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New findings on the relationships among New Guinea tree monitor lizards of the *Varanus prasinus* (SCHLEGEL, 1839) complex
(Squamata: Sauria: Varanidae)

Neue Erkenntnisse zur Verwandtschaft innerhalb der neuguineischen Baumwarane
aus dem *Varanus prasinus* (SCHLEGEL, 1839) - Komplex
(Squamata: Sauria: Varanidae)

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KURZFASSUNG

Gewebeproben von 36 Waranen neun unterschiedlicher Arten aus dem *Varanus prasinus* (SCHLEGEL, 1839) - Komplex wurden hinsichtlich eines 519 bp Fragments des mitochondrialen 16S Gens zur Erhellung ihrer Verwandtschaftsbeziehungen untersucht. Der Datensatz, der die ersten Sequenzdaten von *V. reisingeri* EIDENMÜLLER & WICKER, 2005 und *V. bogerti* MERTENS, 1950 enthält, wurde mit publizierten Sequenzdaten (ZIEGLER et al. 2007) verglichen. Die vorliegenden Ergebnisse bestätigten frühere Studien und deuten darüber hinaus auf eine unerwartet nahe phylogenetische Verwandtschaft von *V. bogerti* mit *V. kordensis* hin. Obwohl sichtbare Unterschiede in Färbung, Pholidose und den Meßwerten zwischen *V. reisingeri* und *V. prasinus* vorhanden sind, war ein genetischer Unterschied in den mitochondrialen Sequenzen zwischen diesen beiden Taxa nicht feststellbar. Die neuen Erkenntnisse werden hinsichtlich der Biogeographie der Neuguinea-Region diskutiert.

ABSTRACT

Tissue samples of 36 monitor lizards of nine species of the *Varanus prasinus* (SCHLEGEL, 1839) complex were investigated regarding a 519 bp fragment of the mitochondrial 16S gene to elucidate their systematic relationships. The dataset, which contains the first sequence data for *V. reisingeri* EIDENMÜLLER & WICKER, 2005, and *V. bogerti* MERTENS, 1950, was aligned to published sequence data (ZIEGLER et al. 2007). The present results generally support the findings of an older study, and furthermore propose an unexpected close phylogenetic relationship of *V. bogerti* to *V. kordensis* (A. B. MEYER, 1874). Despite of obvious differences in coloration, pholidosis, and morphometrics, no sign of molecular differentiation in the studied mitochondrial sequence data was detected between *V. reisingeri* and *V. prasinus*. The new findings are discussed in the light of the biogeography of the New Guinea region.

KEY WORDS

Reptilia: Squamata: Sauria: Varanidae; *Hapturosaurus*, *Varanus prasinus* complex, *Varanus bogerti*, *Varanus reisingeri*, mitochondrial 16S gene, systematics, New Guinea region

INTRODUCTION

Within the varanid subgenus *Hapturosaurus* BUCKLITSCH, BÖHME & KOCH, 2016, the members of the highly arboreal *Varanus prasinus* (SCHLEGEL, 1839) group share a set of characteristic and synapormorphic morphological features, clearly separating them from their more terrestrial sister group of the *V. indicus* (DAUDIN, 1802) complex of the subgenus *Euprepiosaurus* FITZINGER, 1843 (BUCKLITSCH et al. 2016). The body is always fairly long and slender with considerably long legs, and a prehensile tail, which does not occur in any other species of monitor lizard. The curved claws are very sharp. In the palmar, plantar, and subdigital regions, several scales form cushion-like arrangements that are somewhat adhesive. All these morphological features are ecological adaptations to a highly specialized arboreal life style, enabling these monitor lizards to venture out on the thin, outer tree branches in the rainforest canopy, inaccessible to other congeneric species (GREENE 1986).

The geographical distribution of the members of the *V. prasinus* complex is restricted to New Guinea and several offshore islands. One species, *V. keithhornei* (Wells & Wellington, 1985), inhabits the Cape York Peninsula of Australia (Fig. 1). Among the members of the complex, *V. prasinus* has by far the widest distribution; it covers the entire land mass of New Guinea and the small islands of the Torres Strait separating northern Australia from New Guinea. Notably, there exist unconfirmed but trustworthy observations and reports of green tree monitor lizards from the Cape York Peninsula (see references in Lemm 2014), substantiating the possibility of a sympatric occurrence of two tree monitor lizard species.

