



# On the Cover: Varanus rosenbergi

The juvenile *Varanus rosenbergi* depicted on the cover and inset of this issue was photographed by **Barry Hatton** in Royal National Park, NSW on the morning of 10 October 2006. The specimen (ca. 25-28 cm in total length) was first noticed beneath a shrub in the heathland of the park while photographing a whip snake (*Demansia psammophis*). The *V. rosenbergi* was approachable, and allowed photographs to be taken from a distance of less than a meter.





## **BIAWAK**

## Quarterly Journal of Varanid Biology and Husbandry

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The International Varanid Interest Group is a volunteer-based organization established to advance varanid research, conservation, and husbandry, and to promote scientific literacy among varanid enthusiasts. Membership to the IVIG is free, and open to anyone with an interest in monitor lizards and the advancement of varanid research. Membership includes subscription to *Biawak*, a quarterly journal of varanid biology and husbandry, and is available online through the IVIG website.

# BIAWAK

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Varanus panoptes panoptes. Townsville, Queensland. Photograph by Brad Rowden.

## **NEWS NOTES**

## Denver Zoo Hatches Komodo Dragons

The Denver Zoo announced the hatching of four Komodo dragons (*Varanus komodoensis*), with four others expected to hatch shortly. This marks the third time the facility has hatched this species. The zoo's last breeding success occurred in 2003. Denver Zoo is the second Northern American facility to produce Komodo dragons this year; the other being the Los Angeles Zoo (see *Biawak* 4(3): 79). The hatchlings will eventually be put on public display.

Source: http://denverpost.com; 16 November 2010

## **Malaysian Officials Seize Monitor Lizards in Raid**

Malaysian officials at the Wildlife and National Parks Department seized several monitor lizards (*Varanus*  sp.) along with more than fifty other animals in a raid on two farms owned by convicted wildlife trafficker Anson Wong. Nicknamed the "Lizard King", Wong first gained notoriety with his conviction in 2000 of wildlife trafficking and was sentenced earlier this year on yet another count. The animals, seized from Wong's farms at Teluk Bahang and Balik Pulau, have been temporarily sent to the Penang National Park.

Source: New Straits Times; 8 November 2010

## Finnish Zoo Receives Eggs from Black Water Monitor

The Helsinki Tropicario announced that their black water monitors (*Varanus salvator 'komaini*<sup>2</sup>) have laid several eggs. This form (downgraded to synonymy with the widespread *V. s. macromaculatus* several years ago) has rarely been reproduced in captivity. Only two previous successes are known; in 2007 and 2008, both in Costa Rica (see Dwyer & Perez. 2007. *Biawak* 1[1]: 13-20 and



*Varanus g. griseus* seizes *Uromastyx*. Assoumaan Desert, Central Province, Saudi Arabia. Photograph by **Ibrahim S. Abu-Neamah** http://www.flickr.com/photos/23576634@N08/



*Varanus g. griseus* struggles with *Uromastyx*. Assoumaan Desert, Central Province, Saudi Arabia. Photograph by **Ibrahim S. Abu-Neamah** http://www.flickr.com/photos/23576634@N08/

Dwyer & Perez. 2007. *Biawak* 1[2]: 89). At least two eggs from the clutch are believed to be viable, and the young are expected to hatch in eight to ten months. The three animals held by this facility are believed to be the only specimens of this *Varanus salvator* race to be held in public European collections.

Source: Helsingin Sanomat; 28 October 2010

## Monitor Lizard Skins Seized in Alaska

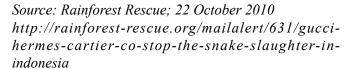
An illegal shipment of monitor lizard (*Varanus* sp.) skins on its way from New York to Taiwan was seized by USFWS inspectors. Officials confiscated them due to problems with the shipping invoice. Notice that the skins, worth over \$4,200 USD, were seized was issued and if no one comes forward to claim them, they may end up being auctioned off.

Source: Anchorage Daily News; 26 November 2010

## Organization Details Reptile Skin Trade Practices

The organization Rainforest Rescue (http://www. rainforest-rescue.org/) has detailed practices in the Indonesian reptile leather trade which appear to demonstrate excessive animal cruelty and what is likely an unsustainable harvest from wild areas. The Swiss news broadcast "Rundschau" aired video depicting processing routines including the confinement of large numbers of animals in constrained and cramped conditions for days, as well as excessively cruel slaughter methods including the skinning of still-living water monitors (Varanus salvator) and the use of water hoses inserted into live snakes in order to stretch them. The CEO of Swiss watch manufacturer Swatch has promised to eliminate products which are obtained by 'dubious' means. However, other companies were less responsive. Cartier and Hermès both stated merely that their companies follow existing laws and the Swiss company Bally responded that their products come from Indonesian breeding farms; the existence of which was disputed by Swiss officials. Another implicated company, Gucci, had no comment. Jean-Daniel Pasche, the chairman of the Federation of the Swiss Watch Industry, also did not comment since the issue of animal welfare has not yet been addressed by the respective companies.

Besides the issues of animal cruelty, questions have also been raised concerning sustainability. Export quotas are set by the individual nations, often with little or no scientific basis, and even these limits are readily ignored according to the non-governmental organization TRAFFIC. False documentation is commonly used; often by smuggling animals into Malaysia to be listed as exports from that country instead. Though specific studies on population declines are not given, numbers of animals taken by collectors have fallen sharply recently presenting problems for sustainability, biodiversity, and ecological balance.





Thousands of water monitor skins are processed each year in Indonesian factories. Macassar, SW Sulawesi, Indonesia. Photograph by **André Koch** 

Monitor skins pass through several processing stages including soaking. Skin factory, Macassar, SW Sulawesi, Indonesia. Photograph by **André Koch**.

Monitor skins are bleached before they are stained and processed into high-quality leather products for western consumers. Skin factory, Macassar, SW Sulawesi, Indonesia. Photograph by **André Koch**.

# International Symposium at ZFMK honoring Prof. Dr. Wolfgang Böhme

On 20 November 2010, an international symposium honoring Prof. Dr. Wolfgang Böhme was held at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn, Germany, on the occasion of his retirement after 39 years of professional work at ZFMK.

Attended by almost 100 friends, colleagues, and family members from Germany, Europe and the United States, the symposium began with an opening address by Johann Wolfgang Wägele, director of the Museum Alexander Koenig. He gave a short introduction to Wolfgang Böhme's vita and emphasized his merits for the ZFMK over almost 40 years. Next, Philipp Wagner (ZFMK) held a talk about African herpetology, another focus of Wolfgang Böhme's research. After a coffee break, Miguel Vences (University of Braunschweig) presented new insights into the phylogeny and diversity of the Chamaeleonidae, comparing Wolfgang Böhme's results and hypotheses in hemipenial morphology about the relationships of chameleons with new findings from molecular studies. Before lunch break, André Koch (ZFMK) introduced the audience to "The Monitor Man" and told "A Story of Stunning Discoveries and Charismatic Creatures" -the story of Wolfgang Böhme's

numerous contributions to monitor research including the descriptions of several new species (for details see Koch *et al.* on page 122 of this issue).

In the afternoon, participants of the symposium had the opportunity to attend a guided tour with Wolfgang Böhme through the herpetology collection. Led by André Koch, the leaders of the AG-Warane (Kay Dittmar) and the Waranforum (Frank Mohr) together with Mrs. Kielmann, used this time for a detailed look at the monitor lizard collection at the ZFMK. Wolfram Freund (ZFMK) opened the afternoon session with an entertaining talk about 29 years of expeditions to the Neusiedler See (Lake Neusiedl), Austria/Hungry, by Wolfgang Böhme. The symposium was closed with a laudatio in honor of Wolfgang Böhme given by Aaron Bauer (Philadelphia), a close friend and colleague since the early 1980s, who emphasized that the knowledge and broad research interests of Wolfgang Böhme's were not restricted to amphibians and reptiles, but also included mammalogy, ornithology, paleontology, cryptozoology, the history of herpetology, and zoo-ethnology.

A special issue of the Bonn Zoological Bulletin published by the Zoologisches Forschungsmuseum Alexander Koenig (http://zfmk.de/web/Forschung/Buecher/Beitraege/index.en.html) is dedicated to Wolfgang Böhme. Among others, it contains an updated checklist of the living monitor lizards of the world by Koch *et al.* (for details see the Recent Publications section of this issue).



Attendees of the symposium in the ZFMK exhibit.

## Announcement of the Third Annual Meeting of the "AG Warane" of the DGHT

The AG Warane is pleased to announce that its third annual meeting is in preparation. The meeting will take place on 9-10 April 2011 at the Zoologisches Forschungsmuseum Alexander Koenig in Bonn, where the three Multidisciplinary World Conferences on Monitor Lizards were held in 1989, 1997 and 2005. For the first time, the annual meeting will last two days. This should give attendees enough time for conversation and exchange of experiences. The meeting starts on Saturday at 10:00 a.m.

## Location:

Zoologisches Forschungsmuseum Alexander Koenig Adenauerallee 160 53113 Bonn http://zfmk.de

## **Preliminary Program:**

## Saturday, 9 April 2011

10:15 a.m.	Welcome Address by the leaders of the AG-Warane	10:00 a.m. 10:15 a.m.	Start André Koch (Bonn): "The Monitor
10:30 a.m.	Frank Mohr (Würzburg): "Keeping		Man: Wolfgang Böhme's contributions
	and breeding of Varanus kordensis with		to monitor lizard research" (in
	remarks on keeping tree monitors in		German). See essay by Koch et al. in
	groups" (in German).		this issue of <i>Biawak</i> , pp. 122-142.
11:00 a.m.	Ralf Sommerlad (Frankfurt) and	10:45 a.m.	Thomas Hörenberg (Stuttgart):
	Natascha Behler (Bonn): "Danau		"Keeping and breeding of <i>Varanus t</i> .
	Mesangat: Basics and update about		tristis" (in German).
	an exciting conservation project in	11:15 a.m.	General meeting of the members of
	Borneo" (in German).		the AG-Warane (incl. executive board
12-13 p.m.	Lunch break		member elections)
13:00 p.m.	Departure to the Cologne Zoo (with	12-13 p.m.	Lunch break
	own cars or public transport)	13-14 p.m.	Guided tour through the exhibit of the
14-17 p.m.	Visit of the Cologne Zoo (possibly	_	Museum Alexander Koenig (André
_	with guided tour through the		Koch)
	Aquarium)	15:00 p.m.	End of the annual meeting 2011
18:00 p.m.	Return trip		_

## Further information can be found in early 2011 on the AG Warane homepage at www.ag-warane.de, or contact Kay Uwe Dittmar (working group leader) at dittmar@ag-warane.de or André Koch (scientific leader) at a.koch.zfmk@uni-bonn.de.



