ZOO VIEW

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Tales of Monitor Lizard Tails and Other Perspectives

Since I—about 30 years ago—got my first living Nile monitor and became acquainted with his life habits in the terrarium, the monitor lizards have fascinated me all the time, these 'proudest, best-proportioned, mightiest, and most intelligent' lizards as [Franz] Werner strikingly called them.

—*Robert Mertens (1942)*

Modern comparative methods allow the examination of the probable course of evolution in a lineage of lizards (family Varanidae, genus *Varanus*). Within this genus, body mass varies by nearly a full five orders of magnitude. The fossil record and present geographical distribution suggest that varanids arose over 65 million yr ago in Laurasia and subsequently dispersed to Africa and Australia. Two major lineages have undergone extensive adaptive radiation within Australia: one evolved dwarfism (subgenus *Odatria*, pygmy monitors), whereas the other Australian lineage (subgenus *Varanus*) remained large, and several of its members evolved gigantism.

—*Eric R. Pianka (1995)*

Monitor lizards adopt characteristic defensive postures, flattening themselves from side to side and extending their gular pouches, presumably to make themselves appear as large as possible. Often they hiss loudly and flick their tongues. Big species lash their tails like whips with considerable accuracy. Some species stand erect on their hind legs during such displays.

Male monitor lizards engage in ritualized combat, fighting over females. Larger species wrestle in an upright posture, using their tails for support, grabbing each other with their forelegs and attempting to throw their opponents to the ground. Blood is sometimes drawn in such battles. Smaller species grapple with each other while lying horizontally, legs wrapped around each other as the roll over and over on the ground. The victor then courts the female, first flicking his tongue all over her and then, if she concurs, climbing on top of her and mating by curling the base of his tail beneath hers and inserting one of his two hemipenes into her cloaca. (Male varanids have a unique cartilaginous, sometimes bony, support structure in each hemipenes, called a hemibaculum).

—*Eric R. Pianka and Laurie J. Vitt (2003)*

Maintenance of the existing diversity of varanids, as well as clade diversity of all other extant lizards, will depend increasingly on our ability to manage and share beleaguered spaceship Earth. Current and expanding levels of human populations are unsustainable and are direct and indirect causes of habitat loss. They also contribute to escalating rates of climate change. To address anthropogenic habitat loss and climate change, we will have to make major changes in our resource use.

—*Eric R. Pianka (2012)*

It is evident that the international pet trade in monitor lizards originating from Southeast Asia and the Indo-Australian Archipelago impacts a much higher number of species compared to those involved in the commercial skin trade…Trade impact in live *Varanus* species still remains poorly understood, given the fact that field conservation studies are almost completely lacking, particularly in the tropics…Current Indonesian legislation appears nontransparent and incomplete to conserve Indonesia's currently recognized 28 monitor lizard species. One major reason is that traders, particularly those harvesting species, next to collectors and middlemen, react highly responsive to lucrative opportunities which are generated by international demand… Traders have largely benefited from the paucity of information available from the wild. In addition, the complex geography of this vast island region together with the taxonomic uncertainty in look-a-like species and the lack of capacity building programs, training material and guides in the countries of origin hamper an efficient trade control.

—*Koch et al. (2013)*

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In Babylon in the 3rd millennium B.C., monitor lizards (also known as varanids and, in Australia, goannas) were beloved by the chief god, Marduk (the long, split tongue can be recognized in reliefs). Monitor mummies are known from Egypt and monitors appear in hieroglyphs; in the late Egyptian era (1st century B.C.) there were genuine "lizard cults" (Brentjes 1975). Aristotle, in the fourth century B.C., might have been the first person to study the anatomy of monitor lizards, most likely the Bengal Monitor (*Varanus bengalensis*)—brought back with many other animal specimens from Alexander the Great's Asiatic expeditions (Cresswell 1862). A wonderful representation of an incarnation of Gautama Siddhartha, adorned with a water monitor's head, resides in a Thai Buddhist temple in Bangkok (Fig. 1). Before he achieved nirvana and became the Buddha, Gautama Siddhartha

PHOTO BY PRAWAT THANANITHAPORN AND INFORMATION BY JESSICA AMANDA SALMONSON

FIG. 1. Thai Buddhist temple representation of an incarnation of Gautama Siddhartha, adorned with a monitor's head. The story began in India, where Buddha had been a Bengal Monitor. We believe that the monitors on either side are likely *V. bengalensis* and the scene is in a Buddhist temple in Bangkok, Thailand. The only other species it could be is *V. salvator*; however, because water monitors are despised in Thai culture (the Thai word for them - 'hĭia' is one of the most deplorable insults you can call someone), we suggest that *V. bengalensis* is a more appropriate fit.

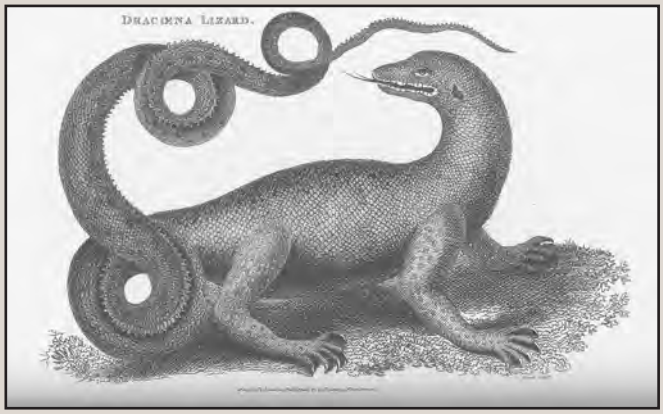

FIG. 2. Bengal Monitor (called *Lacerta Dracæna*) from "General Zoology or Systematic Natural History. Volume III. Amphibia" by George Shaw (1802).

was the Bodhisatta of Many Lives. Legend has it that in one of these lives the Bodhisatta, who was born as a lizard. His life was that of a lizard along a river, hunting for food and basking in the sun, which sounds like a pretty nice lifestyle to us.

Monitor lizards have proven to be interesting subjects for behavioral studies. H.-G. Petzold (1984, translated from German) stressed the importance of observations made on monitors in captivity. "In appropriately equipped large terraria—or in climatically favorable regions, held in outdoor enclosures, monitors are impressive show animals and biologically interesting study objects at the same time. Their care in zoos goes back to the times of the menageries; only a few decades ago, successful breeding was among the rarest of zoo events. A large part of our knowledge about the behavior and reproduction of individual species of the genus *Varanus* is based on terrarium observations." At the Smithsonian National Zoological Park (SNZP), a female Komodo Dragon (*V. komodoensis*) demonstrated play behavior, interacted with inanimate objects and human caretakers (Burghardt et al. 2002; Murphy and Walsh 2006). A recent study by Loh et al. (2018) summarized the state of peer-reviewed research in AZA zoos and aquariums.

A sizeable threat to smaller Australian varanids is the invasive Cane Toad (*Bufo marinus* = *Rhinella marina*), that has expanded its range across the top half of the country. One of the most disastrous examples of human miscalculation has been the introduction of these highly toxic anurans into the sugar cane fields of Queensland in 1935 to control invertebrate pests. However, the Yellow-spotted Goanna (*V. panoptes*) is a large (up to 1.5 m TL) monitor inhabiting woodlands and floodplains in New Guinea and northern Australia. Ujvari and Madsen (2009) radio-tagged nine lizards to investigate predation on the toads; they discovered > 90% mortality in the study area due to ingestion of toxic toads.

The introduction of two invasive mammal predators—European Red Fox (*Vulpes Vulpes*) and feral House Cat (*Felis catus*)—in Australia has resulted in direct and indirect mortality of goannas. Both foxes and cats kill monitors, and these alien predators are also responsible for the widespread use of poisoned baits to control their populations. There is a critical need to instruct land managers to properly use bait products. Jessop et al. (2013) studied bait effects on Lace Monitors (*V. varius*) and found that these lizards can remove and ingest surface-laid Curiosity© baits. Depending on daily weather conditions, up to 22% of baits per day were removed by varanids during the summer.

A study by Woinarski et al. (2018) listed astronomical numbers of reptiles killed by feral cats. These figures are sobering and disquieting: feral cats in Australia's largely natural environments kill more than one million reptiles per day, and individual cats take, on average, more than 225 individual reptiles each year, with almost all of these being native species:

> "THE LOSS OF ~1.8 MILLION NATIVE REPTILES PER DAY DUE TO PREDATION BY CATS PROVIDES FURTHER EVIDENCE OF THE POTENTIAL CONSERVATION IMPACT OF THIS INTRODUCED PREDATOR ON AUSTRALIAN BIODIVERSITY, AND UNDERSCORES THE VALUE OF EFFORTS NOW BEING MADE TO MANAGE FERAL CAT POPULATIONS (E.G. THROUGH LOCAL-SCALE EXCLOSURES, ENHANCED ISLAND BIOSECURITY, BROAD-SCALE PREDATOR CONTROL PROGRAMS) AND THE PREDATION PRESSURE THEY EXERT (E.G. MANAGEMENT OF FIRE AND GRAZING PRESSURE), ESPECIALLY TARGETING CONSERVATION MANAGEMENT FOR SPECIES WHOSE POPULATION VIABILITY IS MOST VULNERABLE TO CAT PREDATION."

Woinarski has also published studies on native birds and mammals, mirroring the results shown for reptiles. The effects of feral cats on local goanna populations can be significant. For example, Sweet (2007) had six of 50 radio-tracked Spotted Tree Goannas (*V. scalaris*) and Black-headed Monitors (*V. tristis*) at his study site in Kakadu National Park, NT, that were predated by a single feral cat, and observed several additional cases of feral cat predation on non-tagged individuals. Nutt (2011) listed *Varanus* sp. as among the 20 most important prey categories of feral cats in north-central Queensland.

We have listed many excellent papers concerning varanids in the Literature Cited: Rotter (1963), Minton and Minton (1973), Auffenberg (1981, 1994, 1998), Pianka (1986), Pianka et al. (2004), Pianka and Vitt (2003), Bennett (1998, 2003), Burden (1927), King and Green (1993, 1998, 1999), Surahya (1989), Vincent and Wilson (1999), Murphy et al. (2002), Rogner (2007), Eidenmüller (2007, 2016), Swan (2009), Lenz (1995), and Brown (2012). In the series *Mertensiella*, a supplement to *Salamandra*, Wolfgang Böhme and Hans-Georg Horn edited a volume called *Advances*

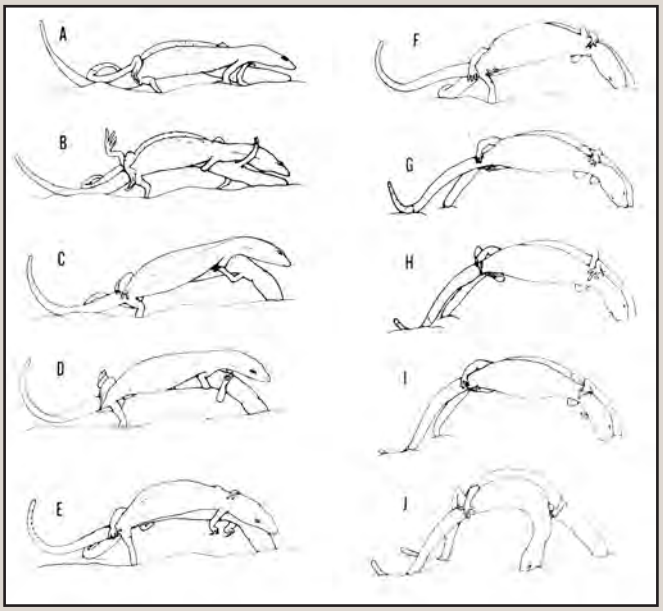

Fig. 3. The videotaped sequence of actions during arching bout of two *Varanus gilleni* males at Dallas Zoo. From Carpenter et al. (1976).

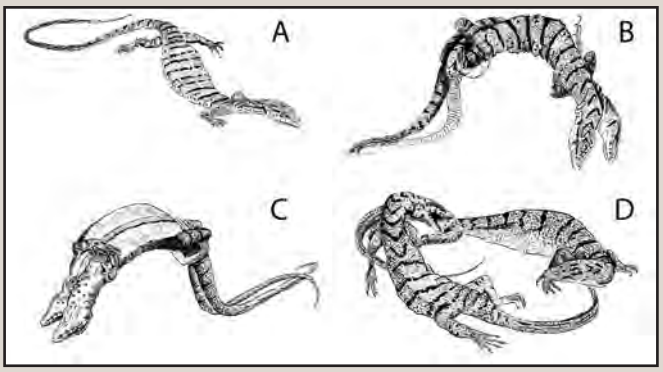

Fig. 4. *Komment-Kampf* or ritual struggle of male *Varanus gilleni* at Dallas Zoo. A) First sequence, prior to contact. B) Second phase, now in combat. C) Each male either inflates body with gular pumping motion and rotates upon longituinal axis or deflates trunk in order to overpower rival. D) Struggle concludes with winning male on left biting subordinate loser. Because these lizards were kept in a relatively small enclosure, the subordinate could not flee and became immobile. The dominant male switched from aggression to courtship behavior and attempted copulation. From Murphy and Mitchell (1974).

in Monitor Research (1991). Two additional edited volumes of *Advances in Monitor Research* were produced in 1999 (Horn and Böhme) and 2007 (Horn et al.). Recently, proceedings from the Interdisciplinary World Conference on Monitor Lizards held in Bangkok, Thailand in 2015 have been published by Michael Cota (2016).

