, Ø., Harper, D. A. T., and Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* **4**, 9.
- Harvey, M. B., and Barker, D. G. (1998). A new species of blue-tailed monitor lizard (genus *Varanus*) from Halmahera Island, Indonesia. *Herpetologica* **54**, 34–44.
- International Union for Conservation of Nature (2001). 'IUCN Red List Categories and Criteria, Version 3.1.' (IUCN Species Survival Commission: Gland, Switzerland & Cambridge, UK.)
- Jennings, W. B., and Pianka, E. R. (2004). The tempo and timing of the Australian *Varanus* radiation. In 'Varanoid Lizards of the World'. (Eds E. R. Pianka and D. R. King.) pp. 77–87. (Indiana University Press: Bloomington, IN.)
- Koch, A., Auliya, M., Schmitz, A., Kuch, U., and Böhme, W. (2007). Morphological studies on the systematics of south east Asian water monitors (*Varanus salvator* ssp. Complex): nominotypic populations and taxonomic overview. *Mertensiella* **16**, 109–180.
- Koch, A., Arida, E., Riyanto, A., and Böhme, W. (2009). Islands between the realms: a revised checklist of the herpetofauna of the Talaud Archipelago, Indonesia, with a discussion about its biogeographic affinities. *Bonner Zoologische Beiträge* **56**, 107–129.
- Lever, C. (2003). 'Naturalized Reptiles and Amphibians of the World.' (Oxford University Press: Oxford.)
- Mayr, E. (1942). 'Systematics and the Origin of Species.' (Columbia University Press: New York.)
- McCoid, M. J. (1993). Reproductive output in captive and wild mangrove monitors (*Varanus indicus*). *Varanews* **3**, 4–5.
- McCoid, M. J., and Wittman, G. J. (1993). *Varanus indicus* (mangrove monitor). Diet. *Herpetological Review* **24**, 105.
- McGarigal, K., Cushman, S., and Stafford, S. G. (2000). 'Multivariate Statistics for Wildlife and Ecology Research.' (Springer: New York.)
- McGuire, J. A., Brown, R. M., Mumpuni, , Riyanto, A., and Anayani, N. (2007). The flying lizards of the *Draco lineatus* group (Squamata: Iguana: Agamidae): a taxonomic revision with descriptions of two new species. *Herpetological Monographs* **21**, 179–212. doi: 10.1655/07-012.1
- Mertens, R. (1926). Über die Rassen einiger indo-australischer Reptilien. *Senckenbergiana* **8**, 272–279.
- Mertens, R. (1942a). Die Familie der Warane. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **462**, 1–116.
- Mertens, R. (1942b). Die Familie der Warane. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **465**, 117–234.
- Mertens, R. (1942c). Die Familie der Warane. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **466**, 235–391.
- Mertens, R. (1963). Liste der rezenten Amphibien und Reptilien: Helodermatidae, Varanidae, Lanthanotidae. *Das Tierreich* **79**, 1–26.
- Philipp, K. (1999). Niche partitioning of *Varanus doreanus*, *V. indicus* and *V. jobiensis* in Irian Jaya: preliminary results. *Mertensiella* **11**, 307–316.
- Philipp, K., Böhme, W., and Ziegler, T. (1999). The identity of *Varanus indicus*: redefinition and description of a sibling species coexisting at the type locality. *Spixiana* **22**, 273–287.
- Rastegar-Pouyani, N. (2005). A multivariate analysis of geographic variation in the *Trapelus agilis* complex (Sauria: Agamidae). *Amphibia-Reptilia* **26**, 159–173. doi: 10.1163/1568538054253474
- Van Rooijen, J., and Vogel, G. (2008). An investigation into the taxonomy of *Dendrelaphis tristis* (Daudin, 1803): revalidation of *Dipsas schokari* (Kuhl, 1820) (Serpentes: Colubridae). *Contributions to Zoology (Amsterdam, Netherlands)* **77**, 33–43.
- Van Steenis-Kruseman, M. J. (1950). Malaysian plant collectors and collections. *Flora Malesiana* **1**, 1–639.
- Vogel, G., and van Rooijen, J. (2008). Contributions to a review of the *Dendrelaphis pictus* (Gmelin, 1789) complex – 2. The eastern forms. (Serpentes: Colubridae). *Herpetozoa (Wien)* **21**, 3–29.
- Wikramanayake, E. D., and Dryden, G. L. (1988). The reproductive ecology of *Varanus indicus* on Guam. *Herpetologica* **44**, 338–344.
- Ziegler, T., and Böhme, W. (1997). Genitalstrukturen und Paarungsbiologie bei squamaten Reptilien, speziell den Platynota, mit Bemerkungen zur Systematik. *Mertensiella* **8**, 3–207.
- Ziegler, T., and Böhme, W. (1999). Genital morphology and systematics of two recently described monitor lizards of the *Varanus* (*Euprepiosaurus*) *indicus* group. *Mertensiella* **11**, 121–128.
- Ziegler, T., Böhme, W., and Philipp, K. M. (1999a). *Varanus caerulivirens* sp. n., a new monitor lizard of the *V. indicus* group from Halmahera, Moluccas, Indonesia (Squamata: Sauria: Varanidae). *Herpetozoa (Wien)* **12**, 45–56.
- Ziegler, T., Philipp, K. M., and Böhme, W. (1999b). Zum Artstatus und zur Genitalmorphologie von *Varanus finschi* Böhme, Horn & Ziegler, 1994, mit neuen Verbreitungsangaben für *V. finschi* und *V. doreanus* (Meyer, 1874) (Reptilia: Squamata: Varanidae). *Zoologische Abhandlungen. Staatliches Museum für Tierkunde* **50**, 267–279.
- Ziegler, T., Böhme, W., Eidenmüller, B., and Philipp, K. M. (2001). A note on the coexistence of three species of Pacific monitor lizards in Australia (Sauria, Varanidae, *Varanus indicus* group). *Bonner Zoologische Beiträge* **50**, 27–30.
- Ziegler, T., Böhme, W., and Schmitz, A. (2007a). A new species of the *Varanus indicus* group (Squamata, Varanidae) from Halmahera Island, Moluccas: morphological and molecular evidence. *Mitteilungen des Museum für Naturkunde Berlin. Zoologische Reihe* **83**(Suppl.), 109–119. doi: 10.1002/mmzn.200600034
- Ziegler, T., Schmitz, A., Koch, A., and Böhme, W. (2007b). A review of the subgenus *Euprepiosaurus* of *Varanus* (Squamata: Varanidae): morphological and molecular phylogeny, distribution and zoogeography, with an identification key for the members of the *V. indicus* and the *V. prasinus* species groups. *Zootaxa* **1472**, 1–28.