*Varanus niloticus*. Tarangire National Park, Tanzania. Photograph by **Ria Koppen**.

## Sunday, 10 April 2011

## **ARTICLES**

Biawak, 4(4), pp. 117-124 © 2010 by International Varanid Interest Group

## The Origin of *Varanus*: When Fossils, Morphology, and Molecules Alone Are Never Enough

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Abstract: One of the many interesting questions in evolutionary studies of varanid lizards is the origin of the genus *Varanus*. The fossil record indicates the earliest emergence of this genus on Gondwana, although the remains of early varanid lizards have been discovered in Laurasia. The relationships among extant *Varanus* can generally be inferred using molecular phylogenetic techniques, although several attempts to generate a phylogeny of *Varanus* have used morphological characters. We identify two key-regions of global dispersal for varanid lizards that may be used to test hypotheses on the origin of this genus in a phylogeographic framework. The landmass currently connecting Africa and Asia as well as the Lesser Sunda Islands in southern Wallacea may have facilitated intercontinental radiation of varanid lizards, which are distributed in Africa, Asia, and Australia. We consider that an integrated approach such as phylogeography might better explain the origin of this charismatic lizard group than any single analytical method.

## Introduction

Current views on the evolution of varanids oppose a Gondwanan to a Laurasian origin. On one hand, the lineages of varanid lizards were thought to have diversified in Australia, a fragment of Gondwana, and dispersed through Southeast Asia to their current distribution. On the other hand, varanids were thought by others to have originated in Asia, a fragment of Laurasia, and dispersed to Australia via the Indonesian Archipelago. Here we review morphological and molecular studies and propose two key routes for inter-continental dispersal. Present land connection between Asia and Africa as well as the Lesser Sunda Islands are two critical regions for deducing the origins of global varanid radiation. In spite of resolved phylogenetic relationships among almost

all extant varanid species, an approach describing the pattern of lineage distribution over geographic space is still needed to deduce the dispersals of extant species.

Two prevailing scenarios on the origin and radiation of varanid lizards are hypothesized based upon two different bases. A Gondwanan hypothesis is based on species diversity, whereas a Laurasian hypothesis is based on the fossil record. We review these two hypotheses by taking into account selected published phylogenetic studies based on morphological and molecular datasets and discuss them in light of paleontological data. The two scenarios for the origin of *Varanus* are presented below.

## Laurasian origin: central Asia

Based on the fossil record, Estes (1983) postulated a radiation of varanid lizards from an ancestral source in Asia. Having radiated from what is now Mongolia during the Late Cretaceous to Early Cenozoic (80-50 Ma), early varanid lizards dispersed to almost all major fragments of Laurasia and Gondwana, including North America, Europe, Africa, and Australia. Extant Asian varanids are descendants of the Mongolian lineages, while those that dispersed to North America and Europe (30-45 Ma, Oligocene-Eocene) are now extinct. So far, we know from fossils that modern varanids reached some Gondwanan fragments i.e., Africa, India, and Australia, and might have failed to reach others i.e., Antarctica, Madagascar, and South America. To date, no fossil monitor lizards have been found in South America or Madagascar. The absence of varanids in South America is presumably due to the disappearance of connections between Africa and South America about 100 Ma. Varanids seem to be also lacking in Madagascar, probably because this island has been separated from Africa since about 155 Ma (Rabinowitz et al., 1983; Torsvik et al., 1998; Wells, 2003; Ali & Aitchison, 2008). Similarly, no fossil varanid has been reported from Antarctica. This view of Laurasian origin is supported by morphological (e.g., Sprackland, 1991) and molecular data (e.g., Fuller et al., 1998). On the other hand, varanids seem to first appear on Gondwanaland much later in Africa. A fossil of Varanus stem-clade was recovered from the Early Oligocene Egypt (Smith et al., 2008). The oldest evidence of varanid lizards on all Gondwanan fragments is recently reported as a Varanus from the Late Eocene (37 Ma) of Egypt, which is also thought as an indication of the emergence of this genus in Africa (Holmes et al., 2010). Therefore, varanids in general are likely to have emerged first in Laurasia, while the genus Varanus, in particular, may have evolved during a later period on Gondwana. Nonetheless, overall records of fossil varanids so far found on Gondwanan fragments i.e., Africa and Australia are much younger than those found in central Asia, with the oldest Laurasian and Gondwanan varanid fossils differ by about 40 Ma.

## Gondwanan origin: Australia

Hutchinson & Donnellan (1993) argued that varanids could have originated in Gondwanaland. Several lines of evidence support the hypothesis that ancestral forms of varanids may have gone through a major diversification in Australia and radiated to Southeast Asia. First, the

primitive subgenus *Varanus* is distributed in Australia. Second, immunological data show a deep divergence within Australian varanids (Baverstock et al., 1993). Third, twenty-four out of fifty-eight recognized species currently occur in Australia (Böhme, 2003). Thus, more than a third of the total currently described varanid species are distributed in Australia alone. This hypothesis of a Gondwanan origin assumes a dispersal route from Australia to the Indonesian Archipelago. Active dispersal from Australia into Asia should have occurred relatively recently i.e., during or after the Miocene, when Australia was closer to Southeast Asia. Otherwise, varanids might have reached Asia by vicariance during the Early Eocene, after India drifted and collided with Eurasia (~57 Ma). eventually raising the Himalayan Mountains and Tibetan Plateau by 35 Ma (Ali & Aitchison, 2005, 2008). The latter scenario assumes the occurrence of ancestral monitor lizards on the Indian fragment of Gondwanaland following the break-up of this supercontinent during the Middle Jurassic. Thus, early varanids are assumed to have occurred on Gondwana before it broke into two fragments about 170 Ma. One fragment included India, Madagascar, the Seychelles, Australia, and Antarctica, whereas the other included Africa and South America (Ali & Aitchison, 2008).

## Morphology of varanids

Varanid lizards are relatively conservative in their morphology, despite the high interspecific variation in body size (Pianka, 1994). External morphological characters are conventionally used to describe monitor lizard species and are categorized into meristic and morphometric features. Meristic characters are those that can be quantified using numbers or counts (e.g., number of scales around mid-body), whereas morphometric characters are quantified by measurements (e.g., distance between nostril and eye). Robert Mertens (1942) based his classification of 24 species of Varanus on external morphology and cranial structure, and assigned them to eight subgenera. He grouped these characters into four categories i.e., body form, nostril shape and its relative location on the head, scalation and the coloration of scales, as well as the shape of the skull and dentition. Based on this observation, Mertens considered monitor lizards to have originally evolved within Asia, and then radiated from there to their present distributions, including in Australia and Africa. He argued that South Asia and the Indonesian Archipelago together are the focal points of monitor lizard evolution, because seven out of eight subgenera prevail within this region. Mertens pointed out that only two out of eight subgenera succeeded in Australia, while the number of species in Australia was similar to that in Asia. Furthermore, he regarded the morphological characters of African species as derived from those of Asian varanids. A later approach to characterize species was through the use of internal morphological characters. Hemipenes morphology (Branch, 1982; Böhme, 1988) and lung morphology (Becker et al., 1989) have been used to reconstruct the phylogeny of some representative species distributed in Africa, Asia, and Australia. A general agreement between hemipenal and lung studies implies a varanid radiation out of Australia to Asia and Africa. Both studies placed V. griseus basal in the African radiation, signifying this species was an intermediate form between African and Asian species.

Sprackland (1991) examined 23 varanid species using a total of 57 characters. Although most of these characters were morphological, molecular and ecological characters were also included. Groups based upon hemipenal structure (Böhme, 1988) were incorporated as distinguishing characters along with groups defined using karyotype morphology (King & King, 1975; King et al., 1991) and protein electrophoresis (Holmes et al., 1975). Sprackland's study was aimed at clarifying relationships of the *V. prasinus* group, which was hypothesized as being derived from *V. indicus* stock. In his study, Sprackland postulated west-to-east clinal evolution and implied that the ancestors of Odatria (small Australian varanids) were of Asian origin. Additionally, Sprackland's phylogeny showed that V. komodoensis was the sister to V. varius, both of which formed a lineage that, in turn, is the sister to Odatria. It is important to note, that in this Asian radiation scenario, V. gouldii was believed to have arisen from an Asian ancestor and evolved later into V. priscus, which is now extinct. However, a relatively close affinity of V. gouldii with an extant or extinct Asian Varanus may still have to be determined to support this west-to-east theory. On the other hand, the Asian V. salvator has been suggested to have a close relationship with three Australian species, i.e. V. komodoensis, V. priscus, and V. varius based on skull morphology (Head et al., 2009).

## Molecular phylogeny of varanids

The rapidly growing molecular systematic techniques have allowed hypotheses of varanid lizards phylogenies based on DNA sequences. Ast (2001) performed a phylogenetic analysis involving 40 living species of all varanid subgenera and designated three varanoid

species as outgroups. She confirmed the monophyly of the superfamily Varanoidea and the family Varanidae, and proposed that the African clade is basal within the family. Asian and Australian species were described as sister groups, which was reflected in the split between Indo-Asian and Indo-Australian clades. The Indo-Asian clade gave rise to two subclades, each of which has a separate geographic range. The subclade Indo-Asian A encompassed all Asian species distributed in the Indonesian Archipelago to Sulawesi, which lies on the western part of Wallacea. The subclade Indo-Asian B nested those species distributed to the east of Sulawesi through to the Pacific islands off of New Guinea. The Indo-Australian clade separated large- and small-bodied *Varanus* into *gouldii* group and *Odatria*, respectively.

To date, the phylogeny of Ast (2001) is probably the most comprehensive and reliable study inferring relationships among extant varanid lizards, because it is well sampled across the taxonomic classification and geographic distribution. Three major clades in this phylogeny are monophyletic, and they seem to be concordant with a pattern of geographic distribution. The African clade consists of species distributed in Africa and western Asia, whereas the large Asian clade consists of species distributed in Asia. The Australian clade contains all species occurring in Australia, as well as the New Guinean V. salvadorii and V. komodoensis, which occurs only in the Lesser Sundas. The relationship among V. varius, V. komodoensis, and V. salvadorii in this phylogeny is determined monophyletic. The clade containing these three species that are distributed in Australia, Asia, and New Guinea is basal in the larger Australian clade, and may suggest Australia as the origin of varanid radiation to Asia and New Guinea. However, a Gondwanan source of varanid radiation is rejected based on mitochondrial gene re-arrangement data (Amer & Kumazawa, 2008).

