Monitors, Mammals, and Wallace's Line

Samuel S. Sweet & Eric R. Pianka

Abstract

Although varanid lizards have achieved parity with mammals in many parts of the world, they exploit very different metabolic strategies and sensory mechanisms, and are properly regarded as convergent on the lifestyle of small predatory mammals. In parts of island southeast Asia and in Australia small monitors appear to fill ecological niches occupied by cats, mustelids and viverrids in other parts of the world. Species diversity of large monitor species (>1.3 m TL) does not change across Wallace's Line, which is the distributional boundary for nearly all small, carnivorous placental mammals, but the diversity of small monitor species (<1.2 m TL) increases abruptly from this line east. Small monitor species can coexist with dasyurid marsupial carnivores, but apparently not with placental carnivores (this is being tested now with the establishment of feral cats in Australia). Because juveniles of large monitor species can survive in communities with placental carnivores to the west of Wallace's Line, we speculate that predation rather than resource competition has influenced the observed pattern. Large monitors produce large clutches and their juveniles soon grow out of the vulnerable size range, whereas small monitor species (despite being more fecund, when body size is factored out) produce fewer eggs, are always subject to mammalian predation, and may not be able to coexist over evolutionary time with placental carnivores.

Key words: Squamata: Varanidae; mammalian carnivore competitors; Indo-Australia; Wallace's Line.

Introduction

Predators and their prey are locked in a coevolutionary arms race over time. By selecting against less sophisticated prey individuals, predators favor prey with better escape abilities. This selects for predators better able to capture evasive prey, steadily raising the bar for both. In addition to increased speed, agility and strength, carnivores commonly evolve larger brains and increased development of integrative centers than do their herbivorous prey (Jerison 1973). Greater information-processing capacity may include adaptations for refined neuromuscular coordination, use of complex sensory modalities with a low signal-to-noise ratio, and/or enhanced problem-solving abilities. Combinations of these functions are driven by ecological and behavioral differences. For predatory animals, solitary vs. pack hunting behavior, ambush vs. widely-foraging tactics, and reliance on visual, auditory or olfactory input each influences the nature and sophistication of information-processing abilities required.

Consequences of these differences are familiar (compare, for example, dogs to cats, or either to sheep), but even broader questions can also be asked: how would small theropod dinosaurs have fared in a match with modern mammals, given the state of the information-processing arms race in Mesozoic times? More realistically, can other lineages of predators compete successfully with modern mammals, and, if so, how is this parity achieved?

Varanid lizards are obvious candidates for this sort of inquiry. This group of about 60 living species has representatives in nearly all terrestrial environments at low latitudes throughout the Old World. Monitors are relatively conservative in morphology, but come in a broad range of sizes (20 g to over 50 kg as adults; see Pianka 1995, 2004b). As a group, monitors are alert and agile diurnal carnivores that typically search widely for prey, relying on acute vision and extremely sensitive chemoreception. Superb predators, they are the most advanced and most intelligent of all lizards. Physiologists, students of behavior, ecologists, and those who simply appreciate monitor lizards have used terms such as mammal-like, near-mammalian, and so on, to the extent that the concept is almost a cliché in the literature. However, saying that monitors are mammal-like is misleading and obscures the issue. Attributes of monitors that are functionally equivalent to mammalian adaptations certainly evolved convergently, since their last common ancestor lived ca. 300 mya. Monitor lizards similar to species living today have coexisted with sophisticated mammalian carnivores since at least the mid-Cretaceous (see Molnar 2004 for a review of fossil varanids).

The stem ancestor of diapsid reptiles and mammals must have lacked the aerobic metabolic scope, visual and chemoreceptive abilities, and information-processing adaptations that characterize modern monitors and mammals. Monitors are ectotherms that operate at body temperatures equal to or greater than those of mammals, with circulatory and respiratory systems that permit long periods of sustained activity, albeit without the costly molecular and physiological control mechanisms required by endotherms. Reptilian and mammalian eyes are reasonably similar in structure (Röll & Horn 1999) but the ways that visual information is edited and processed in the brain differ greatly between the two groups (Jerison 1973, Northcutt 1984). Mammals rely almost entirely on receptors in the nasal epithelium for their olfactory prowess, whereas monitors (like snakes) use their tongues to transfer compounds into an elaborate vomeronasal organ (Schwenk 1995, Schwenk & Wagner 2001), which is vestigial in many mammals or used principally to detect sex pheromones. Both monitors and mammals retain and use detailed "map knowledge" of features within their extensive home ranges (Tsellarius & Menshikov 1994), and both employ complex foraging strategies that show considerable plasticity and at times appear to deceive their prey to facilitate capture (Hermes 1981, Horn 1999, 2004, Sweet & Pianka 2003). Mammals conduct complex neural integration in an enlarged isocortex, whereas the neural processing pathways of reptiles and birds emphasize the anterior dorsal ventricular ridge and tectum mesencephali (Pearson 1972, Ulinski 1990, ten Donkelaar 1998).