Despite their partly colorful appearance and up to 120 cm total length, several species of tree monitor lizards were described only in recent years. These are the light blue and black *V. macraei* Böhme & Jacobs, 2001, from Batanta Island, the black and yellow *V. boehmei* Jacobs, 2003, from Waigeo Island, and the yellow-green *V. reisingeri* Eidenmüller & Wicker 2005, from Misol Island. Other species, such as *V. telenesetes* Sprackland, 1991 from Rossel Island or *V. bogerti* Mertens, 1950, inhabiting the Trobriand, D'Entrecasteaux and Louisiade islands off southeastern New Guinea are known only from a single or a few historical voucher specimens, respectively (Koch et al. 2014). The phylogenetic relationships between the various members of the *V. prasinus* group were first investigated by Ziegler et al. (2007), but in this initial study not all taxa involved were available. Hence, samples of *V. telenesetes*, *V. bogerti* and the recently described *V. reisingeri* were lacking. The present study aims to remedy this lack of information in order to elucidate the systematic relationships of the New Guinea tree monitor lizards.

MATERIALS AND METHODS

The authors obtained blood samples of 23 monitor lizards of the *V. prasinus* complex from Dr. Markus Baur, head of the reptile sanctuary at Munich, including six samples of specimens that were identified as *V. reisingeri*, based on their distinctive black and yellow coloration. All these specimens were confiscated by German customs at Frankfurt Airport, a major hub in Europe for the international trade with exotic animals (Valaoras 1998; Auliya 2003). In addition, blood samples were obtained from ten specimens held in private collections in Germany. The taxonomic allocations of all specimens were based on their external appearance as compared with an illustrated identification key (Koch et al. 2013) and the respective original species descriptions. Tissue samples of *V. telenesetes* (QMJ1190) and *V. keithhornei* (QMJ65052) were kindly provided by Patrick Couper (Queensland Museum Brisbane, Queensland, Australia). A sequence from the sample of *V. telenesetes* was not obtained, probably due to the long-time preservation of the specimen collected about 100 years ago (Koch et al. 2014). *Varanus caerulivirens* Ziegler, Böhme & Philipp, 1999, of the *V. indicus* (Daudin, 1802) species group, the sister clade of the tree monitor lizards, was chosen as outgroup sample.

Andreas Schmitz (Geneva) provided a sequence of the mitochondrial 16S gene of a specimen of *V. bogerti* (Bishop Museum, Honolulu, Hawaii, USA - BPBM 16053) obtained using the same primers as given below. The newly generated sequences were aligned to 20 16S sequences of monitor lizards of the *V. prasinus* complex that were found in the NCBI (National Center for Biotechnology Information) database Genbank®. They all were published by Ziegler et al. (2007), who applied the same primers used for this study (see below).

For analysis of the mitochondrial 16S gene, DNA extractions were carried out, by vacuum extraction, using a vacuum extraction kit (Pall GmbH, Dreieich, Germany), following the instructions of the manufacturer. DNA concentration was checked elektrophoretically. A 532 bp fragment of the mitochondrial 16S gene was amplified by PCR, using primers as published by Vences et al. 2005 (forward: 16SA-L, 5'-CGCCTGTTTATCAAAAACAT-3'; reverse: 16SB-H, 5'-CCGGTCTGA ACTCA GATCACGT-3'). PCR reactions were run with 1 µL DNA template, 2.5 µL Reaction Buffer (PeqGold), 2.5 µL 2.5 mM dNTPs, 0.5 µL Taq Polymerase (PeqLab), 16.5 µL H_2O, and 10 pmol of each primer. Reaction mixes were processed by the following protocol: Initial denaturation: 180 s at 94 °C; denaturation: 15 s at 94 °C; hybridization: 60 s at 51 °C; elongation: 60 s at 72 °C; repeated for 39 cycles; final elongation: 120 s at 72 °C. Sequencing the PCR products was done at the laboratories of the Biodiversität und Klima - Forschungszentrum (BIK-F), Frankfurt am Main.

Sequences were automatically aligned, applying the ClustalW Algorithm (Larkin et al. 2007) as implanted in MEGA.5 software (Tamura et al. 2011); alignments were checked manually. A matrix of uncorrected, pairwise distances was computed (Table 1). Maximum likelihood analyses were run in PAUP 4.01 (Swofford 2001), performing a heuristic search, applying TBR (Tree-Bisection-Reconnection) branch swapping and computing 1000 bootstrap replicates. Just as for Bayesian analyses (Fig. 2), evolutionary models were used, which were found using jmodeltest (Posada 2008) under assumptions of AIC (Akaike's information criterion).

Bayesian analyses were run in MrBayes v3.1.2. (Ronquist & Huelsenbeck 2003). Four Markov chains were run twice for 2,000,000 generations, sampling every 100th generation. The increase in likelihoods was checked by visualizing the p-files provided by the program in an EXCEL spreadsheet. The first 1,000 generations were discarded as "burn in". The Genbank® accession numbers of the newly acquired sequences are provided in Table 1.

