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This variety and beauty, even the strangeness, the ugliness, and the unexpectedness we find everywhere in nature excite in us admiration, wonder, and curiosity — the three emotions which stimulate first our attention, then our determination to learn.."

-Alfred Russell Wallace, 1910

ABSTRACT

The monitor lizards of the subgenus *Euprepiosaurus* Fitzinger, popularly known as the Pacific monitor lizards, are widely distributed on islands in the southwest Pacific region where they often form conspicuous components of the local faunal communities. Despite their notable size, importance as top predators, and the widespread use of their meat and skins by local communities, the number of species, phylogenetic relationships, and distribution of these lizards have remained poorly known. Most species have been described recently and known to science only from colonial-era museum collections or from animals reaching Europe through the international pet trade. The number of recognized species has risen from two to fourteen since 1990, both as a result of revisions of populations previously assigned to *Varanus indicus,* and from the discovery of completely new species.

This dissertation investigates the phylogenetic relationships and taxonomy of *Euprepiosaurus* throughout its extensive geographical range. It relies on a combination of molecular, morphological, and field data to reveal species boundaries and species distributions. Tissue samples were collected over twelve months of fieldwork in the Papua New Guinean island provinces, and sampled from existing museum collections. The results are presented in four separate chapters (one manuscript and three published articles).

The first chapter is the most well-sampled molecular phylogeny of the subgenus *Euprepiosaurus* and *Hapterosaurus* Bucklitsch to date. It includes 96 samples representing 14 recognized species and several apparently new species. Two mitochondrial genes (*ND4* and *16S*) were sequenced and Maximum Likelihood, Parsimony and Bayesian inference approaches were used for phylogenetic reconstructions. BEAST was used to estimate lineage divergence times. All analyses retreive both *Euprepiosaurus* and *Hapterosaurus* as monophyletic. Within *Euprepiosaurus* three clades, or species-groups, are recovered as monophyletic with varying support. These are the *V. doreanus* group, the *V. indicus* group, and the *V. jobiensis* group (currently consisting of a single species).

The *V. doreanus* group consist of four recognized species – all of which are well-supported and monophyletic in our analysis. *Varanus doreanus* which is geographically widespread on New Guinea, Cape York, Aru and other satellite islands positions as a sister taxon to a clade containing the single-island endemics *V. finschi, V. semotus* and *V. yuwonoi*.

The *V. indicus* group is estimated to have radiated rapidly during the Pleistocene, resulting in a number of allopatric island endemics. *Varanus indicus* is the most widespread species and occurs throughout New Guinea and its offshore islands, New Britain, Cape York and parts of the Northern Territory. Other well supported monophyletic lineages include *V. cerambonensis, V. melinus, V. douarrha,* and several apparently new species from insular PNG, the Solomon Islands, Western Micronesia, and the Moluccas.

The *Varanus jobiensis* specimens included in this study are resolved as a well-supported monophyletic clade consisting of several divergent lineages. The populations from the western and eastern part of the range are estimated to have diverged 3-7 million years ago, suggesting that *V. jobiensis* may represent a species complex.

The second chapter is a study of the identity of *V. indicus.* Described by Francois Daudin in 1802, the original type specimen has since been lost and more recently replaced by a neotype. Field and museum studies (this study) indicate that the neotype neither originates from the type locality, nor does it represent the species described by Daudin. An application has therefore been made to the ICZN to replace the neotype with a well-documented specimen that agrees with other known specimens from Ambon and surrounding islands. This will have the effect of synonymizing *V. cerambonensis* with *V. indicus* and making *V. indicus* a species endemic to the islands of the central Moluccas. *Varanus chlorostigma* is proposed as the valid name for the taxon occurring on New Guinea and surrounding islands.

The third chapter is the description of *V. semotus,* a new species of the *V. doreanus* group from Mussau island in northern Papua New Guinea. It is described on the basis of molecular and morphological characters. *Varanus semotus* is the first endemic reptile described from Mussau, and the only member of the *V. doreanus* group that is known to occur on a remote oceanic island. It is the third monitor lizard recorded from the Bismarck Archipelago. The distribution of the related *V. finschi* is also discussed and narrowed down to New Britain.

The fourth chapter is a re-description and re-validation of *V. douarrha,* a species originally described in 1830 by the French naturalist René Lesson. The original type specimen has been lost from the museum in Paris and the name was for a long time considered synonymous with *V. indicus.* With the description of *V. finschi* (1994) the name *douarrha* was designated a *nomen dubium* due to the possible sympatry of two species on New Ireland. An examination of the collections from New Ireland and recent fieldwork on New Ireland, Djaul and Lavongai showed that only one species of *Varanus* occur there confirming the identity of *V. douarrha.* Morphological and molecular studies further showed that this species is distinct from both *V. indicus* and *V. finschi* and warrants recognition as a valid species.

TIIVISTELMÄ

Euprepiosaurus-alasuvun varaanit ovat laajalle levinneitä eteläisen Tyynenmeren alueella, jossa ne muodostavat tärkeän osan paikallisista saarieliöyhteisöistä. Varaanit ovat kookkaita huippupetoja ja riistalajeina merkittäviä myös ihmisen kannalta. Tästä huolimatta niiden lajirikkaus, fylogenia ja levinneisyysalueet tunnetaan vielä heikosti. Valtaosa lajeista on kuvattu tieteelle vasta kolmen viime vuosikymmenen aikana. Lajikuvaukset ovat perustuneet pääosin vanhoihin museonäytteisiin tai yksilöihin, jotka ovat päätyneet Eurooppaan kansainvälisen eläinkaupan kautta. Vuoden 1990 jälkeen *Euprepiosaurus*-alasuvun varaanien lajimäärä on kasvanut kahdesta lajista neljääntoista.

Tämä väitöskirja käsittelee kattavasti Tyynenmeren saaria asuttavien varaanien fylogeniaa, taksonomiaa ja eliömaantiedettä. Tutkimus pohjautuu pitkäaikaisiin kenttä- ja kokoelmatutkimuksiin sekä laajoihin morfologisiin ja geneettisiin aineistoihin. Kenttätutkimusten aikana selvitettiin varaanien biologiaa ja kerättiin kudosnäytteitä Papua-Uuden-Guinean saariilla. Kudosnäytteitä kerättiin myös australialaisiin ja yhdysvaltalaisiin eliökokoelmiin tallennetuista varaaniyksilöistä. Väitöskirja koostuu neljästä artikkelista, joista kolme on jo julkaistu kansainvälissä tieteellisissä sarjoissa.

Väitöskirjan ensimmäinen luku esittelee *Euprepiosaurus*- ja *Hapterosaurus*-varaaniryhmien aikakalibroidun molekyylifylogenian joka pohjautuu kahden mitokondriaalisen geenin (*ND4* ja *16S*) sekvensseihin. Sekvenssiaineisto analysoitiin käyttäen Bayesian-, Maximum Likelihood-, ja Parsimonia-menetelmiä. Aika-arviot on tehty BEAST-ohjelman avulla hyödyntäen sekä fossiiliaineistoon että aikaisempiin tutkimuksiin perustuvia kalibrointipisteitä. Tutkimuksen mukaan *Euprepiosaurus*-alasuku koostuu kolmesta monofyleettisestä lajiryhmästä: 1) *Varanus doreanus*, 2) *V. indicus* ja 3) *V. jobiensis*.

V. doreanus-ryhmä kattaa neljä tunnettua lajia. Uuden-Guinean alueella laajalle levinnyt *Varanus doreanus*-laji on ryhmän kolmen muun lajin sisarlaji. Kolme muuta lajia (*V. finschi*, *V. semotus* ja *V. yuwonoi*) ovat kotoperäisiä yksittäisille saarille Bismarckin ja Pohjois-Molukkien alueella ja muodostavat yhdessä hyvin tuetun monofyleettisen ryhmän.