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Appendix 1. Additional specimens of the *Varanus indicus* species complex included in this study

Specimens that have been examined for the first time are indicated by an asterisk

Species	Specimens
<i>V. rainierguentheri</i>	3 specimens: ZFMK 85404 (holotype, Halmahera); USNM 23438 (paratype, Halmahera); MZB Lac. 6145* (Halmahera).
<i>V. indicus</i>	21 specimens: ZFMK 70650 (neotype, Ambon); ZMA 11146c (Ambon); ZMA 10202 (New Guinea); RMNH 21053–54 (New Guinea, 2 specimens); RMNH 21055a (New Guinea); RMNH 21046–47 (New Guinea, 2 specimens); RMNH 21042 (New Guinea); RMNH 21036a,b,e (New Guinea, 3 specimens); MZB Lac. 6445* (Weigeo); ZMA 10192a–h (Weigeo, 8 specimens).
<i>V. cf. indicus</i>	1 specimen: ZFMK alive* (without locality data, formerly in the Cologne Zoo).
<i>V. yuwonoi</i>	4 specimens: UTA-R41281 (holotype, Halmahera); UCM 58747 (paratype, Halmahera); MZB Lac. 2722* (Ternate?); ZFMK 70594 (Halmahera).
<i>V. zugorum</i>	1 specimen: USNM 237439 (holotype, Halmahera).
<i>V. caerulivirens</i>	5 specimens: ZFMK 68874 (holotype, Halmahera); ZFMK 6877 (paratype, Halmahera); SMF 32805 (paratype, Halmahera); RMNH 3149 (Halmahera); MZB Lac. 6144* (Halmahera).
<i>V. melinus</i>	8 specimens: ZFMK 65737 (holotype, 'Obi'); ZFMK 74278 (paratype, 'Obi'); ZFMK 66357 (paratype, 'Obi'); ZFMK 70441 (paratype, 'Obi'); ZFMK 66358 ('Obi'); MZB Lac. 2226*–27* (Halmahera?, 2 specimens); MZB Lac. 2723* (Sula Islands?).