RESULTS

The results obtained are generally in accordance with the findings of earlier authors (Ziegler et al. 2007) regarding the molecular phylogenetic relationships between the different species of the *V. prasinus* complex. As in the previous study by Ziegler et al. (2007), all samples of *V. kordensis* form a well-supported clade, the sister group to all other taxa in the phylogram (Fig. 2). However, the sample of *V. bogerti* lies embedded in this clade, separated from the other specimens only by a quite long branch length. In the Maximum Likelihood Analysis, and a preliminary Neighbor Joining Analysis, *V. bogerti* was positioned as sister group to *V. kordensis*. Since this genealogical grouping was supported by very weak bootstrap values only, the *V. bogerti* clade collapsed. Another puzzling peculiarity regarding this clade is caused by a sample of the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK 70604) from Ziegler et al. (2007) which these authors had labeled *V.* cf. *prasinus*. In the heat map graphic (not shown), these two aforementioned samples are well separated from the other specimens of the *V. kordensis* clade. Six of the seven samples assigned to *V. kordensis* share a common haplotype, from which specimen KOR6 differs by only 0.2 % uncorrected sequence distance (p-distance). From this common haplotype, the sequence of *V. bogerti* differs by a p-distance value of 1.2 % and the sequence of ZFMK 70604 by 1.0 %. The p-distance value between the sequences of *V. bogerti* and ZFMK 70604 is 1.7 %, which explains the problems of the Bayesian analysis to resolve the relationships within this clade.

Another well-defined but weakly resolved clade contains the samples assigned to *V. macraei*, *V. boehmei*, *V. prasinus* and *V. reisingeri*. Within this clade, the three samples of *V. boehmei* (two from Ziegler et al. 2007: ZFMK 77837, ZFMK 79122 and a new sample: BOE1) are grouped together as a distinct subclade. They all share a common haplotype. Similarly, the samples assigned to *V. prasinus* and *V. reisingeri* form a separate sub clade. The samples assigned to *V. macraei* that all share the same haplotype, form a basal polytomy, from which

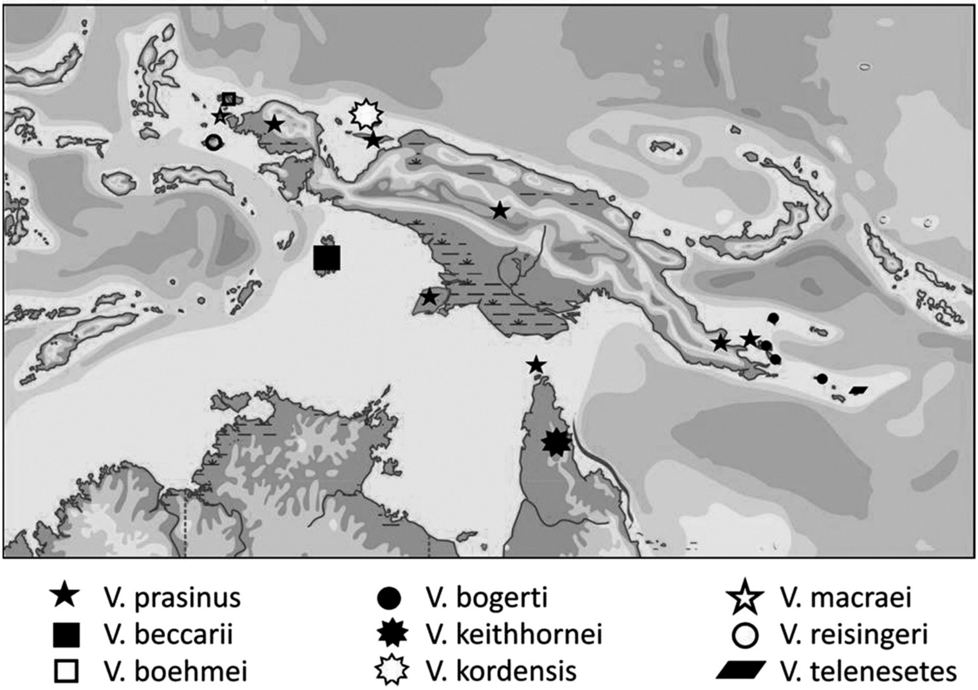

Fig. 1: Geographical distributions of the members of the *Varanus prasinus* complex in the region of New Guinea and northern Australia.

Abb. 1: Geographische Verbreitung der Arten des *Varanus prasinus*-Komplexes im Gebiet von Neuguinea und dem nördlichen Australien.

these two groupings arise. However, in a less conservative phylogenetic analysis, *V. boehmei* might well be considered a sister clade to *V. macraei*, *V. prasinus*, and *V. reisingeri* (see MP and NJ trees in ZIEGLER et al. 2007). The p-distance values between *V. boehmei* and the *V. prasinus* / *V. reisingeri* clade are 1.6 – 1.9 % (on average 1.6 ± 0.001 %), those between *V. boehmei* and *V. macraei* are 1.4 ± 0 %. The specimens colorwise assigned to *V. reisingeri* are not delimitable from most of the *V. prasinus* samples. Ten of the 14 samples within this clade share a common haplotype. This haplotype was found in four samples of *V. prasinus* and six of *V. reisingeri*. Average p-distances between the *V. prasinus* / *V. reisingeri* clade and the single haplotype found in *V. macraei* are only 0.2 – 0.6 % (on average 0.3 ± 0.001 %).