V. indicus-ryhmän arvioidaan levittäytyneen Tyynenmeren saarille nopeasti ja laajasti Pleistoseenikauden aikana, mikä on johtanut monien allopatristen ja yksittäisille saarille kotoperäisten lajien syntyyn. Monofyleettinen *Varanus indicus* on näistä levinneisyydeltään laajin. Pienempien saarten kotoperäiset *V. cerambonensis, V. melinus* ja *V. douarrha* ovat myös monofyleettisiä. *V. indicus*-ryhmä sisältää myös monia erillisiä fylogeneettisiä linjoja, jotka edustavat mahdollisesti tieteelle uusia lajeja. Nämä elävät esimerkiksi Manussaarella, Louisiaadiensaarilla, Tanimbarsaarella, Salomonsaarten eri osissa ja Mikronesiassa.

Aineiston mukaan myös *V. jobiensis*-lajin tutkitut yksilöt muodostavat monofyleettisen kokonaisuuden, jonka läntiset ja itäiset populaatiot näyttävät eronneen toisistaan noin 3-7 miljoonaa vuotta sitten. *V. jobiensis* onkin mahdollisesti monien lajien kompleksi.

Väitöskirjan toinen luku käsittelee *V. indicus*-lajin taksonomiaa. Ranskalainen François Marie Daudin kuvasi lajin vuonna 1802 Molukkien Ambonsaarelta kerätyn yksilön perusteella. Tyyppiyksilö kuitenkin katosi, minkä vuoksi lajille määriteltiin neotyyppi. Uudet kenttä- ja museotutkimukset osoittavat, että

kyseinen neotyyppi ei kuitenkaan edusta Daudinin alun perin kuvaamaa lajia. Väitöskirjan toinen luku vetoaa kansainväliseen eläintieteen nimistökomiteaan (ICZN), jotta neotyyppi vaihdettaisiin sellaiseen yksilöön, joka on todistetusti peräisin alkuperäiseltä tyyppipaikalta ja edustaa Daudinin kuvaamaa lajia. Muutoksen jälkeen *V. cerambonensis*-lajista tulisi *V. indicus*-lajin nuorempi synonyymi. *V. indicus*-nimi viittaisi muutoksen jälkeen lajiin, joka on kotoperäinen Keski-Molukkien saarille. *V. chlorostigma*-nimeä ehdotetaan lajille, joka elää Uudessa-Guineassa ja Australiassa.

Väitöskirjan kolmannessa luvussa kuvataan tieteelle uusi *V. semotus*-laji, joka elää Uuden-Irlannin provinssin Mussausaarella. Lajikuvaus perustuu sekä geneettiseen että morfologiseen aineistoon. *V. semotus* on ensimmäinen kotoperäinen Mussausaarelta kuvattu matelijalaji. Tämän lisäksi laji on *V. doreanus*-ryhmän ainoa edustaja, joka elää syrjäisellä valtamerisaarella.

Väitöskirjan neljännessä luvussa kuvataan uudelleen *V. douarrha*-laji. René Lesson kuvasi lajin alun perin jo vuonna 1830, mutta tyyppiyksilön kadottua Lessonin kuvaaman lajin uskottiin olevan joko *V. indicus* tai *V. finschi*. Tutkimuksen mukaan Lessonin alun perin kuvaama laji on validi, ja se elää kotoperäisenä ainoana varaanilajina Uuden-Irlannin-, Djaul- ja Lavongaisaarilla.

TABLE OF CONTENTS

LIST OF ORIGINAL ARTICLES

I. Weijola V, Vahtera V, Lindqvist C. A comprehensive mtDNA phylogeny and divergence time estimates for the Pacific monitor lizards (*Varanus*: *Euprepiosaurus*) reveal high levels of cryptic diversity and local endemism. Manuscript.

II. Weijola V (2015) *Tupinambis indicus* Daudin, 1802 (currently *Varanus indicus*; Reptilia, Squamata): proposed conservation of usage of the specific name by replacement of the neotype. *Bulletin of Zoological Nomenclature* 72: 134–141.

III. Weijola V, Donnellan SC, & Lindqvist C (2016) A new blue-tailed Monitor lizard (Reptilia, Squamata, Varanus) of the *Varanus indicus* group from Mussau Island, Papua New Guinea. *ZooKeys* 568: 129-154

IV. Weijola V, Kraus F, Vahtera V, Lindqvist C & Donnellan SC (2017) Reinstatement of *Varanus douarrha* Lesson 1830 as a valid species with comments on the biogeography of monitors in the Bismarck Archipelago, Papua New Guinea. *Australian Journal of Zoology* 64 (6): 434-451

Contributions to the original articles.

	I	**II**	**III**	**IV**
Original idea	VW	VW	VW	VW
Field work	VW	VW	VW	VW
Laboratory	CL, SD		CL, SD	CL
Data analysis	VV,VW	VW	SD, VW	VV, SD, VW
Writing	VW, VV	VW	VW, SD	VW, FK, VV

VW = Valter Weijola

VV = Varpu Vahtera

CL = Christer Lindqvist

SD = Steve Donnellan

FK = Fred Kraus

1. INTRODUCTION

The Pacific Ocean occupies roughly one third of the world´s surface area and encompasses climates ranging from tropical to polar. With tens of thousands of islands dispersed throughout this vast sea it is a uniquely diverse region that has fascinated western explorers and naturalists for the past 500 years. These islands and their faunas played key roles in the development of the theory of speciation and evolution (Darwin 1858; Wallace 1858) and continued to inspire many of the early key concepts in biology such as biogeography and systematics (e.g. Wallace 1876, 1881; Mayr 1942). These early pioneers lacked many of the tools available to scientists today, critically, an understanding of plate tectonics and genetics, both of which are fundamental to modern biogeographers (Emerson 2008). Instead they relied upon the existing knowledge of species distributions, much of it gained personally during long periods of field collecting.

Islands have continued to play an important setting for studies in evolutionary biology, biogeography, and conservation (Wilson 1959; MacArthur & Wilson 1967; Diamond 1975; Lack 1976; Simberloff 1976). The most intensely studied systems are those easily accessible to scientists and with relatively well-developed infrastructure such as the Caribbean, Galapagos, Hawaiian, and Canary islands, all of which have provided classic examples in island biology (e.g., Lack 1947; Schoener 1968; Williams 1972; Ricklefs & Cox 1972; Losos 2009).

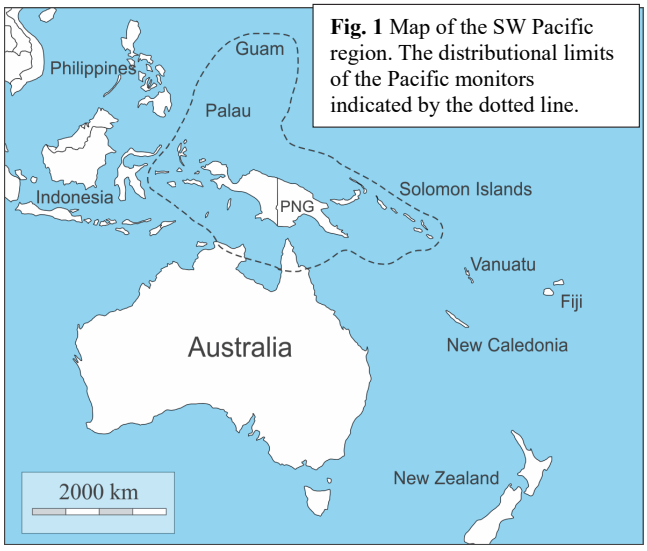

Fig. 1 Map of the SW Pacific region. The distributional limits of the Pacific monitors indicated by the dotted line.