## The role of phylogeography

Present distribution of varanids is limited to three continents, namely Africa, Asia, and Australia, where the climate can be relatively warm. The discovery of fossil varanids beyond the range of the living forms generally suggests a larger historical distribution for these lizards. In turn, the broader distribution of varanids in the past may reflect a wider distribution of a warmer zone on Earth. Indeed, it has been suggested that Cretaceous greenhouse warming effectively raised temperatures at high latitudes while reducing equator-to-pole temperature gradients (Ufnar *et al.*, 2004). Given the

wider distribution of varanids in areas of warmer climate in the past, we may be able to infer the diversification processes for varanids. The extent of genetic divergence among populations of closely related species in the present geographic range can be estimated from DNA sequences, in order to assess patterns of lineage distribution. In turn, an association between geographic distribution of lineages and the level of differentiation among populations of various varanid species may be used to formulate a scenario about varanid radiation in light of the past geological processes that have formed today's geography.

The extent of the geographic distribution of a species, their phylogenetic relationships, and their dispersal ability is discussed in phylogeography. Studies in phylogeography often integrate at least three components to elucidate present geographic distribution of a species i.e., genealogical relationship (intraspecific phylogeny) based on molecular data, dispersal ability, and geography. Intraspecific phylogeny is used to infer relationships among haplotypes that may correlate with geographic distance and show population structure. Dispersal ability is an important factor in the distribution of species that involves active movement of individuals, which may be influenced by geography e.g., water barriers to strictly terrestrial species. Phylogeography may be a powerful tool to demonstrate population structuring as well as speciation processes, for example, to clarify the relationships among populations of member species within the *V. indicus* spp. complex. Within the last decade, a number of new species have been recognized from this varanid group by re-evaluations of described species as well as a result of discoveries from remote islands (Böhme, 2003). Given the distribution of these cryptic species on islands, a hypothesis of speciation through isolation may be tested in a phylogeographic study for this species complex. A hypothesis of speciation through isolation may also be tested for some other varanids, for example V. togianus, which is distributed in a limited range and shows a high degree of endemism. This species was formerly recognized as a subspecies of the widespread V. salvator (Koch et al., 2007).

## Key-regions of varanid intercontinental radiation

We identify two key-regions across the present-day varanid distribution range that may be useful in helping to clarify the intercontinental radiation of *Varanus*. These two regions are: 1) the land connection between Africa and Asia that lies in the Middle East, and 2) the Lesser Sunda Islands, which coincide with southern Wallacea.

Varanids might have radiated through these regions independently and this hypothesis can be a highlight in phylogeographic studies. Phylogeny alone would not be sufficient to show species radiation, because it does not take into account dispersal and geographic factors that are indispensable to shedding light on population-level divergence. We explore two hypotheses of varanid radiation through these two regions below.

Varanus griseus is distributed along the landmass connecting Africa and Asia. This area is mostly dry and may have allowed the unique adaptive evolution of this monitor lizard to such an extreme habitat. In Africa, the distribution of V. griseus includes the northern regions of the Saharan Desert (Bayless, 2002), whereas the populations in Asia are distributed in Central Asia, the Arabian Peninsula, and southwestern Asia to northwestern India (Böhme, 2003). The relationships among regional populations in Africa and Asia may be determined by analyzing the population structure across its range in conjunction with morphological data. Further analyses investigating the relationships between V. griseus and its closely related species might eventually reveal a pattern of species radiation across the region. Two closely related species that overlap in their distribution with V. griseus are V. niloticus in northern Africa, and V. bengalensis in northwestern Asia. Interestingly, an hypothesis on the relationship between African and Asian varanids has come from several phylogenetic studies which placed Asia as a possible source of radiation to Africa (e.g., Böhme, 1988; Baverstock et al., 1993; Amer & Kumazawa, 2008). An investigation on the morphological characters of V. griseus is currently running at ZFMK in Bonn, Germany. Results of this study may be applicable for a future phylogeographic analyses among populations of V. griseus in Africa and Asia, which is central in the varanid evolutionary history studies.

The Lesser Sunda Islands lie in southern Wallacea. This region coincides with the margins of the Eurasian and Indian-Australian plates (Hall, 2002), which is characterized by the presence of small islands clustered in chains. The presence of small islands in this region seems to confound scenarios of varanid radiation between Asia and Australia that are essentially the contradictory hypotheses of the Laurasian versus Gondwanan origin of varanids. It is thanks to the shallow (~200 m) water barrier between Australia and New Guinea (Hall, 2002) and the Pleistocene Glacial Maxima (Kuhle, 1988) that the distribution of varanid lizards on the nearby Sahul Shelf may be understandable. The presence of *V. panoptes*, *V. indicus*, and *V. prasinus* populations in

southern New Guinea and northern Australia has been the source of a hypothetical scenario of varanid radiation in this region, which was based upon their recent divergence in the Late Pleistocene about 20,000 years ago. During that time, the land bridge between New Guinea and Australia disappeared due to increased sea levels and the populations on New Guinea and Australia started to diverge (Baverstock et al., 1993). Nevertheless, the divergence between Asian and Australian varanids is still subject to a detailed assessment. Information from phylogeny alone is not sufficient to infer the patterns of intra- and interspecific divergences at population level, which are among the important features in understanding their evolutionary history. Additionally, it is interesting to note, that some ecological factors such as predation by mammalian species could prevent the diversification of small varanids in the Lesser Sunda Islands and also Wallacea in general (Sweet & Pianka, 2007). Thus, a bias for large-size species may be expected in the distribution of varanids in this joint periphery of Asia and Australia.

The complex zoogeography of Wallacea seems to be generally influenced by the geological evolution of this region (Hall, 1998). During the formation of islands in Wallacea, animal species evolved through processes of vicariance and dispersal. Plate tectonics seem to affect the distribution of both Asian and Australian species particularly in the Lesser Sundas, which is situated in the southern part of Wallacea. The current distribution of V. komodoensis in the Lesser Sundas is an intriguing fact in the biogeography of Varanus. Phylogenies for extant varanids suggest V. varius, of eastern Australia, as the sister species to V. komodoensis (e.g., Ast, 2001). On the other hand, the extinct V. priscus of central Australia is also considered a sister species to V. komodoensis (Head et al., 2009). Thus, based on its relationships with both extant and extinct varanids, V. komodoensis is suggested to have a close affinity with Australian species. It is possible, that the island of Timor in the Lesser Sundas might have been a stepping-stone in the dispersal of ancestral V. komodoensis from Australia to the Lesser Sundas. However, this hypothesis should also be tested in a phylogeographic context, because information from phylogenies and fossil is not adequate to explain processes that operate at population level, such as dispersal. The fossil V. bolkayi found on Java and two varanid vertebrae from western Timor were presumed to represent a subspecies of V. komodoensis (Hooijer, 1972), suggesting a wider distribution for V. komodoensis from Timor to Java. If dispersal occurred from Australia to the Lesser Sundas, it should have occurred relatively recently. Timor lies on the Indian-Australian Plate and

was relatively distant from the Lesser Sundas. Only in the Late Miocene, about 5 Ma (Hall, 2002), the Indian-Australian Plate moved northward, bringing Timor closer to the Lesser Sundas. Thus, V. komodoensis might have dispersed from Australia to the Lesser Sundas not more than 5 million years ago. Indeed, fossils of V. komodoensis from Pliocene Australia suggest an origin of this species in Australia at least 3.8 Ma (Hocknull et al., 2009). Nevertheless, fossil V. komodoensis might also be found in Southeast Asian sites such as the Southeast Asian savanna corridor, which spanned between mainland Southeast Asia and Australia during the last glaciation period (Bird et al., 2005). Savanna is one of the occupied habitats for *V. komodoensis* in the Lesser Sunda Islands besides monsoon forest and grassland (Auffenberg, 1981). However, no reliable fossil is currently recorded from Asia, presumably because this savanna corridor is now submerged under the sea.

## Conclusion

We acknowledge that the origin of varanid lizards of the genus Varanus still remains debatable, despite the advances in phylogenetic studies for this lizard group. Fossils are reliable evidence of ancestral species and their historical distribution. However, fossils are relatively scarce and may be underrepresented in some parts of the world. As phylogeny and fossils may be still insufficient to substantiate either view on the origin of varanids in general, one may expect to seek hints from the relationships among populations of extant species within the two key-routes of intercontinental dispersal. These two regions include the landmass connecting Asia and Africa, as well as the Lesser Sunda Islands in southern Wallacea. The latter coincides with the margin of the Eurasian and Indian-Australian plates, for which the complex geology may reflect current distribution patterns of fauna in this region. An approach to solving this riddle is the application of phylogeographic methods, which makes possible an identification of the population structure with regard to their phylogenetic relationships and dispersal processes. This approach also seems to be useful for making inferences about the historical dispersal of V. komodoensis, for which the extant populations only occur on several islands within the Lesser Sundas. However, support from paleogeographic and geological data as well as multiple fossil records from both sides bordering this island group is needed to make a robust hypothesis about the evolutionary processes that gave rise to the restricted *V. komodoensis* populations. Eventually, patterns for varanid radiation between Asia and Australia could also be well-corroborated by using similar approaches. The application of phylogeography may be extended to unravel relationships among African and Asian species with regard to the direction of the geographic radiation of *V. griseus*.

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Fig. 1. The evolution and dispersal route of varanid lizards. Laurasian hypothesis is based on fossil records (Estes, 1983) and indicated by grey arrows, whereas Gondwanan hypothesis is based on species diversity (Hutchinson & Donellan, 1993) and indicated by white arrows. Map shows Late Cretaceous-Tertiary transition (~65 Ma), redrawn after a paleogeographic map available at http://jan.ucc.nau.edu/~rcb7/globaltext2.html by Ron Blakey, Geology Department, Northern Arizona University. Laurasian and Gondwanan fragments are indicated in this map with the letters "L" and "G", respectively.