In accordance to ZIEGLER et al. (2007), *V. keithhornei* and *V. beccarii* DORIA, 1874, are considered the sister clade to the clade of *V. macraei* / *V. prasinus* / *V. reisingeri*, although this grouping is not well-supported. However, three samples that were assigned to *V. prasinus* (cf. PRA 7, PRA 3) and *V. reisingeri* (REI 3) are positioned within this clade, as a basal polytomy to *V. beccarii*. These samples sharing a common haplotype are separated from the rest of the *V. prasinus* / *V. reisingeri* samples by p-distances of 2.3 – 2.7 % (on average 2.4 ± 0.0014 %), whereas the p-distances to *V. beccarii* are merely 0.4 – 0.6 % (on average 0.4 ± 0.0007 %). To verify this unexpected finding, i.e., to rule out the possibility that this is an artifact caused by cross contamination, these three samples were run again in an independent trial (from DNA extraction on). However, the authors obtained the same result in the second run and thus are confident, that the results are correct (but see discussion).

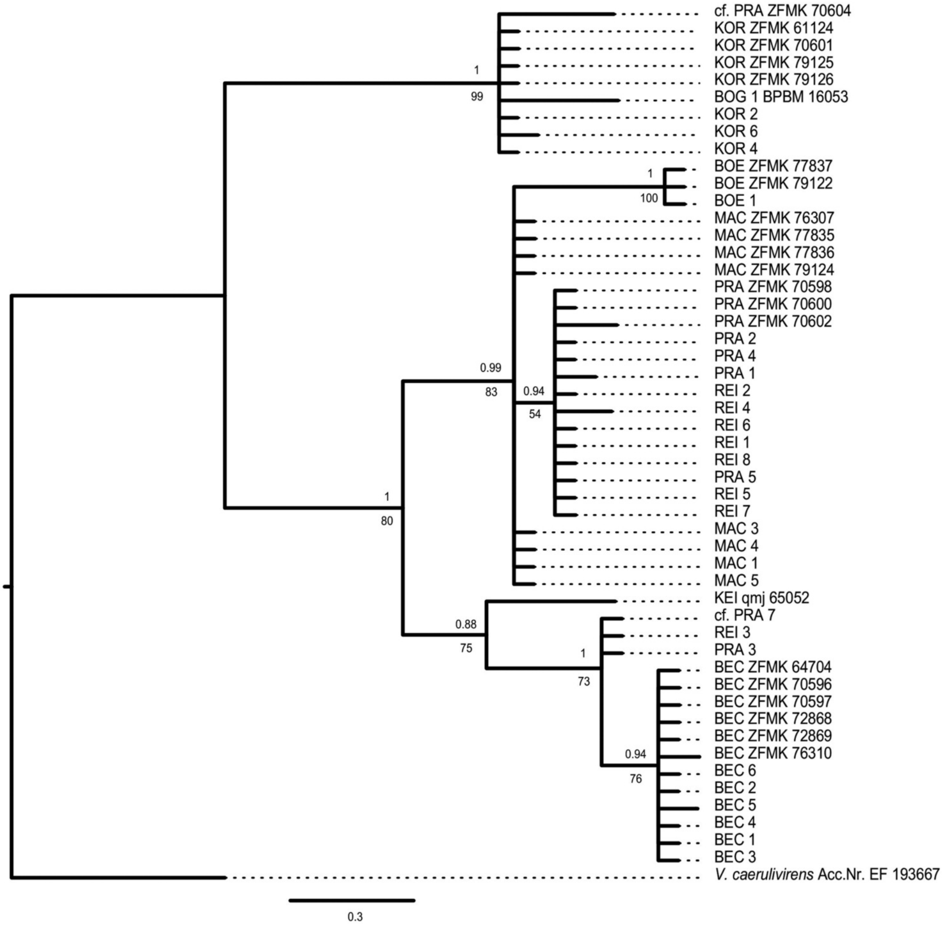

Fig. 2: Bayesian phylogram of the combined datasets. Numbers above branches are posterior probability values from Bayesian analysis, numbers below branches are bootstrap values from maximum likelihood analysis, inferred from 1,000 pseudoreplicates.

Abb. 2: Phylogramm der kombinierten Datensätze nach Bayesianischer Analyse. Zahlen über den Ästen sind Posterior Probability-Werte der Bayesianischen Analyse. Zahlen unter den Ästen sind Bootstrapwerte (1000 Pseudoreplikationen) der Maximum Likelihood Analyse.