Biogeography

Throughout Africa and southern Asia, monitors coexist quite successfully with a wide range of carnivorous mammals, though their species richness is rather low, and most are large (>1.3m in total length [TL] as adults) and relatively bulky lizards. Five species occur in Africa (one of which extends well into central Asia), and an additional seven species are distributed across mainland southern Asia. Monitor species richness increases sharply in offshore Southeast Asia, with 15 species in the East Indies and Philippines (four shared with the mainland), and 15 species in New Guinea and the Bismarck and Solomon islands. Species richness peaks in Australia, with 29 named species (five shared with New Guinea). Over a dozen more, as yet undescribed, species also occur in Australia. In parts of northern Australia up to 8 or 9 (exceptionally, 10-11) species may co-occur, partitioning resources by differences in body size and habitat (Pianka 1994, Shine 1986, Sweet 1999, this volume). Australian monitors are often considered to be ecological equivalents that fill niches occupied elsewhere by small carnivorous mammals such as cats, weasels, mongooses and civets (Storr 1964, Pianka 1969, Keast

1972, Hecht 1975; but see also Wroe 2002, and Wroe et al. 2004). A novel feature of the Australasian radiations is that over half of the species are small (<1.3m TL) and of slender build. These belong to monophyletic clades (Ast 2001) in the subgenera *Euprepiosaurus* and *Odatria*, and also differ from other varanids in having determinate growth (de Buffrenil, Ineich & Böhme 2004).

The high species richness of small monitors in eastern Indonesia and Melanesia (see Pianka & King 2004) has only recently been recognized, principally through the efforts of Wolfgang Böhme and his colleagues. Prior to 1990, only four small species were recognized in the region: a widespread and highly variable mangrove monitor (*Varanus indicus* ssp.); the green tree monitor (*V. prasinus* ssp.) and animals referred to *V. scalaris* occurring in New Guinea, and *V. timorensis* (Timor). Fifteen more species have been added (another three have been proposed which may prove to be valid), increasing the species richness of the family Varanidae by about 25%. Some of these new taxa are local (often insular) derivatives of the widely-ranging *V. indicus* and *V. prasinus* groups, and should perhaps be considered members of superspecies complexes. Others, while clearly allied to these complexes, are very distinct. These exciting developments allow a new perspective on varanid diversity in the Australasian region, and suggest a reevaluation of the ecological and historical interactions of monitors and mammals.

Wallace's Line overlies a complex tectonic boundary zone passing between the Sunda Arc islands of Bali and Lombok, between Borneo and Sulawesi, and east of the Philippines (Fig. 1). No land connection across it has ever existed. Wallace's Line marks the eastern limit of many terrestrial arthropods and vertebrates having Southeast Asian affinities and linked to the great ancient northern landmass of Laurasia. Conversely, it is the western limit for most plant and animal groups that evolved on the Australia-New Guinea landmass as it traveled north from its old Gondwanan connections during the last 50 my of the Cenozoic (Metcalfe et al. 2001). Within the region termed Wallacea (comprising the islands between Wallace's Line and the western limits of the Sahul Shelf linking Australia and New Guinea) the present day islands include microcontinental fragments, elevated sea bed, and island arcs derived from what might be termed the geological equivalent of gastrulation. Several small crustal plates and plate fragments are being compressed, rotated and/or subducted between the Asiatic mainland and the Australian and Pacific plates (Hall & Holloway 1998, Hill & Hall 2003, http://www.gl.rhul.ac.uk/searg/current_research/plate_tectonics/index.html). Within the period that monitors have occupied these landmasses, landscape effects include the accretion of microcontinents and island arcs as the north coastal mountains of New Guinea (Polhemus & Polhemus 1999), the elevation of the central massif of that island, strong shearing and westward displacement of Australian plate fragments to form parts of Halmahera, Obi, the Sula archipelago and the adjoining east arm of Sulawesi (Ali, Hall & Baker 2001), the appearance and loss of volcanic and forearc islands within the inner and outer Banda arcs, the Sangihe Arc and Halmahera Arc (Nichols & Hall 1999, Hall & Wilson 2000), and significant changes in exposed land area on the Sahul Shelf and elsewhere. Patterns of distribution and differentiation of monitor species in Wallacea are thus the results of dispersal (whether by direct land connections, island hopping, or sweepstakes rafting) and vicariance in this complex and dynamic tectonic region. For some vagile organisms, this meeting zone is a filter barrier between Asia and Australia, while for other lineages less capable of overwater dispersal

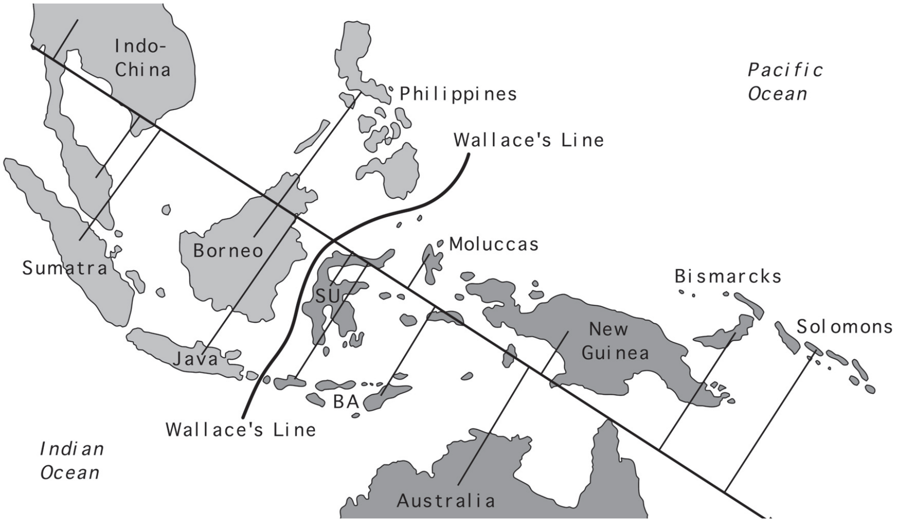

Fig. 1. Wallace's Line and the transect used to prepare Fig. 2. Lines at right angles to the transect mark (in sequence) the units shown in Fig. 2. The island east of Borneo marked "SU" is Sulawesi. BA = Banda Arcs.