Early artistic renditions often show varanids and other lizards with coiled tails held over the body, a position now known to be a bit of an exaggeration (see Shaw 1802; Fig. 2). Many illustrations of reptiles beginning in the 15th century are not terribly accurate, perhaps because the artists may not have viewed living examples and updated technology (engravings, etchings, lithographs, and so on) was not available at the time. Dennis and Adler (2003) traced the evolution of herpetological art and improving technologies for showing amphibians and reptiles. An historical overview of varanid illustrations is in preparation for the journal *Biawak* (see Mendyk et al. 2016).

Tail Use

The degree of variation and specialization in tail morphology across monitor species is remarkable. Bedford and Christian (1996) studied the relationship between tail morphology and habitat in monitor lizards. Wide ranges of fascinating uses of the tail have been recorded. One of the most dramatic examples of tail use is that of male Pygmy Mulga Monitors (*V. gilleni*) embracing conspecifics in an arching posture during combat rituals at the Dallas Zoo (DZ) (Murphy and Mitchell 1974; Carpenter et al. 1976; Radcliffe and Murphy 1983; Figs. 3–4). Aquatic, semiaquatic, rock-dwelling, and terrestrial varanids utilize ritualized combat to establish dominance with conspecifics. A few examples reflect differences in combat between species from different habitats. Davis et al. (1986) recorded ritualized combat in captive Dumeril's Monitors (*V. dumerilii*). Honegger and Heusser (1969) contributed an analysis of the behavioral inventory of the Asian Water Monitor (*Varanus salvator*). Horn et al. (1994) provided a description of the four or five elements comprising varanid combat:

We think it appropriate to combine these single elements to the following four or five phases:

Display phase: aggressive tongue-flicking, body flattening.

Encompassing phase: combatants encompassing each other with lateral display, partly accompanied by head jerks.

Clinch phase: bipedal stance in wrestling pose with mutual embrace.

Catch phase: tilting over each other and twisting and turning around to achieve the superior position.

Subpressive phase: after the fight mounting the inferior specimen (pseudocopulation), biting (and chasing if it retreats).

The following varanid species have been observed to carry out ritual combat or encounters interpreted as such: *Varanus albigularis* (Branch 1991), V. *b. bengalensis* (Deraniyagala 1957), Auffenberg 1981), *V. dumerilii* (Davies et al. 1986), *V. flavirufus* (Thompson et al., in press, as *V. gouldii*), *V. gouldii horni* (this paper), *V. gouldii rubidus* (Bennett 1992), *V. indicus* (McCorn & Hensley 1989), *V. komodoensis* (Horn 1985), *V. mertensi* (Greer 1989; this paper), *V. niloticus* (Clements 1968, Branch 1991), *V. olivaceus* (Auffenberg 1988), *V. salvator marmoratus* (Gaulke 1989), *V. s. salvator* (Honnegger & Heusser 1969, Vogel 1979a, b, Rese 1986), *V. spenceri* (Waite 1929; not *V. giganteus*: Horn 1981), *V. varius* (Worrell 1963, Breeden & Breeden 1972, Horn 1980, Twigg 1988, and this paper); from the *Odatria* section of *Varanus* have to be added: *V. caudolineatus* (Thompson et al., in press), *V. gilleni* (Murphy & Mitchell 1974, Carpenter et al. 1976), *V. semiremex* (Horn 1985), *V. similis* (Horn 1985; this paper), and *V. timorensis* (Horn 1985). It is important to note that monitors show their agonistic behavioural inventory not only in the field under natural conditions, but also in the laboratory; when kept properly, after many years. Even captive-bred specimens (e.g. *V. similis*, see above) display it. Therefore, the inherited nature of these stereotyped behavioural patterns is proven.

Rock-dwelling Ridge-tailed Monitors (*V. acanthurus*) at Dallas Zoo (DZ) used the spiny tail to wrap around human fingers when held. In one case, the monitor also bit the space between

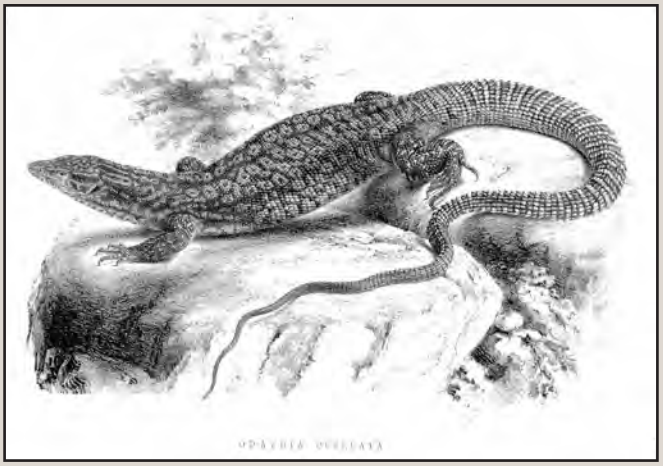

Fig. 5. Illustration of *Odatria ocellata* now *V. acanthurus* from "The Lizards of Australia and New Zealand" by John E. Gray and Albert Günther from 1845 to 1875. The spiny tail seems to be used to block entrances to burrows. This publication was reissued by SSAR in 1995.

two fingers with surprising force and held this position for ca. 15 min, causing considerable pain. The tail may have been used to position the bite. Auffenberg (1994) recalled a *V. acanthurus* that drew blood from his index finger by forcefully pushing its spiny tail scales against the finger after it was jammed into the captive's burrow. Horn (1999) observed captives using their tails to probe for prey under rocks. The enclosures at DZ had many flattened rocks that accommodated small rodent and invertebrate prey hiding from the monitors; the use of the tail as a probe was never seen (Fig. 5). Wilson and Knowles (1988) described tail use to block the entrances to burrows, presumably as a defense against predators.

Sprackland (1980) described peculiar tail use in a captive Storr's Monitor (*V. storri*):

> "I had been sifting the sand in the cage and pulled the male lizard out from under his retreat. Once exposed, he moved a short distance away from my hand, flattened the body to face me, and, with nose in the sand and hips upraised, began to rattle the tip of his tail. The latter third of this organ would be rapidly vibrated in a series of 2–3 second bursts, until I withdrew my hand. Later observations showed that this display would be invoked when another lizard encroached upon the male's perch, or, when intimidated by me or large prey items. If the vibrating tail came into contact with any solid material (rocks or twigs), the sound produced was a distinct buzz, similar to that produced by young rat and bull snakes (*Elaphe* sp. and *Pituophis* sp., respectively)."

Sprackland also noted that when manually restrained, a *V. storri* forcefully rubbed the spines of its tail against his hand, slightly abrading his skin.

Patanant (2012) described tail-probing behavior in a King's Monitor (*V. kingorum*) and listed three other literature accounts describing this behavior in other varanid taxa (Gaulke 1989; Eidenmüller 1993; Horn 1999). Patanant (2012) recorded that prey is located using vision and/or olfaction. If the crevice is too narrow for the lizard to enter with its head, the lizard forms a semicircle with its body and rapidly undulates the tip of its tail to force the prey item out of its hiding spot. When fleeing the hiding spot, the prey is chased and consumed.

Members of the tree monitor, or *V. prasinus* species complex, have long prehensile tails measuring twice the length of the body and are used to assist with climbing and descending from trees. Emerald Tree Monitors (*V. prasinus*) may hang from branches by the prehensile tail tip and lift prey such as rodents held in their jaws from the substrate. In the Dampier Peninsula Goanna (*V. sparnus*), the tail is highly prehensile, similar to that of the Short-tailed Pygmy Monitor (*V. brevicauda*), possibly functioning to assist in navigating through *Triodia* clumps (hummock-forming bunchgrass) and shrubs (Doughty et al. 2014).

In several larger species, the tail can be used as a powerful whip-like weapon for defense. Stirling (1912) referenced claims made by Australian anthropologist Francis James Gillen that he once saw a large Perentie (*V. giganteus*) use its tail to knock down an aboriginal woman with a powerful blow to her legs. He also mentioned a third-hand account of both forelegs of a dog being broken in a similar manner. Mitsch (1936) reported that an irritated *V. varius* broke the glass window of its terrarium with a blow from its tail. Kent-Seville (1897) noted that a zookeeper at Regents Park sustained severe lacerations to the neck from the tail of a *V. varius* as he attempted to clean its enclosure. At DZ, when three adult Crocodile Monitors (*V. salvadorii*) were placed on the floor, all three lizards accurately used the long tail tip to strike at JBM's eyes. In several cases, his eyes were nearly struck so he started using a welder's mask to avoid injury. [As an aside, these lizards regularly showed blood and saliva in the labial region and dental arcade. At first, it was interpreted as a medical issue but there were no outward signs of pathology. Examination of published photos of captive lizards indicated that this was a regular occurrence, so we speculated that this condition might be similar to the exudate from mouths seen in Komodo Dragons. This phenomenon is frequently seen in captives of species with exceptionally long teeth—e.g., *V. salvadorii, V. doreanus, V. yuwonoi*—and might be related to normal tooth replacement (S. Sweet, pers. comm.).]

The laterally compressed tails of semi-aquatic species such as Mertens' Water Monitor (*V. mertensi*), the Nile Monitor (*V. niloticus*), and *V. salvator* allow for powerful swimming but can also aid in sequestering food. A *V. mertensi* at SNZP used its laterally compressed tail to corral live feeder cichlids into the shallows of a smaller pool that had a rock perimeter. This monitor chased the fishes from the larger pool into the smaller one where they were more vulnerable. The tail was pressed into the spaces between rocks separating both pools or raised above the rocks to trap the fishes. Some of the fishes leaped over the monitor, who caught them in mid-air in many cases (JBM, pers. obs.). This behavior has been observed in other captive (Vincent and Wilson 1999b) and wild *V. mertensi* (Hermes 1981), and has also been documented in wild *V. niloticus* (Keith and Ginsburg 2010). Mayes et al. (2005) observed a *V. mertensi* at an irrigation channel drain in East Kimberly in Western Australia during the late wet season. The monitor was standing on the edge of an artificial waterfall and snatched three fish out of the air. In Sri Lanka, Wikramasinghe et al. (2010) observed a *V. salvator* using thrashing tail movements to displace water and small fish from small shallow pools during the dry season, where they were easily captured and consumed on land.

Christian (1981) described a truly remarkable positioning of the monitor tail:

> One habit of the Black-headed Monitor [*Varanus t. tristis*] that helps distinguish it from other monitors (particularly at a distance) is its tendency to curve the long tail in a high arc over its head while sunbaking. I have never seen [this] in any

other species of monitor, including the Freckled Monitor [*V. tristis orientalis*], resting in this fashion. This classic posture is followed by an amazing burst of speed as the lizard is approached and in a flash it has disappeared amongst the spinifex.

This behavior was observed in juvenile *V. tristis orientalis* in captivity (McDonald 1999).

McDonald (1999) also observed tail-luring behavior in captive-bred hatchlings of this species, as well as an individual that used its tail to flick a cricket off branches inside its enclosure. *Varanus tristis* have been reported to use their tails to rustle leaf litter and stir up small skinks and insects so they could then be seized (Sweet 2007); this behavior has also been observed in captive specimens of the Kimberly Rock Monitor (*V. glauerti*) (RWM, pers. obs.).

Lizard ecologists can often create indirect behavioral profiles by examining tail markings in the substrate. In the Desert Monitor (*V. griseus*), Michael Stanner (in Pianka et al. 2004) listed indirect communication by spoor:

"While running fast, the monitor raises its body and leaves only footprints. Occasionally the tail may slightly touch the sand, leaving a short straight traction mark; 2) While walking or running slowly, the monitor leaves a sinuous traction mark of the tail with footprints on both sides; 3) After defecation, *V. griseus* wipes its cloacal region in the sand, leaving a broad traction mark. During this act, the monitor propels itself forward with the forelimbs only. The hindlimbs are raised and do not touch the sand; 4) Tsellarious and Mensshikov (1994) coined the term 'drag' for the fourth type of traction mark. The monitor presses its tail and/or its cloaca and hind part of the belly into the sand and leaves a distinct mark of up to 10 m long, using all four limbs to propel itself forward."

If the trail is several hours old, the male can track the female in the right direction; if several days old, it is hit-or-miss. Farlow and Pianka (2000) described variation in the trackway patterns of Australian desert-dwelling monitors, noting that different species left their own conspicuous tail drag-marks.

Threat and Defensive Behavior, Mimicry

An adult *V. mertensi* was placed in a mixed lizard exhibit at DZ that housed several West Indian Iguanas (*Cyclura*) to see if they would be compatible. The monitor immediately assumed a threat posture that was described by Murphy (1969) and Murphy and Lamoreaux (1978).

Tsellarius and Tsellarius (1997) described threat behaviors of *V. griseus* during encounters with conspecifics:

"Fights were rarely noted and only between unfamiliar lizards. It is proposed that ritual combat arises from displays of dominance and not from a ritualization of the fight. The behavior of monitors during contacts is highly varied and not stereotypical. Data from observations attests to the existence of a complex, mammal-like social structure in the population."