DISCUSSION

Within monitor lizards, the *V. indicus* complex is regarded to be the sister group of the *V. prasinus* group (Böhme 1988; Sprackland 1991; Ast 2001; Ziegler et al. 2007). Genetically, this split was dated at the early Miocene about 20 million years ago (mya) by Vidal et al. (2012). Both monitor lizard groups broadly co-exist on New Guinea and its surrounding islands, where they sympatrically inhabit evergreen tropical rainforests. Hypothetically, once the evolutionary split between the *V. indicus* group and the *V. prasinus* group had occurred (possibly through sympatric specia-

Table 1 (this and opposite page): Matrix of uncorrected, pairwise distances. The table reads from the left page to the right page, its upper portion being continued in the lower portion.

	KOR ZFMK 61124	KOR ZFMK 70601	KOR ZFMK 79125	KOR ZFMK 79126	KOR 2	KOR 4	KOR 6	BOG BPBM 16053	MAC ZFMK 76307	MAC ZFMK 77835	MAC ZFMK 77836
KOR ZFMK 61124											
KOR ZFMK 70601	0,000										
KOR ZFMK 79125	0,000	0,000									
KOR ZFMK 79126	0,000	0,000	0,000								
KOR 2	0,000	0,000	0,000	0,000							
KOR 4	0,000	0,000	0,000	0,000	0,000						
KOR 6	0,002	0,002	0,002	0,002	0,002	0,002					
BOG BPBM 16053	0,012	0,012	0,012	0,012	0,012	0,012	0,014				
MAC ZFMK 76307	0,041	0,041	0,041	0,041	0,041	0,041	0,043	0,047			
MAC ZFMK 77835	0,041	0,041	0,041	0,041	0,041	0,041	0,043	0,047	0,000		
MAC ZFMK 77836	0,041	0,041	0,041	0,041	0,041	0,041	0,043	0,047	0,000	0,000	
MAC ZFMK 79124	0,041	0,041	0,041	0,041	0,041	0,041	0,043	0,047	0,000	0,000	0,000
MAC 1	0,041	0,041	0,041	0,041	0,041	0,041	0,043	0,047	0,000	0,000	0,000
MAC 3	0,041	0,041	0,041	0,041	0,041	0,041	0,043	0,047	0,000	0,000	0,000
MAC 4	0,041	0,041	0,041	0,041	0,041	0,041	0,043	0,047	0,000	0,000	0,000
MAC 5	0,041	0,041	0,041	0,041	0,041	0,041	0,043	0,047	0,000	0,000	0,000
BOE ZFMK 77837	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,045	0,014	0,014	0,014
BOE ZFMK 79122	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,045	0,014	0,014	0,014
BOE1	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,045	0,014	0,014	0,014
PRA ZFMK 70598	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
PRA ZFMK 70600	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
PRA ZFMK 70602	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,006	0,006	0,006
cf. PRA ZFMK 70604	0,010	0,010	0,010	0,010	0,010	0,010	0,012	0,017	0,045	0,045	0,045
PRA 1	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,004	0,004	0,004
PRA 2	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
PRA 3	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
PRA 4	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
PRA 5	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
cf. PRA 7	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
REI 1	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
REI 2	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
REI 3	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
REI 4	0,047	0,047	0,047	0,047	0,047	0,047	0,048	0,052	0,006	0,006	0,006
REI 5	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
REI 6	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
REI 7	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
REI 8	0,043	0,043	0,043	0,043	0,043	0,043	0,045	0,048	0,002	0,002	0,002
BEC ZFMK 64704	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC ZFMK 70596	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC ZFMK 70597	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC ZFMK 72868	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC ZFMK 72869	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC ZFMK 76310	0,047	0,047	0,047	0,047	0,047	0,047	0,048	0,052	0,023	0,023	0,023
BEC 1	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC 2	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC 3	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC 4	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
BEC 5	0,047	0,047	0,047	0,047	0,047	0,047	0,048	0,052	0,023	0,023	0,023
BEC 6	0,045	0,045	0,045	0,045	0,045	0,045	0,047	0,050	0,021	0,021	0,021
KEI QMJ 65052	0,047	0,047	0,047	0,047	0,047	0,047	0,048	0,052	0,023	0,023	0,023