Wallace's Line offers a convenient natural experiment, since virtually none of the small carnivorous mammals of Southeast Asia (cats, weasels, civets or mongooses) have crossed it on their own. A single species of civet is native to the island of Sulawesi. Two other civets and a mongoose have been introduced to Sulawesi, two species of civets have been introduced to some of the Lesser Sunda Islands, and two mongooses are established on scattered islands of the Moluccas (Corbett & Hill 1992, Nowak 1999). If monitor lizards and small mammalian carnivores are ecologically complementary, we might expect to see an increase in monitor species richness immediately east of Wallace's Line.

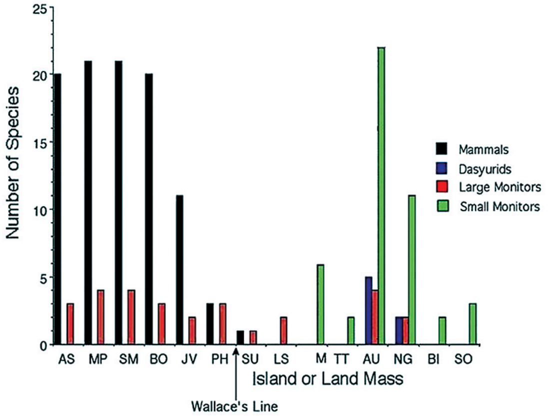

Fig. 2. Transect from NW to SE showing numbers of species of small carnivorous placental mammals, small carnivorous marsupials (dasyurids), large monitors, and small monitors from islands and landmasses located along the transect shown in Fig. 1. AS = Asia, MP = Malay Peninsula, SM = Sumatra, BO = Borneo, JV = Java, PH = Philippines, SU = Sulawesi, LS = Lesser Sundas, M = Moluccas, TT = Timor-Tanimbar, AU = Australia, NG = New Guinea, BI = Bismarcks, and SO = Solomon Islands.

Tab. 1. Database for Fig. 2, including the geographic distributions of species of carnivorous placental and marsupial mammals of <5kg body mass (see text), and of "small" and "large" varanid lizards. Values for viverrid and herpestid mammals in parentheses refer to introduced species.

		Felids	Mustelids	Viverrids	Herpestids	Total Placentals	Dasyurid Marsupials	Monitors <1.3m TL	Monitors >1.3m TL
1	Mainland SE Asia	4	1	10	2	17	0	0	3
2	Malay Peninsula	4	2	9	4	19	0	0	4
3	Sumatra	5	3	8	2	18	0	0	4
4	Borneo	4	2	8	2	16	0	0	3
5	Java	2	2	4	1	9	0	0	2
6	Philippines	1	0	2(1)	1	4(1)	0	0	3
7	Sulawesi	0	0	1(2)	0	1(2)	0	0	1
8	Lesser Sundas	1	0	0(3)	0	1(3)	0	0	2
9	Northern Moluccas	0	0	0(2)	0(1)	0(3)	0	7	2
10	Timor-Tanimbar	0	0	0(1)	0	0(1)	0	2	0
11	New Guinea	0	0	0(1)	0	0(1)	2	11	2
12	Australia	0	0	0	0	0	5	22	4
13	Bismarcks	0	0	0	0	0	0	2	0
14	Solomons	0	0	0	0	0	0	2	1

Tab. 2. Body masses (range) and geographic distributions of placental mammals in the areas designated on Fig.1. Entries in parentheses refer to species introduced and established (X), or introduced but not confirmed as established (?). Abbreviations as in Fig. 1, except A = Aru Islands, B = Bali, K = Komodo, L = Lombok, and P = Palawan.

Taxon	Mass (kg)	AS	MP	SU	BO	JV	PH	SU	LS	MO	TT	NG	AU	BI	SO
Carnivora															
Felidae															
Catopuma badia	2.3 - 4.5				X										
C. temmincki	5.0 - 16	X	X	X											
Felis chaus	4.0 -16	X													
Pardofelis marmoratus	2.0 - 6		X	X	X										
Prionailurus bengalensis	4.5 - 6.8	X	X	X	X	X	X		(X) BL						
P. planiceps	1.8 - 2.7		X	X	X										
P. viverrinus	4.9 - 11	X		X		X									
Mustelidae															
Martes flavigula	2.0 - 3	X	X	X	X	X									
Mustela lutreolina	0.30 - 0.35			X		X									
M. nudipes	0.30 - 0.35		X	X	X										
Viverridae															
Arctogalidia trivirgata	2.0 - 2.7	X	X	X	X	X			(?) K						
Cynogale bennettii	3.0 - 5		X	X	X										
Diplogale hosei	0.8 - 1.2				X										
Hemigalus derbyanus	1.0 - 3	X	X	X	X		X P								
H. owstonii	0.8 - 1	X													