Fewer detailed studies on conceptual questions have been conducted in the biologically complex islands of the tropical SW Pacific (Fig.1), which continues to be logistically challenging to work in. Many of the important publications by Jared Diamond, Ernst Mayr, and Edward Wilson were, however, heavily based on field-studies on islands surrounding New Guinea (Mayr 1942, 1963; Wilson 1961; Diamond 1972, 1975).

New Guinea is the second largest tropical island in the world and famous for its biodiversity and high degree of species endemism (estimated to be 60-90% in plants) (Takeuchi 2007). While the surrounding islands and archipelagos are less species rich they host various numbers of local endemics which raises the total number of species for the region significantly (Allison 1996). This region remains a frontier for biodiversity inventories, where species diversity of land vertebrates remains incompletely known. For some groups such as amphibians the island of New Guinea is mega-diverse and may prove to be richer in species than any other corresponding area (Allison 2007a).

The biological exploration of Melanesia (New Guinea, the Bismarck Archipelago, the Solomon Islands) started in earnest in the late 1800´s and a large part of the existing biological collections originate from that

time and until the end of the colonial-era in the early 1970´s (Allison 2007b, Frodin 2007). These early ambitious efforts, such as the Archbold, Whitney South Sea, and Noona Dan expeditions collected broadly over the taxonomic spectrum and continue to be some of the most valuable collections from the region.

From 1987 through the mid 1990s the Western Australian- and Bogor Museums undertook large herpetological collecting expeditions in the Lesser Sunda Islands and southern Moluccas (How & Kitchener 1997). The Australian Museum ran a series of important expeditions throughout Melanesia and the Moluccas from 1989–1993 (Flannery 1995). Led by mammalogist Tim Flannery these expeditions assembled large general collections including herpetological specimens. Since 2001 Fred Kraus and Allen Allison from the Bishop Museum have led several productive expeditions to Papua New Guinea (PNG) focused on the diversity of the herpetofauna. As of November 2016 this work had resulted in the description of an impressive 77 new amphibians and 19 new reptiles (F. Kraus pers. comm.).

All of these expeditions have collected monitor lizards opportunistically and produced useful voucher material from many localities. Monitors are however secretive animals that are difficult and time-consuming to find, and they are easily missed by general collectors not specifically targeting them (Pianka & Sweet 2016). Often they are either incidentally captured in the process of general herpetofaunal surveys, caught unintentionally in mammal snap-traps, or brought in by experienced local hunters. Thus, there has been a need for a study specifically focused on monitors, with detailed sampling throughout the Pacific region that could provide insight into the biogeography and systematics of these poorly known animals. The number of detailed molecular phylogenetic and biogeographic studies for Melanesian lineages in general is still relatively low (although see Pulvers & Colgan 2007; Smith & Filardi 2007; Hagen et al. 2012; Rowe et al. 2011; Jønsson et al. 2014; Andersen et al. 2015; Klein et al. 2016; Strickland et al. 2016; Timm et al. 2016; Toussaint et al. 2016; Jønsson et al. 2017; Oliver et al. 2017a), adding further value to a detailed case study of the widespread Pacific monitors.

1.1. Systematics and distribution of the Pacific monitor lizards

Monitor lizards all belong to a single genus (*Varanus*) containing 80 recognized species (Böhme 2003). With the exception of a few frugivorous species the members of this genus are predators that form important components of the food webs they are part of (Pianka 1970; Auffenberg 1981; Pianka 1994; Purwandana 2016). Some species are exploited for the fashion industry and live-animal trade with hundreds of thousands of monitors being harvested each year (De Buffrenil & Hemery 2007; Natusch & Lyons 2012). In many parts of their range their meat and skins are highly valued by local subsistence hunters.

Monitor species vary widely in size, their lengths ranging from less than 20 cm to more than 300 cm and weights from less than 17 g to more than 100 kg. However, all species occurring to the west of Wallace´s line are relatively large (adult length >130cm), while to the east of this biogeographical barrier many of the species are small (normal adult length <130cm). According to Sweet & Pianka (2003, 2007) the absence of placental predators has allowed for the impressive radiation of small and medium sized monitors in Australia, New Guinea and the Pacific islands.

The genus *Varanus* is currently divided into 12 subgenera, eight of which are represented in the Pacific east of the Sunda shelf. Of these, one (*Philippinosaurus*) occurs only in the Philippines, one (*Soterosaurus*) primarily west of Weber´s line, and five (*Euprepiosaurus, Hapterosaurus*, *Odatria*, *Papusaurus, Varanus*) are restricted to Australia, New Guinea (including some land-bridge islands) and some of the Lesser Sunda Islands. The monotypic subgenus *Solomonsaurus* is restricted to parts of the western Solomon Islands (McCoy 2015).

The most species rich and widely distributed subgenus in the Pacific islands is *Euprepiosaurus* (Fig. 2). *Euprepiosaurus* was previously divided into two species groups: the medium sized terrestrial/aquatic/arboreal *V. indicus* group recognizable by their laterally compressed tails, and the more specialized and smaller arboreal *V. prasinus* group. These two species groups were recently given their own subgenera with the *V. indicus* group keeping the former subgeneric name and the *V. prasinus* group given the new name *Hapterosaurus* (Bucklitsch et al. 2016).

There are currently 15 recognized species of *Euprepiosaurus,* three of which are widespread in the Papuan region, and twelve that are endemic to smaller islands or island groups. This subgenus can be divided into at least three separate species-groups: a *V. indicus* group, a *V. doreanus* group, and a *V. jobiensis* group (Paper I). Additionally, there are a few species for which no genetic material was available for this study and which are difficult to clearly allocate to any of these based on morphology, including *V. caerulivirens* Ziegler, Böhme & Philipp 1999*, V. zugorum* Böhme & Ziegler 2005, and an undescribed species from the northern Moluccas.

The *V. indicus* group has the largest distribution with populations occurring on almost every island between the Sula Islands in the west to San Cristobal in the east, Guam in the north and as far south as northern Australia (Fig. 3A). It is thus one of the most widespread species groups of terrestrial vertebrates in the SW Pacific islands. The members of this group are generally most abundant in habitats along coasts such as mangrove forests, and along larger rivers, but they also occur at lower densities in inland forests up to at least 900 m elevation (Weijola 2010; Weijola & Sweet 2010; Weijola & Sweet 2015; Paper IV).

The *V. indicus* group was long considered to comprise one variable and widespread species: *Varanus indicus* Daudin 1802 (Boulenger 1885, de Rooij 1915, Mertens 1942). A few other island populations were subsequently named, *Monitor douarrha* Lesson 1830, *M. chlorostigma* Gray 1831, *V. indicus rouxi* Mertens 1926, *V. tsukamotoi* Kishida 1929, but these were all subsequently synonymized with *V. indicus* (Boulenger 1885; Mertens 1942).

More recent taxonomic efforts started with the discovery of *V. melinus* Böhme & Ziegler 1997 from the Sula Islands, and then continued with several more species descriptions: *V. cerambonensis* Philipp, Böhme & Ziegler 1999 from Seram, Ambon and Buru, *V. juxtindicus* Böhme, Philipp & Ziegler 2002 from Rennell, *V. rainerguentheri* Ziegler et al. 2007 from Halmahera, *V. lirungensis* Koch et al. 2009 from Talaud, *V. obor* Weijola & Sweet 2010 from Sanana, and now the revalidation of *V. douarrha* Lesson 1830 from New Ireland (Paper IV). All described species are allopatric but there is evidence for sympatric occurances between described and undescribed species on a couple of islands (Weijola unpublished).