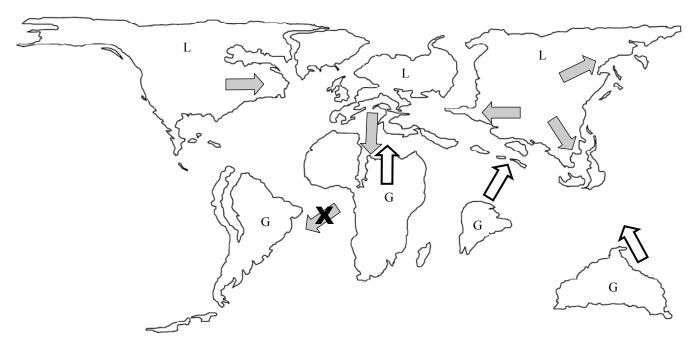
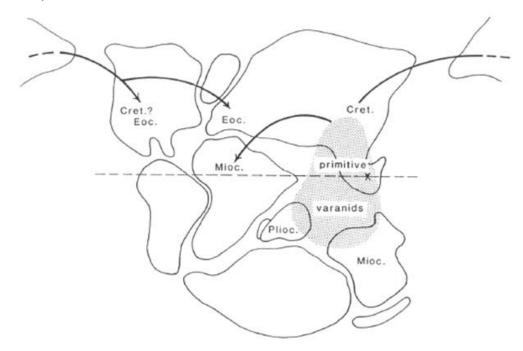


Fig. 2. Hypothetical dispersal of ancestral varanids from Asia as illustrated in Estes (1983). Varanid lizards are thought to have originated in central Asia during the Cretaceous (~80 Ma) based on fossils found in Mongolia, whereas the genus *Varanus* is thought to have emerged in Africa sometime in the Eocene, more than 37 Ma (Holmes, 2010).



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## Observation of a Wild Pair of Spiny-tailed Monitors (*Varanus acanthurus*) Engaged in Breeding Activity

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Abstract: Because of the alert and secretive nature of monitors, observations of reproductive events in the wild are somewhat rare, especially in smaller species belonging to the subgenus *Odatria*. A wild pair of *Varanus acanthurus* was observed copulating on the grounds of the Alice Springs Desert Park, NT. August through October 2010 had above average rainfall, and a warm sunny day on 8 October was likely a trigger for this event.

The spiny-tailed monitor, *Varanus acanthurus*, has an extensive range across northern Australia, which includes the region of Alice Springs in the southern part of the Northern Territory. This species is generally associated with sandy or stony areas and often shelters in burrows excavated beneath rocks (Husband, 1980). Typical of most deserts, the extremes of this area include temperature, moisture levels, and prey abundance. Reproductive activity of *V. acanthurus* in captivity usually coincides with warming temperatures, increases in moisture levels, and prey abundance, which provide the energy necessary for reproductive output (pers. obs.).

During August, September, and the first week of October 2010, the Alice Springs area saw copious amounts of rainfall, making it one of the wettest years on record.

At 1100 h on 8 October 2010, myself, my father, and Jochem van der Reijden were searching a rock pile in the Alice Springs Desert Park for *V. acanthurus*, in an area where the species had previously been observed by Jochem (pers. comm.). Some rustling was heard across from the rock pile we were searching, and upon further investigation, a pair of *V. acanthurus* (both ca. 25.4-30.5 cm in snout to vent length) was observed copulating underneath a small rock ledge, near the entrance to a



Fig. 1. Copulating pair of Varanus acanthurus.



Fig. 2. Male *V. acanthurus* basking.

burrow (Fig. 1). Observed copulation took place for around three minutes while photographs were taken, being careful not to disturb the pair. The female retreated down a burrow under the rock, possibly as a result of our intrusion, leaving the male in place. It remained there for several minutes tongue-flicking, and was apparently unaware of or unconcerned by our presence. The female then emerged from the first burrow, moving underneath vegetation and rock overhangs to another burrow situated underneath a large rock approximately one meter away. The male then moved from the site of copulation to a sunny spot on the nearest rock to bask (Fig. 2). Around two minutes after moving to the second burrow, the female also emerged to bask on a rock situated between the two burrows (Fig. 3). After basking for approximately five minutes, the male retreated to a burrow and the female was left to bask undisturbed (Fig. 4).

The background color of the female matched the yellow-orange base color of the surrounding rocks (Fig. 4), whereas the male had a more reddish ground color (Fig. 2). The dorsal occelli of the female were mostly interconnected, making for an intricate maze-like pattern. Spots in the centers of the occelli were present in the male, but were largely absent in the pattern of the female. Both animals were fairly robust with fat tails, suggesting prominent fat reserves or a recent abundance of prey. This was not surprising, as plentiful amounts of locusts and other insects were observed throughout the surrounding area, which are commonly taken by this species (King, 2008). The burrows appeared to be well-used, and the surface of the soil was damp from the rain of the previous week.

Ovaries and ova of *V. acanthurus* have been shown to increase in size from April to May, remaining enlarged from June to October, and oviductal eggs were present



Fig. 3. Female *V. acanthurus* basking



Fig. 4. Female (left) and male (right) V. acanthurus basking

between August to November (King & Rhodes, 1982). Based on observations in captivity, *V. acanthurus* has a gestation period of around two to four weeks (Husband & Bonnett, 2009). This would place oviposition for the female *V. acanthurus* in the present report towards the end of October or early November, thus falling within the timeframe reported by King & Rhodes (1982).

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## Mammal-like Feeding Behavior of *Varanus salvator* and its Conservational Implications

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Abstract: The sequence of a 70-minutes observation of a *Varanus salvator* feeding on a suckermouth catfish (*Hypostomus*) in Lumpini Park, Bangkok, Thailand is described. The monitor tore off chunks of meat with its jaws, using its forefeet for assistance. After a large amount of the fish had been eaten, the monitor separated the hind part of the fish and swallowed it anterio-posteriorly. The conservational aspects of this feeding behavior are discussed.

## Introduction

Monitor lizards are equipped with cranial kinetic capabilities – inferior to those of snakes, but superior to those of other lizards. Cranial kinesis enables monitor lizards to swallow large prey wholly and quickly. As in snakes, infrequent consumption of large meals is advantageous to monitor lizards, enabling them to lower energy expenditure associated with long and frequent forays in search of smaller prey species, hence, decreasing the amount of time vulnerable to predation while foraging. Contrary to snakes that can only swallow their prey whole, where prey size is limited by their swallowing capabilities, mammalian carnivores can rip their prey apart and eat smaller chunks at a time; hence, they can feed on comparatively large prey and their prey-size is limited only by their abilities to catch and subdue prey. In many, but not all cases, the latter constraint can be overcome by group-hunting (e.g., wolves, spotted hyenas, African hunting dogs), and for scavengers, this constraint is usually irrelevant. Monitor lizards do not hunt in groups, but based on the observation described herein of a water monitor Varanus salvator eating a suckemouth catfish in Lumpini Park in Bangkok, Thailand, I postulate that at least for several large or medium-large Varanus species, prey size may not be solely limited by their swallowing capabilities, but rather by their ability to catch and subdue the prey. For Varanus species that scavenge for food, this constraint is usually irrelevant.

## **Observation**

Lumpini Park is a fenced 58 ha public park located in the heart of Bangkok, surrounded by a hyper-urban environment and heavily trafficked roads. The park includes several ponds, water canals, paved pedestrian roads, and various sporting and recreational facilities. The park is open to the public during daytime hours and is usually teeming with people engaged in jogging and other sporting and recreational activities. Lumpini Park includes a notable (and probably dense) population of V. salvator. I have seen monitors of all size-classes - from small juveniles (ca. 30 cm in total length [TL]) to very large adults of 2.5 m TL or more (estimated from a distance). The monitors are easily spotted, either swimming in the ponds or canals or on the shores, usually within 10 m from the water's edge. Less frequently, they may move away from the water - 50 m or more from the water's edge. Juveniles and small adults (≤ ca. 80 cm TL) climb trees, concrete fences and other manmade structures. The monitors also regularly enter the park's underground draining system. Contrary to most other places in Thailand, people refrain from fishing in Lumpini Park, therefore the ponds seem to hold sizable populations of fish, turtles and other aquatic animals. I have observed water monitors feeding on walking catfish (Clarias sp.), swamp eels (Fluta alba), barbs (Puntius sp.), suckermouth catfish (Hypostomus plecostomus), Asian box turtle (Cuora amboinensis) and food leftovers discarded by picnickers in the park. The V. salvator of Lumpini Park are habituated to humans and seem to be indifferent to their presence at distances of 2-3 m or

more. Below 2-3 m, they usually flee (usually into the water) or display various threatening postures.

At 1405 h on 6 January 2010, I spotted a V. salvator (ca. 140 cm TL; estimated from a distance + another ca. 10 cm of missing tail tip) outside the fence surrounding Lumpini Park, ca. 5 m from a water canal. The monitor was engaged in eating a suckermouth catfish H. plecostomus (ca. 45 cm TL, estimated from a distance). At first, the monitor tore a hole in the skin and bore its head into the body, much like a vulture eating softer inner parts of a carcass. It then proceeded to rip the body apart with its jaws using its forefeet for assistance, consuming smaller chunks of meat at a time (Fig. 1). By 1440 h, a substantial amount of the fish had been eaten; parts which remained included the head, pectoral fins, vertebral column, and tail (Fig. 2). At 1453 h, the monitor succeeded in severing the vertebral column, separating the hind part of the body (altogether ca. 20 cm), and took less than 3 min to swallow it whole in an anteriorposterior orientation (Fig. 3). During this process, the monitor stopped all eating activities and observed me motionlessly for ca. 2 min. What remained of the fish at this stage included most of the head, especially the hard dorsal part covered with bony shields, the pectoral fins, and about 10 cm of the anterior spinal cord that remained attached to the head (Fig. 3). The monitor then left the fish, defecated, and foraged in the area for ca. 5 min, using typical varanid foraging behaviors (see below), eating smaller chunks of meat and other leftovers from the fish that were scattered in the immediate vicinity. At 1503 h, the monitor returned to the remains of the fish carcass and continued to rip it apart. At 1505 h, it yawned, then unsuccessfully tried to tear off parts of the head. It then moved ca. 4 m away from the fish, walked under the fence into the park and then returned to the vicinity of the fish where it resumed foraging, characterized by thorough searching accompanied by repetitive tongue flicks, traveling back and forth into and out of the park. At 1515 h, another two V. salvator emerged from the nearby canal (ca. 2 m and 1 m TL).



Fig. 1. Varanus salvator tearing off chunks of meat from the body of a suckermouth catfish using its jaws and forefeet.



Fig. 2. The remains of a suckermouth catfish after a large part of it had been eaten. Eating intermission – the monitor stops all eating activities to motionlessly observe its surroundings.



Fig. 3. After severing the vertebral column and separating the hind part of the fish's body, the monitor swallows the hind part anterio-posteriorly. The remains of the fish's anterior lie near the monitor's right front foot.