Taxon	Mass (kg)	AS	MP	SU	BO	JV	PH	SU	LS	MO	TT	NG	AU	BI	SO
Macrogalidia musschenbroekii	3.8 - 6.1							X							
Paguma larvata	3.6 - 6	X	X	X	X										
Paradoxurus hermaphroditus	2.4 - 4	X	X	X	X	X	(X)	(X)	(X)	(X)	(X)	(X) A			
Prionodon linsang	0.7 - 1	X	X	X	X	X									
P. pardicolor	0.6 - 0.8	X													
Viverra tangalunga	5.0 - 11	X	X	X	X		X	(X)		(X)					
V. zibethica	5.0 - 11	X	X												
Viverricula indica	2.0 - 4	X	X	X		X			(X)						
Herpestidae															
Herpestes brachyurus	0.4 - 0.6		X	X	X		X P								
H. javanicus	0.4 - 0.7	X	X			X		(?)	(?)	(X)					
H. semitorquatus	0.7 - 1		X	X	X										
H. urva	2.0 - 4	X	X												

A simple approach to assessing this is to create a transect from mainland Asia through New Guinea and Australia to the Solomon Islands, project the positions of various islands or landmasses onto it, and plot the numbers of species in each of four groups for each area (Fig. 2). These groups are small placental carnivores, marsupial carnivores, and "small" and "large" varanid lizards. For this analysis (data in Tab. 1), we considered potentially competing placental mammals to include all indigenous carnivorous species in the families Felidae, Herpestidae, Mustelidae (excluding hog-badgers) and Viverridae having adult weights of 5 kg or less (Tab. 2). Here we employed the taxonomy and distributional data accepted by Corbett & Hill (1992). Additional records for the current distributions of introduced civets and mongooses were assembled from several sources (e.g., Flannery 1989). We also included distributional information for the largest extant marsupial carnivores (quolls and phascogales; Strahan 1989, Flannery 1995) whose current distributions overlap those of monitors. We made an admittedly arbitrary distinction between "small" and "large" monitor species native to the region, on the basis of maximum reported total lengths being less than or greater than 1.3 m. This division corresponds in part to the current phylogeny (Ast 2001), which is phylogeographically concordant but suggests that small body size has evolved independently twice within the trans-Wallacean clades (Pianka 2004b).

Fig. 2 documents that species richness of large monitors remains about the same across Wallace's Line, while distributions of small monitor species and small mammalian carnivores are mutually exclusive, but with an informative twist. Fig. 2 also illustrates the distribution of carnivorous marsupial mammals (six species of quolls and a phascogale). These are fierce and active carnivores, yet they are sympatric with the majority of small monitor species native to New Guinea and Australia.

Here we consider two explanations for the observed biogeographic pattern. We first discuss a phylogeographic interpretation, in which the pattern is simply a result of the separate evolutionary histories of varanids in Africa and Asia versus on the Australian plate, and of the inability of small species to cross Wallace's Line. We then consider a macroecological explanation for the regional proliferation of small monitor species, which is enforced by limits related to ecological complementarity between monitors and mammals. This second interpretation is also causally related to Wallace's Line, but here as it has served as a barrier to the eastward dispersal of small carnivorous mammals.

Monitor Phylogeography

An area cladogram for extant varanoid lizards (Fig. 3), based on the phylogeny derived by Ast (2001), is broadly consistent with a Laurasian origin of both Varanoidea and *Varanus*. The oldest presently-known fossils unambiguously assigned to the Varanoidea (*Parviraptor*, middle and late Jurassic) are Laurasian, known from Asia, western Europe and North America (Molnar 2004, Molnar & Pianka 2004). Similarly, the earliest known *Varanus* (ca. 45 mya) is central Asian. Following King & King (1975), Estes (1983), King, King & Baverstock (1991), Sprackland (1991), Baverstock et al. (1993), Card & Kluge (1995), and Fuller et al. (1998), a Laurasian origin model based on karyotypic, molecular, morphological and fossil evidence has achieved general acceptance. Pepin (1999) provided a useful analysis of fossil varanids and concluded

Table 3. Summary of reproductive tactics data for 47 species of *Varanus*. Abbreviations: E/W = Distribution relative to Wallace's Line, Sm/Lg = adult size <1.3m, >1.3m, CS = clutch size, HSVL = Hatchling SVL (mm), HWt = Hatchling Mass (g), AdSVL = Adult SVL (mm), AdWt = Adult Mass (g), EPP = Expenditure per Progeny, RCM = Relative Clutch Mass. Data are from the species accounts in Pianka and King 2004, except as noted.

