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New data on the rare *Varanus bogerti* Mertens, 1950 and *V. telenesetes* Sprackland, 1991 (Squamata: Varanidae), two endemic monitor lizard taxa from island groups off southeastern New Guinea

André Koch¹, Nicole Ernst¹, Bernd Eidenmüller² & Fred Kraus³

¹Zoologisches Forschungsmuseum Alexander Koenig, Leibniz Institute for Animal Biodiversity, Section of Herpetology, Adenauerallee 160, D-53113 Bonn, Germany

²Griesheimer Ufer 53, 65933 Frankfurt, Germany

³Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA

Some monitor lizards are among the least studied of all vertebrate species, being known only from a handful of old voucher specimens in museum collections. This includes tree monitors related to *Varanus prasinus* (Schlegel, 1839), namely *V. telenesetes* and the melanistic *V. bogerti*, which inhabit the Trobriand, D'Entrecasteaux and Louisiade islands off southeastern New Guinea. We provide new data about morphological variation and natural history for *V. bogerti* supplemented by a detailed description of the colour pattern in hatchlings. The exact distribution range of *V. bogerti* is still insufficiently known, and a historical record from the Trobriand Islands needs verification. We also discuss the taxonomic status, distribution and origin of the holotype of *V. telenesetes*, the only known specimen of this taxon, in relation to *V. bogerti* and *V. prasinus*. The examination of specimens of *V. prasinus* from southeastern New Guinea allows a discussion about the putative sympatric occurrence of, and past gene flow between multiple tree monitor species on the D'Entrecasteaux islands in light of climate-induced sea level changes during the Pleistocene. Only further field work and future investigations will yield sufficient answers to the open questions surrounding these rare New Guinean tree monitors.

Key words: D'Entrecasteaux Islands, *Euprepisaurus*, Louisiade Islands, melanism, Milne Bay, Reptilia, *Varanus prasinus* species group

INTRODUCTION

Melanism, the predominance of dark pigmentation, is a common phenomenon in the genus *Varanus* Merrem, 1820 and can be observed in various, unrelated species groups (Mertens, 1942; Bennett, 1998; Koch et al., 2007). Among the group of arboreal monitors related to *V. prasinus* (Schlegel, 1839) from New Guinea and its offshore islands are two taxa that are entirely black as adults (Ziegler et al., 2007). These are *V. beccarii* (Doria, 1874) from the Aru Islands, off southwestern New Guinea, and *V. bogerti* Mertens, 1950 from the Trobriand, D'Entrecasteaux, and Louisiade islands off southeastern New Guinea (Fig. 1). In addition, the taxa *V. boehmei* Jacobs, 2003 from Waigeo Island off western New Guinea and *V. keithhornei* Wells & Wellington, 1985 from northern Australia show only faint light markings on a dark-grey to blackish background colour. Of these partly or entirely melanistic tree monitors, *V. bogerti* is very rare, being known only from a handful of old voucher specimens in a few museum collections.

In 1950, *V. bogerti* was described by Robert Mertens as a subspecies of the Emerald-Green Tree Monitor, *V. prasinus* (Fig. 2). Mertens (1950) named the species in honour of Charles M. Bogert (1908–1992), curator of the Department of Amphibians and Reptiles at the American Museum of Natural History between 1937 and 1968. The description was based on three specimens (AMNH 41638–40) collected by R.H. Beck in March 1929 during the Whitney South Sea Expedition at Fergusson (=Moratau) Island, D'Entrecasteaux Archipelago, off the southeastern tip of New Guinea. Burt & Burt (1932) reported on the herpetological results of this expedition. These authors were aware of Boulenger's (1885, 1895a) accounts about *V. kordensis* (Meyer, 1874) from the New Guinean islands of Mysore (=Biak) and Fergusson, respectively, and accordingly also referred their three black specimens from the latter island to this supposedly melanistic species. Misleadingly, however, Boulenger (1885, 1895a) had identified some black specimens from Fergusson Island (BMNH 95.4.26.14–16, three juvenile specimens, collected by A.S. Meek, Fig. 5) and southeastern New

Correspondence: André Koch (andrepascalkoch@web.de)

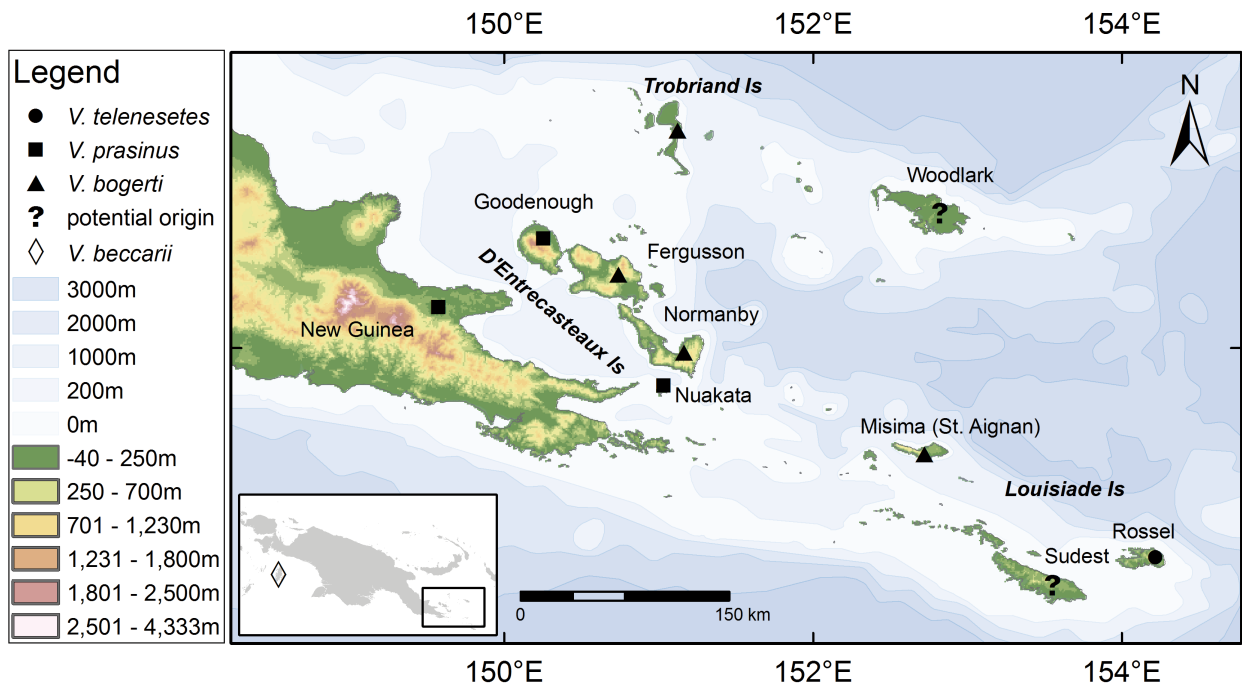


Fig. 1. Map of southeastern New Guinea, including the offshore island groups of the D’Entrecasteaux, Louisiade, and Trobriand archipelagos, where the endemic *Varanus bogerti* and *V. telenesetes* occur. Note that the origin of the latter species is not sufficiently known (see text). Also the exact distribution of *V. bogerti* on the Trobriand Islands is unclear. Question marks indicate islands of possible provenance. The wide-spread *V. prasinus* inhabits mainland New Guinea and the islands of Goodenough and Nuakata. The inserted map shows the geographic range of the melanistic *V. beccarii* in the Aru Islands.