Bels et al. (1995) provided a threat analysis of *V. griseus*:

"The threat behaviour in *Varanus griseus* was investigated with highspeed cinematography and Xray films. Lizards exhibit threat display involving throat movements and associated throat, thorax and mouth movements. The functional anatomy of the buccopharyngeal region is described and threat displays are kinematically studied and functionally interpreted."

Johnson (1976) published the following observations seen in captive monitors:

"The adult male *V. gouldii* (s-v length 91.0 cm) demonstrated a high degree of aggressiveness and displayed the characteristic threat posture with back arched, neck and throat inflated, and at times rapidly inflated and deflated the body. Loud hissing and rapid tongue flicking always accompanied such behaviour. Occasionally after this initial threat display, rapid tail vibration, increased tongue flicking, hissing and bipedal (rearing up on the hind limbs) stance was assumed. The author has also observed this latter bipedal stance with extreme harassment in captive *V. varius* and *V. spenceri*. At times the tail was used defensively in a whip-like action. Often the *V, gouldii* after assuming the bipedal stance lunged forward at the investigator. These latter responses were only elicited when cornered and highly agitated. When grabbed *V. gouldii* often discharged the cloacal contents and attempted to claw and bite."

Cota and Krebs (2015) proposed that newly hatched *V. dumerilii*, which have bright red heads and glossy black bodies with creamish transverse dorsal bands, may use Batesian mimicry to avoid predation by raptors and mammals. There are several highly toxic red, orange, and yellow-headed venomous elapid snakes in the geographic range of this lizard—King Cobra (*Ophiophagus hannah*), Red-headed Krait *(Bungarus flaviceps*), and Malaysian Coral Snake (*Calliophis bivirgata flaviceps*)—which might well be the models. The non-venomous Red-headed Reed Snake (*Calamaria schlegelii*) may also be related to this mimicry complex, and the Red-headed Pipe Snake (*Cylindrophis ruffus*) conceals its head among body coils, flattens the tail and arches it upward to display its red pattern, mimicking that of coral snakes.

When captured and physically restrained, some monitors appear to use defecation as a defense strategy. RWM recalls an unfortunate incident involving the late varanophile Mark K. Bayless, in which he brought one of his White-throated Monitors (*Varanus albigularis albigularis*) to the veterinarian for an examination. While restraining the animal and holding it out vertically for the veterinarian to inspect its dorsum, the irritated monitor forcefully evacuated the contents of its bowels, spraying liquefied feces onto Bayless' face and into his open mouth.

Thermoregulation

One recent development in maintaining captive monitors successfully is recognition of the need to provide broad thermal gradients with high surface basking temperatures (Mendyk et al. 2014). Christian and Weaver (1996) examined thermal profiles in four species of Australian varanids:

"Abstract: The aims of this paper are to compare the thermal ecology of four species of varanid lizards that occupy a range of habitats and climatic regions, and to assess the efficacy of methods for evaluating the extent to which ectothermic animals exploit their thermal environments. Hertz et al. (1993) have proposed several indices of thermoregulation, and these are evaluated with respect to our data from varanid lizards. The thermoregulatory

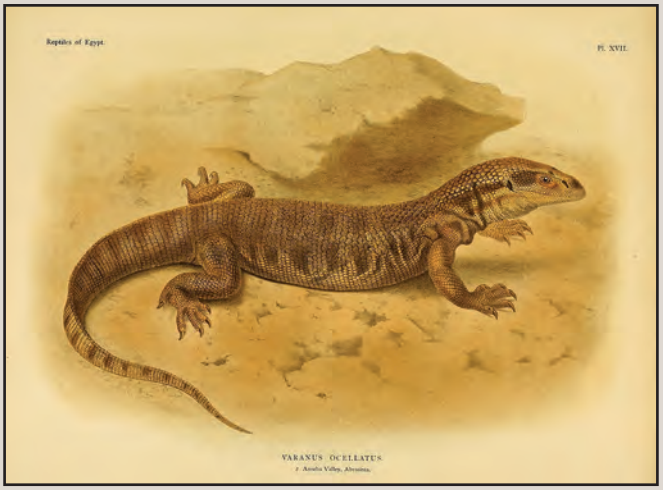

Fig. 6. *Varanus albigularis* in John Anderson's "Zoology of Egypt" in 1898.

> characteristics of three tropical monitor lizards (*Varanus panoptes*, *V. gouldii*, and the semiaquatic *V. mertensi*), and the temperate-zone *V. rosenbergi* were studied throughout the year. Radiotelemetry was used to measure the body temperatures (Tb's) of free-ranging animals, and microclimatic data were collected to determine the range of possible Tb's that an animal could achieve. Operative temperatures (Te's) were estimated by biophysical models for each set of animal characteristics and microclimatic conditions. The Tb's selected by animals in a laboratory thermal gradient were used to determine the set-point range of Tb's that the animals voluntarily select."

Bartholomew and Tucker (1964) outlined the effects of size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanids, emphasizing physiological differences in size rather than species given that varanids have roughly the same body plan across taxa. Two important papers by Mendyk et al. (2014, 2016) concern thermal husbandry of varanids and should be consulted by those who maintain these lizards in captivity. Walsh et al. (1999) compared dramatically differing thermal preferences in wild and captive *V. komodoensis* at SNZP. They hypothesized that the life style of captives is less energetic than in their wild counterparts.

Reproduction

Of the 80 or so species of varanids currently known to science, at least 65 have been maintained in captive collections and of these, around 50 species have successfully reproduced at least once in captivity. Horn and Visser (1989) reviewed reproduction of 20 species in captivity and data on their biology (1991; Fig. 6). Horn and Visser (1997) also provided an updated account on reproduction that covered behavior, diet, egg incubation, light, reproduction, sexing, and taxonomy. Mendyk (2012) presented reproductive data for 12 species of monitors kept at the Bronx Zoo over a 33-year period, including five species that were successfully hatched at the zoo. Brotzler (1965) outlined the breeding of *V. mertensi* in in the Wilhelma Zoo in Stuttgart, Germany. This species later reproduced on several occasions at the Bronx Zoo through the late 1990s and 2000s (Lee 2000; Lee and Friedman 2000; Mendyk 2012). Müller (1970) bred *V. salvator* at the Leipzig Zoo, David (1970) at the Ahmedabad Zoo, and Hairston and Burchfield (1992) at the Gladys Porter Zoo in Brownsville, Texas. Herrmann (1999) documented husbandry and captive breeding of *V. salvator* in the Cologne Aquarium at the Zoo. At the Frankfurt Zoo, Wicker et al. (1999) kept and bred the beautiful Cuming's Water Monitor (*Varanus cumingi*); this species was recently bred by the Cologne Zoo (Anonymous 2017; T. Ziegler, pers. comm.). Ziegler et al. (2009) documented the first captive breeding of the Blue Tree Monitor (*V. macraei*) at the Plzen and Cologne Zoos, and Ziegler et al. (2010) described the first F_2 breeding of the Quince Monitor (*V. melinus*) at the Cologne Zoo. Wesiak and Koch (2009) reported on the husbandry, first breeding, and juvenile development of Rennel Island Monitors (*V. juxtindicus*). De Zeeuw (2010) described husbandry and reproduction of *V. glauerti* in captivity. The Dallas Zoo hatched one Butaan (*V. olivaceus*) in 1992 that died shortly after hatching (Card 1995), perhaps due to a congenital heart defect. More recently, the Los Angeles Zoo has experienced repeated success in reproducing this species (Recchio 2016). Mendyk (2015c, 2016, 2017, 2018) prepared annotated bibliographies on captive reproduction in several *Varanus* subgenera.

Brown (2009) recommended using hemipenial trans-illumination as a sexing technique in varanids. Recchio and Kasielke (2017) described a successful blood collection technique for sex determination of incubating *V. komodoensis* eggs at Los Angeles Zoo. Judd et al. (1977), Morris and Alberts (1996), and Morris et al. (1996) explored sex determination in *V. komodoensis* and *V. albigularis* at San Diego Zoo.

The Gembira Loka Zoo in Jogjakarta, Indonesia has successfully bred *V. komodoensis* for many years, producing well over 100 hatchlings (Walsh et al. 1998). The offspring are maintained in large groups in movable enclosures and are placed in sunlight daily (Busono 1974). Gaulstaun (1973) reported that *V. komodoensis* eggs were deposited in the Zoological and Botanical Garden of Jakarta, Indonesia; Osman (1967) prepared a note on the breeding behavior of *V. komodoensis* at Jogjakarta Zoo; and Sunter (2008) at London Zoo. Walsh and Rosscoe (1993) and Walsh et al. (1993) reported on the history, husbandry, and breeding of *V. komodoensis* at SNZP. Birchard et al. (1995) followed oxygen uptake in these *V. komodoensis* eggs and the energetics of prolonged development. In 2006, Phillip et al. described parthenogenesis in *V. komodoensis* at London and Chester Zoos:

> "This reproductive plasticity indicates that female Komodo dragons may switch between asexual and sexual reproduction, depending on the availability of a mate — a finding that has implications for the breeding of this threatened species in captivity… It occurs in captive snakes and has been implicated in one other species Argus monitor lizard (*Varanus panoptes*)."

Parthenogenesis has now been observed in at least seven species of *Varanus* (Lenk et al. 2005; Konáš 2007; Hennessy 2010; Weichmann 2012; Hörenberg 2013; Grabbe 2014; Grabbe and Koch 2014; RWM, unpubl.). Additionally, given its apparent prevalence in captive varanids, an older case of suspected delayed fertilization in Gould's Monitor (*V. gouldii*) at DZ (Doles and Card 1995) might have been a case of parthenogenesis.

Perry et al. (1993) described the first captive reproduction of *V. g. griseus* at the Research Zoo of Tel Aviv University in Israel (Figs. 7, 8). Visser (1981, 1985) provided notes on the breeding of *V. albigularis* and the Yellow Monitor (*V. flavescens*) in Rotterdam Zoo. Bosch (1999) bred *V. prasinus* in the Löbbecke Museum + Aquazoo, Düsseldorf (Germany). Barker (1984)

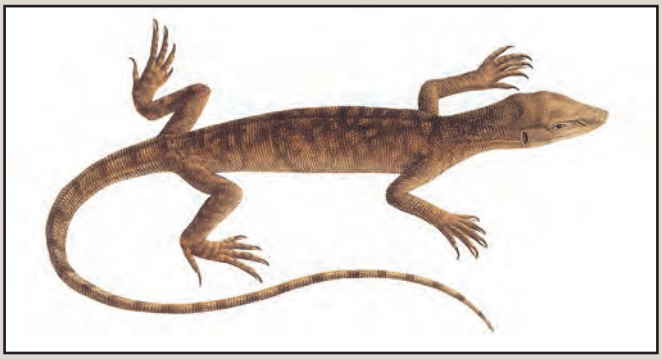

Fig. 7. *Varanus griseus* from "Symbolae Physicae-Zoologica" by Christian Gottfried Ehrenberg in 1828.

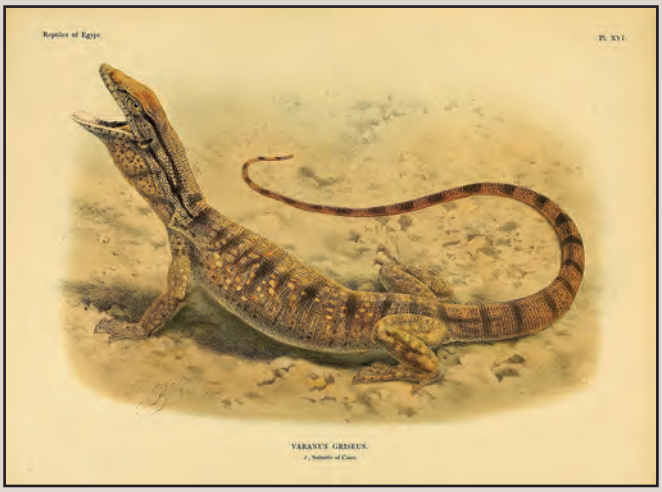

Fig. 8. *Varanus griseus* in John Anderson's "Zoology of Egypt" in 1898.

reproduced Biak Tree Monitors (*V. kordensis*) at DZ. Boyer and Lamoreaux (1983) and Horn (1978) bred *V. gilleni*; Husband (1991) bred this taxon at the Australian Reptile Park. Mitchell (1990) reported on the reproduction of *V. gouldii*, and Card (1994) reported double clutching in *V. gouldii and V. olivaceus* at DZ. Radford and Paine (1989) hatched five *V. dumerilii* and one Black Tree Monitor (*V. beccarii*) at Buffalo Zoo in 2005. Fisher (2012) described husbandry and reproduction of *V. beccarii*. Irwin (1996) described courtship, mating and egg-deposition by *V. giganteus* at the Queensland Reptile and Fauna Park (now Australia Zoo) and DZ (W. Card, pers. comm.). Rehák (1996) followed the reproductive biology of the Mangrove Monitor (*V. indicus*) in Prague Zoo; several important studies on the biology of this species have resulted from the captive-bred individuals hatched at this zoo (Frýdlová et al. 2011; 2013a,b; 2017a,b; Frynta et al. 2010; Gregorovicova 2012). Wicker (1993) presented reproductive data on *V. acanthurus* at Frankfurt Zoo. Stirnberg (1997) described care and breeding of *V. varius* in Bochum Zoo that led to 2nd generation offspring.