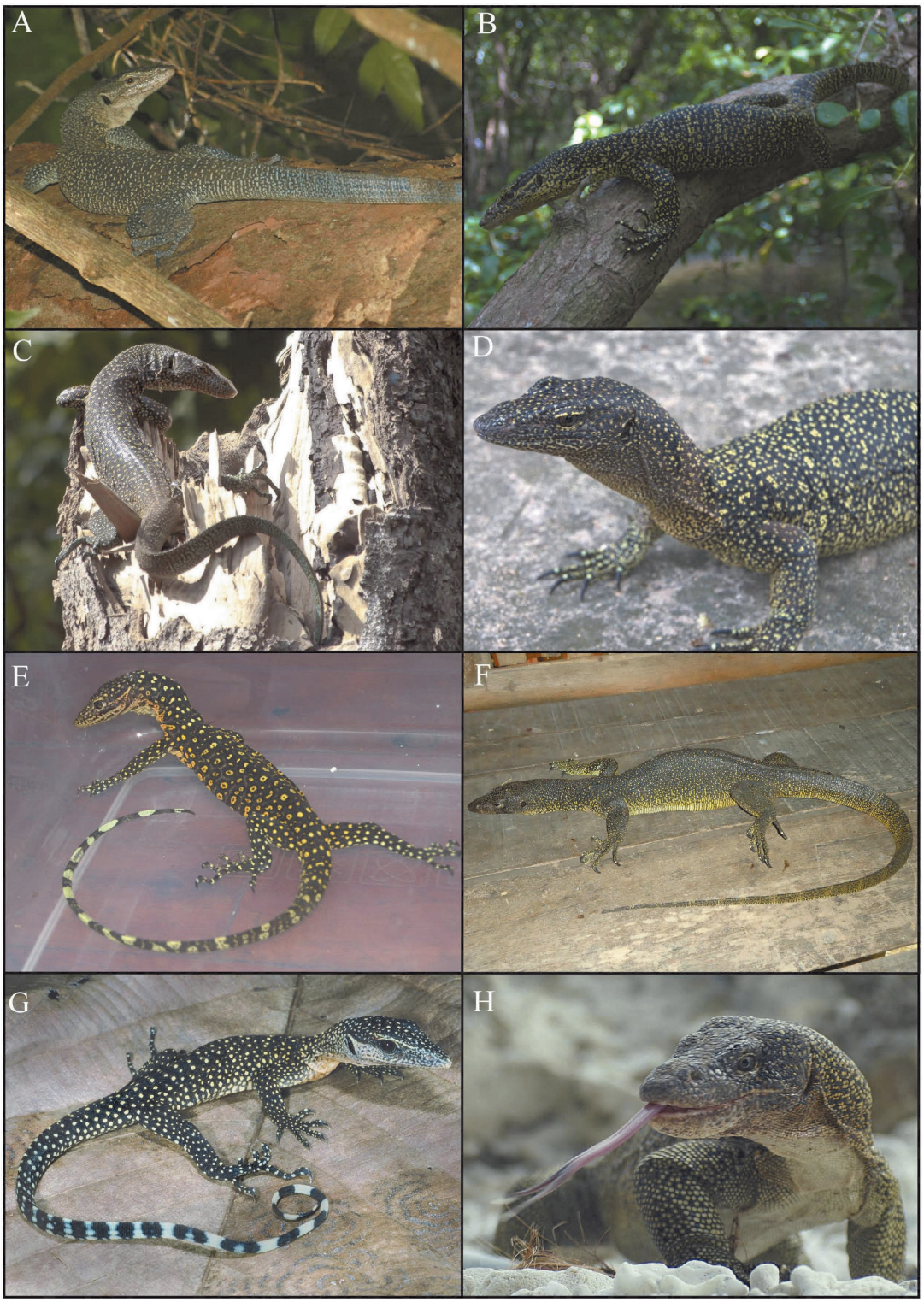
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Fig. 2. Members of the subgenus *Euprepiosaurus: Varanus caerulivirens* (A), *V. cerambonensis* (B), *V. doreanus* (C), *V. douarrha* (D), *V. finschi* (E), *V. indicus* (F), *V. jobiensis* (G), *V. juxtindicus* (H), *V. melinus* (I), *V. obor* (J), *V. rainerguentheri* (K), *V. semotus* (L), *V. yuwonoi* (M) & *V. sp.* from Misima (N). Photos by VW except C (Anders Zimny), G (Pavel German) and L (Quetzal Dwyer).

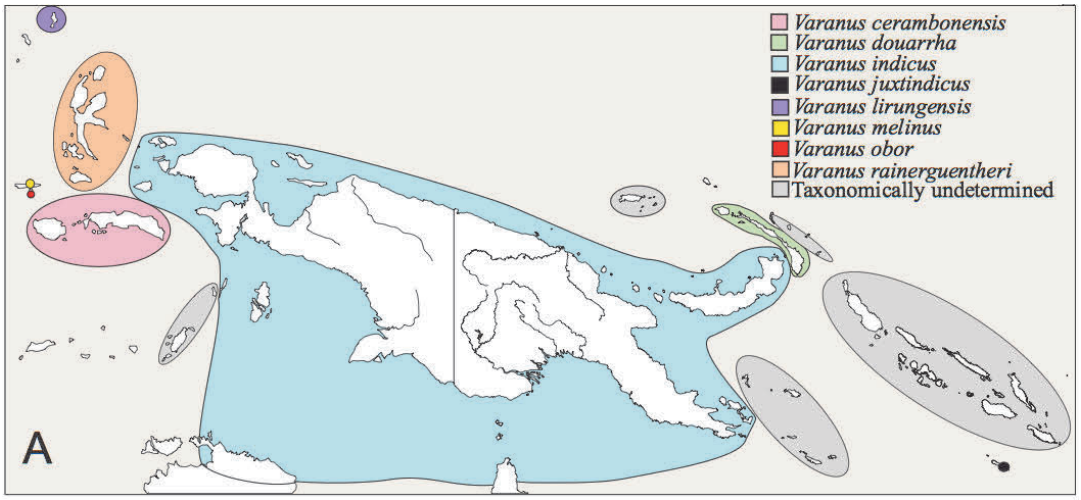

Fig. 3A. Distribution of the *Varanus indicus* group in the Moluccas, New Guinea and Melanesia revised from Philipp et al. 1999, Koch et al. 2009, Böhme et al. 2002, Weijola 2010, Weijola & Sweet 2010, Weijola & Sweet 2015, papers II-III and unpublished reviews of museum specimens.

The *V. doreanus* group contains four recognized species, three of which have been discovered since 1994: *Varanus doreanus* Meyer 1974 is present on New Guinea, Aru, Salawati, Waigeo, Biak, Karkar and far northern Queensland, *Varanus finschi* Böhme, Horn & Ziegler 1994 is a New Britain endemic, *V. yuwonoi* Harvey & Barker 1998 is a Halmahera endemic, and *V. semotus* Weijola, Donnellan & Lindqvist 2016 is endemic to Mussau (Fig. 3B). Little is known about the ecology of these species despite that all of them, except for *V. yuwonoi,* appear to be relatively common and conspicuous in many areas where they occur (Philipp 1999; Weijola 2010; Paper III).