Guinea (BMNH 76.7.6.2, an adult with imprecise locality data [but see comments below], collected by “–Comree, Esq.”) as *V. kordensis*, although he had an alleged syntype (BMNH 46.9.1.92, an adult specimen called “a”) from the type locality “Kordo, Mysore (=the village of Kordo on Biak Island)” at hand in the British Museum. This voucher specimen shows the characteristic colour pattern of a black network on an olive-green background (Boulenger, 1885:322). Later, Meyer (1887) reported Boulenger’s (1885) mistake about the alleged type status of the *V. kordensis* specimen “a”, which Marquis G. Doria from the natural-history museum in Genova (Genoa), Italy, had presented to the British Museum in London. Possibly, this specimen had been collected by Odoardo Beccari (1843–1920), an Italian naturalist and namesake of *V. beccarii*. In this regard, Meyer (1887) stated that he had collected only a single voucher specimen (field number 365) of his new species, i.e. the holotype of *V. kordensis*, which was deposited at the royal museum for natural history in Dresden, of which Adolf B. Meyer (1840–1911) was director between 1874 and 1906. Consequently, Boulenger’s non-type *V. kordensis* specimen from the type locality merely represents a toptotypical voucher without any taxonomic relevance. In addition, Boulenger (1885) incorrectly synonymised Doria’s (1874) melanistic taxon *beccarii* with Meyer’s green *kordensis*, of which he certainly never saw the type specimen in the Dresden museum. The holotype was later destroyed in World War II (Obst, 1977; see also Böhme & Koch, 2010). So possibly Boulenger (1885) confused the second entirely black (and therefore misidentified *V. kordensis*) specimen “b” (BMNH 76.7.6.2) with *V. beccarii*, a melanistic tree

monitor that was collected and described by Doria (1874) the same year as the taxon *kordensis* (Meyer, 1874). Also, Barbour (1912) and de Rooij (1915) followed Boulenger’s (1885) misleading classification uncritically, while Roux (1910) referred to the taxon *beccarii* as a distinct subspecies of *V. kordensis*.

Mertens (1942) was the first to recognise the morphological and taxonomic distinctness of the black monitors from Fergusson Island vis-à-vis all other tree monitor species known at that time, including the phenotypically similar melanistic *V. beccarii* from the Aru Islands. Later, he described *V. bogerti* as another black subspecies of *V. prasinus* (Mertens, 1950). After studying further voucher specimens from New Guinean



Fig. 2. Dorsal view of the male holotype of *V. bogerti* (AMNH R-41639) from Fergusson (=Moratau) Island, D’Entrecasteaux Archipelago. It was collected by R. H. Beck in March 1929 during the Whitney South Sea Expedition and described by Mertens (1950) as a subspecies of *V. prasinus*. Photo: David Kizirian.

offshore islands at the British Museum of Natural History in London (BMNH), Mertens (1959) later extended the geographic range of *V. bogerti* to include the “Trobriand Islands” (imprecise locality, BMNH 96.7.8.1, a juvenile, collected by A.S. Meek) and St. Aignan (=Misima Island, BMNH 1889.7.1.8, a female, collected by B.H. Thomson) in the Louisiade Archipelago (Fig. 1). Note that earlier de Rooij (1915) had already mentioned the existence of (black) tree monitors from these islands without having examined specimens. Of these additional voucher specimens, however, no morphological data were provided by Mertens (1959) and none has been published since. Nor did Mertens (1959) mention the exact number of specimens he investigated or the respective collection numbers of the examined material (see above). Thus, *V. bogerti* has to be regarded as a little-known endemic to the small island groups southeast of New Guinea.

In 1980, Czechura (1980) reported on the discovery of tree monitors from the Cape York Peninsula of northern Australia; these were subsequently described as *V. keithhornei* by Wells & Wellington (1985). At the same time, Czechura (1980) mentioned a specimen from Rossel Island, the southeastern-most island of the Louisiade Archipelago, housed in the Queensland Museum collection (QMJ1190) that was a member of the *V. prasinus* species group but could not be assigned to any known taxon. Reviewing geographical variation in the tree monitor group, Sprackland (1991) elevated the taxon *bogerti* to species status and allocated the single specimen (QMJ1190) from Rossel Island to a hitherto undescribed species, *V. telenesetes*. According to the author, this new species differs from *V. prasinus* and *V. bogerti* in colour pattern and scalational characters (Sprackland, 1991). Later authors either regarded Sprackland’s (1991) new species description with scepticism (e.g., Green, 2004; J. A. Covacevich, pers. comm. to B. Eidenmüller) or followed his opinion without comment (e.g., Böhme, 2003; Ziegler et al., 2007). Although he claimed to have examined five specimens from the natural history museums in New York (AMNH 41638–39, 76722) and London (BMNH 76.7.6.2 and BMNH 89.7.1.8), Sprackland (1991) only provided morphological data for the three type specimens as given by Mertens (1950) in the original description. Sprackland also apparently examined two of the six *V. bogerti* specimens that Mertens (1959) had found in the BMNH collection (and incorrectly referred to all voucher specimens he examined as paratypes), but he did not provide data on those specimens. Further, Sprackland (1991:569) erroneously stated that Mertens (1959) had examined a monitor specimen from Rossel Island that he had assigned to the taxon *bogerti*. Actually, Mertens (1959) reported the discovery of further specimens of *V. bogerti* in the London collection. This, however, did not include a specimen from Rossel Island (see above).

Therefore, at present the only information available about *V. bogerti* and *V. telenesetes* is the data from the respective original species descriptions (Mertens, 1950; Sprackland, 1991). Given the scepticism expressed regarding the taxonomic status of *V. telenesetes*, and given its reported provenance, it also merits inquiring whether the holotype of *V. telenesetes* merely represents another

specimen of *V. bogerti*. Further, nothing is known about habitat preferences, natural history, or the phylogenetic relationships of these rare monitor species. In the IUCN Red List, *V. telenesetes* is listed as “data deficient” (Bennett & Sweet, 2010) while *V. bogerti* is not listed at all. Consequently, *V. bogerti* and *V. telenesetes* must be regarded as among the least known of all extant monitor lizards (Koch et al., 2013). This article is an attempt to diminish this fundamental lack of knowledge.

MATERIALS AND METHODS

During field work on Fergusson Island in 2002 one subadult specimen of *V. bogerti* was collected by a local and given to FK. As this represents the first voucher specimen known of this rare monitor species since the type series was collected more than 70 years ago and one of only very few known specimens of *V. bogerti*, we here provide additional morphological data as well as the first information about its natural habitat. The new voucher specimen of *V. bogerti* (BPBM 16053) was examined by NE following the protocol, morphological characters, and abbreviations used by Böhme et al. (1994) and Koch et al. (2010). In addition, Flora Ihlow (ZFMK) studied two adult voucher specimens of *V. bogerti* (BMNH 1889.7.1.8 and BMNH 76.7.6.2) in detail and photographed four additional juveniles (BMNH 95.4.26.14–16 and BMNH 96.7.8.1) in the London collection that had earlier been identified by Mertens (1959). Among the latter are the first known juveniles of *V. bogerti* that allow a detailed description of the colour pattern in hatchlings of this species. Hitherto unpublished information about the BMNH specimens of *V. bogerti* and other tree monitor taxa are derived from the collection catalogue entries of the Department of Herpetology and supplemented with data from historical literature sources. In addition, photographs of the *V. prasinus* specimen (AMNH 42373) from Dauila (=Goodenough) Island, that Mertens (1950) had examined along with the *bogerti* type series, were available (Fig. 8A, B). Another specimen of *V. prasinus* from Oro Province of Papua New Guinea was examined by AK in the Vienna Natural History Museum (Fig. 9A, B). Both these specimens allow us to consider the possibility of sympatric occurrence of and/or past gene flow between multiple members of tree monitors on the D’Entrecasteaux Islands in the light of climate-induced sea-level changes during the Pleistocene. Finally, the holotype of *V. telenesetes* (QMJ1190) was studied non-quantitatively twice but independently by BE and FK. The latter examination in February 2005 involved side-by-side comparison with the new *V. bogerti* specimen BPBM 16053.

The distribution map was designed using ArcGIS v.10. Elevation data were obtained from CGIAR SRTM (Jarvis et al., 2008), bathymetry contour lines were obtained from Natural Earth (<http://www.naturalearthdata.com>), and country boundaries were derived from the DIVA-GIS homepage (<http://www.diva-gis.org>).