	PRA 3	PRA 4	PRA 5	cf. PRA 7	REI 1	REI 2	REI 3	REI 4	REI 5	REI 6	REI 7	REI 8
PRA 4	0,023											
PRA 5	0,023	0,000										
cf. PRA 7	0,000	0,023	0,023									
REI 1	0,023	0,000	0,000	0,023								
REI 2	0,023	0,000	0,000	0,023	0,000							
REI 3	0,000	0,023	0,023	0,000	0,023	0,023						
REI 4	0,027	0,004	0,004	0,027	0,004	0,004	0,027					
REI 5	0,023	0,000	0,000	0,023	0,000	0,000	0,023	0,004				
REI 6	0,023	0,000	0,000	0,023	0,000	0,000	0,023	0,004	0,000			
REI 7	0,023	0,000	0,000	0,023	0,000	0,000	0,023	0,004	0,000	0,000		
REI 8	0,023	0,000	0,000	0,023	0,000	0,000	0,023	0,004	0,000	0,000	0,000	
BEC ZFMK 64704	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC ZFMK 70596	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC ZFMK 70597	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC ZFMK 72868	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC ZFMK 72869	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC ZFMK 76310	0,006	0,025	0,025	0,006	0,025	0,025	0,006	0,029	0,025	0,025	0,025	0,025
BEC 1	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC 2	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC 3	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC 4	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
BEC 5	0,006	0,025	0,025	0,006	0,025	0,025	0,006	0,025	0,025	0,025	0,025	0,025
BEC 6	0,004	0,023	0,023	0,004	0,023	0,023	0,004	0,027	0,023	0,023	0,023	0,023
KEI QMJ 65052	0,017	0,025	0,025	0,017	0,025	0,025	0,017	0,029	0,025	0,025	0,025	0,025

tion resulting from ecological divergence), greater New Guinea was probably inhabited by a predominantly black colored, tree dwelling, prehensile tailed monitor lizard with bright markings representing the last common ancestor of all modern tree monitor lizards. With increasing global temperatures and consequently rising sea levels dur-

Tab. 1 (diese und gegenüberliegende Seite): Matrix der unkorrigierten, paarweisen Abstände. Leserichtung von der linken zur rechten Seite, wobei der untere Tabellenblock die Fortsetzung des oberen darstellt.

MAC ZFMK 79124	MAC 1	MAC 3	MAC 4	MAC 5	BOE ZFMK 77837	BOE ZFMK 79122	BOE1	PRA ZFMK 70598	PRA ZFMK 70600	PRA ZFMK 70602	cf. PRA ZFMK 70604	PRA 1	PRA 2
0,000													
0,000	0,000												
0,000	0,000	0,000											
0,000	0,000	0,000	0,000										
0,014	0,014	0,014	0,014	0,014									
0,014	0,014	0,014	0,014	0,014	0,000								
0,014	0,014	0,014	0,014	0,014	0,000	0,000							
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016						
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000					
0,006	0,006	0,006	0,006	0,006	0,019	0,019	0,019	0,004	0,004				
0,045	0,045	0,045	0,045	0,045	0,047	0,047	0,047	0,047	0,047	0,048			
0,004	0,004	0,004	0,004	0,004	0,017	0,017	0,017	0,002	0,002	0,006	0,048		
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	0,000
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	0,000
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	0,000
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	0,000
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,006	0,006	0,006	0,006	0,006	0,016	0,016	0,016	0,004	0,004	0,008	0,050	0,006	0,004
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	0,000
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	0,000
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	0,000
0,002	0,002	0,002	0,002	0,002	0,016	0,016	0,016	0,000	0,000	0,004	0,047	0,002	0,000
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,023	0,023	0,023	0,023	0,023	0,033	0,033	0,033	0,025	0,025	0,029	0,050	0,027	0,025
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,023	0,023	0,023	0,023	0,023	0,029	0,029	0,029	0,025	0,025	0,029	0,050	0,027	0,025
0,021	0,021	0,021	0,021	0,021	0,031	0,031	0,031	0,023	0,023	0,027	0,048	0,025	0,023
0,023	0,023	0,023	0,023	0,023	0,033	0,033	0,033	0,025	0,025	0,029	0,050	0,027	0,025

BEC ZFMK 64704	BEC ZFMK 70596	BEC ZFMK 70597	BEC ZFMK 72868	BEC ZFMK 72869	BEC ZFMK 76310	BEC 1	BEC 2	BEC 3	BEC 4	BEC 5	BEC 6	KEI QMJ 65052
0,000												
0,000	0,000											
0,000	0,000	0,000										
0,000	0,000	0,000	0,000									
0,002	0,002	0,002	0,002	0,002								
0,000	0,000	0,000	0,000	0,000	0,002							
0,000	0,000	0,000	0,000	0,000	0,002	0,000						
0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000					
0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000				
0,002	0,002	0,002	0,002	0,002	0,004	0,002	0,002	0,002	0,002			
0,000	0,000	0,000	0,000	0,000	0,002	0,000	0,000	0,000	0,000	0,002		
0,021	0,021	0,021	0,021	0,021	0,023	0,021	0,021	0,021	0,021	0,023	0,021	

ing the Pliocene (with a maximum about 3.5 mya), some areas of this formerly contiguous landmass around New Guinea were divided into distinct smaller islands and the various local tree monitor populations became geographically and genetically isolated, giving rise to divergent evolutionary lineages and disjunctive insular distribution patterns as was the case in many other Australo-Papuan vertebrates (see e.g., Heads 2002; Rawlings & Donnellan 2003; Outlaw & Voelker 2008).