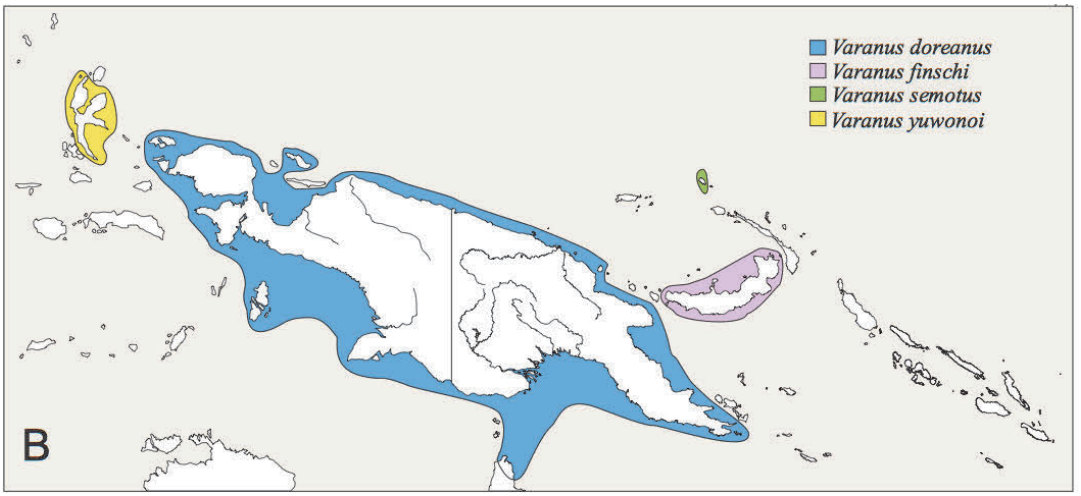

Fig. 3B. Distribution of the *Varanus doreanus* group revised from Weijola 2010, Milenkaya & McKay, papers II-III and unpublished reviews of museum specimens.

Varanus jobiensis Ahl 1932 is the only taxon described from what appears to be a complex of species distributed throughout New Guinea, Japen, Biak, Waigeo and the D´Entrecasteaux islands (Paper I, Fig. 3C). Populations morphologically divergent from the type locality (Japen) occur at least on Biak, Batanta, Waigeo and in eastern New Guinea (Weijola pers. obs.). Taxonomic work on this group is difficult due to the paucity of voucher collections from many areas and the absence of a comprehensive genetic sampling. They occur from lowland forests up to at least 1300 m elevation and probably persist at higher altitudes than any other species of *Euprepiosaurus*. The only field observations have been published by Philipp (1999).

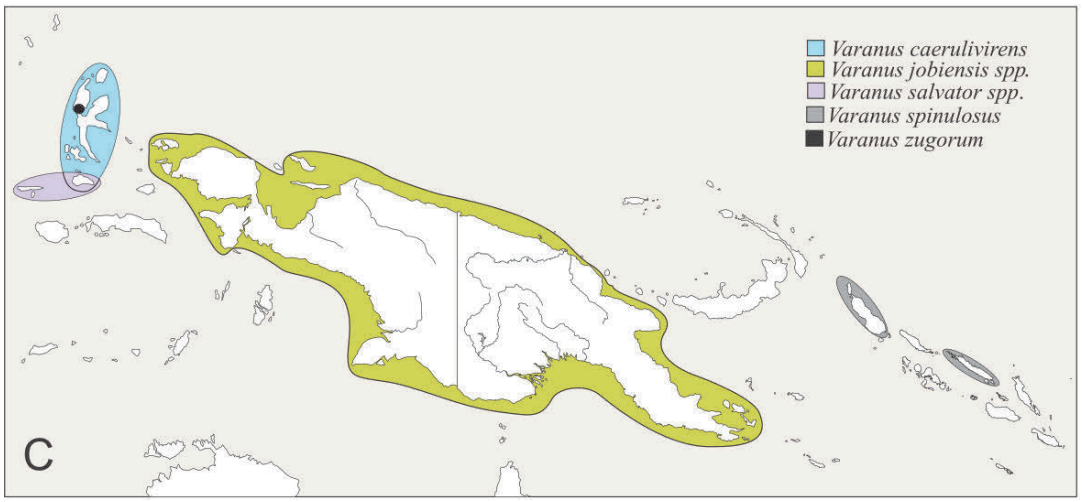

Fig. 3C. Distribution of *V. jobiensis spp., V. caerulivirens, V. salvator spp., V. spinulosus* and *V. zugorum* after Böhme & Ziegler 2007, Weijola 2010, Weijola & Sweet 2010, McCoy 2015 and unpublished reviews of museum specimens.

2. AIMS OF THE THESIS

The fauna of Papua New Guinea has in general been studied in more detail than that of West Papua and the Moluccas, but here *Varanus* has been an exception. The majority of taxonomic work on *Euprepiosaurus* has been made by European taxonomists who have relied heavily upon colonial era collections in European museums of which the largest are from the Dutch East Indies (Indonesia). A number of Indonesian species have also been described from animals reaching Europe through the pet trade.

The existing phylogenetic and taxonomic studies have been limited to morphological characters (Mertens 1942; Brandenburg 1983; Philipp et al. 1999; Sprackland 2004) and molecular-phylogenetic studies with limited sampling (Ziegler et al. 2007A). As many of the species are cryptic and morphologically conservative, descriptions of new taxa have principally been restricted to species highly distinct in colour-pattern (Böhme and Ziegler 1997; Weijola & Sweet 2010) and to those for which genetic material has been available (Ziegler et al. 2007B; Koch et al. 2009).

The primary aim of this study is to produce a geographically well-sampled molecular phylogeny, and to use the results for taxonomic work including new species descriptions. The monitors of insular Papua New Guinea (and many other regions) are still poorly known and my aim for the fieldwork in 2012-2013 was to visit and collect voucher material from the Admiralty Islands, Bismarck Islands, Louisiade Islands, D´Entrecasteaux Islands and Woodlark Island.

Another objective is to resolve the identity and nomenclature of *V. indicus,* the first species of *Euprepiosaurus* to be described. The original type specimen had been lost and subsequently the name of this taxon had shifted to a different species presumed to coexist at the type locality (Philipp et al. 1999). This became apparent during my fieldwork on Ambon and surrounding islands in 2009 and was confirmed during later work on museum collections.

3. MATERIAL AND METHODS

3.1. Fieldwork and study sites

The fieldwork was carried out over a period of 21 months, in the Moluccas 2008-2009, and in 2012-2013 in the island provinces of Papua New Guinea and parts of the Solomon Islands (Fig. 4). A total of 40 different islands were visited for durations spanning a few days to several months. Fieldwork was done in close co-operation with experienced local hunters who functioned as guides and informants. Monitors were most often located by active search, mostly by foot, and more infrequently by canoe or rowing boat. Tracks were only useful occasionally, particularly on sandy beaches and in mangrove forests. At each location efforts were always made to visit both coastal and inland habitats, and where possible hill forests up to several hundred meters in altitude (Fig. 5). The highest field site was at the Lelet plateu on central New Ireland where the elevation is approximately 900 meters. Monitors were noosed and examined when possible, otherwise identified with binoculars by their color-pattern. Photographs were additionally taken for later inspection. A set of variables was recorded for each sighting including time, location, habitat, activity and altitude.