Collection abbreviations are as follows: AMNH: American Museum of Natural History, New York, USA; BMNH: The Natural History Museum (formerly British

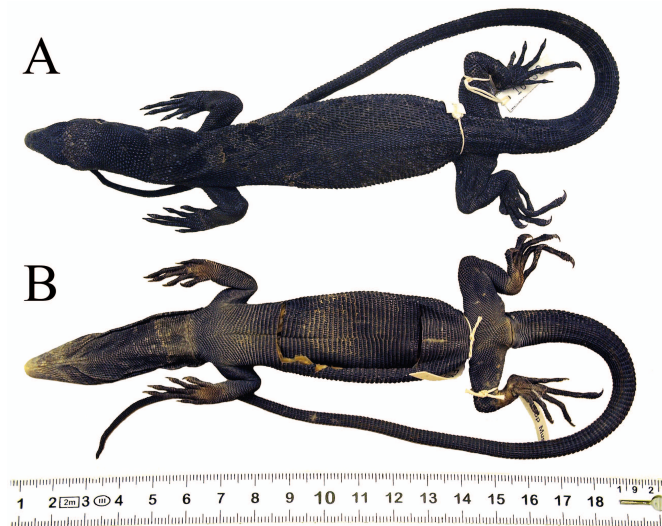


Fig. 3. The new voucher specimen of *V. bogerti* (BPBM 16053) from Fergusson Island. (A) Dorsal view; (B) Ventral view. Note the relatively short tail of this subadult specimen. The dorsal, narrow yellow crossbars made of scattered yellow scales were only visible in life. Photos: Nicole Ernst.



Fig. 4. Dorsal view of the head of *V. bogerti* (BPBM 16053). Typical of the *V. prasinus* group are the enlarged scales of the interorbital region located between the likewise enlarged supraoculars. Note also the strongly keeled nuchal scales, which are diagnostic for *V. bogerti*. Photo: Nicole Ernst.

Museum of Natural History), London, UK; BPBM: Bernice Pauahi Bishop Museum, Honolulu, Hawai'i, USA; NMW: Naturhistorisches Museum, Vienna, Austria; QM: Queensland Museum, Brisbane, Australia; RMNH: Naturalis National Museum of Natural History, Leiden, The Netherlands; ZMA: formerly Zoological Museum, University of Amsterdam, Amsterdam, The Netherlands (now integrated in RMNH).

Definitions and abbreviations for the morphological characters examined are as follows: SVL: snout-to-vent length measured from snout tip to cloaca; TL: tail length measured from cloaca to tail tip; Index 1: relative tail length [=TL/SVL]; A: head length measured from snout tip to anterior margin of ear opening; B: head width measured across maximum width; C: head height above the eyes; Index 10: relative head length [=A/B]; Index 11: head length in relation to head height [=A/C]; G: snout length measured from anterior rim of eye to centre of nostril; H: snout length measured from centre of nostril to snout tip; Index 2: position of nostril between eye and tip of snout [=G/H]; P: scales around head from rictus to rictus; Q: scales around tail base; R: scales around tail after first third of its length; S: number of midbody scale rows; T: transverse rows of ventral scales measured from gular fold to insertion of the hind legs; N: ventral scales from tip of snout to gular fold; X: transverse dorsal scale rows from hind margin of tympanum to gular fold; Y: transverse dorsal scale rows from gular fold to insertion of hind legs; XY: dorsal scales from hind margin of tympanum to insertion of hind legs [=X+Y]; m: scales around neck anterior to gular fold; U: differentiated (=enlarged) supraocular scales (right/left); c: supralabials exclusive the rostral scale. Measurements were taken to the nearest millimetre.

RESULTS AND DISCUSSION

Description of the new voucher specimen of *V. bogerti*

BPBM 16053 (field number FK 6264, Figs. 3–4), a subadult from Lauoya (9.4678°S, 150.8224°E), 1 km west of Basima, Fergusson Island, Milne Bay Province, Papua New Guinea, 40 m elevation, caught by a local collector, given to F. Kraus, 2 September 2002.

Morphology: The body is slender. SVL 154 mm, TL 253 mm, ToL 407 mm. The tail is roundish in cross section and 1.64 times as long as the snout-vent length (index 1=TL/SVL); head length 29 mm, head width 15 mm (index 10=A/B=1.93), head height 11 mm (index 11=A/C=2.63); distance from anterior margin of eye to nostril 8.5 mm, distance from nostril to tip of snout 6.8 mm (index 2=G/H=1.25). Head scales rounded, rugose. Three and four enlarged supraocular scales above the right and left eyes, respectively. As in the holotype of *V. bogerti* (AMNH 41639), three rows of enlarged scales span the interorbital region. Weight 44 g in life. The proportion indices and scalational features of the subadult voucher specimen coincide well with those data provided by Mertens (1950) for the three adult types (Table 1). Notably, however, the tail of BPBM 16053 is significantly shorter, being only 1.64 times as long as SVL compared to about 2.0 times in the type series of *V. bogerti* and other members of the *V. prasinus* group (Mertens, 1942; 1950). This difference could be due to the specimen's young age, with the tail becoming proportionally longer with increasing age in tree monitors. In support of that notion, hatchlings of *V. prasinus* and *V. beccarii* have a tail that is only about 1.5 times the SVL (Mertens, 1942; Eidenmüller, 1998; Eidenmüller & Wicker, 1993).

Colouration in life: Colour notes were taken by FK: “Dorsum black with narrow yellow crossbars made of scattered yellow scales. Head ash grey; tail black. Venter ash grey changing to black on posterior two-thirds of tail. Tongue pink with violet tip; mouth pink.” In preservative, only the circumocular scales and the margins of the labial scales are brightly coloured, although the pale crossbands remain faintly evident; the tongue is flesh-coloured but is light blue anterodorsally beginning just posterior to the bifurcation.

Natural history of V. bogerti: As the new voucher specimen reported herein was collected by a local, direct information about its natural habitat is unavailable, but the specimen presumably came from secondary lowland rainforest, which dominates the area west of Basima. On nearby Normanby Island (Fig. 1), the species is frequently found in mangrove forest, although it also occurs in lowland rainforest (pers. comm. of local inhabitants to FK).

The historical voucher specimens of *V. bogerti* in the BMNH collection

The following six specimens of *V. bogerti* are housed in the BMNH collection. They were all collected more than a hundred years ago and although Mertens (1959, 1963) referred to them repeatedly, no morphological data have since been published. Data in quotation marks (‘’) are derived word for word from the collection catalogue page of ‘‘*Varanus prasinus kordensis*’’. See the introduction for an explanation as to why these *V. bogerti* specimens were erroneously allocated to the taxon *kordensis* by the former curator George A. Boulenger (1858–1937). Notably, the comment ‘‘deleted 1991’’ has been added behind the name ‘‘*kordensis*’’. This most probably resulted from the taxonomic revision of the tree monitor group by Robert Sprackland, who first visited the BMNH in 1989, and subsequently synonymised the younger taxon *kordensis* with the older *prasinus* (Sprackland, 1991). More recently, however, the original species status of *V. kordensis* was revalidated by Jacobs (2002).

Table 1. Morphological data of the new specimen of *V. bogerti* as compared to two historical voucher specimens, the type series (AMNH 41638–40), and three other melanistic taxa of the *V. prasinus* species group from Australo-Papua including *V. telenesetes*. ^aThe three newly examined specimens of *V. beccarii* are BMNH 1910.4.26.25–26 and BMNH 1905.11.29.4. ¹Sprackland (1991) provided only one value for the supraoculars. From the photograph of the dorsal side of the head of the holotype provided by Sprackland (1991:568) it is evident that three and four supraoculars are enlarged on the right and left side, respectively. ²Ditto for the enlarged supralabial scales. ³Only the supralabials on the right side were counted. ⁴Note that slight differences exist in calculating the relative position of the nostril between Mertens (1942, 1950) and Brandenburg (1983) and this study.