Species	**Clade**	**E/W**	**Sm/Lg**	**CS**	**HSVL**	**HWt**	**AdSVL**	**AdWt**	**EPP**	**RCM**	**Source**
V. acanthurus	Odatria	E	Sm	7.9	62.9	3.9	250	180	0.022	.171	
V. albigularis	African	W	Lg	24.5	114.4	22.5	500	6000	0.004	.092	
V. baritji	Odatria	E	Sm	7.3	58.7	3.5	252	180	0.019	.142	
V. beccarii	Sm Asian	E	Sm	4	93	12.3	340				
V. bengalensis	Lg Asian	W	Lg	20.2	94	78	580	2600	0.03	.606	
V. brevicauda	Odatria	E	Sm	2.5	46.5	1.77	110	12.5	0.142	.354	
V. caudolineatus	Odatria	E	Sm	4.3		1.95	123	19	0.103	.441	
V. dumerilii	Lg Asian	W	Lg	23	88.7	13.5	500	2950	0.005	.105	Ben Aller, pers. com.
V. eremius	Odatria	E	Sm	3.6	64.8	2.6	160	41.5	0.063	.226	
V. exanthematicus	African	W	Lg	18	89.5	15	320	709	0.021	.381	
V. finschii	Sm Asian	E	Sm				305				
V. flavescens	Lg Asian	W	Lg	16	77.6	6	410	1040	0.006	.092	
V. giganteus	Lg Australian	E	Lg	8.5	150.2	46.7	700	4784	0.01	.083	
V. gilleni	Odatria	E	Sm	5.25	63.7	2.9	186	46.2	0.063	.330	
V. glauerti	Odatria	E	Sm	3	72.6	4.2	250	141	0.03	.089	
V. glebopalma	Odatria	E	Sm	6	87.5		305	300			
V. gouldii	Lg Australian	E	Lg	6.2	106.3	16.7	655	4000	0.004	.026	
V. griseus	African	W	Lg	15.4	109.1	19.3	625	800	0.024	.372	
V. indicus	Sm Asian	E	Sm	10	111	22	520	2300	0.011	.096	
V. jobiensis	Sm Asian	E	Sm	4	112	47	450	1300		.145	
V. keithhornei	Sm Asian	E	Sm	3	98	10.5	260	230	0.046	.137	
V. kingorum	Odatria	E	Sm	4.5		1.82	114				
V. komodoensis	Lg Australian	E	Lg	18.7	420	100	1530	54000	0.002	.035	
V. kordensis	Sm Asian	E	Sm	3.5	85	7.9	270				Vincent den Breejen, pers. comm..

V. mabitang	Lg Asian	E	Lg	9			640	3533			
V. macraei	Sm Asian	E	Sm	5.25	89	5.7	350				Robert Mendyk, pers. comm.
V. melinus	Sm Asian	E	Sm	4.8	112	22	420				
V. mertensi	Lg Australian	E	Sm	8.15	125.7	29.1	475	1320	0.022	.180	
V. mitchelli	Odatria	E	Sm	9.8	68	3.9	300	360	0.011	.106	
V. niloticus	African	W	Lg	23.8	119	25.5	644	3500	0.007	.173	
V. olivaceus	Lg Asian	E	Lg	6.7	160	25	509	4650	0.005	.036	
V. ornatus	Africaa	W	Lg	16.5	117	23	925	7500	0.003	.051	
V. panoptes	Lg Australian	E	Lg	11	111	40.1	740	7000	0.006	.063	
V. pilbarensis	Odatria	E	Sm	4	55.5	2.55	169	60	0.042	.170	
V. prasinus	Sm Asian	E	Sm	4	84.2	9.2	245	237.5	0.039	.155	
V. primordius	Odatria	E	Sm	3.6	44	1.5	120	32.8	0.046	.165	
V. rosenbergi	Lg Australian	E	Sm	15.3	155	19.9	470	1140	0.017	.267	
V. rudicollis	LgAsian	W	Lg	8	103	21	590	4000	0.005	.042	D. McGinnity pers. comm.
V. salvadorii	Lg Australian	E	Lg	6.45	115	53.78	745	13000	0.004	.027	
V. salvator	Lg Asian	W	Lg	12.4	128.9	53.4	839	7280	0.007	.091	
V. scalaris	Odatria	E	Sm	7.7	63	3.6	253	135	0.027	.205	
V. semiremex	Odatria	E	Sm	12.5	73.94	4.58	270	222	0.02	.258	
V. spenceri	Lg Australian	E	Lg	19.9	124	19.75	525	6000	0.003	.066	
V. storri	Odatria	E	Sm	3.9	54.2	2.85	132				
V. timorensis	Odatria	E	Sm	9	65.8	3.6	225	120	0.03	.270	
V. tristis	Odatria	E	Sm	10	70.8	4.4	305	250	0.018	.176	
V. varius	Lg Australian	E	Lg	8	105	24.9	765	1400	0.018	.142	

that a Laurasian ancestry was the most parsimonious concept.

Ast (2001) presented a well-corroborated phylogenetic hypothesis for varanoids that resolved many of the points of conflict among prior reconstructions. Ast concluded that *V. griseus* (northern Africa to central Asia) and the African *Varanus* species form the sister group to the remainder, which consists of two major units: an Australasian lineage having two weakly-supported clades; and a second lineage nearly restricted to Australia and New Guinea that includes three major clades. One of the Australasian clades is restricted to southern Asia and the lands of the Sunda Shelf save for members of the *V. salvator* complex, which occur well to the east of Wallace's Line in the Lesser Sundas and Sulawesi (and perhaps in the northern Moluccas, as discussed below), as well as being distributed throughout the Philippines. The other Australasian clade has the *V. olivaceus* group (Philippines) as the sister taxon to the small species placed in the subgenus *Euprepiosaurus* (*V. indicus* and *V. prasinus* groups), with all species of *Euprepiosaurus* confined to lands east of Wallace's Line. Ast's second Australasian clade places the small Australian *Odatria* spp. as sister to two lineages, one containing *V. salvadorii*, *V. komodoensis* and V. *varius*, and a second containing the larger Australian *Varanus*.