It can be assumed that the last common ancestor of the members of the subgenera *Euprepiosaurus* and *Hapturosaurus* was a generalist, as is the case in most Indo-Australian varanids (Horn & Visser 1991; Bennett 1998; King & Green 1999). The evolutionary split into the strictly tree dwelling taxa of the *V. prasinus* complex and the more terrestrial taxa of the *V. indicus* complex could be explained by specializing in certain food preferences and availability. Most likely, the green background coloration of some members of the *V. prasinus* complex evolved as an adaption to their life in the foliage of the canopy. In this special environment, being of green color represents a selective advantage since it provides camouflage. Thus, Greene (1986) regarded the green coloration in *V. prasinus* as a derived character state and an adaptation to strongly arboreal habits. Members of the *V. prasinus* complex mostly feed in the upper tree canopies (Irwin 1994), and accordingly, stomach content studies mainly detected katydids and other arthropods (Greene 1986), whereas members of the *V. indicus* complex mainly forage in the lower vegetation and on the ground (but see Koch et al. 2009), and often also near the shoreline. Consequently, Philipp et al. (2007) revealed that a high percentage of prey items found in stomachs of their *V. indicus* study group consisted of crustaceans, reptile eggs and vertebrates (especially skinks). Only in the examined specimens of *V. jobiensis* the food consisted of a large proportion of insects (Philipp et al. 2007).

The area of New Guinea, northern Australia, and the neighboring islands experienced a very dynamic geological and climatological history (Heaney 1991; Hall & Holloway 1998; Lohman et al. 2011) that most likely played an important role in the diversification of tree monitor lizards (Ziegler et al. 2007). Their dispersion began at the Miocene-Pliocene transition about five to six mya (Vidal et al. 2012), an epoch characterized by a global sea level minimum (Outlaw & Voelker 2008). Associated with cyclical glaciation events in the northern hemisphere during the Pliocene and particularly during the following Pleistocene, global sea levels repeatedly dropped substantially (Jongsma 1970; Chappell & Shackleton 1986). From the Oligocene to the early Pliocene (ca. 33.8 to 2.5 mya) sea levels changed by an altitude of about 30 to 60 meters, while greater changes only began during the Pleistocene (Miller et al. 2005). Associated with the glaciation events during this period, the sea level in the area lowered and rose substantially and repeatedly (Heatwole 1987; Voris 2000) depending on cold and warm periods during glacification. For instance, about 130,000 years ago, sea levels off the north-eastern coast of New Guinea were 60 to 80 meters lower than today (McCulloch et al. 1999). As a consequence of falling sea levels, Australia, New Guinea, and the associated offshore islands, many of which are under water today, were united in a contiguous landmass connected by the currently submerged continental Sahul shelf.

Accordingly, land bridges between the islands formed and disappeared, connecting and disconnecting repeatedly during each glacial and interglacial period, enabling populations of animals to segregate and mix genetically. The longer the forested land bridges existed, the longer animals could migrate in both directions and the exchange of genetic information was increased. According to Heatwole (1987), about 14,000 years ago, as large amounts of water were bound through the glaciation in the northern hemisphere, the sea level in the area was about 120 m below its present level and Australia, New Guinea, and most of their offshore islands were united in a contiguous landmass, which was probably inhabited by tree dwelling, prehensile-tailed monitor lizards, in areas where suitable habitats occurred.

The authors of this paper are convinced that the aforementioned climatological, ecological, and zoogeographic factors induced the radiation and distribution of the *V. prasinus* subgroup and, thus interpret the results of their molecular investigation in the light of these repeated events.

Under these past conditions which also affected the Raya Ampat Archipelago (west of New Guinea), Batanta Island, the distribution range of *V. macraei*, was repeatedly connected to New Guinea. These two islands' tight geographical connection and the close genetic affiliation of *V. macraei* to *V. prasinus* as discovered by Ziegler et al. (2007) and supported by the present study, suggest that introgression and hybridization during glacial periods with overland connections between former island territories are probably responsible for the presented phylogenetic findings.

When global sea levels were 30 meters below present levels, also Misol Island, the range of *V. reisingeri*, was connected to mainland New Guinea (Voris 2000). Because of the pronounced differences in coloration, scalation and overall appearance it may be intuitively assumed that *V. reisingeri* was geographically isolated from *V. prasinus* for a longer period of time than *V. macraei*. Such an assumption, however, is not supported by the phylogenetic estimates presented here. Whether or not these external morphological differences strictly correspond to the geographical range, with yellow specimens being restricted to Misol Island, while emerald green being exclusive to New Guinea, awaits confirmation by comparison of voucher specimens with detailed locality data or observations from the field. Statements of local reptile dealers are not reliable since they often obscure the exact origin of traded specimens. In this regard, it is worth mentioning that captive specimens of *V. reisingeri* changed their coloration from yellow to green, possibly depending on nutrition or artificial lighting (D. Kielmann pers. comm.) Weijola (pers. comm.) mentioned, that *V. reisingeri* was clearly distinguished from *V. prasinus* when a different mitochondrial DNA sequence (e.g., ND4) was analyzed.