Taxon, specimen(s)	<i>V. bogerti</i> (BPBM 16053)	<i>V. bogerti</i> (BMNH [18]76.7.6.2)	<i>V. bogerti</i> (BMNH 1889.7.1.8)	<i>V. bogerti</i> (type series, n=3)	<i>V. telenesetes</i> (QM J1190, holotype)	<i>V. keithhornei</i> (n=3/3, incl. holotype)	<i>V. beccarii</i> (n=6/2)	<i>V. beccarii</i> (n=3) ^a
Source of data	this study	this study	this study	Mertens (1950)	Sprackland (1991)	Czechura (1980)/ Sprackland (1991)	Mertens (1942)/ Brandenburg (1983)	this study
Locality	Fergusson Isl.	‘‘South of Huon Gulf’’ (but see comments above)	St. Aignan (= Misima) Isl.	Fergusson Isl.	Rossel(I) Isl.	Cape York peninsula, North Australia	Aru Islands	Aru Islands
Age	subadult	adult	adult female	adult	subadult	adult	?/adult	adult
Index 1	1.64	1.92	1.87	2.00–2.10	1.96	1.98–2.10/ 1.98–2.02	1.90–2.10/ 1.90–2.20	1.71–1.90
Index 2	1.25	-	-	1.15–1.29 ⁴	-	1.26–1.32/-	1.46–1.53 ⁴ / 1.10–1.21	-
Index 10	1.93	-	-	2.01–2.14	-	~2.00/-	1.61–1.74/1.79	-
Index 11	2.63	-	-	2.37–2.56	-	~1.70/-	1.94–2.00/2.50	-
P	40	42	40	44–48	40	35–36/36	32–37/28–33	35–38
Q	62	66	67	-	-	-	-/51–59	62–69
R	24	30	27	-	-	-	-	26–29
S	96	101	95	95–99	100	90–99/90–93	81–92/82–93	95–101
T	81	85	78	87–90	92	86–89/84–91	70–79/73–80	76–82
N	73	79	75	-	-	-	-/61	70–74
XY	104	113	102	-	-	-	-/97–98	93–104
M	108	-	-	-	-	-	-/89	-
U	3/4	4/2	3/3	3–3	3/4 (7 ¹)	~5–5/6–7	-	4–5
c	41	20 ³	23 ³	-	22 ²	-/21–23 ²	42–43/-	20–21 ³

1) **BMNH 1889.7.1.8**: A female from St. Aignan (=Misima Island), Louisiade Archipelago, collected by “B.H. Thomson Esq. [=esquire]”. Sir Basil Home Thomson (1861–1939), a colonial administrator and later police officer, travelled the Louisiade and D’Entrecasteaux Islands in 1888. The island of St. Aignan was visited between 20 and 24 October. Although he mentioned wallabies and collected birds and butterflies on the various islands that were visited during the cruise (see Tristram, 1889; Kirby, 1889), no reference was made to the black monitor lizard specimen (Thomson, 1889). Apparently, no subsequent report about the reptiles (and amphibians) Thomson collected was published.

2) **BMNH [18]76.7.6.2**: An adult from “New Guinea, South of Huon Gulf” with imprecise locality data, collected by “Comree, Esq.”. From the first digit (76) of the entire collection number it is obvious that this specimen was collected prior to 1876, which might help to identify the odd collector. Most likely, “Comree” refers to Dr. Peter Comrie, a naturalist and medical officer of the royal navy, who accompanied Captain John Moresby (the namesake of Papua New Guinea’s capital Port Moresby) twice aboard the HMS Basilisk during his voyages in southeastern New Guinea and the D’Entrecasteaux Islands (Frodin, 2007). Subsequently, Sclater (1876) reported some bird specimens collected by Dr. Comrie and named a new species after him, the curl-crested Manucode (*Manucodia comrii*). Comrie was also listed as a collector of birds from Huon Gulf in southeastern New Guinea by Sharpe (1906). Strangely, however, we were not able to find a reference to a person called Comrie or Comree in Captain Moresby’s (1876) travel narrative. Instead, he repeatedly mentioned a navigating-lieutenant Connor. Comrie (1877), who published some “Anthropological Notes on New Guinea”, mentioned that he had found drums of the natives made from the skin of a large monitor lizard during the voyages of the Basilisk. The skin most probably was from the wide-

spread *V. indicus* (Daudin, 1802) that inhabits the islands together with the smaller tree monitors (Kraus & Allison, 2004). From the narrative by Moresby (1876) and from Comrie’s (1877) account it is obvious that the specimen BMNH [18]76.7.6.2 was most probably also collected on the D’Entrecasteaux Archipelago. Among other islands of this group, the Basilisk made a stop on Fergusson Island.

3) **BMNH [18]95.4.26.14–16**: Three juvenile specimens from “Fergus[s]on Island, D’Entrecasteaux Group”, collected by “A.S. Meek” (Fig. 5).

4) **BMNH [18]96.7.8.1**: A juvenile from the “Trobriand Islands”, collected by “A.S. Meek”. In his detailed travel narrative, Meek (1913) never differentiated between the islands he visited in the Trobriand Archipelago but steadily merely referred to “the Trobriands”. Also Boulenger (1895b), who published the herpetological results of Meek’s Trobriand collection, did neither mention this young monitor specimen nor did he provide any further information about the exact origin of the other voucher specimens, which included two species new to science. Only Thomas (1896) mentioned Kiriwina Island, the main island of the Trobriand Archipelago, as source of a supposedly new subspecies of cuscus (*Phalanger orientalis kiriwinae*=*P. intercastellanus* Thomas, 1895) collected by Meek. Notably, Heatwole (1975) listed merely the widespread Pacific or mangrove monitor *V. indicus* for several of the Trobriand, Lusancay and Louisiade islands he visited in 1969. Therefore, it remains unclear, on which of these islands *V. bogerti* occurs, if at all.

Morphological variation and ontogenetic change of colour pattern in *V. bogerti*

Morphology: Morphological data are provided for BMNH 1889.7.1.8, an adult female from Misima (=St. Aignan) Island, and BMNH [18]76.7.6.2, an adult from “South of Huon Gulf” (see comments above), respectively.

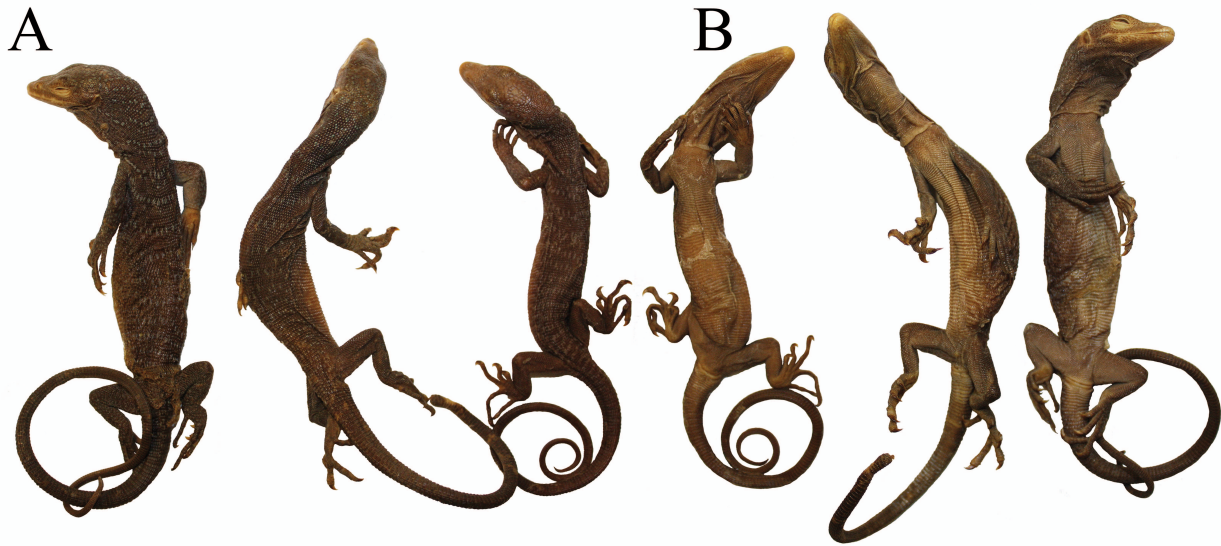


Fig. 5. Three juveniles of *V. bogerti* (BMNH [18]95.4.26.14–16) from Fergusson Island collected by A.S. Meek. (A) Dorsal view; (B) Ventral view. Note the faint dorsal colour pattern of transverse rows as is typical for many tree monitor taxa and which fades with age. Photos: Flora Ihlow.