A number of varanids lay eggs in termite mounds (Green et al. 1999):

"The internal temperature of termitaria of *Nasutitermes exitiosus*, the mound species used by *V. rosenbergi*, is maintained by the termites at around 30°C for most of the year, but shows a mid-winter decline to around 20°C…In addition, humidities are high throughout the year…There is a protective earthen outer wall that is comparatively soft and friable, but about 10cm beneath the mound surface there is an extremely hard inner layer of material (about 14cm thick) that is difficult to penetrate…On the inner side of this layer are the warm nursery galleries, and these consist of a flaky material that is easily broken."

Kirshner (2016) described various aspects of the termite mound nesting biology of Rosenberg's Monitor (*V. rosenbergi*). Carter (1999) described nesting and evidence of parental care by *V. varius. Varanus varius* lay eggs in the center of mounds. The eggs incubate within the mound for about 290 days and hatch in mid-spring. At hatching, the adult (probably the female) digs into the termite mound to release the hatchlings. What is remarkable is that the adult remembers the location of the eggs after ca. 8 months.

At DZ, a pair of *V. varius* were observed courting, followed by copulation. The male slowly followed the female until she stopped moving, then began scratching her dorsum with his foreclaws. After this behavior, which lasted about 5 min, he straddled her and twisted his tail to align their cloacae and inserted the hemipenis. Copulation lasted about 15 min. No eggs were produced. Complete descriptions of the reproductive biology of captive *V. varius* were published by Kirshner (2007) and Horn (1991).

Eidenmüller and Wicker (1991) covered captive breeding, artificial egg incubation, development and surgical removal of impacted eggs in *Varanus similis* at Frankfurt Zoo. Stefani (2008) outlined husbandry protocols and reproduction of the Peach-throated Monitor (*Varanus jobiensis*) in captivity (earlier referred to as *V. karlschmidti*). Jackson (2005) outlined history, natural history, captive breeding, and husbandry in the Rusty Monitor (*V. semiremix*).

Interactions with Humans

In 1942, Gustav Lederer published observations on captive *V. komodoensis* at Frankfurt Zoo, including a photograph of a woman with a large dragon. Lederer discovered that dragons are able to distinguish one person from another. At this zoo, the dragon knew the veterinarian after the second treatment and could no longer be persuaded to leave its hiding place when the vet appeared. The lizard even recognized the operating table and fled from it (Lederer 1931). He described the habits of this tame dragon that lived at the Frankfurt Zoo between 1927–1944. It was taken on long walks through the zoo by the director. The dragon was in excellent health up to its death from an Allied bombing raid in which the facility was demolished, thus living 16 years, 8 months, and 21 days. At DZ, curator Ruston Hartdegen and associates discovered that a dragon could discriminate among its permanent keeper, another reptile keeper who had less contact with the dragon, and a keeper from another animal department. The dragon was calm with the familiar caretaker, nervous around the less-familiar reptile keeper, and displayed defensive behavior to the keeper from another animal department (R. Hartdegen, pers. comm.). Kraken, the first dragon hatched at SNZP in 1992, exhibited the same individualized responses toward familiar and unfamiliar persons.

London Zoo reptile curator Joan Beauchamp Procter (1928) examined dragon behavior:

"The question of the ferocity of these lizards is, perhaps, the most misunderstood of all. All the lizards of the genus

Fig. 9. *Varanus niloticus* in John Anderson's "Zoology of Egypt" in 1898.

> *Varanus* are savage, predatory, and highly strung, and they use their teeth, claws and slashing tails with great effect, as I have personal cause to know. At the Zoo we consider any large monitor more dangerous to deal with than a crocodile twice its size. But, allowing for this, *V. komodoensis* is the gentlest, most intelligent, and most tractable of them all. This is comparing them with specimens only half their weight of species such as *niloticus*, *albigularis*, *bengalensis*, *salvator*, *nebulosus*, *varius*, and so on. It is quite true that they are very nervous, and also that they could no doubt kill one if they wished, or give a terrible bite when taking food from the hand greedily, but there is no vice in them."

Procter included a photograph of a two-year-old child standing next to an adult dragon and wrote:

> "The dragon, whose name is Sumbawa, walked around a very long table, and without paying attention to the audience ate a large fowl, several eggs, and a pigeon from her hand, allowing itself to be scratched and patted even when swallowing the fowl with enormous gulps, treatment which even dogs will not always permit … She [at death proved to be a male] would tear a pig to pieces but can be trusted with children."

Sumbawa was the host at children's tea parties a few weeks after arrival at the Zoo and was perfectly tame with all the guests. Sumbawa accompanied Procter on strolls through the Zoo during her inspections investigating everything that might be of interest. The lizard responded to the voice of its keeper or curator but disliked having its tympanum touched. Procter's experiences and her fondness for Komodo Dragons have recently been turned into a children's book, *Joan Procter, Dragon Doctor: The Woman Who Loved Reptiles* (Valdez and Sala 2018).

Murphy and Walsh (2006) and Murphy et al. (2002) described many instances of dragons and humans interacting without incident. Gordon Burghardt of the University of Tennessee filmed sequences of a dragon at Zoo Knoxville interacting with a cardboard box, Frisbee, bucket, small balls, shopping bag containing a shoe within a cardboard box, and exploratory tongue-flicking on his torso. The lizard stuck its head into the bucket and shoe and carried both around the enclosure. At DZ, a tame adult *V. niloticus* (Fig. 9) was used in demonstrations for several years. Atypical for the species, this lizard was completely tractable and allowed many visitors to pet and hold it.

A most enjoyable read is an account by Eric R. Pianka and Samuel S. Sweet (2016)—*Field Observations by Two American Varanophiles*. For many herpetologists, studying monitor lizards in Australia would be a dream come true but to actually do so is very challenging: biting insects, difficult terrain, isolation, finding and catching lizards in blasting dry heat and dangerous rainstorms while avoiding injuries from the monitors. ERP spent about 48 months over a 42-year period in the Great Victoria Desert. SSS worked 31 months in the field over 13 years in tropical northern Australia, primarily in Kakadu National Park. The superb *in situ* photographs show the beauty and difficulty in traversing the study sites within the various habitats and the magnificence of these varanids living there. ERP remembers:

> "For one of my birthdays, Helen embroidered an accurate and beautiful *Varanus eremius* on the back of a nice shirt. Sadly, I have grown too fat and can no longer fit into this fine shirt! When I was still lean and mean, I wore it proudly to a herpetological society meeting — as I was walking along, someone behind me called out my name — the guy turned out to be none other than my good buddy fellow varanophile Jim Murphy who knew *Varanus eremius* was my favorite lizard and who recognized the species."

Great Escapes

Because of their intelligence and problem-solving abilities, captive monitor lizards can be quick to exploit defects or flaws in their exhibits and enclosures or take advantage of keeper errors. As a result, there are numerous accounts of escapes in zoos; in some cases it took several days or weeks to apprehend an animal, and in others, captives were never retrieved. While working at the Long Island Reptile Museum (LIRM), a former reptile zoo in New York (see Mendyk 2015), RWM witnessed several monitor escapes worth noting. A male *V. melinus* escaped from its exhibit and worked its way up into the ductwork in the ceiling of a service corridor where it could not be retrieved. Keepers would periodically encounter the animal basking out in the open under overhead skylights in the museum's gallery when they would arrive for work in the morning, but it managed to evade recapture for several weeks. A 1.2-m long *V. salvadorii* acquired through a seizure from a local drug dealer's residence managed to squeeze through a small gap and access the crawl space in the ceiling above its exhibit. Perched on ladders with their heads poking up through the ceiling tiles on opposite ends of the exhibit, RWM and a fellow keeper attempted to direct the animal towards either side by poking at it with broomsticks. Poked from the opposite side of the enclosure, the monitor lunged towards RWM with its mouth agape, causing him to fall backwards off the ladder and into the exhibit's shallow pool below. The resulting sprained ankle was an acceptable alternative to a bite to the face given the impressive dentition of the species. RWM was told of an incident involving an escaped *V. cumingi* at the LIRM that managed to crawl behind a wall in the main exhibit gallery. Without hesitation and in front of numerous museum visitors, the facility's owner took to the wall with a sledgehammer, proceeding to punch large, gaping holes in the drywall until the animal could be located and captured by hand. Unaware of why this was going on, the looks on the museum visitors' faces were priceless (T. Baez, pers. comm.).

Despite varanids' reputation and propensity for exploiting weaknesses in enclosures or keeper errors (e.g., leaving an

enclosure door unlocked), sometimes escaped individuals do not travel far, or even depart when given the opportunity to do so. Ruston Hartdegen recalled an incident at DZ where he transferred an older *V. olivaceus* to an attached shift enclosure while the glass window of its exhibit was waiting to be replaced. The following morning, the curator commented on how great the *V. olivaceus* looked on display, having shifted the animal back into its exhibit the previous night. Knowing that the glass had not yet been replaced, a perplexed Hartdegen went to check on the exhibit to find the monitor basking contently on a perch just a few feet away from the missing window pane of the exhibit!

Some accounts document monitors returning back to the enclosures they originally escaped from. For example, Kent-Seville (1897) reported on a *V. varius* that returned to its outdoor enclosure 10 days after escaping, but now missing part of its tail and in poor physical condition. Kent-Seville (1897) also referenced a monitor (species not identified, but probably *V. salvator*) that escaped from its holding enclosure in northern Borneo that was found back at its enclosure just a few days later.

Grossly underestimating their climbing abilities, keepers at the Bronx Zoo were surprised when one of two Komodo Dragons that arrived in 1955 promptly escaped from their enclosure—a former Galapagos Tortoise exhibit (Dunto 1955; Bridges 1959). A *V. komodoensis* nearly escaped from the Antwerp Zoo when it was taken outside into an uncontained area for photographs and took off running; luckily a keeper was able to grab its tail at the last moment before it got away (Berg 1959). Possibly unsatisfied with the nesting options provided to her, a gravid female *V. salvadorii* managed to escape from its enclosure at the Honolulu Zoo by squeezing through a two-inch gap in the corner of its exhibit (Meier 2000). When captured and returned to its enclosure, it immediately returned to the precise spot where it had escaped from, demonstrating remarkable spatial memory. Conners (2004) noted that a juvenile *V. komodoensis* escaped its outdoor enclosure at Zoo Miami and was free for more than two months. In his 1958 book, *Zoo Hunt in Ceylon*, German animal dealer Heinz Randow described the escape of an enormous 3-m long *V. salvator* that had been captured and held at his facility in Ceylon (now Sri Lanka) awaiting export to a European aquarium. There, it was housed in a large wooden crate and fed a diet of flying foxes every other day. One day it managed to escape but was found shortly thereafter dragging the heavy wooden crate behind it, to which it had been tethered.

Escapes from private reptile keeper collections are far more extensively documented in local newspapers, and date back to the late 1800s (Zandera 1895; Kent-Saville 1897). It is suspected that escaped or intentionally released pet *V. niloticus* are responsible for the introduction and establishment of the species in southern Florida, USA, where there are now at least three known populations (Enge et al. 2004; Wood et al. 2016).

Feeding Behaviors

Several authors have described that varanid lizards are capable of modulating their transport kinematics in response to different prey. Although these lizards use inertial prey transport, they also modulate tongue and hyoid movements in response to different prey types. Schaerlaeken et al. (2011) wrote:

> "The ability to modulate feeding kinematics in response to prey items with different functional properties is likely a prerequisite for most organisms that feed on a variety of food items. Variation in prey properties is expected to reveal variation in feeding function and the functional role of the different phases in a transport cycle. Here we describe the kinematics of prey transport of two varanid species, *Varanus niloticus* and *Varanus ornatus*."

Smith (1986) described varanid feeding:

> "The morphology and function of the tongue and hyoid apparatus in *Varanus* were examined by anatomical and experimental techniques. Morphological features unique to *Varanus* include a highly protrusible tongue that has lost a roughened dorsal surface, an exceptionally strong and mobile hyobranchial apparatus, a welldefined joint between the ceratohyal and anterior process, and a series of distinct muscles inserting at the anterior hyobranchial region. *Varanus* is also unusual among lizards in a number of feeding behaviors; it ingests prey entirely by inertial feeding, as the tongue does not participate in food transport."

Thompson (1995) followed the feeding behavior of *V. gouldii* in the wild. The abstract from that paper reports:

> "Two Gould's goannas (*Varanus gouldii*) were intensively observed in the semi-urban environment of Karrakatta Cemetery, Perth, Western Australia. After emerging and basking to increase their body temperature, they spent most of their time out of their burrows foraging, primarily in leaves between grave covers, and under trees and shrubs. Mean speed of movement between specific foraging sites was 27.6 m min^{-1}, whereas the overall mean speed while active was only 2.6 m min^{-1} because of their slower speeds while foraging. A number of specific body postures were observed, including; vigilance, walking, erect, and tail swipes. Specific feeding and avoidance behaviours were also recorded, along with the influence that two species of birds had on their selection of foraging sites."