Immediately upon their arrival, the original monitor retreated to the canal and disappeared in the water. The larger of the two monitors seemed to be more shy and weary of my presence and dove into the canal where it disappeared. Shortly thereafter, the smaller individual also retreated to the canal and disappeared from sight.

At 1525 h, it began to rain and the observation was terminated. The net observation time for the feeding behavior lasted 70 min and was carried out from a distance of 3-4 m. Although the feeding monitor usually ignored me completely, it does appear that my presence did cause minor disturbance since it occasionally stopped eating to observe me and the surroundings for 5-30 sec (Fig. 2) before resuming eating; these pauses infrequently lasted longer than a minute (1-2 min). On several occasions, the monitor carried the fish 3-5 m away from me in an effort to continue eating behind vegetation and a fence.

## **Discussion**

It is well known that *V. komodoensis* occasionally preys on feral domestic horses and water buffaloes (Auffenberg, 1981) that obviously cannot be swallowed wholly. In terms of feeding and foraging behavior and hunting tactics, *V. komodoensis* constitutes a category of its own, somewhat detached from other varanids (Auffenberg, 1981). There are no reports on such a behavior in *V. griseus*, but it cannot be ruled out (Stanner, 1983). Morphologically, there is no reason why *V. griseus* (or other medium-sized varanids that are strong enough) would not use such prey-handling techniques. In that respect, unlike snakes whose teeth are posteriorily curved, conical and round in transverse-

section, and adapted only for holding the prey in place and preventing it from sliding out of the mouth during the process of swallowing, the teeth of Varanus are bi-laterally compressed and serrated (Mertens, 1942; Gaulke & Horn, 2004), which enables cutting and tearing off pieces of flesh. Karunarathra et al. (2008) observed a 2 m V. salvator swallowing a 50 cm suckermouth catfish in the Bellanawila-Attidiya Sanctuary in Sri Lanka; hence, it can be concluded that water monitors are capable of either swallowing suckermouth catfish wholly, or ripping them apart into smaller pieces with their jaws and feet as described above. The monitor in Bellanawila-Attidaya was 2 m long (vs. 1.4 or 1.5 m in Lumpini Park) and the fish - 50 cm (vs. 45 cm in Lumpini Park); therefore, predator/prey length-ratio in Bellanawila-Attidaya was 4, vs. 3.1 or 3.3 respectively in Lumpini Park. It can therefore be postulated that upon attempting to eat a suckermouth catfish, or any other type of prey for that matter, V. salvator considers either or all of the following factors: the species of the prey, its morphology, and the predator/prey size-ratio. If the predator/prey size ratio is large, the monitor will consume the prey in the easiest and quickest way possible, by swallowing it whole. If the predator/prey size ratio is not large, or if the prey's morphology makes it too difficult, hazardous or impossible to swallow, the monitor will rip the prey apart instead.

The suckermouth catfish is an introduced omnivorous fish from South America that is causing problems in local Thai ecosystems. The fish was introduced into Thailand in the 1970's as a cleaning fish for aquaria. When the fish grew and became too large for aquarists, it was released in local fresh water ecosystems (water canals,

ponds, swamps, rivers, etc.). Since its introduction, it has succeeded to spread in many provinces in central and northern Thailand, eating fish-eggs, including those of commercially-important species (Tangkrock-olan, unpub.). Surprisingly, Thais that readily eat almost any type of animal, do not eat suckermouth catfish, claiming that its flesh does not taste good. Thus, devoid of a major predator, suckermouth catfish could multiply and spread more rapidly.

Monitor lizards are the most loathed animals in Thailand, and of the four species native to Thailand, V. salvator is by far the most loathed. The Thai name for this species is "Hia", which is considered an extremely offensive and abusive word that Thais are reluctant to even mutter. Due to their unpopularity, Thais do not consider monitor lizards in general, and water monitors in particular, as worthy species for protection and conservation. Varanus salvator can eat suckermouth catfish of all size-classes; hence, they may now have an opportunity to change their negative image, become the main biological controller of suckermouth catfish, and help save fresh-water ecosystems of Thailand. Moreover, V. salvator routinely scavenge for food and are capable of eating decaying carrion (Stanner unpub. data; Traeholt, in Bennett, 1998). Water monitors can eat large prey by ripping it apart (this study) and are capable of eating carrion of all size-classes including human corpses (survey in Bennett, 1998). Contrary to the general public, Thai officials that are responsible

for the management and maintenance of fresh-water ecosystems usually acknowledge the important role of water monitors in maintaining sanitation in fresh-water reservoirs and ecosystems, all of which may be useful for promoting the conservation of this species.

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# The Monitor Man: A Story of Stunning Discoveries and Charismatic Creatures\*

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Abstract: On the occasion of Prof. Dr. Wolfgang Böhme's retirement from curatorship of the herpetology section at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn, Germany after 39 years, we summarize his many achievements and contributions to the study of systematics and diversity of the extant members of the lizard family Varanidae. For the last 25 years, monitor lizards of Africa and Southeast Asia have been one of his main research activities which have resulted in nearly 80 publications about monitor lizard, including the descriptions of 15 new monitor taxa (viz., two subspecies, 12 species and one subgenus). Due to these decade-long taxonomic investigations of monitors, the herpetological section at ZFMK now houses one of the most important and most complete collections of monitor lizards both in terms of type material (including 12 primary type specimens and paratypes of four additional monitor species) as well as the total number of species represented. Today, 58 different *Varanus* species are housed in the ZFMK collection, representing nearly 80% of the global monitor lizard diversity. Without doubt, Wolfgang Böhme has played an important role in the advancement of monitor research and belongs to the most successful students of the systematics and taxonomy of extant monitor lizards.

## The monitor man: how everything started

On the occasion of Prof. Dr. Wolfgang Böhme's (Fig. 1) retirement from the position as deputy director and curator of herpetology at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn, Germany after 39 years, we summarize

his achievements and contributions to the study of systematics and diversity of the extant members of the lizard family Varanidae. For the last 25 years, monitor lizards of Africa and Southeast Asia have been one of his main research activities.



Fig. 1. Wolfgang Böhme in August 2006. Photograph by **André Koch**.

As early as 1974 (i.e., three years after he had taken up the post as curator of amphibians and reptiles at the ZFMK), Prof. Dr. Hans-Georg Horn, Sprockhövel, drew the attention of Wolfgang Böhme to the fact that specimens of *V. panoptes* from New Guinea were morphologically distinct from their Australian conspecifics. At that time, a shipment of juvenile and subadult specimens from Merauke, southern New Guinea reached Germany. However, the lack of an adult specimen prevented the description of a novel taxon until 1988 when Böhme (1988a) finally erected the new allopatric subspecies V. panoptes horni, which was dedicated to his colleague and friend Hans-Georg Horn, with whom he would initiate and organize three consecutive "Multidisciplinary World Conferences on Monitor Lizards" between 1989 and 2005 (see below). This taxonomic description was the beginning of a most fruitful series of further monitor lizard discoveries which still continues today.

## The "TV monitor" and other amazing discoveries

Many people may think that in order to find fascinating new species, scientists must survey poorlyexplored regions of the globe such as mountainous areas, rainforests, or remote islands. Sometimes, however,

extraordinary discoveries are made under somewhat different circumstances. It was indeed an unusual circumstance in 1985 that began the long series of novel monitor lizard discoveries by Wolfgang Böhme and colleagues, when he sat comfortably at home watching a television documentary about the Arabian Republic of Yemen. After viewing images of Yemen's landscapes, he was much surprised to see a large monitor lizard climbing up a tree, because no monitor species was hitherto known from northern Yemen. To get a hold of this undetermined species, Wolfgang Böhme first contacted the author of the documentary to obtain information about the exact locality where this monitor specimen had been filmed. Next, in early 1986, he sent out two students to the same locality to find and secure this monitor lizard for further investigations (Böhme et al., 1987). Despite three months of intense efforts, not a single specimen could be found. However, during the rainy season half a year later, Beat Schätti, from the Zoological Museum in Zurich, traveled to the area again and encountered eight specimens of the unknown monitor lizard. For further taxonomic comparisons, they were exported to Switzerland and Germany, where the live specimens were displayed in the vivariums of the Berne Zoo and the ZMFK, respectively. Finally, the investigations culminated in the description



Fig. 2. *Varanus yemenensis*, the new monitor species Wolfgang Böhme discovered by watching a TV documentary, in the arms of his eight-year old son Peter. Photograph by **Wolfgang Böhme**.

of *V. yemenensis* (Fig. 2), the Yemen monitor (Böhme *et al.*, 1989). Due to its extraordinary discovery many colleagues still fondly refer to this species as the "TV monitor".

## Untangling the underestimated diversity of Indo-Australian monitor lizards

After this promising opening, Wolfgang Böhme's focus shifted from African to Indo-Australian monitor lizards. Although he never set foot in Southeast Asia, this presented hardly any obstacles for him to significantly enhance knowledge about the monitor diversity of this tropical region. For instance, by comparing the original type specimens Böhme (1991) showed that *V. karlschmidti* Mertens, 1951 is a junior synonym of *V. jobiensis* Ahl, 1932, and thus did not have nomenclatorial priority over the latter name. So, *V. jobiensis* was resurrected and is still in use today for the peach-throated monitor from New Guinea.

Until the 1990s, Indo-Australian monitor lizards comprised only seven long-recognized species. These were the infamous Komodo dragon *V. komodoensis* Ouwens, 1912 from the Lesser Sunda Islands, the widespread water monitor *V. salvator* (Laurenti, 1768) (with several subspecies) inhabiting continental Southeast Asia, the Greater and Lesser Sunda Islands, Sulawesi, and the Philippines (see Koch *et al.*, 2007), the polytypic emerald tree monitor *V. prasinus* (Schlegel, 1839) (with four allopatric subspecies), the crocodile monitor *V. salvadorii* (Peters & Doria, 1878), the peach-throated monitor *V. jobiensis* Ahl, 1932, and the mangrove monitor *V. indicus* (Daudin, 1802) (with three different subspecies), all of which inhabit New Guinea and adjacent islands, and *V. timorensis* (Gray,

1831) (likewise polytypic) from Timor, New Guinea and northern Australia (Böhme, 1988b, 1997; see also Mertens, 1963).