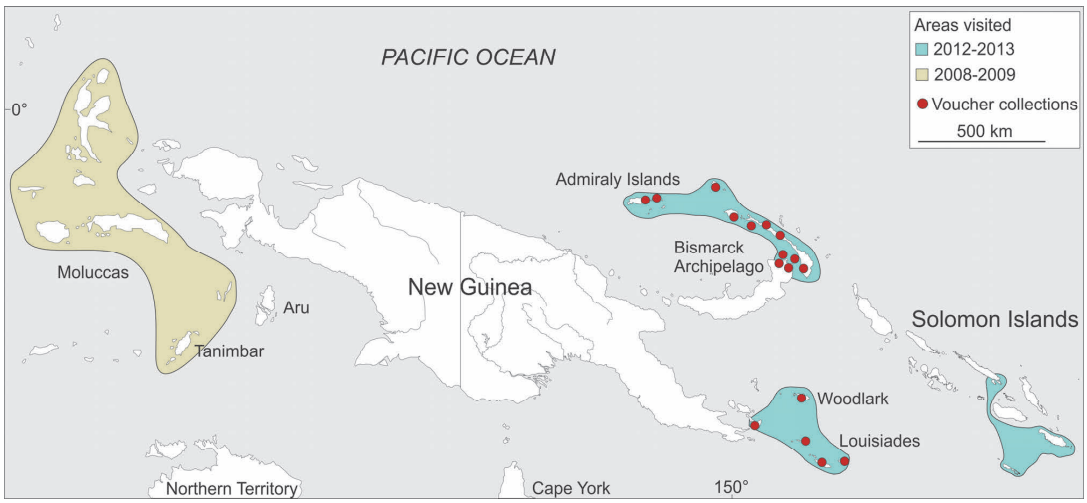

Fig. 4. Islands visited during fieldwork.

Voucher specimen and tissue collections were made in 2012 and 2013 on the following Papua New Guinean islands. Bismarck- and Admiralty groups: New Britain, New Ireland, Duke of York, Mioko, Watom, Djaul, Mussau, Lavongai, Manus and Los Negros, and in the Milne Bay province: Normanby, Woodlark, Misima, Sudest and Rossel islands.

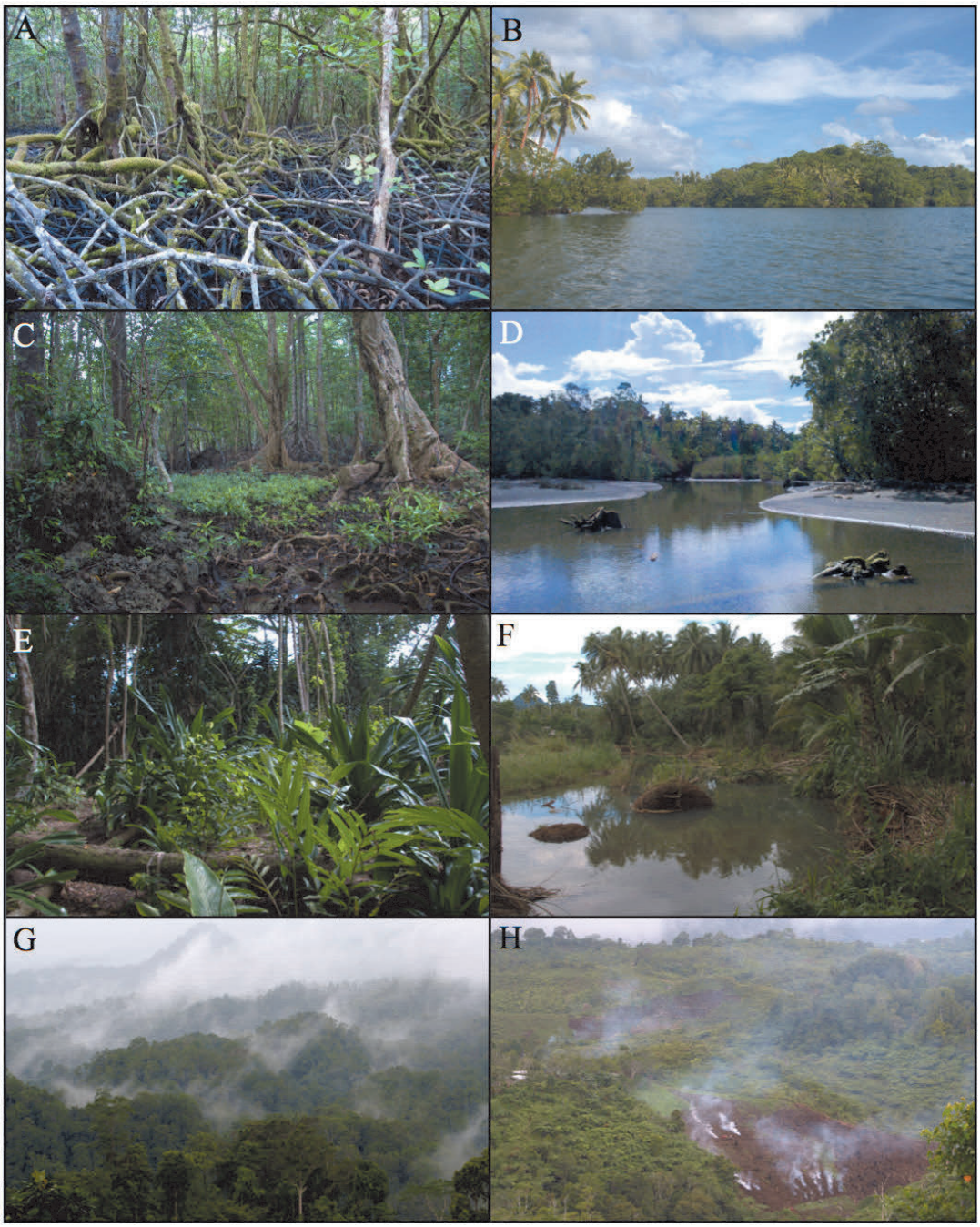

Fig. 5. Typical habitats where field-surveys were carried out: A.) Mangrove forest on Woodlark. B.) Freshwater lake on Rennell Island C.) Mangrove forest on Lavongai. D) River mouth on New Ireland. E) Coastal forest on Los Negros Island. F) Freshwater swamp on Lavongai Island. G) Inland rainforest on Manus Island. H) Mixed secondary vegetation and plantations on the Lelet plateu, New Ireland. Photos by VW.

Animals collected for vouchering as specimens were usually captured with noosing poles or rarely tracked with hunting dogs. Tissue samples (muscle, tailtip or liver) were collected and stored in 95% ethanol. Voucher specimens were fixed in 10% formalin and then stored in 70% ethanol. A total of 46 voucher specimens and 48 tissue samples were collected. All specimens are currently deposited at the Zoological Museum of the University of Turku (ZMUT), with part of the collection to be transferred to the National Museum and Art Gallery in Port Moresby. Additional tissue samples were obtained from existing museum collections.

All specimens and tissue samples were collected and exported under the relevant permits by the National Research Institute and the Department of Environment and Conservation of Papua New Guinea as well as CITES authorities in both countries. Local permits from the provincial governments and local landowners were also always obtained prior to initiation of fieldwork.

3.2. Museum collections

The collections of the following museums were examined: The American Museum of Natural History, New York (AMNH); The Australian Museum, Sydney (AMS); The National Museum of Natural History, Washington D.C. (NMNH); The National Museum and Art Gallery, Port Moresby (PNGNM); The Naturalis Museum, Leiden (RMNH); Museum National d´Histoire Naturelle, Paris (MNHN); The Queensland Museum, Brisbane (QM); The Western Australian Museum (WAM). Additional specimens were accessed as loans from the Zoological Museum of the University of Copenhagen (ZMUC) and Zoologische Museum der Humboldt Universität, Berlin (ZMB).

3.3. Morphology

The scalation and morphometric characters used for *Varanus* have changed little since they were standardized by Brandenburg (1983), and for all practical and comparative purposes the same were used in Papers III & IV. Measurements were taken from vouchered specimens with measuring tape or calipers to nearest mm (body) or 0.5mm (head) and from the literature (Brandenburg 1983). Scalational data were analysed with Principal Components Analysis using PAST and R in Papers III & IV (Hammer et al. 2011; R Core Team 2013).