Large varanids forage in a slow deliberate manner, swinging the head from side to side and following prey trails by using the forked tongue to evaluate both sides of the trail without requiring the lizard to constantly shift from side to side (Schwenk 1994, 2000). Young (1997) reported that monitors lack taste buds. At DZ, Garrett and Card (1993) found that rapid tongue-flicking enables monitors to pick up olfactory cues. Losos and Greene (1988) examined the ecological and evolutionary implications of diet in monitor lizards. Arboreal monitors have unique ways to handle prey. Irwin (1994) reported on the behavior and diet of the Canopy Goanna (*V. keithhornei*) at the Queensland Reptile and Fauna Park (now Australia Zoo). Hartdegen et al. (1999) observed feeding behavior of *V. beccarii* at DZ. These lizards often take struggling prey to a horizontal branch used as a permanent killing station, much like raptors.

Should prey be hidden inside a hole in a tree branch and the opening too small to accommodate the lizard's head, a clever alternative is employed by members of the *V. prasinus* complex. Once the prey item is detected by smell or by sight, *V. beccarii* and *V. prasinus* tongue-flicked around the opening to investigate its content, then stuck their snouts in the opening, only to discover that the food was out of reach. After the unsuccessful attempt with their snouts, they reached into the hole with a forelimb while maintaining eye contact with the food, and the prey was hooked with the claws. Both species have exceedingly

Fig. 10. *Varanus beccarii* using the forelimb to probe for inaccessible prey. From Mendyk and Horn (2011).

Fig. 11. Illustration of *Monitor gemmatus* (now *V. bengalensis*) from "The Animal Kingdom" by Baron Cuvier and P. A. Latreille (Plates, Vol. II, Reptiles–Fishes) in 1834.

sharp claws on their forefeet which are inserted into the opening to impale rodent prey, which is quickly extracted and consumed. Extraction of food items out of a small opening requires highly coordinated movements of the forelimb, wrist, and digits (Fig. 10; see Mendyk and Horn 2011; Mendyk 2012; Kuppert 2013). Shuter (2014) reported that a 13-yr old captive-bred male *V. prasinus* submerged itself underwater to secure prey at the Bronx Zoo. Hartdegen et al. (2000) described prey laceration by using the sharp foreclaws of *V. prasinus* and *V. beccarii* at DZ.

Traeholt (1993) found that *V. salvator* dispatches live mice by seizing them consistently behind the head/cervical region (76.7%) rather than the stomach (9.0%) or tail (5.0%). [In contrast, venomous snakes that are ambush predators such as pitvipers and true vipers carefully strike rodents. If the mouse or rat approaches frontally, they often wait until the prey offers a lateral view and strike. Usually the prey is released after the strike, especially if the rodent is too large and possibly dangerous, and the snake accurately follows the trail (see Boyer et al. 1996).] He divided treatment of prey into three broad categories"Shake", "Scrape" and "Crush Head and Neck." Horn (1999) mentioned teamwork between two *V. niloticus* as they may cooperate when raiding bird or crocodile nests. At DZ, an adult *V. indicus* recently collected from the wild in West Papua passed shell fragments from a newly hatched Fly River Turtle (*Carettochelys insculpta*).

Jaman et al. (2007) evaluated population status and feeding of *V. bengalensis* and *V. flavescens* in Bangladesh (Figs.11, 12). The study showed that *V. bengalensis* preferred invertebrates whereas *V. flavescens* sought vertebrate prey. The authors concluded that there was significant niche separation. These differences suggested that future conservation plans should be aware of population numbers. *Varanus bengalensis* are significantly more numerous than *V. flavescens*.

Eight *V. gouldii* hatched at DZ in 1996 were used to compare chemosensory behavior and prey trail-following (Garrett et al. 1996; Fig. 13). In the trail-following experiment, an S-shaped trail was laid on a paper substrate and a dead mouse carcass was pulled along the trail and hidden behind a barrier at the end. The following variables were recorded: time when the lizards contacted the trail; time when rodent was located; amount of time the lizard's head was within the trail area; total number of tongue-flicks while in the testing arena; and total number of tongue-flicks within trail. Naturally, the trails followed lizard bodies. A series of experiments were performed using these recently-hatched lizards as a stimulus to study tail-luring in Death Adders (*Acanthophis antarcticus*). These lizards were separated from the snakes with a glass panel and were susceptible to the lure, lunging at snake tails.

Captive *V. albigularis* were observed by John (Andy) Phillips at San Diego Zoo, who found that these lizards are capable of numerical discrimination (Pianka et al. 2004). The varanids were fed four snails in an enclosure with separate compartments with movable partitions—opened one at a time allowing a monitor to eat each of the four snails. After the last snail was consumed, the lizard was allowed access into another adjacent chamber containing four more snails. After the lizard became conditioned to expect four snails, one snail was removed from some snail groups—all the test lizards searched extensively for the missing fourth snail, even when the door to the next group was open.

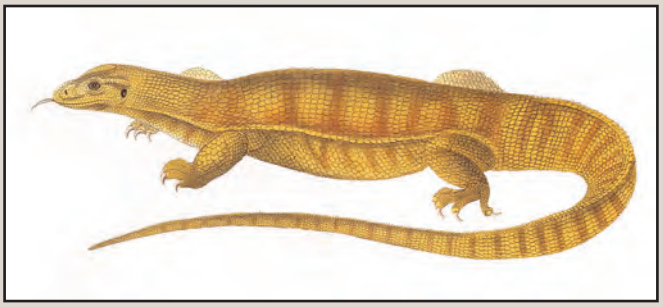

Fig. 12. *Varanus flavescens* from "Illustrations of Indian Zoology Chiefly Selected from the Collection of Maj.-Gen. Hardwicke" by John Edward Gray in 1830–1835.

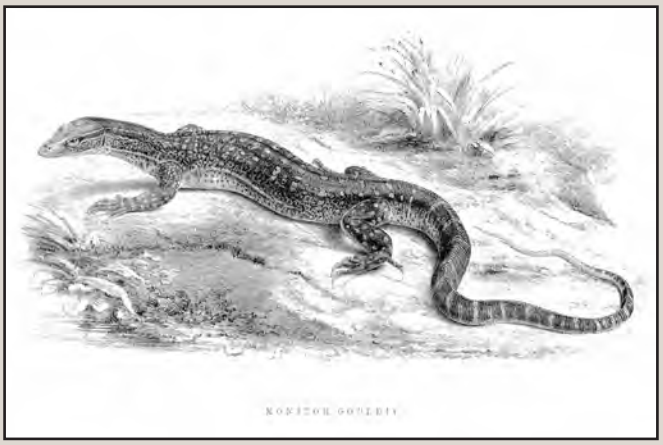

Fig. 13. Illustration of *Monitor gouldii* now *V. gouldii* from "The Lizards of Australia and New Zealand" by John E. Gray and Albert Günther from 1845 to 1875.

Fig. 14. *Varanus dumerilii* from "Verhandelingen over de natuurlijke geschiedenis der Nederlandsche overzeesche bezittingen…" by Salomon Müller in 1839–44.

This clever experiment was expanded to demonstrate that these monitors can count up to six. If snails were offered in groups of larger than six, the monitors gave up counting, eating all before moving on to the next chamber. This ability to count possibly evolved as a consequence of raiding nests of mammals, birds, and reptiles, since average clutch or litter size of prey would probably be less than six. Phillips and associates have extensively studied varanid biology, publishing their findings in a series of papers from 1992 to 1998. *Varanus albigularis* regularly consumes venomous snakes, including Puff Adder (*Bitis arietans*), African Viper (*B. caudalis*), Egyptian Cobra (*Naja haje*), and Black-Necked Spitting Cobra (*Naja nigricollis*). JBM saw a nature film of this monitor attacking an adult *N. nigricollis*. The snake was grabbed at mid-body and was vigorously shaken and battered against the rocky substrate, preventing accurate spraying of the venom. When the snake was disoriented after about 15 min, the lizard released it and quickly seized the head. The snake was still moving weakly during swallowing until the end of the episode. It never was able to bite the lizard during the violent struggle.

One of the most interesting papers on *V. albigularis* was written by Bill Branch in 1991 called "*The Regenia registers of Brown (1869–1909). "Memoranda on a species of Monitor or Varan.*" Branch covers all aspects of Alfred 'Gogga' Brown's extensive observations—sex ratio, size, body proportions, hemipenial morphology, visceral fat bodies, coloration, diet, cause of death, longevity, reproduction, gestation period, egg laying, oviposition, eggs, clutch size, hatchling size, incubation period, growth, behavior, mating behavior, shedding, thermoregulation, predation, parasites, exploitation, seasonal activity, and retreats. The amount of information that Gogga collected on his captive lizards and on wild counterparts in the late 19th century is truly astounding.

JBM saw a film at a European monitor conference of an adult *V. dumerilii* attacking a large crab (Figs. 14, 15) and it was grisly. The lizard began by pulling off both pinching claws, then removing each leg until only the carapace remained. Each part was quickly ingested. The crab was still alive but finally died when the monitor crushed it in its jaws and swallowed it piecemeal. This behavior was discussed by Krebs (1979, 1991, 2016).

Three frugivorous and largely arboreal monitors occur in the Philippines: Sierra Madre Forest Monitor (*Varanus bitatawa*), Mabitang (*V. mabitang*), and *V. olivaceus*. Fruits, snails, and palm nuts are eaten by wild *V. olivaceus* but four captives at DZ refused all available fruits, snails, and nuts available from local Asian markets but fed voraciously on mice and rats. Invertebrates such as crabs and insects were ignored as well as birds and bird eggs. Yuyek (2012) described husbandry and reproduction of *V. olivaceus* at the Avilon Montalban Zoological Park; thawed chicken parts and rodents were accepted. Recchio (2016) outlined husbandry and reproduction at Los Angeles Zoo, which included a diet comprised of several fruit items. Sweeney et al. (2017) compared nutritional elements in captive versus

Fig. 15. Hatchling *Varanus dumerilii* have bright red heads and glossy black bodies with creamish transverse bands to potentially mimic several highly venomous sympatric snakes. Illustration by Carel Pieter Brest van Kempen ("A Kerangas Forest Floor – Hatchling Dumeril's Monitor," 2012. Acrylic on illustration board, 30" x 20"). Kerangas is an Iban term referring to the fact that the soil is too poor to grow rice. Dominant tree species usually belong to the mangosteen family. Orchids show the greatest species diversity. Species of melastomes, laurels, myrtles, and gingers are also commonly represented. Many plant species bear nitrogen-fixing bacterial nodules on their roots, and carnivorous plants also thrive. Species of the pitcher plant genus *Nepenthes* trap insects in leaves that are modified into water-bearing pitchers. Bladderworts (*Utricularia* spp.) and Sundews (*Drosera* spp.) also trap small arthropods.

wild lizards and found that the sugary cultivated fruits typically offered in captivity were vastly different nutritionally from the fruits consumed in nature.

Tourists arrive by ship several times a week to Komodo Island to watch demonstrations of dragon feeding behavior. A 46-kg *V. komodoensis* ate a 41-kg wild pig, which left its belly grossly distended and dragging on the ground (Auffenberg 1981). JBM watched dragon feeding behaviors on Rinca and Komodo Islands. The visitors stood on a high overlook on Komodo Island and the rangers tossed dead goats down to the dragons. At the former site, a freshly killed adult goat was presented by the rangers to 20 lizards ranging in size from adult males to subadults. The largest lizards were near the carcass and the smaller ones dashed in to grab scraps flung by the bigger ones since cannibalism was a real danger. The time span between the carcass hitting the ground and until nary a speck of goat remained was 7 min. Surprisingly, the lizards did not bite one another. After the feeding, two adult males engaged in vigorous bipedal combat for ca. 15 min; no biting took place and the subordinate animal quickly left the arena (see Schuett et al. [2009] for explanation of evolution of bipedal postures). The rangers tied the hindquarters of a goat to a tree, so the lizards had to adopt a bipedal stance; they never jumped to reach the food. The rangers also tied the hindquarter to a long rope and ran with the lizards following like the pied piper; fortunately, the humans were faster than the lizards. The dragons were habituated to the area, waiting for goats to fall from the sky and no longer showed predatory behavior. The rangers were worried that the demonstrations led to deleterious effects, so these shows were discontinued. Quentin Bloxam from Jersey Wildlife Preservation Trust (pers. comm.) documented that after the cessation of artificial feeding some of these varanids simply remained in place and starved to death.

On Rinca, JBM observed a subadult dragon foraging for over two hours with no success. Every rock or hiding place was investigated with rapid tongue flicking; the tail was not used to frighten hidden prey in to the open. A Sambar deer bellowed a plaintive stress call next to a dirt trail. Ten minutes later, an adult lizard slowly crossed the trail, presumably tracking the deer, about 3 m in front of JBM and totally ignored him.

Chris Wemmer told JBM that many years ago, SNZP herp keepers routinely fed dead animals from the collection after necropsy to reptiles. Head keeper Lee Schmeltz acquired a carcass of a Muntjac (known also as the Barking Deer from Asia, Sri Lanka, Taiwan, Indonesia islands, and central China) that recently died in the collection and fed it to the *V. komodoensis* during visiting hours. The dragon seized the muntjac by the belly and tossed its head in a violent slashing motion which eviscerated the deer, splashing the glass front of the enclosure with blood, metabolic by-products, and entrails. Predictably, the incident was reported in record time to higher authorities and Schmeltz was warned never to let it happen again (Murphy and Xanten 2007, Murphy 2015). Kuppert (2013) recorded trailing behavior in a dragon at SNZP:

> "The scent trail experiment clearly shows this Komodo Dragon's RTF increased greatly as it approached the prey and was in immediate proximity to it. The experiment gives insight in how the trailing behaviour is manifested. Shorter and more tongue flicks also indicate intensified investigatory behaviour. Knowing that Komodo Dragons have the ability to follow prey over several kilometres can be the basis for an olfactory-based enrichment regimen. One approach could be to construct an artificial scent trail that leads to a buried food item, similar to the one in the experiment conducted. This approach stimulates the animals to be active. Since many Komodo Dragons in captivity are overweight (J. Gerrits, personal communication 15. Feb. 2012), this feeding approach might increase an individual's physical exercise and be a mental stimulus."