Again it was Prof. Dr. Hans-Georg Horn, an attentive monitor lizard keeper and successful breeder for many decades (e.g., Horn, 1977, 1991), who got the ball rolling. As early as the 1970s, he observed significant differences between certain V. indicus forms with a dark versus a light tongue (Horn, 1977). The latter, very beautifully-colored specimens were referred to as V. indicus "kalabeck" by pet traders. In the first step of a thorough revision towards a resolved taxonomy of the seemingly variable mangrove monitor lizards, Böhme et al. (1994) examined the traceable, original type specimens of all available names, and then revalidated the taxon doreanus A. B. Meyer, 1874 (Fig. 3) for the light-tongued and blue-tailed monitors from New Guinea. This decision was corroborated by Böhme's (1991) earlier findings, which had revealed differences in hemipenial morphology between both forms. At the same time, Böhme et al. (1994) described V. doreanus finschi, a new allopatric subspecies from the Bismarck Archipelago, which differed from typical V. doreanus by an unpatterned, bright throat and the lack of blue pigmentation on the tail. Later, this taxon was elevated to species status due to the confirmed sympatric occurrence of both taxa on New Guinea and northern Australia (Ziegler et al., 1999a, 2001)

In their note on the synonymy and taxonomy of the *Varanus bengalensis* complex, Böhme & Ziegler (1997a) clarified the complicated and confusing nomenclatural situation caused by the descriptions of *V. irrawadicus* Yang & Li, 1987 and *V. vietnamensis* Yang & Liu, 1994. *Varanus irrawadicus* was already synonymized with *V. b. bengalensis* by Auffenberg (1994), but some



Fig. 3. The blue-tailed monitor *V. doreanus* remained long unrecognized but was resurrected from synonymy of *V. indicus* by Böhme *et al.* (1994). Photograph by **Amir Hamidy**.

misspellings and other errors still caused considerable confusion. Thus, the nomenclatural discussion and first revisionary action of Böhme & Ziegler (1997a) towards the correct spelling irrawadicus summarized that this taxon and the spellings irrawardicus, irriwadicus, and irriwardicus are in fact synonyms of. V. b. bengalensis (Daudin, 1802). Böhme & Ziegler (1997a) also showed that V. vietnamensis has to be regarded as a synonym of V. bengalensis nebulosus (Gray, 1831). In addition to this assessment, the authors provided new evidence to reevaluate the taxonomic status of the two formal subspecies of V. bengalensis. Based on well-known differences in scalation (undifferentiated versus differentiated supraocular scales, number of oblique ventral scale rows) in combination with new genital morphological findings, Böhme & Ziegler (1997a) showed that the populations of bengalensis and nebulosus have achieved a divergent status surpassing the subspecies level. Besides the morphological evidence for a distinct specific rank of bengalensis and nebulosus,



Fig. 4. Wolfgang Böhme with a specimen of the colorful quince monitor *V. melinus*. Photograph by **Thomas Ziegler**.

the authors also demonstrated for the first time that the distribution ranges of these taxa, which were formerly considered to be allopatric, are parapatric and, in part, even sympatric. However, Böhme & Ziegler (1997a) closed their note with the challenge for more detailed distribution analyses at the geographical borderline between both taxa in order to document sympatry - with or without hybridization - also in other localities.

While these initial investigations were based on the examination of voucher specimens housed in natural history collections, several subsequent discoveries of new Indonesian monitor lizards were real surprises because they were reptile trade-based. At first, some astonishingly yellow-colored monitors (Figs. 4 & 5), purported to have originated from Obi Island in the Moluccas, came to the attention of Wolfgang Böhme and his former student Thomas Ziegler from photographs taken by traders in Jakarta. Later, some live specimens reached Germany and were encountered in a pet store in Duisburg, North Rhine-Westphalia. One specimen, the subsequent holotype, was made available for further investigations and display in the vivarium of the ZMFK through the generous support of Horst Dintelmann, Bonn, a long-standing friend and supporter of the museum. This live individual, together with three additional voucher specimens served as the type series of the quince monitor V. melinus (Böhme & Ziegler, 1997b). Later, the pet-trade-based type locality Obi turned out to be an error and was corrected by Ziegler & Böhme (1999). Due to their colorful appearance, quince monitors are focal species of monitor enthusiasts all around the world. The first successful breeding of V. melinus was published by Dedlmar & Böhme (2000), and subsequently, the first F2 breeding by Ziegler et al. (2010a). However, still nothing is known about the biology of wild *V. melinus* populations.

Next to *V. melinus*, further hitherto unknown monitor lizards were regularly exported from Indonesia and appeared in the international pet trade towards the end of the last millennium. For instance, in 1998, another breathtakingly colorful monitor lizard, the tri-colored monitor *V. yuwonoi* (Fig. 6) from Halmahera Island, fascinated the international community of monitor lizard enthusiasts. A few years earlier, the first evidence for the existence of this third blue-tailed monitor species was collected by wildlife trader Frank Yuwono during an expedition to the Moluccan Islands. This time, however, the species was described by colleagues from the United States (Harvey & Barker, 1998). Confirmed assignment to the *V. indicus* species group was subsequently provided by Ziegler & Böhme (1999) based on synapomorphic



Fig. 5. *Varanus melinus* is one of the most colorful new monitor lizard species, and was discovered by Wolfgang Böhme and Thomas Ziegler through the pet trade in the 1990s. Photograph by **Thomas Ziegler**.



Fig. 6. When Wolfgang Böhme held *V. yuwonoi* in his hands, it had already been described by colleagues from the United States. Photograph by **Thomas Ziegler**.



Fig. 7. *Varanus caerulivirens* from the northern Moluccas was also discovered through the international pet trade. Photograph by **Kai Philipp**.

outer genital structures. The year 1999 was also very prolific for monitor lizard research because it saw the description of two new Indonesian species. Ziegler et al. (1998) had already published a photograph of a monitor specimen with a turquoise tinge and a light-colored tongue (Fig. 7), which could not be allocated to any known species of the V. indicus group. The following year, it was described as V. caerulivirens (Latin for turquoise) by Ziegler et al. (1999b) after a juvenile specimen with reliable locality data (Halmahera Island) had been found in the Senckenberg Museum, Frankfurt. The true identity of this historical voucher specimen had not been recognized by Robert Mertens. Only with the development of a new taxonomic concept of the widespread V. indicus (Böhme et al., 1994; Philipp et al., 1999; see also Koch et al., 2009 a), could the underestimated diversity of these Pacific monitor lizards be revised.

The ninth member of the growing *V. indicus* group within the subgenus *Euprepiosaurus* was subsequently named *V. cerambonensis* from the Moluccan Islands of Ceram and Ambon, central Indonesia (Philipp *et al.*, 1999). In contrast to former studies, this time morphological data from voucher specimens collected by Kai Philipp (Baden Baden) on several Moluccan Islands and New Guinea were combined with specimens from various German and Dutch natural history museums. The systematic investigations revealed the sympatric existence of two distinct monitor lizard species on Ambon, the type locality of *V. indicus* (Daudin, 1802). Therefore, Philipp *et al.* (1999) designated a neotype for Daudin's taxon in order to allocate the species

epithet to a name-bearing voucher specimen for future investigations.

The next new monitor species of considerable size was found by Wolfgang Böhme during a visit to his late friend and colleague Jens B. Rasmussen at the Zoological Museum in Copenhagen, Denmark. This time, a series of specimens identified as V. indicus and collected in 1962 by the Danish Noona Dan Expedition on Rennell, a remote islet of the Solomon Islands, did not exhibit the typical dorsal double keel along the tail. Apart from this unique feature, the new species, named V. juxtindicus (Figs. 8 & 9) due to its phenetic resemblance with the mangrove monitor *V. indicus*, is characterized by a vivid pattern of many small yellow dots (Böhme et al., 2002). Until recently, V. juxtindicus was known only from the type specimens in the Copenhagen museum. Wesiak & Koch (2009), however, demonstrated that this "rare" monitor species was already kept and bred unrecognized in captivity more than 10 years before its formal description in 2002. The morphological similarity of both species together with the lack of a taxonomic concept of true V. indicus at that time inhibited identification (Wesiak & Koch, 2009).

Another unexpected discovery took place in summer 2002, when Wolfgang Böhme visited his colleague George Zug at the US National Museum of Natural History (USNM), Smithsonian Institution in Washington D.C., which maintains one of the largest amphibian and reptile collections in the world. Among its numerous *V. indicus* specimens, Wolfgang Böhme recovered a peculiar specimen from Halmahera Island, Moluccas, which showed no traces of a color pattern.



Fig. 8. Wolfgang Böhme holds the adult holotype of *V. juxtindicus*. Photograph by **Kai Philipp**.

It was subsequently named *V. zugorum* by Böhme & Ziegler (2005) in gratitude for George Zug and his wife. Until today, this single voucher specimen, which had been collected in the early 1980s, remains the only known example of this species.

It was also during this visit to the USNM that Wolfgang Böhme discovered a specimen of *V. spinulosus* (USNM 120886) which had likewise escaped the attention of herpetologists for nearly sixty years because it had been misidentified as *V. indicus* (Böhme & Ziegler, 2007). This voucher specimen from the island of Bougainville represented the first country record of *V. spinulosus* for Papua New Guinea (PNG) and expanded its known range by almost 400 km. At the same time, two specimens of true *V. indicus* (USNM 120161, -62) with the same locality and collecting data documented sympatry, and possibly even syntopy, of both species on Bougainville (Böhme & Ziegler, 2007).

These discoveries of novel monitor lizard species in natural history museums impressively demonstrated the importance of historical herpetological collections and the need for further taxonomic investigations into Indo-



Fig. 9. Until recently, *V. juxtindicus* was only known from the historical type specimens. Photograph by **André Koch**.

Australian monitor lizards. In 2007, a third new monitor species from Halmahera Island in the northern Moluccas was described. *Varanus rainerguentheri* was dedicated to Rainer Günther, the former curator of herpetology at the Museum für Naturkunde in Berlin (ZMB), at the occasion of his retirement (Ziegler *et al.*, 2007).

Despite the description of *V. rainerguentheri*, the year 2007 experienced no increase in species numbers of the growing *V. indicus* group. Based on the examination of the hemipenes, *V. spinulosus* (Fig. 10), originally described by Mertens (1941) as a subspecies of *V. indicus*, was excluded from the *V. indicus* species group (Böhme & Ziegler, 2007). Due to unique features in genital morphology and scalation, *V. spinulosus* is now not even considered a member of the subgenus *Euprepiosaurus*. Therefore, this monitor species from the Solomon Islands is currently treated *incertae sedis*, and probably represents a distinct subgenus of its own (Böhme & Ziegler, 2007).