The Laurasian origin model thus involves early dispersal from central Asia into Africa and south Asia, with two derived lineages crossing Wallace's Line and radiating as (a) the subgenus *Euprepiosaurus* (chiefly in Wallacea and New Guinea), and (b) *V. komodoensis* in the Lesser Sundas, and *Odatria* and the larger Australopapuan *Varanus* on the lands of the Sahul Shelf. Two presumably more recent crossings of Wallace's Line involve different members of the *V. salvator* complex, which ranges far into the Lesser Sundas, and also has reached Sulawesi and nearby islands. Because Australia lay far to the south of the Asian mainland in late Cretaceous and early Tertiary time, the implied dual invasion of Wallacea and Australia is unlikely to have occurred much prior to the middle Tertiary, and the oldest varanid fossil material known from Australia is dated at the Oligocene-Miocene boundary at 24 mya (Molnar 2004). Access to fragments of present-day Wallacean islands and the Australian continental platform by mid-Tertiary is not as problematic as might be assumed from a broad view of the geography of regional plates. In part this is because the leading edge of the Australian plate contacted the Philippine Sea plate (far to the south of its present remnants) by 50 mya (Hall 1998, http://www.gl.rhul.ac.uk/searg/current_research/plate_tectonics/index.html),

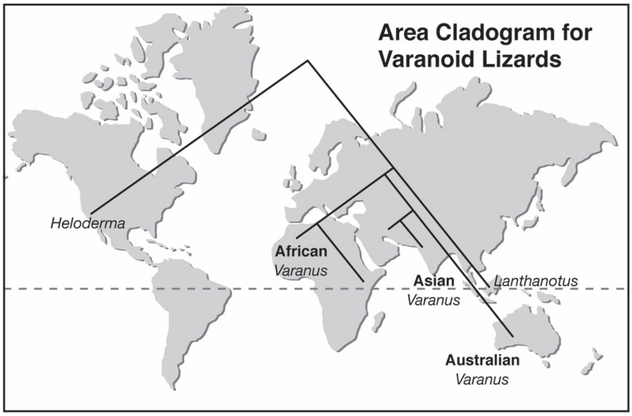

Fig. 3. Area cladogram for varanoid lizards, supporting the concept that Varanoidea is a Laurasian lineage.

and subduction along this front created island arcs (similar to the present-day Lesser Sundas) that moved northward as Australia approached the Asian mainland. Detailed tectonic reconstructions (Hall 1998, 2002) show an extensive island arc system extending from the Sunda Shelf across the northern margin of New Guinea from the Oligocene onward, as well as fragments of Sulawesi, Halmahera, the East Philippines, and the Vogelkop of present-day New Guinea distributed between major land masses. While some of the structure has been lost to subduction, the general picture is that the proto-Wallacean region has been dotted with islands throughout the last 30 my, and was tectonically active from about 50 mya.

An alternative to the Laurasian model was recently offered by Schulte, Melville & Larson (2003). Based on parallel re-analyses of mtDNA phylogenies for agamid and varanid lizards and molecular clock evolutionary rate estimates, Schulte et al. proposed that the major divisions in each family are far older. By their analysis, Asian and Australian agamid lineages putatively diverged ca. 150 mya, African *Varanus* diverged ca. 145 mya, and major clade boundaries among Asian and Australian varanids date to 112-120 mya. This invokes a Gondwanan origin for both families and an early history tied to Jurassic and early Cretaceous plate movements. In this scenario, the phylogeny and current distribution derives from vicariant cladogenesis in Africa, India and Australia as those units separated and traveled northward to contact the Eurasian landmass, with dispersal from the Indian subcontinent into mainland SE Asia possible after ca. 50 mya (Hall 1998). The fragmentation, transport and accretion of the Cimmerian terranes that make up much of present-day SE Asia involves earlier events (Metcalfe 1998) that pre-date the origin of varanoids under the model proposed by Schulte et al. (2003). Their area cladogram for varanids is of the type termed the Northern Gondwana Pattern by Sanmartin & Ronquist (2004).

Ascribing the deep history of varanid lizards to Gondwanan vicariance creates a number of significant difficulties. These include that all Cretaceous and Paleogene varanoid fossils so far described, and all Paleogene fossils assigned to the family Varanidae, come from Eurasia and North America; Molnar (2004) lists 22 named species (of *Saniwa*, *Iberovaranus* and *Varanus*) from a larger set of fossils and Laurasian localities. The earliest known varanid fossils of African (17-19 mya), Indian (early Pliocene), and Australian (23-24 mya) provenance are all of Neogene age. Similarly, the fossil record of monstersaurs and helodermatids is exclusively Laurasian (Molnar & Pianka 2004), and the only fossil questionably assigned to the Lanthanotidae is of late Cretaceous age, from Mongolia (Pianka 2004a). The Gondwanan vicariance proposal also predicts that varanoid lizards had access to South America before its progressive separation from Africa (ca. 110-95 mya), and (via Antarctica) from Australia until perhaps 40 mya (Veevers et al. 1991), but no varanoids have ever been identified in the South American fossil record, and large teiids fill the monitor niche on that continent at present.

Schulte et al. (2003) do not address these difficulties with their Gondwanan vicariance proposal, which hinges on an accurate calibration of the evolutionary rate of this portion of the mitochondrial genome (reviewed by Weisrock et al. 2001). Instead, they assign dates to certain basal divergences within *Varanus*, which on examination are difficult to reconcile with their biogeographic scenario. A divergence dated at 120.5 mya partitions a clade containing all southeast Asian species, plus *V. olivaceus* and the

Wallacean clade *Euprepiosaurus*, from the lineage containing *V. komodoensis* and all other Australopapuan *Varanus* plus *Odatria*. The divergence between *V. olivaceus* and *Euprepiosaurus* is dated at 112 mya. Because Africa and India separated from Gondwana no later than 130 mya (HALL 1998, McLOUGHLIN 2001), any vicariant events dated to ca. 120 or 112 mya must have involved Australia alone. However, each of these divisions of *Varanus* contains lineages that occur on both sides of Wallace's Line – in each case the next younger divergence (undated by SCHULTE et al.) partitions Asian from trans-Wallacean clades.