Defecation

For smaller species of monitor lizard and juveniles of larger taxa, it may be advantageous for an individual not to defecate close to its refuge site, where pythons and other olfactory-driven predators could potentially track down their whereabouts. In captivity, monitors are limited in the distance they can travel

to defecate, which can pose a problem for dispersing their feces. With impeccable precision, *V. beccarii* in RWM's private collection learned to aim and direct their feces out a small gap along the bottom edge of the door to their enclosure, leaving a mess on the room's floor daily. Probably serving a similar anti-predatory function, water monitors belonging to the *V. salvator* complex are notorious for defecating in their water in captivity – leaving keepers with the task of frequently cleaning out water tubs and pools with some of the most vile and putrid sewage produced in the herpetological world. Even worse was the keeper at the LIRM who stumbled while carrying a tub full of rancid *V. salvator* water and ended up sloshing it all over himself. Without a shower at the facility or a change of clothes, he had no other option but to rough it out for the remainder of the workday in his soiled clothing. Another keeper sustained a serious bite to the hand by a *V. cumingi* while it was submerged in a putrid pool of fouled water which, in addition to major reconstructive surgery to the hand, required months of aggressive antibiotic therapy.

Defecation could also be used to confuse predators. At the Bronx Zoo, a female Ornate Monitor (*V. ornatus*) regularly defecated on top of her freshly nested clutches of eggs (Lee 2000)—possibly as a scent deterrent to egg predation. A female *V. salvadorii* at the Denver Zoo defecated exclusively on top of her nest site for a period of more than three months (Trout, 2007). Similar behaviors have also been observed in several other monitor species in captivity (RWM, unpubl. data; F. Retes, pers. comm.).

Enrichment and Training

Hayes et al. (1981) called for zoo workers and others working with captive animals to include amphibians and reptiles in their enrichment schemes, countering a common belief that they possessed limited cognitive and emotional needs. Behaviorist Gordon Burghardt has researched environmental enrichment and cognitive complexity in reptiles, including varanids, focusing on implications for captive populations (Burghardt 1977, 2013). In White-throated Monitors (*V. a. albigularis*), a large carnivorous species, Burghardt and associates found that sensory cues and foraging decisions were influenced by various snail presentations (Kaufman et al. 1996). In his many papers on improper environmental effects and deleterious end results in captive reptiles, he outlines ways to make the complex lives of varanids and other reptiles far more interesting (see Burghardt et al. 2002 for unexpected behavioral elements in *V. komodoensis*).

Monitors have shown remarkable learning abilities. As an example, 16 Black-throated Monitors (*V. albigularis microstictus*) reared from hatching at the Dallas Zoo in off-exhibit housing were used in trials to track differences in learning between lizards in complex, enriched settings and others in stark enclosures as described in Manrod (2003) and Manrod et al. (2008):

> "A transparent food tube contained several prey. The food tube allowed the monitors to obtain prey by using hinged doors at either end of the tube to access food. All eight lizards learned to open the tube, insert head, and capture the prey within 10 min."

Not surprisingly, varanids in complex environments learned more quickly.

A prey density-dependent foraging experiment by Kaufman et al. (1996) is described in the paper's abstract:

> "Results showed that at high prey density, these lizards selected large over small snails. At low prey densities, however, large and small snails were selected at an equal rate. Apparently, when prey densities are high, the lizards have the opportunity to select the larger prey items without incurring locomotor costs. These data support optimal foraging theory but are unique in that they are an example from a little-studied, widely foraging species of lizard."

Using several taxa of varanids at Zoo Atlanta (*V. komodoensis, V. griseus, V. rudicollis, V. albigularis*), Diaan Gaalema ran multiple experiments for food choice, reinforcer preference, and visual discrimination. The results show that these types of trials can be undertaken in a zoo.

Firth et al. (2003) examined responses by *V. ornatus, V. albigularis,* and the Savannah Monitor (*V. exanthematicus*) to a repeated food source, asking if this was evidence for association learning.

> "Food location times have been recorded in three captive monitor lizards (*Varanus* spp.). The results, in the form of regression equations, showed that in general the time taken to locate the food decreased with the number of times the food was offered."

Hellmuth et al. (2012) provided suggestions for operant conditioning and training, using *V. niloticus, V. beccarii,* and *V. komodoensis* in examples of trained behaviors for facilitating veterinary procedures in reptile species in zoos. Murphy and Walsh (2006) discussed various examples of training in *V. komodoensis*:

> "At the London and Houston Zoos, ultrasonography without anesthesia is used to determine sex and assess reproductive condition on dragons; the dragons remain calm during the procedure.
>
> In London, a large male dragon (named Raja) was trained to use a restraint box for target training. Dragons are trained to associate a target on a stick with a food reward. The target is moved into and out of the restraint crate so that the dragons become comfortable entering this restricted space, which facilitates moving them. This interesting example of operant conditioning used food as the initial cue — then the reward frequency was gradually reduced, using a clicker (sound producing device) as a bridge between the target and reward (R. Gibson, pers. comm.).
>
> At the Pittsburgh Zoo, a study was initiated to test a dragon's spatial memory by examining whether dragons use proximal (near-by) or distal (far away) visual cues to remember the location of a food reward hidden in the lizard's exhibit. Preliminary results support the hypothesis that a dragon used proximal cues to remember the location of the food and additional experiments are underway to determine if a dragon can use distal cues in other circumstances (H. Ellerbrock, pers. comm.)."

Several zoos have focused on conditioning large varanids for voluntary participation in routine veterinary procedures including radiographs (Anonymous 2006; Ainsworth 2013), nail trimmings (Herndon 2001; Ainsworth 2013), weight measurements (Herndon 2001; Anonymous 2006), blood (Anonymous 2006; Camina et al. 2013) and saliva collection (Gully 2013), and crate training for transport (Mader and Divers 2003; Helmuth et al. 2012) or medical procedures (Fleming and

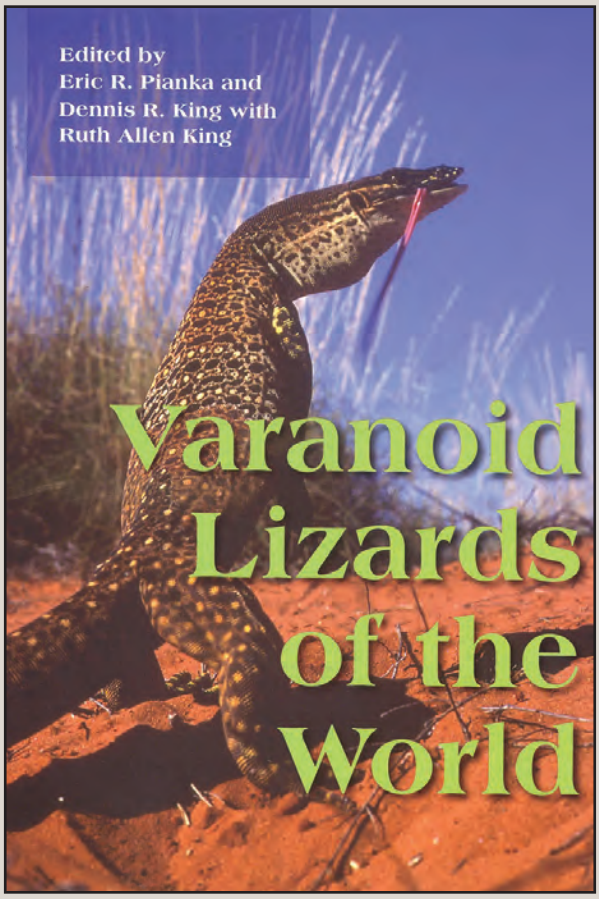

Fig. 16. This superb volume incorporates virtually all information on varanid lizards. Thirty-five of the most prominent authors studying monitor biology provide up-to-date overviews on all taxa. The volume also includes information on the varanoid clade—helodermatids, and the taxon *Lanthanotus borneensis*. The species *Estesia mongoliensis* is known exclusively from fossils.

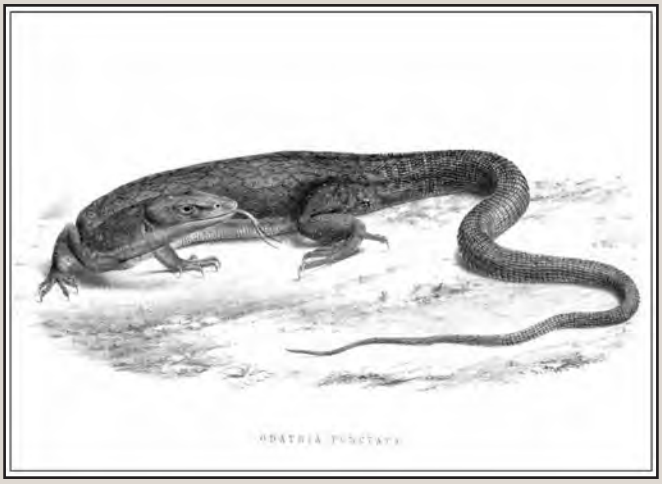

Fig. 17. Illustration of *Odatria punctata*, now *V. tristis* from "The Lizards of Australia and New Zealand" by John E. Gray and Albert Günther from 1845 to 1875.

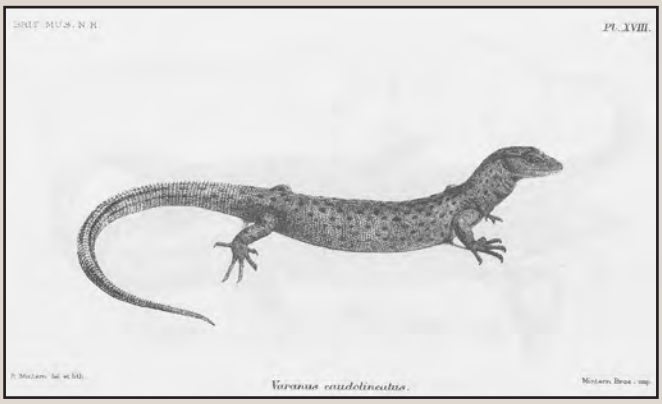

Fig. 18. Illustration of *Varanus caudolineatus* from "Catalogue of the Lizards of the British Museum, Volume III" by George A. Boulenger in 1887.

Skurski 2013). At Taronga Zoo, Boylan (2011) recalled training a *V. komodoensis* to walk through the zoo to its new enclosure, and Donato (2008) mentioned training a large *V. salvadorii* at the Saint Augustine Alligator Farm for use in educational demonstrations.

"Lizard Kings"

In 2009, the US Public Broadcasting System (PBS) presented an award-wining film on varanids in the series NOVA called "Lizard Kings," created by Gisela Kaufmann and Carten Orlt. Segments included history, hatching, a Perentie attacking and consuming a highly venomous Eastern Brown Snake (*Pseudonaja textilis*), reactions to wildfires, and interactions with humans.

A number of research projects and observations by prominent biologists are presented. Lizard Man Eric Pianka discusses his long-term lizard diversity studies in the Red Sands, Great Victoria Desert in Australia with field assistant Stephen Goodyear. The film shows views of his field camp, use of pit traps, trailing by following tail marks left in sand, construction of daily nocturnal burrows by *V. gouldii* for thermoregulation, and tracking using Lizardcam with Oxford biologists Lucas Bluff and Christian Rutz. Eric's sense of humor is in full bloom—his personal contest called "flies out of my face" where he swats at the unbelievable density of these annoying creatures and is quite pleased with himself when he kills two with one stroke. Imagine his unbounded pleasure if three or more are smashed! Two nightmares follow—a giant monitor chasing and swallowing him and "War Crimes," a Nuremberg-like trial explaining the thousands of lizards (35,000+) killed for his studies with a *V. giganteus* as judge and many lizards (thorny devils, frilled lizards, bearded dragons and so on) as jury: Verdict—DEATH by hanging!

Pianka has watched lizard diversity negatively impacted by climate change over the past several decades in Australia. Due to a ca. 20% increase in rainfall, spinifex and other desert plants have been replaced by shrubs and other moisture-loving flora, causing a dramatic shrinkage in saurian biodiversity.

Gordon Burghardt and associated researchers demonstrate target training experiments with *V. exanthematicus* at the University of Tennessee. Former Curator Ian Stephens at London Zoo shows an array of different human-dragon interactions such as trailing, targeting, and allowing keepers to brush off dead skin with soapy water on the entire body of the famous dragon, Raja.

Michael Cota and others show an amazing sequence of *V. salvator* combatting, mating, and foraging for table scraps between and around the diners' feet/legs and on top of the tables at Dusit Zoo, Thailand.