Fig. 6. The holotype of *V. telenesetes* (QMJ1190), which lacks any green pigmentation today, in contrast to Sprackland's (1991) original description. Its collector and origin are unknown. Photos: Patrick Couper.

The body is slender. SVL=286 and 321 mm, TL=534 and 615 mm, and ToL=820 and 936 mm, respectively. The tail is roundish in cross section and 1.87/1.92 times as long as the snout-vent length (index 1=TL/SVL); nostril closer to tip of snout (index 2=G/H=1.27 for BMNH 1889.7.1.8). Head scales rounded, rugose. 2/4 and 3/3 enlarged supraocular scales above the right and left eyes, respectively. In both specimens, three rows of enlarged scales span the interorbital region. Overall, the morphometric ratios and scalational features of these two specimens coincide well with those data provided by Mertens (1950) and those of the new voucher specimen from Fergusson Island (Table 1). In summary, and based on six adult and subadult specimens, the extended morphological variation of *V. bogerti* is as follows: Tail length (index 1) 1.64–2.10 times the snout-vent length; position of nostril (index 2) 1.15–1.29 times nearer the tip of the snout than to the eye; head length 1.93–2.14 times the head width (index 10) and 2.37–2.63 times the head height (index 11); 40–48 scales around the head from rictus to rictus (P); 62–67 scales around tail base (Q) and 24–30 scales around tail after one third of its length (R); 95–101 scales around midbody (S); 78–90 ventrals from gular fold to insertion of hind limbs (T) and 73–79 ventral scales from tip of snout to gular fold (N); 102–113 dorsal scales from tympanum to hind limbs (X+Y); 108 scales around the neck (m); 2–4 enlarged supraoculars above each eye (U); and 20–23 supralabials on each side. For details see Table 1.

In addition, the neck scales in the three juvenile specimens from Fergusson Island (BMNH [18]95.4.26.14–16) are flat and roundish rather than oval, tuberculated and spinose as in the subadult and adult specimens. Also the dorsal head scales are flat and not rugose as described by Mertens (1950) and seen in the type specimens of *V. bogerti* (less so in AMNH 41638 as he already noticed).

Colouration: While further morphological data about the first known juveniles of *V. bogerti* are not available,



Fig. 7. Dorsal view of the head of the holotype of *V. telenesetes* (QMJ1190). Similar to *V. bogerti* and other tree monitors, this specimen has enlarged scales in the interorbital region. Photo: Steve Wilson.

the photographs taken allow a detailed description of the colour pattern in hatchlings of this monitor species. The three juveniles from Fergusson Island (BMNH [18]95.4.26.14–16) show a faint dorsal colour pattern of about 15 to 19 transverse rows of lighter spots comprising one to five slate-blue (in preservative) scales each on an ash-grey background. These irregular transverse rows extend across the neck and dorsum of each specimen (Fig. 5A). The ventral side is lighter brownish ash grey as is the head and particularly the areas around the labials and below the eyes (Fig. 5B). In contrast, the only juvenile from the Trobriand Islands (BMNH [18]96.7.8.1) lacks any dorsal pattern of light spots, and also the venter and head are darker ash grey.

As with adults of *V. beccarii* from the Aru Islands, both adult BMNH specimens of *V. bogerti* are unicoloured black dorsally, showing no traces of a colour pattern. The ventrum is ash grey. The heads, however, are lighter coloured (particularly in BMNH 1889.7.1.8 from St. Aignan [=Misima Island]), as is the case in the three juveniles from Fergusson Island (Fig. 5). In the specimen from Misima Island the tongue, in contrast to the new voucher specimen (see above), is entirely pink. So obviously, some morphological variation in colouration and pattern of *V. bogerti* occurs across its assumed distributional range. This involves on the one hand an ontogenetic change in colour pattern and probably also some geographic variation between the different populations of the D'Entrecasteaux, Trobriand and Louisiade islands. On the other hand, given the odd distribution of the old voucher specimens of *V. bogerti* (no other endemic amphibian and reptile species from the Milne Bay islands occurs across all three archipelagos [F. Kraus pers. obs.]), they may represent more than one taxon, or the provenance of some of the early material is incorrect (see discussion above). Therefore, only further field work and future investigations will reveal the entire morphological variation and systematics of this melanistic New Guinean tree monitor.

Table 2. Morphological data of the widespread *V. prasinus* including the holotype (RMNH 4812), specimen AMNH 42373 from Goodenough Island, d’Entrecasteaux Archipelago, and an aberrant specimen (NMW 12392) from Cape Nelson, Papua New Guinea. The latter specimen shows some differences in colour pattern (see Fig. 9) as well as in scalation characters (*in italics*). ¹Brandenburg (1983) provided only the number of supralabials on one side.

Taxon, specimen(s)	<i>V. prasinus</i> (RMNH 4812, holotype)	<i>V. prasinus</i> (n=25, incl. holotype)	<i>V. prasinus</i> (AMNH 42373)	<i>V. cf. prasinus</i> (NMW 12392)
Source of data	Brandenburg (1983)	Brandenburg (1983)	Burt & Burt (1932)	this study
Locality	West coast of New Guinea	New Guinea and some offshore islands	Goodenough Isl.	Cape Nelson, Papua New Guinea
Age	adult male	various	adult	subadult
Index 1	1.83	1.51–2.15 (mean=1.92)	-	<i>ca.</i> 2.18
Index 2	1.25	1.10–1.41 (mean=1.21)	-	<i>1.44</i>
Index 10	1.87	1.80–2.13 (mean=1.95)	-	1.91
Index 11	2.77	2.60–2.97 (mean=2.72)	-	2.33
P	40	35–44 (mean=40)	-	56
Q	64	52–68 (mean=62)	-	70
R	-	25–35	-	29
S	97	81–112 (mean=93)	102	106
T	78	70–87 (mean=77)	85	83
N	67	63–80	-	86
XY	114	93–133 (mean=107)	-	123
m	92	80–96 (mean=88)	-	<i>108</i>
U	5/6	3–6	-	3/3
c	48	21–26 ¹	-	23/23 (46)

Is *V. telenesetes* a valid taxon? A comparison with *V. bogerti* and *V. prasinus*

In the original description of *V. telenesetes*, Sprackland (1991) declared that the specimen was similar to *V. prasinus* in “... being green above, with indistinct dark chevrons ...” As evident from the photographs depicted by Sprackland (1991:568) himself, those provided by S. Wilson (see also Kirschner et al., 1996; Eidenmüller & Philippen, 2008), and by new pictures taken by one of us (BE) during a visit at the Queensland Museum in Brisbane in 2011, the holotype of *V. telenesetes* (QMJ1190) now appears as another rather melanistic tree monitor lacking any green pigmentation or obvious colour pattern on the dorsal side (Figs. 6–7). These findings are corroborated by the observations of R. Sprackland, who first examined the type specimen of *V. telenesetes* in 1983. Thirty years ago, the “nape, plus parts of the dorsum and tail were visibly dark green” (R. Sprackland, pers. comm. to AK). However, when re-examined in 1999 and 2003 by him “it did appear darker, more chalk-board gray than green.” Unfortunately, Czechura (1980) provided neither a description nor photographs of this unique specimen but merely mentioned that it could not be assigned to any known taxon using available literature and specimens. In contrast to the original diagnosis, the type specimen today is entirely dark grey without any green colouration, but obscure, narrow, dark crossbands are faintly evident on the specimen when held in alcohol (FK, pers. obs.). The head is lighter, appearing white laterally (Fig. 6).