This difficulty is inherent in AST's (2001) phylogeny. Members of the *V. salvator* complex occur widely in the Lesser Sundas, on Sulawesi and the Togian Islands, and old specimens exist from Obi and Halmahera (W. BÖHME, pers. com., 2005). Remaining taxa in the *V. salvator* complex range from Sri Lanka to the Philippines, suggesting that *V. salvator* s.l. has crossed Wallace's Line twice. The five other species in this clade are exclusively Asian. The sister clade to this Asian lineage has *V. olivaceus* (Philippines) as its basal member, while the remaining species comprise the *V. prasinus* and *V. indicus* groups centered in New Guinea, and restricted to lands east of Wallace's Line. An Australian plate origin for the *V. olivaceus* + *Euprepiosaurus* clade is possible (but not at 112 mya), since tectonic reconstructions (HALL 2002) show the East Philippines terrane being approached by the New Guinea margin of the Australian plate by about 25 mya, before being translated rapidly northwestward from 16-4 mya to join the western Philippines. However, the same reconstructions show the western Philippines lying adjacent to eastern Borneo at about 50 mya, and linked to Borneo by volcanic arcs more or less continuously since 22 mya, with the principal arc shifting to the east Philippines at about 8 mya (http://www.gl.rhul.ac.uk/searg/current_research/plate_tectonics/index.html).

The Gondwanan vicariance model poposed by SCHULTE et al. (2003) does not explain how varanids reached Asia, because the times they estimate for major divisions within the genus preclude a role for the Indian subcontinent. If the ancestry of the Asian clade is African, no mechanism is evident to place its sister group *Euprepiosaurus* exclusively east of Wallace's Line at 112 mya. Conversely, if all non-African clades have Australian ancestry, the implicit 120-112 mya divergence between the Asian clade and *Euprepiosaurus* fails to explain how the Asian clade reached the mainland before late Tertiary times. In either case, AST's (2001) phylogeny requires a minimum of two major clades crossing Wallace's Line <u>prior to</u> 112 mya under the timeframe proposed by SCHULTE et al. SCHULTE et al. (2003) also analyzed an agamid phylogeny and obtained one similar estimate for the divergence of Australian and Asian clades. However these results are based on comparing only four Asian species with 70 Sahulian spp. (most Australian, a few from New Guinea, but none from Wallacea itself). Thus, this sample cannot provide a robust test for their hypothesis. HUGALL & LEE (2004) have argued that the divergence dates proposed by SCHULTE et al. contain significant methodological errors, and cannot support divergence times in excess of 14-41 mya for agamids, or by extension for varanids as well.

Given the serious mtDNA evolution rate estimation error and extensive incompatibility with the fossil record, plate tectonics and varanid phylogeny, we regard the Gondwanan vicariance model of SCHULTE et al. (2003) as untenable. A Laurasian origin for

Varanus with early Tertiary dispersal into Sundaland and mid-late Tertiary colonization of the Australian continent is fully consistent with all evidence except the uncorrected mtDNA evolutionary rate constant employed by Schulte et al. When those rates are properly recalculated (Hugall & Lee 2004), they agree with a Laurasian dispersal model. We propose the following biogeographic scenario for Australasian *Varanus*, based on Ast's (2001) phylogenetic hypothesis.

(1) An old Australian clade reached that continent by dispersal along the island arcs and microcontinents arrayed along the S margin of the Philippine Sea Plate no earlier than ca. 50 mya (Hall 2002). This clade is represented by the *V. varius* group (of which *V. spinulosus* may be a member [Böhme & Ziegler, this volume]), the subgenus *Odatria*, plus remaining Australian species of *Varanus*.

(2) A clade consisting of the *V. olivaceus* group and the ancestor of the subgenus *Euprepiosaurus* reached the west Philippines via Borneo no earlier than ca. 50 mya (Hall 2002), with the *V. indicus* and *V. prasinus* groups dispersing to and radiating on New Guinea and adjoining microcontinental fragments. The tectonics of the Molucca and Celebes seas and bordering lands (see Hall 1998, 2002) are such that relatively short distances have separated volcanic islands of the Sangihe and Halmahera arcs and a collection of Australian plate fragments (including parts of Sulawesi, the Sula Islands, Obi, Halmahera and the Vogelkop of New Guinea) at various times throughout the middle and late Tertiary.

(3) *Varanus salvator* has crossed Wallace's Line twice in the relatively recent past: in the Lesser Sundas (*bivitattus* clade), and from Borneo into Sulawesi (*togianus* clade) and thence eastward (perhaps to Obi and Halmahera).