PHOTO BY R. W. MENDYK

FIG. 19. Arrow shows 2-m *Varanus salvator* swimming at Lumpini Park, Bangkok with city skyline in the background.

PHOTO BY R. W. MENDYK

FIG. 20. *Varanus salvator* is abundant on the grounds and in the waterways of Bangkok's Dusit Zoo. The monitors can even be seen inside various zoo exhibits including those of large carnivores such as tigers.

GENERAL

Ziegler et al. (2016) compiled data on zoo varanid holdings:

> TO GAIN AN OVERVIEW OF MONITOR LIZARDS HELD IN ZOOS, INCLUDING THE SPECIES AND NUMBERS OF INDIVIDUALS KEPT AND THE NUMBER OF KEEPING INSTITUTIONS, WE ANALYZED COLLECTION INFORMATION FROM THE ZOOLOGICAL INFORMATION MANAGEMENT SYSTEM (ZIMS) DATABASE. OUR ANALYSIS PERFORMED IN MARCH 2016 REVEALED THAT THERE ARE 50 SPECIES OF MONITOR LIZARD KEPT GLOBALLY IN 308 ZOOS, WITH 39 OF THESE SPECIES KEPT IN A TOTAL OF 131 EUROPEAN ZOOS. ELEVEN GLOBALLY-KEPT SPECIES WERE LACKING IN EUROPEAN ZOO HOLDINGS, AND NINE SPECIES WERE FOUND EXCLUSIVELY IN EUROPEAN ZOOS. OF THE 79 CURRENTLY RECOGNIZED SPECIES OF MONITOR LIZARD, 30 (38 %) ARE NOT CURRENTLY HELD IN ZOOS. ALTHOUGH ZIMS DATA ARE CERTAINLY NOT COMPLETE, THERE IS A DISCERNIBLE TREND THAT ONLY A FEW SPECIES ARE WIDELY KEPT BY THE ZOO COMMUNITY; WHEREAS MOST SPECIES ARE POORLY REPRESENTED OR NOT REPRESENTED AT ALL.

A fantastic book on varanids was published by Pianka et al. (2004; Fig. 16). Murphy (1971, 1972) provided data on Indo-Australian varanids at DZ and a list of captive monitors in the collection between 1966 and 1993 (Figs. 17, 18). Winston Card published a paper with Arnold Kluge on hemipenial morphology and systematics in 1995. Christie (1982) successfully introduced three incompatible male *V. varius* at the Indianapolis Zoo.

Murphy et al. (2002) investigated factors necessary for the medical and captive management and conservation of *V. komodoensis*. At SNZP, Gray et al. (1966) discovered amoebiasis and Spelman et al. (1996) described anesthesia in *V. komodoensis*. Hyde et al. (2016) found the oral and skin microbiomes of captive dragons are significantly shared with their habitat. Parasite burdens of captive varanids were reported by Bosch (1999).

Köhler (1992) assessed disease in monitors maintained in European collections, and Mendyk et al. (2013) studied mortality in captive varanids at the Bronx Zoo over a 40+ year period. Mendyk (2015) also assessed life expectancy and longevity in seven species of zoo-maintained varanids.

RWM and associates have published a number of varanid papers listed in the references section. He is also the founding editor of the open-access, peer-reviewed online journal *Biawak*, which is devoted exclusively to monitor biology and husbandry.

Some wild monitor lizards occasionally find zoos to be suitable homes. A study by Karunarathna et al. (2008) was conducted on the grounds of the National Zoological Gardens (NZG) in Sri Lanka. *Varanus salvator* and *V. bengalensis* (protected in Sri Lanka) live on zoo grounds. *Varanus salvator* was the first

reptile in Sri Lanka to receive legal protection in 1937 (as well as in the 1992 CITES appendix II list), while *V. bengalensis* has been placed in CITES appendix I (De Silva 1996). It is clear that the NZG is an important suburban refuge for threatened fauna in the wet zone of Sri Lanka. During the survey period, several threats within the NZG were observed, including water pollution and the excessive use of chemicals.

Varanus salvator can be found living in urban environments of many Southeast Asian cities. In Bangkok, Thailand, monitors exceeding 2 m in length roam freely in Lumpini Park, amidst the backdrop of a bustling megacity with towering skyscrapers surrounding the park (Fig. 19). *Varanus salvator* is also abundant on the grounds and in the waterways of Bangkok's Dusit Zoo (see Cota 2011a,b). Here, because of their high population density, conspicuousness, and indifference to human activity, many aspects of the species' biology can be observed easily during a single visit, including ritualized combat, courtship, copulation, and predation on fish and turtles. The monitors here are so abundant that they can even be seen inside various zoo exhibits, including those of large carnivores such as tigers (Fig. 20). At Singapore Zoo, staff must regularly watch out for wild *V. salvator* and Reticulated Pythons (*Malayopython reticulatus*) as they pose a serious threat to collection birds and small mammals (S. Lafebre, pers. comm.).

There are many contrary views of whether Komodo Dragons are venomous. Fry et al. (2009) published a provocative paper:

> "Our multidisciplinary analyses paint a portrait of a complex and sophisticated tooth/venom combined-arsenal killing apparatus in *V. komodoensis* and its extinct close relative *V. priscus*. Thus, despite a relatively weak skull and low bite force, we suggest that the combination of highly and very specifically optimized cranial and dental architecture, together with a capacity to deliver a range of powerful toxins, minimizes prey contact time and allows this versatile predator to access a wide range of prey including large taxa. These results indicate that *V. priscus* was the largest venomous animal to have ever lived."

However, other researchers urged caution in accepting the hypothesis that dragons are venomous until additional evidence is forthcoming (Weinstein et al. 2012; Weinstein et al. 2013; Sweet 2016). Ballard and Antonio (2001) reported on two bites sustained by zoo keepers from *V. griseus* that caused symptoms suggestive of toxicity including dysphagia. Whether it could be considered venom, there does appear to be some active anticoagulatory properties of the saliva that accompanies the bites of at least some species of monitor lizard. Don Gillespie and associates have published on blood and salivary composition (Montgomery et al. 2002; Gillespie et al. 2000; Gillespie et al. 1997). There was a *V. komodoensis* bite at Los Angeles Zoo sustained by a journalist that required reconstructive surgery of the foot and ankle; this report also included a case history of a bite to a zookeeper (Ducey et al. 2016). RWM recalls a colleague receiving a very minor, superficial bite from an adult female *V. melinus* which caused excessive bleeding that took nearly an hour to clot. A surprising amount of bleeding relative to the size of the bite and considerable localized pain was also experienced from the bite of a male *V. beccarii* (RWM, pers. obs.). At SNZP, a juvenile *V. prasinus* bit the finger of a keeper, causing the hand to swell (LA, pers. obs.).

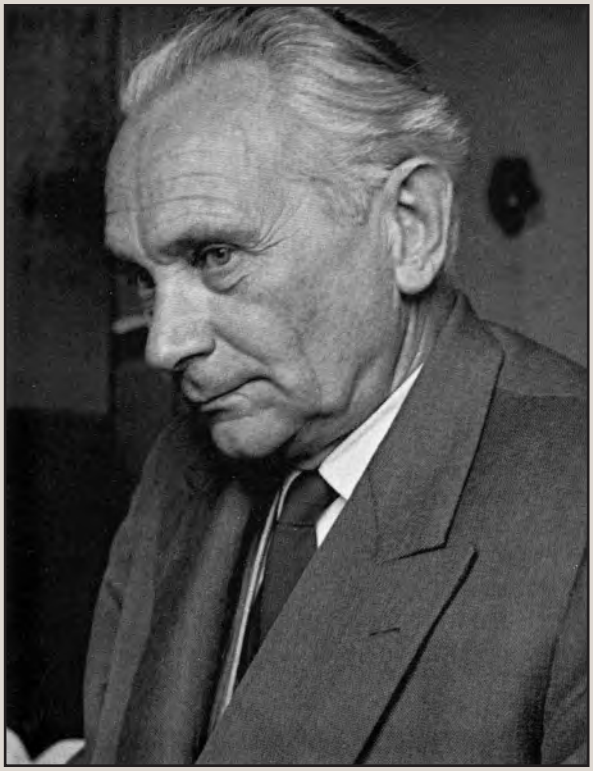

PHOTO COURTESY OF KRAIG ADLER

Fig. 21. Robert Mertens (1894–1975) was a pioneer in the study of varanid lizards. He was the curator at Senckenberg Museum in Frankfurt am Main, Germany.

Seminal Book on Husbandry and Captive Management

This section is based on a German work, *Tasks and Problems of Zoo Biology in Studying the Life Manifestations of Lower Amniotic Animals (Reptiles),* which Hans-Günter Petzold from Tierpark Berlin published in 1984. This compendium, which incorporates terriarum and scientific literature, was completed a few days before his premature death on 19 November 1982. This English translation, *Lives of Captive Reptiles,* was published by SSAR in 2008.

> "Until the middle of the 20th century nothing was known about the incubation times of monitor eggs. In his great monitor monograph Mertens (1942) was able only to express the assumption that the eggs of *Varanus niloticus* lay for about 10 months in termite hills until they hatch. Despite the fact that these are well-known and popular "show" animals in large terraria, no breedings had occurred up to that time in captivity. However, the eggs of *Varanus komodoensis* had already been described in 1932 by Brongersma (up to 11.5 cm long!). In the Batavia (today Djakarta) Zoo the species was said to have reproduced in an outdoor enclosure in 1941/42 (according to Mertens, 1952, without further details); Dathe [personal communication] doubts this as the result of his own later investigation), in the Jogjakarta Zoo, on the other hand, breeding was successful in 1968 (Busono, 1974). — In zoos and in isolated cases involving expert terrarium practitioners the breeding of representatives of these large *Sauria* has been successful only since 1962. The known incubation periods of the eggs vary between a mere 92 days (*Varanus gilleni*, cf. Horn, 1978) and 139 days (*V. timorensis* in the Basle Zoo, Rüegg, 1973) in the smaller species over 170–177

Fig. 22. Illustration of Le Varan à deux bandes (*Varanus bivittatus,* now *V. salvator)* in Alfred E. Brehm' s "Les Merveilles de la Nature. Les Reptiliens et les Batraciens" in 1885.

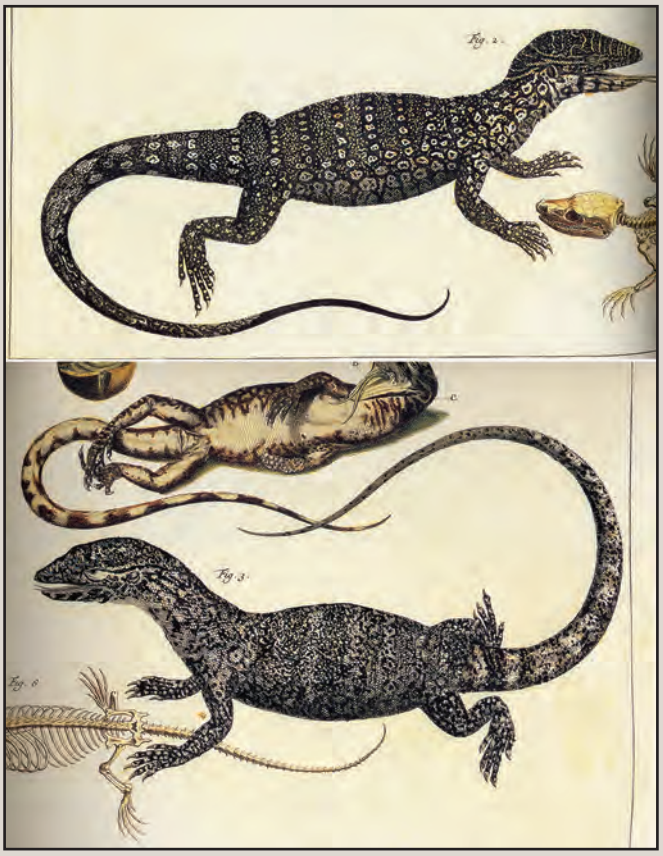

Fig. 23. Illustrations in "Locupletissimi rerum naturalium thesauri" by Albertus Seba in 1734–1765. The lizard pictured may be a Nile Monitor (*V. niloticus* or *ornatus*). Many of the varanid illustrations appearing in Seba's first two volumes of Thesauri were copied by other artists and included in subsequent publications (Shaw, 1802; Goldsmith, 1840). The two species most often pictured by Seba were *Varanus niloticus* and *V. salvator.* Seba's Thesauri is considered to be the most comprehensive survey of biodiversity of the 18th century, and today ranks among the most valuable and sought after illustrated works on natural history, commanding prices of nearly US $500,000 (Aaron Bauer, pers. comm.).