Scale counts reported by Sprackland (1991) are only slightly above or below the variation observed for *V.*

bogerti (see Table 1) and could perhaps be posited as geographic variation in that species if revealed to be conspecific. The close-up of the head of the holotype in Sprackland (1991:568, see also Fig. 7) shows that the scales of the interorbital region are considerably enlarged, as described above for the new specimen of *V. bogerti* (Fig. 4) and as typical for the entire *V. prasinus* group. Similarly, the lighter appearance of the holotype of *V. telenesetes* as compared with the black *V. bogerti* could theoretically be due to fading in long-term preservation. Therefore, based solely on information available in Sprackland (1991), reasonable doubts could perhaps be raised regarding the taxonomic validity of *V. telenesetes*, which could merely represent a synonym of *V. bogerti* (see also Green, 2004).

However, direct, side-by-side comparison of the *V. bogerti* specimen BPBM 16053 with the type of *V. telenesetes* reveals that there are a number of colour-pattern differences between both nominal taxa. In preservative, our subadult *V. bogerti* has (i) a dorsal pattern of vague lighter crossbands on a black ground; (ii) pale scattered scales/punctuations on the tops of the limbs and base of tail; (iii) dark venter; and (iv) palms and soles largely dark (Figs. 3–4). By comparison, the *V. telenesetes* specimen has (i) a dorsal pattern of obscure darker crossbands on a slightly paler ground; (ii) pale, vague rosettes on tops of limbs; (iii) mid-venter pale mottled with small dark squares, and with about ten dark, narrow bars across throat and chest; and (iv) palms and soles white (Figs. 6–7). As well as a more detailed morphological comparison, a phylogenetic

and biogeographic analysis for these crucial island populations of tree monitors is still pending. Therefore, a final decision about the relationships and systematic position of *V. telenesetes* within the *V. prasinus* species group cannot be made here (see also below).

Origin and distribution of *V. telenesetes*: a mystery

Besides concern about its taxonomic status, the only known specimen of *V. telenesetes* raises further questions about its actual origin and distribution. The holotype was collected in the early 1910s without any additional information on the collector(s) or precise locality. Because several specimens from Rossel Island came into the Queensland Museum collections at that time, it was assumed that the specimen of *V. telenesetes* also originated from that island (Czechura, 1980). However, the provenance of this specimen remains uncertain: For instance, Albert Stewart Meek (1871–1943), a travelling naturalist and collector, spent two months on Rossel Island in 1895 but did not mention finding tree monitors there (Meek, 1913). More than a hundred years later, field work in 2002 by FK resulted in obtaining only a representative of the *V. indicus* group on Rossel Island (Kraus & Shea, 2005), and locals stated that this is the only species of *Varanus* on that island. It seems unusual that locals would not observe *V. telenesetes* if it were really present on Rossel Island, so there remains some doubt as to whether the stated locality for the specimen is in error. If that should prove true, then it remains uncertain what its actual origin and distribution are. The only larger islands in the area from which tree monitors are not (yet) recorded, are Sudest (=Tagula Island) and Woodlark (Fig. 1). From the latter island only a member of the *V. indicus* group is reported (Kraus & Allison, 2004; E. Clapp, pers. comm.). Therefore, the authors would like to encourage further field work in this remote island region to resolve the uncertainty about the exact distribution and taxonomic status of *V. telenesetes*.

Putative sympatric occurrence and past gene flow between multiple tree monitor species?

Mertens (1950) suggested the putative sympatric occurrence of *V. bogerti* with *V. prasinus* on the islands of the D'Entrecasteaux Archipelago (Fig. 1). Although this assertion remains unconfirmed until today, both species come closer to sympatry than any other members of the tree monitor group, as has been emphasised by Sprackland (1991). While *V. prasinus* (voucher AMNH 42373, Fig. 8) has been reported from Goodenough Island (Burt & Burt, 1932; Mertens, 1950), *V. bogerti* occurs on Fergusson Island, which is less than 5 kilometres away, and between both islands lie two small islets that further reduce the over-water distance to less than 3 kilometres. So it is very likely that these distinct neighbouring tree monitor populations were repeatedly in spatial contact when both larger islands were, geologically speaking, relatively recently united during Pleistocene global sea-level minima of up to 160 m below present sea-level (Chappell & Shackleton, 1986; Voris, 2000). Similarly, locals have told one of us (FK) that *V. bogerti* is common on Normanby Island, while *V. prasinus* is common on nearby Noakata (Nuakata) Island, separated by only 15 km (Fig. 1).

Although it is uncertain if the Milne Bay islands were united with main island New Guinea during the Pleistocene (McCulloch et al., 1999; Gordon, 2005), two alternate evolutionary scenarios for the tree monitors of New Guinea and its southeastern offshore islands can be postulated. First, facilitated by lowered sea-levels, black (*V. bogerti*) and green (*V. prasinus*) tree monitors may have come in contact with each other on the fused islands of the D'Entrecasteaux Archipelago and evolved independently if they had previously reached the taxonomic level of two separate and reproductively isolated species (Mayr, 1942). Second, specimens of the distinct island populations having not yet achieved reproductive isolation (though some degree of

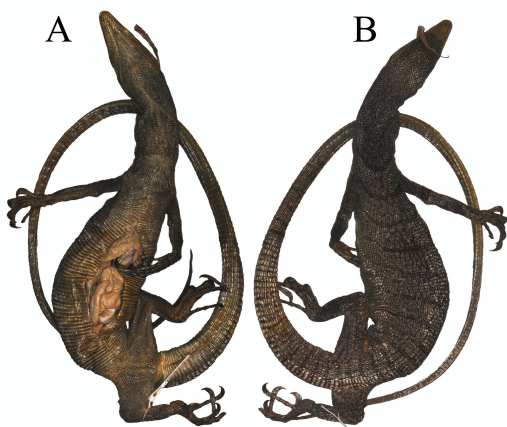


Fig. 8. *V. prasinus* (AMNH 42373) from Goodenough Island. (A) Ventral view showing the unpatterned light (green in life) ventral side. (B) Dorsal view showing the characteristic colour pattern of dark chevrons. Note that the typical emerald-green colouration fades during long-time preservation in alcohol resulting in a slate-blue background colouration. Photos: David Kizirian.



Fig. 9. *V. cf. prasinus* (NMW 12392) from Cape Nelson, northeast coast of Papua New Guinea. (A) Ventral view showing dark marbling on throat and chest, which resembles the pattern seen in the holotype of *V. telenesetes* (see Fig. 6B). (B) Dorsal view showing the colour pattern consisting of indistinct ocelli, which are rather typical for *V. kordensis*. Photos: André Koch.

morphological and genetic differentiation resulting into black [*bogerti*] and green [*prasinus*] island populations, i.e. two different subspecies of a wide-spread tree monitor species), interbred repeatedly in sympatry during global ice ages and consequently experienced gene flow. If the former scenario has happened, both *V. bogerti* and *V. prasinus* should still live unmixed in sympatry to date on these islands. Evidence for this hypothesis could result from future field work but seems unlikely given present information. In turn, if the second scenario is true, then we could expect to find specimens with some degree of intermediate phenotypic characters and genotype resulting from past gene flow.