3.4. Molecular genetics

For phylogenetic analyses a 710 bp fragment of the mitochondrial *NADH* dehydrogenase subunit 4 (*ND4*) gene and a 566 bp fragment of the mitochondrial ribosomal *16S rRNA* gene were sequenced. These genes were chosen because of the comparative sequences available from Genbank and ability to resolve

resent radiations (Fitch et al. 2006; Ziegler et al 2007a). Part of the samples are also included in an ongoing (as of September 2017) next generation sequencing collaboration. Lab protocols are outlined in detail in papers I, III & IV and they followed those of Arevalo et al. (1994) and Palumbi et al. (1991). DNA extractions and PCR amplifications were carried out at the South Australian Museum and Åbo Akademi University by Stephen Donnellan and Christer Lindqvist. PCR products were sent to Beckman Coulter Genomics (Essex, UK) for sequencing.

Sequences were aligned with MUSCLE (Edgar 2004) as implemented in MEGA 6 (Tamura et al. 2013) and manually trimmed to equal length, resulting in a 661 bp fragment of the *ND4* gene and 475 bp fragment of the *16S* gene. Phylogenetic analyses of the concatenated sequences were made with Bayesian inference, Maximum Likelihood, and Parsimony approaches using Mr Bayes (Ronquist & Huelsenbeck 2003) BEAST (Drummond et al. 2012), RaxML (Stamatakis 2006) and TNT (Goloboff et al. 2008). Divergence time estimates were made in BEAST (Papers I & IV) using calibration information from previous molecular estimates (Vidal et al. 2012), and from African and Australian fossils (Molnar 2004, Holmes et al. 2010). The specific molecular phylogenetic procedures are outlined in detail in Papers I, III & IV.

3.5. Species delimitation

The currently recognized species of *Euprepiosaurus* are all allopatric in regards to other members of their respective species groups. While some populations are both morphologically and genetically distinct from their relatives and thus easily diagnosable as species, others are morphologically cryptic and difficult to identify. Integrative approaches such as the unified species concept by de Queiroz (2007) are perhaps the most useful for inferring species boundaries in species-complexes with insular distributions (e.g. Welton et al. 2014).

Following this concept the populations which form clearly distinct evolutionary lineages, are morphologically diagnosable, and reproductively isolated (in these instances by geographical barriers) are considered to be distinct species/candidate species. In Paper IV we also used species delimitation software in the form of Automated Barcode Gap Detection (ABGD) (Puillandre et al. 2011) and a Bayesian implementation of the Poisson tree process model (bPTP) (Zhang *et al*. 2013).

4. RESULTS AND DISCUSSION

4.1. Paper I: Molecular phylogenetics and estimate of divergence times for the Pacific monitor radiation

The BEAST analysis resolved the *V. doreanus* (pp=0.98), *V. jobiensis* (pp=1.00) and *V. indicus* (pp=1.00) species-groups as three separate well-supported clades. A monophyletic *Varanus indicus* (*sensu* Philipp et al. 1999) includes the populations from New Guinea, Australia, Aru, New Britain, the Entrecasteaux Islands, Woodlark and Kei Besar. While populations from other regions currently assigned to *V. indicus,* such as those from the Louisiade Archipelago, Admiralty Islands, western Micronesia, and the Solomon Islands, all form separate monophyletic lineages and probably represent new species. *Varanus cerambonensis* and *V. douarrha* are also well-supported as monophyletic lineages (pp=0.99). The time estimates of divergences based on the fossil calibrations give more recent times than those based on secondary calibrations adopted from Vidal et al. (2012). The *V. indicus* group is estimated to have diversified rapidly and relatively recently: within the past three million years or less, and there are few well-supported relationships among the different species/lineages. The samples from the Moluccas (*V. cerambonensis*, *V. melinus* and *V. sp*. from Tanimbar) form one well-supported clade (pp=1), and the samples from northern Melanesia (*V. douarrha, V. spp.* from Manus, Shortland Isl., Isabel, and New Georgia) another monophyletic clade, although with less node support (pp=0.89). Together they form a sister clade to *V. indicus* and *V. spp* from the Louisiades and western Micronesia but these larger groupings are not well-supported.

The *V. spp.* from Palau and Guam however does form a well-supported (pp=1) clade diverged from each other at an estimated 0.3-0.8 MYA, and from other members of the *V. indicus* group considerably earlier.

The *V. doreanus* and *V. jobiensis* groups have diversified significantly earlier than the *V. indicus* group. *Varanus doreanus* having diverged from *V. finschi*, *V. semotus* and *V. yuwonoi* at an estimated 4-8 MYA, and *V. finschi, V. semotus* and *V. yuwonoi* from each other at 2-4 MYA.

Varanus jobiensis is currently regarded as one species widely distributed on New Guinea, Japen, Biak, Waigeoa and the Entrecasteaux islands. However, our analysis shows that several populations from different parts of New Guinea Waigeo form a number lineages that started diverging from each other around 3-6 MYA and it is likely that some of these represent cryptic speciations making *V. jobiensis* possibly a species complex.

The phylogenetic reconstructions of *Euprepiosaurus* reveal a considerable number of evolutionary lineages within both the *V. indicus* and *V. jobiensis* species groups that suggest a much higher alpha-diversity than is currently recognized. The populations from the Solomon Islands, Manus, Tanimbar, and Western Micronesia currently assigned to *V. indicus* do not form a monophyletic group and many of them clearly represent new species. According to these reconstructions the distributional range of *V. indicus* (*sensu* Philipp et al 1999) is restricted to New Guinea, Australia, and adjacent islands as far east as New Britain.

Our phylogenetic analysis thus largely support the morphologically identifiable *Varanus indicus* occurring on the landmasses of the Sahul shelf (New Guinea, parts of northern Australia, Aru) as well as

nearby islands (New Britain, Duke of York, Watom, D´Entrecasteaux). These populations are all readily referable to *V. indicus* based on the diagnosis provided by Philipp et al. 1999. Additional populations consistent with *V. indicus* that were not included in our analysis exist in the Raja Ampat islands, the Torres Strait islands, Japen and Biak islands.

Most of this region either formed a single landmass during Pleistocene glacial periods (Voris 2000) or is situated relatively near New Guinea (New Britain, D´Entrecasteaux, Biak). Populations genetically clustered within populations of *V. indicus* but highly divergent in color-pattern and some scale-count characters include the populations of Kei Besar and Woodlark islands.

4.2. Paper II: Taxonomic identity and nomenclature of *Varanus indicus*

Unfortunately several of the type specimens from the earlier described species of *Euprepiosaurus* have been lost or destroyed during WW2 bombings (Brygoo 1987, de Lisle 2009). One of these is the specimen used by F.M. Daudin (1802) in the description of *V. indicus*. According to Daudin *V. indicus* was discovered on Ambon by Claude Riche during a stopover by the d´Entrecasteaux expedition in 1792. There is however no evidence that Riche´s zoological collections ever reached Europe and it seems more probable that Daudin studied Riche´s discovery from his surviving notebooks which is evident from some of Daudin´s other descriptions (such as *Cuora amboinensis* Daudin 1802). What is clear from the description is that Daudin had access to a specimen from which he gathered measurements and which modelled for the figure. This specimen presumably part of Daudin´s personal collection which was scattered through a public auction shortly after his death.