The present results regarding *V. boehmei* are in accordance with those of Ziegler et al. (2007) in that this species is a close relative of *V. macraei* and *V. prasinus*. *Varanus boehmei* is restricted to Waigeo Island, located just about 50 km north of New Guinea's Vogelkop Peninsula. However, the sea between Waigeo Island and Western Papua is comparatively deep and thus, Waigeo Island was separated from the main island for a considerably longer time than Batanta or Misol Islands, which offers a plausible explanation why *V. boehmei* is well differentiated from its closest congeners in the data set studied (Fig. 2). According to Voris (2000), the sea level would have to be more than 120 m below the present conditions to connect Waigeo Island to New Guinea which was only the case during Pleistocene glacial maxima, that is, less than 10 % of the time during the last 250,000 years before present (Voris 2000). The relatively pronounced genetic differences between *V. beccarii* and *V. prasinus* correspond well to the greater spatial distance between those islands of the Aru Archipelago (southwest of New Guinea) and New Guinea, although both land masses were connected by a land bridge, when the sea level was just 40 m below the present level (Voris 2000).

The close genetic affiliation of three samples of *V. prasinus* and *V. reisingeri* (PRA 3, cf. PRA 7, and REI 3), respectively, to the *V. beccarii* clade (Fig. 2), suggests a paraphyletic status *V. prasinus*, which is hard to interpret in the absence of reliable locality data, in particular since the voucher specimen of cf. PRA 7 (SMF99805) has the typical coloration of *V. prasinus*. One possible, however very theoretical, explanation would require a common south-central New Guinean origin of the specimens PRA 3, cf. PRA 7, and REI 3, while the rest of the *V. prasinus* samples stem from Western Papua, where most specimens are collected for the pet trade (Luxmoore 1988; Luxmoore & Groombridge 1990; Jenkins & Broad 1994). According to Voris' (2000) paleomaps, the land bridge persisted longest between the islands of the Aru Archipelago and the central southern coast of New Guinea. A population level study incorporating a larger number of specimens of *V. prasinus* from many different localities across the huge land mass of New Guinea is needed to clarify this biogeographic assumption. However, despite the abundance of tree monitor lizards in the pet trade (Shepherd et al. 2005; Pernetta 2009; Koch et al. 2013), there are few voucher specimens with detailed locality data in international museum collections (A. Koch, pers. observ.).

The *V. kordensis* / *V. bogerti* clade is well separated from the other members of the *V. prasinus* complex, which accords well with the assumption, that Biak Island (northwest of New Guinea), the range of *V. kordensis*, was not connected to mainland New Guinea, even when sea levels in the region were as much as 120 m below the present level (VORIS 2000). Although, there are clear genetic differences between these two species in the investigated gene fragment, these differences seem rather subtle, given the huge geographic distance of more than 1,800 km between their respective distribution ranges (*V. bogerti:* d'Entrecasteaux and Trobriand Archipelagos, eastern Papua New Guinea). Since both species occur on islands only 50 km (for *V. kordensis* on Biak Island) and less than 10 km (for *V. bogerti* on Fergusson Island) away from the next populations of *V. prasinus* (KOCH et al. 2014), one would expect that each species is more closely related to the neighboring populations of *V. prasinus* than with each other. The authors could, however, only compare with sequences of *V. prasinus* collected for the pet trade and, consequently, lack exact and reliable locality data. A dataset incorporating *V. prasinus* specimens from the neighborhood of *V. kordensis* and *V. bogerti* may result in a better understanding of the phylogeographic relationships. One can assume, that *V. prasinus* specimens from easily accessible and regularly visited localities on New Guinea are overrepresented, so that the entire genetic diversity within *V. prasinus* is not fully reflected by the dataset under study. *Varanus prasinus* shows some variation in color pattern across the entire distribution range that may correlate with geographic distance (KOCH et al. 2014).

Obviously, the *V. prasinus* group experienced a higher diversification rate in the western parts of its distribution range than in the east with *V. beccarii*, *V. boehmei*, *V. kordensis*, *V. macraei* and *V. reisingeri* being restricted to islands off the Indonesian part of New Guinea (the province called Papua, formerly known as Irian Jaya), while merely *V. bogerti* and *V. keithhornei* (and the dubious taxon *telenesetes*) occur on islands off the coast of Papua New Guinea and on the Australian mainland (Fig. 1). On the other hand, the islands off southeastern New Guinea, namely the Trobriand, D'Entrecasteaux and Louisiade archipelagos, are severely underexplored as to their (herpeto) faunas (BOULENGER 1895a, 1895b; HEATWOLE 1975; KRAUS & SHEA 2005). Therefore, future field work may reveal further undescribed tree monitor taxa from these remote island groups.

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