Mertens (1950) already mentioned the morphological differences between AMNH 42373, the *V. prasinus* specimen from Goodenough Island (Fig. 8), and the specimens from New Guinea. He described the specimen as having “...somewhat narrower and more strongly keeled nuchal and dorsal scales than is characteristic of the [nominotypic] subspecies.” While Mertens (1950) provided no further morphological data of this specimen, Burt & Burt (1932) mentioned that it has 85 ventral scales (T-value) and 102 scales around midbody (S-value) (Table 2). The former value is at the upper limit for *V. prasinus* (T=70–87, on average 77) and within the range of *V. bogerti* (78–90) (see Table 1). Also the S-value of specimen AMNH 42373 is at the upper limit for *V. prasinus* (81–112, on average 92), which according to Brandenburg (1983) usually seems to have less than 100 scales around midbody. Among 25 specimens this author examined, there was only one specimen (ZMA 10224, a male, from Humboldt Bay near Jayapura) with 112 scales (Table 2). In contrast, *V. bogerti* seems to have on average more scales around midbody (S-value=95–101) than *V. prasinus* (see Table 1), which would fit to AMNH 42373 from Goodenough Island. While the colour pattern of this specimen shows no deviations from the typical colour pattern of *V. prasinus*, a third option could be that the high scale counts could be due to founder effects after the successful colonisation of Goodenough Island by *V. prasinus* in the past. Without giving further explanations, but probably due to its unusual scalational features, Mertens (1959) considered the *V. prasinus* specimen from Goodenough Island to represent a close relative of *V. bogerti*, which he regarded a subspecies of *V. prasinus*. Due to their close geographic proximity, Mertens (1950) had already considered *V. bogerti* to be more closely related to the emerald green *V. prasinus* than to the phenotypically similar *V. beccarii* from the more distant Aru Islands (Fig. 1). He ascribed the mutual melanism of both taxa to convergent evolution rather than to phylogenetic propinquity.

There is another remarkable specimen of *V. cf. prasinus* in the collections of the Naturhistorisches Museum in Vienna, which shows some clear deviation in colour pattern. Specimen NMW 12392 is from Cape Nelson along the northeast coast of British (=Papua) New Guinea and was collected/donated by Dr. Rudolf Pöch, an anthropologist, in November 1905 (Fig. 9). The specimen was already examined by Mertens (1942), but was listed with the old collection number NMW 3540, while he

focused on the variation in the dorsal colour pattern of *V. prasinus*. In this specimen, the ventral side is covered with dark marbling forming indistinct thin transverse streaks under chin and chest. Interestingly, these dark streaks on the chest resemble those visible in the holotype of *V. telenesetes* (Fig. 6B). Also, long preservation has left no green colouration in NMW 12392, as is also true for the *telenesetes* type. This renders both specimens ash grey. On the other side, specimens of *V. prasinus* lacking the characteristic black dorsal chevrons are known (AK, pers. observ.). Given these observations, together with uncertainty concerning the origin of the holotype of *V. telenesetes*, it may be possible that *V. telenesetes* will prove to represent an objective synonym of *V. prasinus*.

Notwithstanding these taxonomic considerations, the dorsal colour pattern of specimen NMW 12392, consisting of numerous indistinct ocelli that form the typical *V. prasinus* pattern of dark chevrons (Fig. 9B), resembles the reticulated pattern as is seen in *V. kordensis*. Consequently, this specimen combines characteristic colour pattern features of several distinct tree monitor taxa supporting their close phylogenetic relationships (Ast, 2001; Ziegler et al., 2007; Jacobs, 2008). This somewhat aberrant phenotype may represent the result of past gene flow and/or introgression events during the last and former glacial maxima. During these glacial periods continuous forests probably covered the exposed sea floor of the continental shelf since the strictly arboreal tree monitors also successfully colonised the Cape York Peninsula. The result of the subsequent geographic isolation due to rising sea levels is the endemic *V. keithhornei* of northern Australia (Ziegler et al., 2007).

Since both *V. bogerti* and *V. telenesetes* were not included in the recent species-group phylogeny of the subgenus *Euprepiosaurus* by Ziegler et al. (2007), future taxonomic and molecular investigations are needed to infer the phylogenetic position and status of these taxa within the group of closely-related New Guinean tree monitors.

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REFERENCES

- Ast, J.C. (2001). Mitochondrial DNA Evidence and Evolution in Varanoidea (Squamata). *Cladistics* 17, 211–226.
- Barbour, T. (1912). A Contribution to the Zoogeography of the East Indian Islands. *Memoirs of the Museum of Comparative Zoology Harvard* 44, 1–203.
- Bennett, D. (1998). *Monitor Lizards: Natural History, Biology, & Husbandry*. Frankfurt: Edition Chimaira.
- Bennett, D. & Sweet, S.S. (2010). *Varanus telenesetes*. In *IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1*. Available from: <<http://www.iucnredlist.org>>. Accessed: 20 June 2012.
- Böhme, W. (2003). Checklist of the living monitor lizards of the world (family Varanidae). *Zoologische Verhandelingen* 341, 3–43.
- Böhme, W., Horn, H.-G. & Ziegler, T. (1994). Zur Taxonomie der Pazifikwarane (*Varanus indicus*-Komplex): Revalidierung von *Varanus doreanus* (A. B. Meyer, 1874) mit Beschreibung einer neuen Unterart. *Salamandra* 30, 119–142.
- Böhme, W. & Koch, A. (2010). On the type selection and re-typification of two monitor lizard taxa (Squamata: Varanidae): *Monitor bivittatus celebensis* Schlegel, 1844 and *Monitor kordensis* Meyer, 1874; with some comments and corrections on other name-bearing type specimens. *Zootaxa* 2440, 60–68.
- Brandenburg, T. (1983). *Monitors in the Indo-Australian Archipelago*. Unpublished Thesis, University of Leiden, 98 pp.
- Boulenger, G.A. (1885). *Catalogue of the Lizards in the British Museum (Natural History). Second Edition. Volume II. Iguanidae, Xenosauridae, Zonuridae, Anguidae, Anniellidae, Helodermatidae, Varanidae, Xantusiidae, Teiidae, Amphisbaenidae*. London: Taylor and Francis.
- Boulenger, G.A. (1895a). On a Collection of Reptiles and Batrachians from Ferguson Island, D'Entrecasteaux Group, British New Guinea. *The Annals and Magazine of Natural History* 16, 28–32.
- Boulenger, G.A. (1895b). Descriptions of two new reptiles obtained by Mr. A.S. Meek in the Trobriand Islands, British New Guinea. *The Annals and Magazine of Natural History* 16, 408–409.
- Burt, C. E. & M. D. Burt (1932). Herpetological results of the Whitney South Sea Expedition. VI. *Bulletin of the American Museum of Natural History* 58, 461–597.
- Chappell, J. & Shackleton, N.J. (1986). Oxygen isotopes and sea level. *Nature* 324, 137–140.
- Comrie, R. N. (1877). Anthropological Notes on New Guinea. *The Journal of the Anthropological Institute of Great Britain and Ireland* 6, 102–119.
- Czechura, G. V. (1980). The emerald monitor, *Varanus prasinus* (Schlegel): an addition to the Australian mainland herpetofauna. *Memoirs of the Queensland Museum* 20, 103–109.
- Daudin, F. M. (1802). *Histoire naturelle, générale et particulière des Reptiles, Tome troisième*. Paris: F. Dufart.
- De Lisle, H.F. (2009). Catalog of the genus *Varanus* (Reptilia: Squamata: Varanidae) with new designations of a neotype and a lectotype. *ZooNova* 1, 8–32.
- de Rooij, N. (1915). *The Reptiles of the Indo-Australian Archipelago: I. Lacertilia, Chelonia, Emydosauria*. Leiden: E.J. Brill, Ltd.
- Doria, G. (1874). Enumerazione dei rettili raccolti dal Dott. O. Beccari in Amboina, alle isole Aru ed alle isole Kei durante gli anni 1872–73. *Annali del Museo Civico di Storia Naturale di Genova* 6, 325–357.
- Eidenmüller, B. (1998). Bemerkungen zur Haltung und Nachzucht von *Varanus p. prasinus* (Schlegel, 1839) und *Varanus p. beccarii* (Doria, 1874). *Herpetofauna* 20, 8–13.
- Eidenmüller, B. & Philippen, H.-D. (2008). *Varanoid Lizards – Warane und Krustenechsen*. Terralog 6, Frankfurt: Edition Chimaira.
- Eidenmüller, B. & Wicker, R. (1993). *Varanus (Odatia) prasinus beccarii* (Doria, 1874), Pflege und Zucht. *Salamandra* 28, 171–178.
- Frodin, D.G. (2007). Biological exploration of New Guinea. In *The Ecology of Papua, Part I*, 14–107. Marshall, A.J. & Beehler, B.M. (eds). Singapore: Periplus Editions.
- Gordon, A.L. (2005). Oceanography of the Indonesian Seas and their Throughflow. *Oceanography* 18, 14–27.
- Green, H.W. (2004). *Varanus prasinus* In *Varanoid lizards of the world*, 225–229. Pianka, E.R. & King, D.R. (eds). Bloomington: Indiana University Press.
- Heatwole, H.F. (1975). Biogeography of reptiles on some of the islands and cays of eastern Papu-New Guinea. *Atoll Research Bulletin* 180, 1–41.
- Jacobs, H.J. (2002). Zur morphologischen Variabilität der nominellen Smaragdwaran-Taxa *Varanus prasinus* (H. Schlegel, 1839) und *V. kordensis* (A.B. Meyer, 1874), mit Bemerkungen zur Erstzucht des letzteren. *Herpetofauna* 24, 21–34.
- Jacobs, H.J. (2003). A further new emerald tree monitor lizard of the *Varanus prasinus* species group from Waigeo, West Irian (Squamata: Sauria: Varanidae). *Salamandra* 39, 65–74.
- Jacobs, H.J. (2008). Zucht von *Varanus reisingeri* Eidenmüller & Wicker, 2005 mit Vergleich der Jugendkleider der *V. prasinus*-Gruppe und Bemerkungen zu deren Taxonomie. *Sauria* 30, 5–12.
- Jarvis, A., Reuter, H.I., Nelson, A. & Guevara, E. (2008). Hole-filled seamless SRTM data V4, International Centre for Tropical Agriculture (CIAT). Available from: <<http://srtm.csi.cgiar.org>>. Accessed: 15 May 2012.
- Kirby, W.F. (1889). On the collection of Lepidoptera formed by Basil Thomson, Esq., in the Louisiade Archipelago. *The Annals and Magazine of Natural History* 4, 156–167.
- Kirschner, A., Müller, T. & Seuffer, H. (1996). *Faszination Warane*. Keltern-Weiler: Kirschner & Seuffer Verlag.
- Koch, A., Auliya, M., Schmitz, A., Kuch, U. & Böhme, W. (2007). Morphological Studies on the Systematics of South East Asian Water Monitors (*Varanus salvator* Complex): Nominotypic Populations and Taxonomic Overview. In *Advances in Monitor Research III*, 109–180. Horn, H.-G., Böhme, W. & Krebs, U. (eds). *Mertensiella* 16.
- Koch, A., Gaulke, M. & Böhme, W. (2010). Unravelling the underestimated diversity of Philippine water monitor