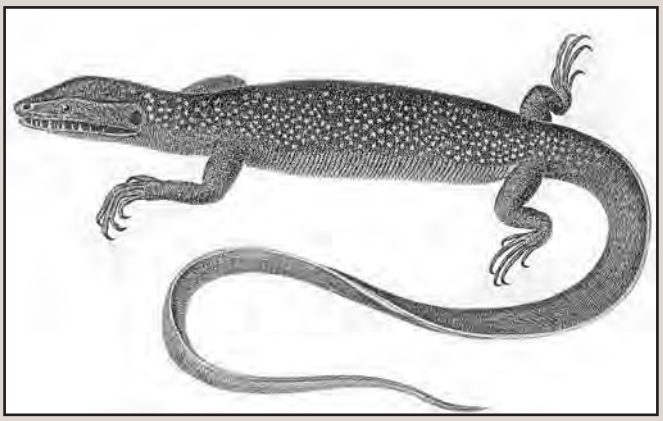

Fig. 24. *Varanus indicus* from "Histoire naturelle, générale et particulière, des reptiles…" by F. M. Daudin, an X-XI [1802–1803].

days (*V. exanthematicus albigularis* in the San Diego Zoo, Staedeli, 1962) up to 327 days (*V. salvator*, variation range 241–327 days under identical incubation conditions, Kratzer, 1973 a; 9 months in the San Antonio, Texas Zoo at 28.9°C, Bowers, 1981). — Up until now we know of successful breedings with corresponding data of nine monitor forms."

"Pellet formation in reptiles is not confined to crocodiles. Hediger (1934) was first to call attention to genuine pellet formation in reptiles at hand of [from] *Varanus indicus* which vomited pellets after feeding with mice, reminiscent in size and composition of those formed by the tawny owl: "They contained parts of skeletons and matted hair." It was possible to undertake more thorough experiments in the Berlin Tierpark with *Varanus salvator* (Petzold, 1967 b). Monitor pellets are less compact and constant in shape than crocodile pellets, more "rag-like"; also, the numerical relations are different (9 mice fed to a dwarf crocodile yielded approximately 100 individual pellets; in monitors only about a tenth as much). The digestive capability of the monitor stomach exceeds that of the owl stomach (only occasionally teeth and bone parts were found, no skulls) but does not equal that of the crocodile and diurnal bird stomach. In the stomach of a *Varanus komodoensis* which had fasted for four months after its catch, Mertens (1942) still found bones of a young Indian sambar."

"As regards squamate reptiles, until now pellets consisting of mammalian remains are known exclusively among monitors, while according to observations made in zoos, pellets composed of bird feathers, claws and beaks are also expelled by Giant snakes (*Liasis fuscus*: Froesch, 1966; *Python molurus bivittatus*: Lederer, 1942 b). Here, too, we are undoubtedly dealing with "genuine" pellets. Lederer (l. c.) also found bird pellets in *Varanus komodoensis*; the feather quills were "actually pasted together." My own attempts to feed *Varanus salvator* with chicken and guinea fowl chicks yielded feathers brought up in the water basin, "but it could not be determined whether during the digestion of birds in the stomach of the monitor pellets was even formed, or whether the feather pellet was only so loosely balled up that — in contrast to the hair pellets — it instantly dissolved in water after being vomited up; the latter is more likely" (Petzold, 1967 b)."

"This compilation, ending *inter alia* [among other things] with the particularly beautiful success of breeding the Emerald monitor, includes only the initial breedings. While at this time we cannot as yet speak of "conservation breeding" of monitors— not all the offspring grew up—we can nevertheless note with satisfaction that international cooperative efforts to build up breeding groups serve this objective (Basel - San Diego 1976

FIG. 25. Illustration of *Varanus gilleni* and *V. eremius. From* Baldwin Spencer (ed.). 1896. "Report on the work of the Horn Scientific Expedition to Central Australia. Part 2: Zoology." These pygmy monitors (subgenus *Odatria*) have often been featured in scientific publications.

WITH *VARANUS KOMODOENSIS*, CF. ANONYMOUS, 1976 B). THE TOTAL INVENTORY OF KOMODO MONITORS IN ZOOS AMOUNTED IN 1980 TO 20 ANIMALS (WITH AN ESTIMATED VOLUME OF POPULATIONS IN NATURE OF 6,000, AMONG THEM, HOWEVER, ONLY ABOUT 400 ♀♀ CAPABLE OF REPRODUCTION)."

"UNTIL THE MIDDLE OF THE 20TH CENTURY THE INCUBATION TIMES OF MONITOR EGGS (CF. THE DATA UNDER 3.1.10) WERE PRACTICALLY UNKNOWN. IN THE MEANTIME, THE PICTURE HAS CHANGED; AT LEAST 9 SPECIES REPRODUCED IN CAPTIVITY — IN PART REPEATEDLY, BUT TO OUR KNOWLEDGE NOT YET EVER IN THE 2ND GENERATION (CF. VISSER, 1975; BUSONO, 1974; INTERNAT. ZOO YEARB., VOL. 1–20)."

"COMMENDABLY THE NUMEROUS PUBLISHED REPORTS OF KEEPING AND BREEDING OF THE LAST TWO DECADES DID NOT LIMIT THE DATES OF NUTRITIONAL STUDIES, CLUTCHES AND INCUBATION, ALTHOUGH THE LATTER ALTOGETHER WERE NEW (CF. 3.1.10.). THE PARTLY EXTREME LONG INCUBATION TIMES REQUIRED MORE COMPARATIVE STUDIES. IN THE SAN DIEGO ZOO THE SEX DETERMINATION OF KOMODO MONITORS WAS ACCOMPLISHED THROUGH QUANTITATIVE MEASUREMENT OF THE STEROID HORMONES IN THE BLOOD; ALSO, THE FIRST KARYOGRAM OF THIS SPECIES WAS MADE (WITH AT FIRST NOT YET FULLY PROVEN INDICATION OF HETEROGAMY OF THE ♀♀; BENIRSCHKE & KUMAMOTO, 1981) AND ALONG WITH THAT, ADDITIONAL MATERIAL WAS COLLECTED TOWARD KNOWLEDGE OF THE CHROMOSOME EVOLUTION IN THE GENUS *VARANUS* (CF. KING & KING, 1975, AS WELL AS SECTION 3.1.1.). EGG MEASUREMENTS AND EGG WEIGHTS AS WELL AS GROWTH RATES AND DEVELOPMENT OF THE OFFSPRING OF SEVERAL MONITOR SPECIES IN VARIOUS ZOOS WERE RECORDED 124. IN ADDITION, ZOOS WERE ABLE TO MAKE OBSERVATIONS OF THE RITUAL COMBAT BEHAVIOR OF THE ♂♂ IN THE FUNCTIONAL SYSTEM OF REPRODUCTION AND ABOUT THE (FOR NOW, ONLY SUSPECTED) BIANNUAL EGG-LAYING OF THE COMMON WATER MONITOR AS WELL AS THE DIGESTIVE-PHYSIOLOGICAL PHENOMENON OF PELLET FORMATION IN MONITORS (CF. SECTIONS 3.1.5. AS WELL AS 3.2.1.)."

"IN THE SAN DIEGO ZOO THE SEX DETERMINATION OF KOMODO MONITORS WAS ACCOMPLISHED THROUGH QUANTITATIVE MEASUREMENT OF THE STEROID HORMONES IN THE BLOOD; ALSO, THE FIRST KARYOGRAM OF THIS SPECIES WAS MADE (WITH AT FIRST NOT YET FULLY PROVEN INDICATION OF HETEROGAMY OF THE ♀♀; BENIRSCHKE & KUMAMOTO, 1981) AND ALONG WITH THAT, ADDITIONAL MATERIAL WAS COLLECTED TOWARD KNOWLEDGE OF THE CHROMOSOME EVOLUTION IN THE GENUS *VARANUS* (CF. KING & KING, 1975, AS WELL AS SECTION 3.1.1.). EGG MEASUREMENTS AND EGG WEIGHTS AS WELL AS GROWTH RATES AND DEVELOPMENT OF THE OFFSPRING OF SEVERAL MONITOR SPECIES IN VARIOUS ZOOS WERE RECORDED]. IN ADDITION, ZOOS WERE ABLE TO MAKE OBSERVATIONS OF THE RITUAL COMBAT BEHAVIOR OF THE ♂♂ IN THE FUNCTIONAL SYSTEM OF REPRODUCTION AND ABOUT THE (FOR NOW, ONLY SUSPECTED) BIANNUAL EGG-LAYING OF THE COMMON WATER MONITOR AS WELL AS THE DIGESTIVE-PHYSIOLOGICAL PHENOMENON OF PELLET FORMATION IN MONITORS (CF. SECTIONS 3.1.5. AS WELL AS 3.2.1.)."

THE FUTURE

Prominent lizard ecologist Eric Pianka (2012) summarized the state of the planet and constructed a pretty depressing picture, especially for future naturalists. Developers, environmental pirates and exploiters, tycoons, and others who view the natural world as something to be only used for human needs and pleasures will have a much easier time getting by as manmade objects continue to litter the world. Those persons who treasure the natural world will be selected against in a true Darwinian fashion.

"IN THE END, THE QUESTION MAY NOT BE SO MUCH WHY DID I WRITE THIS LITTLE BOOK [*THE LIZARD MAN SPEAKS* 1994], BUT RATHER WHY DID YOU READ IT? I LONG FOR A SIMPLER EXISTENCE. I DESPISE STANDING IN LINES OR WAITING FOR TRAFFIC LIGHTS TO CHANGE. OBJECTS AND NOISES OF HUMAN ORIGIN ARE OBNOXIOUS TO ME. I HATE BEING FENCED IN, UNABLE EVEN TO GET OFF THE ROAD. I CANNOT TOLERATE THE THOUGHT OF A WORLD IN WHICH I CAN'T GET TO PRISTINE WILDERNESS, LET ALONE A WORLD WITHOUT ANY WILDERNESS AT ALL. (WE SEEM TO BE ALMOST IMPERVIOUS TO, AND UNAWARE OF, CHANGES OCCURRING AROUND US, PERHAPS BECAUSE THEY OCCUR ON A TIME SCALE OF DECADES, TOO SLOW TO BE PERCEIVED. BUT IF ONE COULD TRAVEL FROM THE 1960'S TO THE 1990'S, THE RESPONSE MIGHT BE MORE LIKE "HEY, WAIT A MINUTE!" UNFORTUNATELY, MUCH OF THE YOUNGER GENERATION DOESN'T EVEN KNOW WHAT THEY'VE LOST AND ARE LOSING.) WE DON'T IMPROVE ON NATURE AS WE LANDSCAPE AND PAVE OVER THE SURFACE OF THE PLANET. I THINK BUILDINGS, FENCES AND ROADS ARE UGLY. I KEEP COMING BACK TO THE OUTBACK IN YET ANOTHER FUTILE ATTEMPT TO ESCAPE FROM CREATIONS OF HUMAN ORIGIN, CROWDING, OVERPOPULATION, AND REGIMENTATION. MY EX-WIFE HELEN USED TO SAY THAT I WAS BORN A CENTURY TOO LATE. PERHAPS WE ALL WERE. PERHAPS YOU READ THIS IN YOUR OWN ATTEMPT TO ESCAPE FROM URBANIZATION."

Pianka continued:

"PEOPLE SOMETIMES ASK ME WHY I STUDY LIZARDS. OR WORSE, SOME SAY "WHAT GOOD ARE LIZARDS?" TO WHICH I RESPOND WITH "WHAT GOOD ARE YOU?" THOSE WHO WOULD THINK, LET ALONE ASK, SUCH A NARROW-MINDED QUESTION SEEM TO ME TO BE HOPELESSLY ANTHROPOCENTRIC. LIZARDS ARE SPECTACULAR AND BEAUTIFUL FELLOW EARTHLINGS THAT

deserve our full respect and care. They were here long before us and deserve to exist on this spaceship, too."

"Sadly, "wildlife management" is somewhat of a farce: Currently we are failing to adequately conserve species or habitats—we humans do not even have the will to limit our own population! Humans have now dramatically altered the ecology of over half of the land surface of this our one and only spaceship planet Earth. Conservation biology is a man-made emergency discipline rather like surgery is to physiology or war is in political science. Wild animals could and would flourish if people could manage to share the planet and leave them large enough undisturbed areas of habitat. However, even if we could somehow designate and maintain large nature reserves, the menace of irreversible global warming seems destined to take a heavy toll on all Earthlings. Hopefully, with new approaches and increased global efforts, lizards, including varanids, will be among the survivors of this current massive anthropogenic extinction event."

Acknowledgments.—This contribution is dedicated to Robert Mertens (1894–1975), a pioneer in the study of varanid lizards (Figs. 21–25). He was the curator at Senckenberg Museum in Frankfurt am Main, Germany. The late Walter Auffenberg at University of Florida in Gainesville (no slouch when it came to studying dragons) was contacted by Mertens as he was planning his first trip to the United States and asked if Auffenberg would take him on collecting trips throughout Florida. Auffenberg quickly agreed and so off they went. Mertens knew the scientific names of every herp, bird, mammal, invertebrate, tree, plant, and so on. Walt was amazed so he asked Mertens how he knew all of the fauna and flora since he had never been to the US. Mertens said that he had memorized all relevant dichotomous keys beforehand in Germany—truly an astounding memory. His experiences throughout his trip are detailed in his book *Zwischen Atlantik und Pazifik* (1951). He kept large living collections at the museum and his home, leading to the classic *Die Warn- und Droh-Reaketionen der Reptilien* (1946). One interesting paper concerned *V. salvadorii* at Wilhelma Zoo (1960). Visitors tried to challenge him to identify an obscure herp; it was said that he never missed! He published a monograph on the Varanidae in 1942, which included 20 plates of many specimens and skulls. On 5 August 1975, he was bitten by an African rear-fanged twig snake (*Thelotornis*) and died 18 days later. In his diary, he wrote "a singularly appropriate end for a herpetologist."

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