When Wolfgang Böhme looked for another student to conduct a project on Indonesian monitor lizards of the *V. salvator* complex, it was the senior author who traveled to Sulawesi and adjacent islands in order to collect new voucher specimens and data representing this taxonomically unresolved monitor group. It was a biogeographic surprise when no members of the *V. salvator* complex were encountered while surveying the remote Talaud Islands in the very north of Sulawesi, but rather an undescribed species of the *V. indicus* group (Koch *et al.*, 2009b). Named after the village of Lirung on Salibabu Island where it was found, *V. lirungensis* has one of the smallest distribution ranges of all known



Fig. 10. Originally described as a subspecies of *V. indicus*, recent hemipenial investigations of *V. spinulosus* have shown that this Solomon Island monitor species does not belong to the subgenus *Euprepiosaurus*. Photograph by **Quetzal Dwyer**.

monitor lizards (Koch *et al.*, 2009a,b). It represents the most northwesterly occurrence of a Pacific monitor lizard species.

## Jewels in the jungle: the *V. prasinus* group

Another monitor lizard group, the colorful New Guinean tree monitors of the *V. prasinus* complex, experienced some astonishing discoveries in the new millennium. One of these spectacular new species was the light-blue and black *V. macraei* (Böhme & Jacobs, 2001), which, without a doubt, is one of the most colorful reptile species of the world (Fig. 11). *Varanus macraei* was successfully bred in captivity just one year after its scientific description (Jacobs, 2002); later, a reproducing zoo population was established (Ziegler *et al.*, 2010b).

Wolfgang Böhme's long-standing contributions to monitor lizard research were honored in 2003 when Hans J. Jacobs (Borchen, Germany), a good friend of Wolfgang and enthusiastic keeper of Indonesian monitors, named a novel species of tree monitor lizard *Varanus boehmei* (Jacobs, 2003). Specimens of the so-called golden-speckled tree monitor, endemic to Waigeo Island off the northwest coast of the Vogelkop (Doberai) peninsula of New Guinea, are still kept and displayed in the public vivarium exhibition of the ZFMK today (Fig. 12).

### The Southeast Asian water monitors

The third Southeast Asian monitor group that saw a growing number of representatives were the widespread water monitors of the *V. salvator* complex. In a first step, Koch *et al.* (2007) re-elevated the three traditionally recognized Philippine taxa *marmoratus* Wiegmann, 1834, *nuchalis* Günther, 1872, and *cumingi* Martin, 1838, as well as the Sulawesian taxon *togianus* Peters, 1872, to their original species status (they had been classified as subspecies of *V. salvator* by Mertens [1942c]). At the same time, the nominotypic subspecies *V. s. salvator* was restricted to the designated type locality of Sri Lanka, while the name *macromaculatus* Deraniyagala, 1944 was resurrected from synonymy for the populations of mainland Southeast Asia, as well as Borneo and Sumatra. The melanistic *komaini* Nutphand, 1987 from Thailand, however, was synonymized with the latter taxon.



Fig. 11. The beautifully-colored *V. macraei* from Batanta Island is one of the most spectacular monitor discoveries in recent years. Photograph by **André Koch**.



Fig. 12. *Varanus boehmei* was named in honor of Wolfgang Böhme's contributions to monitor lizard research in 2003. Today, this species is still displayed in the vivarium of the ZMFK in Bonn. Photograph by **Thomas Ziegler**.



Fig. 13. Varanus palawanensis from the Philippines was recently revealed to be specifically distinct from V. marmoratus. Photograph by Ingo Langlotz.

Recently, the Philippine members of the *V. salvator* complex were re-investigated, resulting in the taxonomic splitting of the polymorphic and disjunct *V. marmoratus* populations (Koch *et al.*, 2010a). Two new species, *V. palawanensis* (Fig. 13) from Palawan Island and *V. rasmusseni* from the Sulu Archipelago, were diagnosed as morphologically distinct species. Interestingly, the latter species is only known from two historical voucher specimens, which like the type series of *V. juxtindicus*, was also collected by the Noona Dan Expedition (see above). In addition, the attractive *V. cumingi* was shown

to be polytypic and a new subspecies of this popular monitor species, *V. cumingi samarensis*, was described from the islands of Samar, Leyte, and Bohol (Koch *et al.*, 2010a).

Even after these two comprehensive revisions of the systematics and diversity of Southeast Asian water monitor lizards, further taxonomic changes and additions are to be expected in the future from various islands of Sulawesi, the Moluccas, and the Lesser Sundas (Koch *et al.*, unpubl. data).

## The Nile monitor and Africa's largest lizard

Discoveries of large, undescribed monitor species are not only to be expected from the many unexplored Indo-Australian and Pacific islands, but may also occur in Africa. In this regard, Böhme & Ziegler (1997c; see also Böhme, 1990) discussed the existence of a further giant monitor lizard species in addition to *V. ornatus* (the rainforest form of *V. niloticus*, which was elevated to full species status by Böhme & Ziegler [1997d]) from the rainforests of Cameroon and Gabon. They cited several independent reports by reliable scientists about a large, gray (monitor) lizard which, in contrast to the forestdwelling *V. ornatus*, was said to taste delicious according to the local people. This interesting feature bares resemblance to the experience of Auffenberg (1988) and could indicate a frugivorous monitor in Africa, as is hitherto only known from the Philippine species V. mabitang and V. olivaceus. Until today, however, no specimen of such a mystery monitor lizard from Central Africa has been secured for science.

Regarding the question of what is Africa's largest lizard, the osteological herpetology collection at ZFMK houses the answer. Based on two skulls from the island of Bioko (formerly known as Fernando Póo) off the west coast of central Africa, Böhme & Ziegler (1997c) showed that the total length of *V. ornatus* distinctly surpasses 250 cm in total length.

## New features in genital morphology and advances in monitor lizard systematics

In monitor lizards, which are generalized active foragers and characterized by a weakly expressed sexual dimorphism, their highly diversified genitals seemed to provide much more reliable information on phylogenetic relationships than traditional classifications based on external morphology (Böhme, 1988b; Ziegler & Böhme, 1997).

In 1988, Wolfgang Böhme's professorial dissertation "Zur Genitalmorphologie der Sauria: Funktionelle und stammesgeschichtliche Aspekte" (= On the genital morphology of saurians: functional and phylogenetic aspects) was published. The monitor lizards (Varanidae) occupied the largest part (32 pages) of the systematic chapters of this 176 page monograph (Böhme, 1988b). Therein, the genital morphology of 26 different monitor lizard taxa was systematically investigated. These hemipenial studies resulted in the surprising finding that the mangrove-dwelling *V. indicus* is actually a close relative of the arboreal *V. prasinus*, which was

traditionally assigned to the round-tailed dwarf monitors of the subgenus *Odatria* from Australia (see Mertens, 1963). This phylogenetic hypothesis which was not supported by lung morphology (see Becker *et al.*, 1989) was later confirmed by molecular studies (Ast, 2001; Ziegler *et al.*, 2007). Thus, both ecologically distinct monitor groups are today united in the subgenus *Euprepiosaurus*. In addition, Böhme (1988b) recognized the morphological distinctness of the hemipenes of Southeast Asian water monitors (*V. salvator* complex), which led to the definition and delimitation of a new monitor subgenus called *Soterosaurus* (Ziegler & Böhme, 1997).

In 1995, Wolfgang Böhme (1995) (re-)discovered miniaturized, paired, evertible and erectile structures in female monitor lizards, for which he proposed the term hemiclitoris. This sexual structure represents the morphological equivalent to the intromittent hemipenis of male squamates. These hemipenis-like organs were also later found in females of other squamates (Ziegler & Böhme, 1997). Ziegler & Böhme (1997, 1999) also demonstrated that these female copulatory organs can be used for taxonomic conclusions and (sub)generic assignments.

The advantages of hemipenial morphology in contrast to traditionally-studied external morphological features (see e.g., Mertens 1942a-c, 1963) to uncover the real systematic relationships of monitor lizards (and other squamate reptile groups) were recently summarized and compared with modern molecular studies by Böhme & Ziegler (2009). Furthermore, Böhme & Ziegler (2009) identified a number of nodes of species groups (including several monotypic ones) where genital morphological clades agreed with molecular inference, such as the subgenera Empagusia, Euprepiosaurus, Polydaedalus, Soterosaurus, and Varanus, to name only a few. Also within groups of closely related species, hemipenial morphology can contribute valuable data and taxonomic insights which are in a broad consensus with molecular data sets. Böhme & Ziegler (2009) suggested that the better agreement in regard to phylogenetic signals between genitalia structures and genetic data may be due to the fact that squamate genital organs are "hidden" inside the tail base and, thus, are not affected by environmentally-effected selective pressures. In contrast to ecologically dependent, peripheral structures, these internal features seem to be merely subject to sexual selection: namely that convergence owing to natural selection is less likely to arise in genital morphology. Based on the recent review of Böhme & Ziegler (2009), it can be stated that genital morphology still plays an important role in squamate taxonomy and phylogeny, and will be crucial for further functional, evolutionary and systematic analyses of monitor lizards and other squamates.

## Other aspects of monitor lizard biology

Next to taxonomic and systematic research, Wolfgang Böhme also supported and supervised ecological studies on monitor lizards. Investigations of the stomach contents of *V. spinulosus* (Böhme & Ziegler, 2007), *V. dumerilii* (Ziegler & Böhme, 1996), and the New Guinean members of the *V. indicus* species group (Philipp *et al.*, 2007) provided important information on the biology and habitat preferences of these monitor species. Wolfgang Böhme also supervised the ecological studies of Sigrid Lenz on the Nile monitor *V. niloticus* in West Africa, which resulted in a detailed monograph on this species (Lenz, 1995).

Wolfgang Böhme also recorded the remarkable age of a male *V. salvator* kept between 1973 and 1999 in a school terrarium in Bonn (Böhme, 2003a). Due to its size when purchased, Böhme (2003a) concluded that the specimen could have attained an individual age of 28 years, which represents the second oldest age ever reported in a member of the Varanidae. This is only surpassed by the Komodo dragon. The skeleton of this *V. salvator* specimen now forms part of the osteological herpetology collection at ZFMK

## The monitor lizard collection of ZFMK

When he commenced his job as curator of herpetology at ZFMK in August 1971, the collection contained only three monitor lizard species. By 1984, this number had increased to 24 species (Böhme & Bischoff, 1984), which represented more than 70% of the then known 30 monitor species. A quarter of a century later, the ZFMK collection now houses 58 different monitor species, which is nearly 80% of the known global monitor lizard diversity. Thanks to Wolfgang Böhme's dedicated efforts and investigations into monitor lizard diversity and systematics for more than 25 years, the herpetological section at ZFMK keeps one of the most important and most complete monitor lizard collections in the world.