Reviewing specimens from Ambon, Philipp et al. (1999) decided to designate a neotype for *V. indicus* and describe a second species from the same island, *V. cerambonensis*. This paper (II) re-examines the identity of *V. indicus* and *V. cerambonensis* in the light of field data gathered on Ambon and several neighbouring islands and a review of museum specimens (Weijola and Sweet 2015), and provides a critical investigation into the original type specimen(s) of *V. indicus* and the neotype designated by Philipp et al. 1999. It shows that there is no evidence that the current neotype was collected on Ambon or that it belongs to the species originally described by Daudin. To the contrary, all evidence points to *V. indicus* being the same taxon that was later described as *V. cerambonensis* (Philipp et al. 1999) and thus that *V. cerambonensis* should be considered a junior synonym of *V. indicus*.

This paper forms a proposal (currently pending before the ICZN) to declare *V. cerambonensis* a junior synonym of *V. indicus* and to exchange the neotype of *V. indicus* for a specimen belonging to the taxon originally described by Daudin. Additionally, it is proposed that *V. chlorostigma* Gray 1831 is resurrected as the valid name for the mangrove monitors of New Guinea, Australia and surrounding islands.

4.3. Paper III: Description of *Varanus semotus*

A new species of *Varanus* discovered during two separate visits to Mussau island in 2012 is described as *V. semotus* (from Latin meaning remote/isolated). Despite the external similarities to *V. doreanus* the phylogenetic analyses place it as a closer relative to *V. finschi* and *V. yuwonoi.* The occurrence of a monitor species belonging to the *V. doreanus*-group on the island of Mussau was surprising, as the other members of this group occur on New Guinea or on islands that are now, or have been, closely associated with New Guinea in the past. Instead, due to the proximity of Mussau to Lavongai and New Ireland it was expected that an insular form of the *V. indicus* group would have inhabited this island.

Philipp et al. 2007 listed *V. finschi* from Mussau based on two specimens collected in 1962 during the Danish Noona Dan Expedition. These are re-identified here as *V. semotus,* and a review is provided for the other published records of *V. finschi* (Ziegler et al. 1999, Ziegler et al. 2001, Philipp et al. 2004, Ziegler et al. 2007A). It is concluded that none of the records from outside of New Britain (New Guinea & Queensland) are based on properly documented specimens, and, that the records from Kei and New Ireland are due to mis-identifications - suggesting that *V. finschi* is in fact endemic to New Britain.

Varanus semotus adds to the known endemic vertebrate assemblage from Mussau that previously included three endemic passerine birds, an undescribed frog, and three undescribed bats (Aplin et al. 2015). More recently a new species of gecko, *Gehyra rohan,* endemic to Manus and Mussau was also described (Oliver et al. 2016).

4.4. Paper IV: Re-instatement of *Varanus douarrha* Lesson 1830

Varanus douarrha was discovered and a single specimen collected by the French naturalist René Lesson at Port Praslin, New Ireland in 1823 during the expedition of *La Coquille*. That specimen is now lost (Brygoo 1987), and considering that no measurements are provided in the 1830 description, and that it is documented that parts of the collections were lost *en route* to Europe (Duyker 2014, Lescuré 2015), it appears questionable whether it ever reached Europe for closer inspection.

This species has been synonymized with *V. indicus* (Boulenger 1885, Mertens 1942), misidentified as *V. finschi* (Ziegler et al. 1999), and designated as a *nomen dubium* by the same authors. A review of museum vouchers at the AM, AMNH and MNHN, and subsequent fieldwork, showed that in the Bismarck Islands *V. finschi* and *V. indicus* are restricted to New Britain and the Duke of York islands, and that previous records of these two species from New Ireland stemmed from misidentifications (of *V. douarrha*).

Morphological and genetic analyses of the monitor populations of New Ireland, Djaul and Lavongai showed that these islands are in fact inhabited by a distinct species of monitor belonging to the *V. indicus* group, for which the name *V. douarrha* was available. According to the BEAST estimate these populations diverged from the ancestor of *V. indicus* more than 2 MYA and from the ancestor of *V. cerambonensis, V. melinus* and *V. spp.* from the Solomon Islands slightly more recently. It indicates that the ancestor of *V.*

douarrha colonized the Bismarck islands prior to *V. indicus,* at a time when New Britain and New Ireland were geographically more distant to each other than they are at present.

New Ireland is relatively depauperate in endemic species. In addition to *V. douarrha* only one other lizard (*Lipinia rouxi*), and a frog (*Cornufer browni*) constitute the known endemic herpetofauna. The endemic mammal and bird faunas are equally depauperate with only one extant mammal (*Pteropus ennisae*) and three birds. Both the mammal- and bird communities were however richer prior to human arrival (Flannery & White 1991, Steadman et al. 1999). *Varanus douarrha* is thus unique on New Ireland in terms of large-growing endemic terrestrial vertebrates to have survived into modern times.

4.5. Conservation

Islands are both disproportionately rich in species and vulnerable to extinctions. Of documented reptile extinctions 81%, of mammals 54%, and of birds 95% have been on islands (Tershy et al. 2015). The native bird fauna of the Pacific island region has been particularly adversely affected with up to 2000 species (20% of global bird diversity) disappearing after human colonization (Steadman 1995). The fossil record of Pacific monitor lizards is extremely limited and only one medium sized species (possibly *Euprepiosaurus*) has been documented to have gone extinct in the Holocene, an undescribed species recently documented from the Pindai Caves in New Caledonia (Anderson et al. 2010). Monitors thus appear to have been relatively resilient to the impacts of human colonization despite being hunted in most parts of their range.

The major traditional threats to species on Pacific island biotas are relatively easy to pinpoint; over-exploitation, introduced species, and habitat loss (Pimm et al. 2006, McCreless et al. 2015). While these continue to be of important concern, the precise effects of human induced climate change on Pacific island biotas remains harder to predict (Allison & Leisz 2009) but as ectotherms reptiles are regarded as particularly vulnerable to the effects of rising temperatures (Sinervo et al. 2010). As sea levels rise, many low-lying islands and coastal areas are being flooded, including important habitats for mangrove monitors (Bellard et al. 2014). During 2016 the disastrous effects of warming temperatures in the South Pacific have already resulted in unprecedented bleaching and dieback not only of coral reefs but also of mangrove forests.

More extreme weather patterns, with prolonged dry periods, are likely to increase the frequency and intensity of wildfires in natural forests and those already degraded from logging and drainage. The extent of damage caused by these fires (often started intentionally) reached catastrophic proportions in Indonesia (including West Papua and the Moluccas) in 2015.

A 2009 analysis of the impacts of climate change on the herpetofauna of the Papuan region concluded that a conservative 35 of the 793 currently recognized species are particularly vulnerable (Allison & Leisz 2009). Species with small ranges and those restricted to cloud forest are particularly exposed (Oliver et al. 2017b). Of mangrove monitors, the numerous populations occurring on small low-lying islands such as Tayandu are thus of particular concern while those on larger and higher islands are less vulnerable.

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THE PACIFIC MONITOR LIZARDS

Monitors are large predatory lizards widely distributed in the Old World from Africa to Australia. A majority of the species inhabiting the Papuan region, the Moluccas and the Solomon Islands belong to the subgenus *Euprepiosaurus*, popularly known as "Pacific monitors" or "Mangrove monitors". Different members of this group occur on most islands of this region and can play important roles as top terrestrial predators. This group of monitors has remained remarkably poorly known and most of the species diversity has only been described during the past two decades. Only a few of the species had ever been observed in the wild by scientists and our understanding of distribution and natural history is fragmentary or non-existant for many species.

This thesis combines almost two years of field studies with collection-based work and molecular genetic investigations, and is the first comprehensive attempt at a rangewide analysis of phylogeny and species diversity in the Pacific monitor clade. It addresses errors in nomenclature and taxonomy caused by missing type specimens and shows that despite the advancements in taxonomy over the recent years, species numbers remain underestimated across the SW Pacific islands and on mainland New Guinea.




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