- lizards (Squamata: *Varanus salvator* complex), with the description of two new species and a new subspecies. *Zootaxa* 2446, 1–54.
- Koch, A., Ziegler, T., Böhme, W., Arida, E. & Auliya, M. (2013). Pressing Problems: Distribution, Threats, and Conservation Status of the Monitor Lizards (Varanidae: *Varanus* ssp.) of Southeast Asia and the Indo-Australian Archipelago. *Herpetological Conservation and Biology* 8 (Monograph 3), 1–62.
- Kraus, F. & Allison, A. (2004). New records for reptiles and amphibians from Milne Bay Province, Papua New Guinea. *Herpetological Review* 35, 413–418.
- Kraus, F. & Shea, G. (2005). Additional Reptile and Amphibian Range Extensions for Milne Bay Province, Papua New Guinea. *Herpetological Review* 36, 471–473.
- Mayr, E. (1942). *Systematics and the Origin of Species*. New York: Columbia University Press.
- McCulloch, M.T., Tudhope, A.W., Esat, T.M., Mortimer, G.E., et al. (1999). Coral record of equatorial sea-surface temperatures during the penultimate deglaciation at Huon Peninsula. *Science* 283, 202–204.
- Meek, A.S. (1913). *A naturalist in cannibal land*. London, Leipzig: T. Fisher Unwin.
- Mertens, R. (1942). Die Familie der Warane (Varanidae). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 462, 465, 466; 1–391.
- Mertens, R. (1950). Notes on some Indo-Australian monitors (Sauria, Varanidae). *American Museum Novitates* 1456, 1–7.
- Mertens, R. (1959). Liste der Warane Asiens und der Indo-australischen Inselwelt mit systematischen Bemerkungen. *Senckenbergiana Biologica* 48, 221–240.
- Mertens, R. (1963). *Das Tierreich. Liste der rezenten Amphibien und Reptilien. Lieferung 79. Helodermatidae, Varanidae, Lanthanotidae*. Berlin: Walter de Gruyter & Co.
- Meyer, A.B. (1874). Eine Mittheilung von Hrn. Dr. Adolf Bernhard Meyer über die von ihm auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. *Monatsberichte der Königlich-Preussischen Akademie der Wissenschaften zu Berlin* 1874, 128–140.
- Meyer, A.B. (1887). Verzeichniss der von mir in den Jahren 1870–1873 im Ostindischen Archipel gesammelten Reptilien und Batrachier. *Abhandlungen und Berichte des Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden* 1887, 1–16.
- Moresby, J. (1876). *New Guinea and Polynesia: Discoveries & Surveys in New Guinea and the D'Entrecasteaux Islands. A Cruise in Polynesia and Visits to the Pearl-shelling Stations in Torres Straits of H.M.S. Basilisk*. London: John Murray.
- Obst, F.J. (1977). Die Herpetologische Sammlung des Staatlichen Museums für Tierkunde Dresden und ihre Typusexemplare. *Zoologische Abhandlungen / Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde* 34, 171–186.
- Roux, J. (1910). Reptilien und Amphibien der Aru- und Kei-Inseln. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 33, 211–247.
- Schlegel, H. (1837–44). *Abbildungen neuer oder unvollständig bekannter Amphibien, nach der Natur oder dem Leben entworfen*. Düsseldorf: v. Arnz & Comp.
- Sclater, P.L. (1876). On the birds collected by Dr. Comrie on the South-east Coast of New Guinea during the survey of H.M.S. 'Basilisk'. *Proceedings of the Zoological Society of London* 1876, 459–461.
- Sharpe, R.B. (1906). Birds. In *The history of the collections contained in the natural history departments of the British Museum, Vol. II. Separate historical accounts of the several collections included in the Departments of Zoology*, 79–515. London: Trustees of the British Museum.
- Sprackland, R. (1991). Taxonomic review of the *Varanus prasinus* group with descriptions of two new species. *Memoirs of the Queensland Museum* 30, 561–576.
- Thomas, O. (1895). On some mammals collected by Mr. Albert Meek on Fergusson Island, D'Entrecasteaux Group. *Novitates Zoologicae* 2, 163–165.
- Thomas, O. (1896). On mammals collected by Mr. Albert Meek on Woodlark Island, and on Kiriwina in the Trobriand Group. *Novitates Zoologicae* 3, 526–529.
- Thomson, B.H. (1889). New Guinea: Narrative of an Exploring Expedition to the Louisiade and D'Entrecasteaux Islands. *Proceedings of the Royal Geographical Society and Monthly Record of Geography* 11, 525–542.
- Tristram, H.B. (1889). On a small Collection of Birds from the Louisiade and D'Entrecasteaux Islands. *Ibis* 31, 553–558.
- Voris, H. (2000). Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography* 27, 1153–1167.
- Wells, R.W. & Wellington, C.R. (1985). A classification of the amphibians and reptiles of Australia. *Australian Journal of Herpetology, Suppl. Series* 1, 1–61.
- Ziegler, T., Schmitz, A., Koch, A., & Böhme, W. (2007). A review of the subgenus *Euprepisaurus* 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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