In the early 1980s, no monitor type specimens were represented in the ZFMK monitor collection (Böhme & Bischoff, 1984). This situation changed some years later with the descriptions of *V. panoptes horni* and *V. yemenensis* in 1988 and 1989, respectively (Böhme, 1988a; Böhme *et al.*, 1989). The current ZFMK

collection is also particularly rich in primary type specimens (i.e., name-bearing specimens) for various new Varanus species and subspecies descriptions. Of 73 currently recognized monitor lizard species, the ZFMK collection currently holds primary type specimens (i.e., holo-, neo-, lecto-, [and syn-]types) of 13 species and subspecies (viz., panoptes horni, yemenensis, doreanus, finschi, melinus, indicus, caerulivirens, cerambonensis, macraei, boehmei, rainerguentheri, s. salvator, and cumingi samarensis). This number is supplemented by paratypes of 4 additional species (juxtindicus, lirungensis, palawanensis, and rasmusseni) (Böhme 2010). For comparison, the Senckenberg collection in Frankfurt (SMF), where Robert Mertens (1894-1975), the father of modern varanid taxonomy worked between 1919 and 1960, contains primary type specimens of eight valid monitor taxa (viz., albigularis microstictus, acanthurus brachyurus, scalaris, griseus koniecznyi, flavirufus, s. storri, reisingeri, and palawanensis), six of which were already there in the 1960s (Mertens, 1967). This equals the number of primary types of valid monitor taxa in the Muséum National d'Histoire Naturelle (MNHN) in Paris (Brygoo 1987, 1990, de Lisle 2009).

## Live monitor lizards in the ZFMK vivarium

Even before the description of *V. yemenensis* in the late 1980s (Böhme *et al.*, 1989), live monitor lizards have regularly been displayed at the Museum Alexander Koenig to show visitors one of the main research foci of the herpetology section (Böhme & Ziegler, 1997c). After the opening of the vivarium in the lower level of the museum building in November 1984, a pair of *V. exanthematicus* lived together with *Kinixys belliana* in a large desert terrarium. In the following years, the newly discovered *V. yemenensis*, *V. melinus*, and *V. yuwonoi* were exhibited. At present, the recently-described *V. boehmei* is displayed on exhibit in the ZFMK vivarium (Fig. 12).

Large monitor species such as the powerful Komodo dragon (*V. komodoensis*) and the New Guinean crocodile monitor (*V. salvadorii*), which due to their enormous total length cannot be kept at ZFMK, are publicly exhibited as painted casts. In 1987, the museum received two adult specimens of *V. salvadorii* from the reptile zoo in Regensburg. The larger of both specimens had a total length of about 255 cm (Fig. 14), which remained the longest specimen of *V. salvadorii* recorded until the late 1990s (Böhme & Ziegler, 1997c). Anecdotal reports of crocodile monitors reaching total lengths of more than 4 m have never been substantiated.

When a male Komodo dragon died in the Rotterdam Zoo in the mid 1980s, it was also used to prepare painted casts. The large *V. komodoensis* specimen had a total length of 265 cm and clearly demonstrated the differences in body proportions between both giant monitor species (Fig. 15). While the skeleton of the specimen remains in the ZFMK collection, three copies of the cast were transported to the Netherlands. Both ZFMK casts of *V. salvadorii* and *V. komodoensis* are today on display at the entrance of the vivarium. The detailed process of making the painted casts was documented and depicted by Böhme & Ziegler (1997c).

## **Conclusions**

Starting in the late 1980s, Wolfgang Böhme initiated and co-organized three successive "Multidisciplinary World Conferences on Monitor Lizards" held at the ZFMK. Many international monitor lizard experts attended these meetings in 1989, 1997 (Fig. 16), and 2005; the contributions of which were published in three

volumes, each co-edited by Wolfgang Böhme (Fig. 17) (see Böhme & Horn, 1991; Horn & Böhme, 1999; Horn *et al.*, 2007).

In the tradition of his scientific idol Robert Mertens (1894–1975) and his important contributions to monitor lizard research (see e.g., Mertens, 1942a-c, 1958, 1959, 1963), Wolfgang Böhme (1997, 2003b) issued two updated and revised taxonomic checklists of extant monitor lizards (Fig. 18). The 2003 "checklist of the living monitor lizards of the world" was prepared on behalf of the CITES (= Convention on international trade in endangered species of wild fauna and flora) Nomenclature Committee due to the growing number of species and far reaching changes in their taxonomy since Mertens' time. This checklist was adopted as the standard reference for the genus Varanus by the 12th Conference of the Parties to CITES in November 2002. A necessary update of the latest checklist by Böhme (2003b) has recently been published by Koch et al. (2010b).

To date, Wolfgang Böhme's research activities on monitor lizards of Africa and Southeast Asia have resulted



Fig. 14. Portrait of a painted cast of *V. salvadorii* with a total length of 255 cm. Photograph by **André Koch**.



Fig. 15. A painted cast of *V. komodoensis* on exhibit at the ZMFK. Photograph by **André Koch**.



Fig. 16. Attendees of the "First Multidisciplinary World Conference on Monitor Lizards" held at the Zoologisches Forschungsmuseum Alexander Koenig (ZFMK) in Bonn, Germany, in September 1989. In front from left to right: Hans-Georg Horn, Brian Green, Dennis King, Gil L. Dryden, David B. Carter, and Max King. At the left margin behind H.-G. Horn is Hans-Otto Becker and behind D. B. Carter and M. King are Hugh I. Jones and Robert G. Sprackland in the background. Photograph by **Wolfgang Böhme**.

in nearly 80 publications (see Appendix 3), including the descriptions of 15 new monitor taxa (*viz.*, two subspecies, 12 species, and one subgenus; see appendix 1), and there is no end in sight to his scientific research and prodigious output of publications. The monitor lizard species described by Wolfgang Böhme and his collaborators in the last twenty-one years represent about 10% of the extant monitor lizard diversity, with further undescribed monitor taxa awaiting formal description (Koch *et al.*, unpubl. data).

Since most of the new monitor species described by Wolfgang Böhme and colleagues are native to the Indo-Australian Archipelago (only *V. yemenensis* originates from the Arabian Peninsula), it is the more amazing that he never set foot on Indonesian soil, or in any other country in Southeast Asia. The discoveries of several of these species in recent years were possible due to the fact that monitor lizards are favorite pets of reptile enthusiasts in Europe.

Today, Wolfgang Böhme belongs to the most successful students of the systematics and taxonomy of extant monitor lizards.

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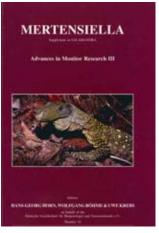


Fig. 17. The proceedings volume "Advances in Monitor Research III" (Mertensiella 16, published 2007) was co-edited by Wolfgang Böhme.



Fig. 18. Wolfgang Böhme's (2003) checklist of the living monitor lizards of the world was adopted by CITES as standard reference of the genus *Varanus*.

colleague, and friend, as well as being an inspiring example in monitor lizard research for many years. He shared his passion and excitement for these fascinating giant reptiles with us and has crucially influenced our personal backgrounds in herpetology. We hope that Wolfgang Böhme will remain a part of the international monitor lizard community, continuing to be productive in publishing and supporting monitor lizard research for many years to come. We wish him all the best for future years in monitor research!

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## Appendix 1: Chronological list of 15 new monitor lizard taxa described by Wolfgang Böhme and colleagues between 1988 and 2010.

Varanus panoptes horni Böhme, 1988
Varanus yemenensis Böhme, Joger & Schätti, 1989
Varanus finschi Böhme, Horn & Ziegler, 1994
Soterosaurus Ziegler & Böhme, 1997
Varanus melinus Böhme & Ziegler, 1997
Varanus caerulivirens Ziegler, Böhme & Philipp, 1999
Varanus cerambonensis Philipp, Böhme & Ziegler, 1999

Varanus macraei Böhme & Jacobs, 2001 Varanus juxtindicus Böhme, Philipp & Ziegler, 2002 Varanus zugorum Böhme & Ziegler, 2005 Varanus rainerguentheri Ziegler, Böhme & Schmitz, 2007

Varanus lirungensis Koch, Arida, Schmitz, Böhme & Ziegler, 2009

Varanus cumingi samarensis Koch, Gaulke & Böhme, 2010

Varanus palawanensis Koch, Gaulke & Böhme, 2010 Varanus rasmusseni Koch, Gaulke & Böhme, 2010

Appendix 2: List of monitor lizard taxa that were (re-)elevated to (original) species status, revalidated from synonymy, or synonymized with older names by Wolfgang Böhme and colleagues:

Böhme (1991):

Varanus jobiensis Ahl, 1932 > revalidated from synonymy of V. indicus Varanus karlschmidti Mertens, 1951 > recognized as junior synonym of V. jobiensis

Böhme et al. (1994):

*Varanus kalabeck* Lesson, 1830 > declared a nomen dubium

Monitor douarha Lesson, 1830 > declared a nomen dubium

*Varanus doreanus* (Meyer, 1874) > revalidated from synonymy of *V. indicus* 

Böhme & Ziegler (1997a):

Varanus nebulosus (Gray, 1831) > elevated to species status

Böhme & Ziegler (1997d):

Varanus ornatus (Daudin, 1803) > elevated to species status

Koch et al. (2007):

Varanus salvator macromaculatus Deraniyagala, 1944 > revalidated from synonymy of V. s. salvator Varanus salvator komaini Nutphand, 1987 > synonymized with V. s. macromaculatus Varanus togianus (Peters, 1872) > re-elevated to original species status Varanus marmoratus (Wiegmann, 1834) > re-elevated

to original species status

*Varanus nuchalis* (Günther, 1872) > re-elevated to original species status

*Varanus cumingi* Martin, 1838 > re-elevated to original species status

# Appendix 3: Chronological list of publications of Wolfgang Böhme about monitor lizards. Numbers in brackets indicate the position in his entire publication record since 1964.

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Varanus giganteus. Osprey Bay, Cape Range National Park, WA. Photograph by Mark and Bill Bell.

## **ERRATA**

On page 108 of Vol. 4 No. 3, the following citation is incorrect:

Indraneil, D. 2010. A Field Guide to the Reptiles of South-East Asia. New Holland Publishers, London. 375pp.

The correct citation is:

Das, I. 2010. A Field Guide to the Reptiles of South-East Asia. New Holland Publishers, London. 375pp.