Two Hypotheses

Small monitors have undergone two adaptive radiations east of Wallace's line (*Euprepriosaurus, Odatria*), but small monitor species do not now occur (and may never have evolved) west of Wallace's Line. The observed pattern could be an artifact of historical geography if small monitors have been limited by dispersal abilities and simply have not been able to cross Wallace's Line to the west (thus, a dispersal limitation hypothesis). Another possibility is that the presence of small carnivorous placental mammals has prevented pygmy monitors from spreading westward, due either to competition or predation (a niche complementarity hypothesis). We can see no straightforward way to exclude either hypothesis, but the weight of distributional and ecological evidence discussed below is concordant with predictions of the niche complementarity model.

Dispersal limitation. – Evaluation of the dispersal limitation hypothesis involves the usual problems of disproving a negative. However, it could be challenged by the observations that *V. timorensis* (*Odatria*) has colonized Timor and adjacent islands by overwater dispersal from Australia, and that members of the *V. indicus* complex have reached remote islands in the Banda Arc, the Solomons, and perhaps the Marianas and Carolines by natural dispersal. Also, no small monitor species inhabits Sulawesi, although *V. melinus* occurs in the Sula Islands immediately offshore. Sulawesi is the only island with wet forests east of Wallace's Line that lacks a radiation of small monitors, but it is also the only Wallacean island with a native carnivorous civet (*Macrogalidia musschenbroekii,* Corbett & Hill 1992). Similarly, the Philippines lack small monitors but have a number of small mammalian carnivores (Tab. 1). Given this consistent pattern and the evident rafting ability of at least some small monitors, a dispersal limitation model may be difficult to support.

Niche complementarity (competitive exclusion). – The complementarity hypothesis has most often been stated in terms of ecological equivalence, wherein competitive release benefits (Australian) monitors that occur in the absence of placental carnivorous mammals (Storr 1964, Hecht 1975). While this may well be true for larger monitor species, small monitors appear to be unlikely to experience strong competition with mammals. Small monitors feed primarily on large insects and other lizards, which are usually widely dispersed and often abundant. Prey species of small lizards are extremely abundant in most Australian habitats, which could be another factor that facilitated diversification of Australian pygmy monitors.

Niche complementarity (predation). – The niche complementarity hypothesis is currently being tested via the introduction of civets, mongooses and feral cats on many Wallacean islands, the presence of feral cats in New Guinea and many Melanesian islands, and especially by the establishment of foxes and feral cats in Australia. For the most part, the evidence from these inadvertent tests remains unexplored, particularly in tropical forest habitats. A number of dietary studies on Australian foxes and cats (see Dickman 1996 for a summary) indicate that small mammals and birds are preferred prey and that varanids are rarely captured. However, most of these studies were conducted in temperate and desert areas rather than tropical woodlands or forests. In a recent field study of small varanids in tropical woodlands in northern Australia (Sweet, this volume) 13 of 54 radiotracked individuals of two species were lost to predation: four were killed by native predators, and nine were taken by a single feral cat. The ambush hunting strategy employed by cats appeared to be particularly effective against small monitors descending tree trunks to forage or travel on the ground. Quolls (*Dasyurus hallucatus*) were common at the study site but failed to catch any of the lizards, perhaps because they tend not to forage at midday and do not employ ambush tactics.

While pygmy monitor species are unknown to the west of Wallace's Line, small individual monitors do occur there, in the form of juveniles of the larger species. To be viable as a concept, the niche complementarity hypothesis should be able to propose why juveniles of large species can coexist in communities with many small carnivorous mammals, whereas small monitor species are unable to do so. One possibility (based on predation) is that the per capita survivorship of small monitors increases as a function of body size, and thus (i) the young of larger species grow quickly and are sufficiently numerous to offset passage through a window of vulnerability, whereas (ii) smaller monitor species produce fewer young and always remain at a size where per capita survivorship cannot be matched by reproductive output.

Reproductive Tactics and Life Histories

Young monitors (of all species) are very secretive and little is known about their ecology. Field investigations typically either do not encounter large numbers of juveniles, or show that they occupy completely different niches than adults. For example, hatchling and juvenile Komodo monitors are arboreal insectivores (Auffenberg 1981), thus avoiding contact with cannibalistic adults. Young Komodos are thus more like the small arboreal species found elsewhere. In our field experience in Australia, juveniles of small species often behave cryptically, more like skinks than monitors. For example, in many months of focused fieldwork in the Great Victoria Desert (ERP) and savannah woodlands in the Northern Territory (SSS), each of us has only encountered a single neonate *V. tristis*. Sweet (1999) observed single neonates of *Varanus glauerti* and *V. glebopalma* in 10 months of intensive field study on the ecology of those species. Juveniles of larger species likewise adopt a very low profile by inhabiting the densest cover available (pers. obs.).

Larger monitors tend to have larger clutch sizes and longer incubation times than small monitors (Thompson & Pianka 2001, Pianka 2004b). With the exception of *V. komodoensis* and *V. spenceri*, large monitors east of Wallace's Line have smaller clutch sizes than those west of Wallace's Line (among the latter group, V. *rudicollis* has an exceptionally small clutch size). Hatchlings of large species also tend to be bigger than those of small species (Tab. 3). However, when hatchling weight is represented as a fraction of adult body weight, larger species on average invest much less (only about one-quarter as much) in each offspring than do smaller ones (Fig. 4).

Hence most small species invest relatively more in each offspring, which requires making fewer progeny. Five small species are exceptions, with relatively larger clutch sizes and smaller progeny than other *Euprepriosaurus* and *Odatria*: these are *Varanus indicus, V. mitchelli, V. semiremex, V. timorensis,* and desert populations of *V. tristis.*

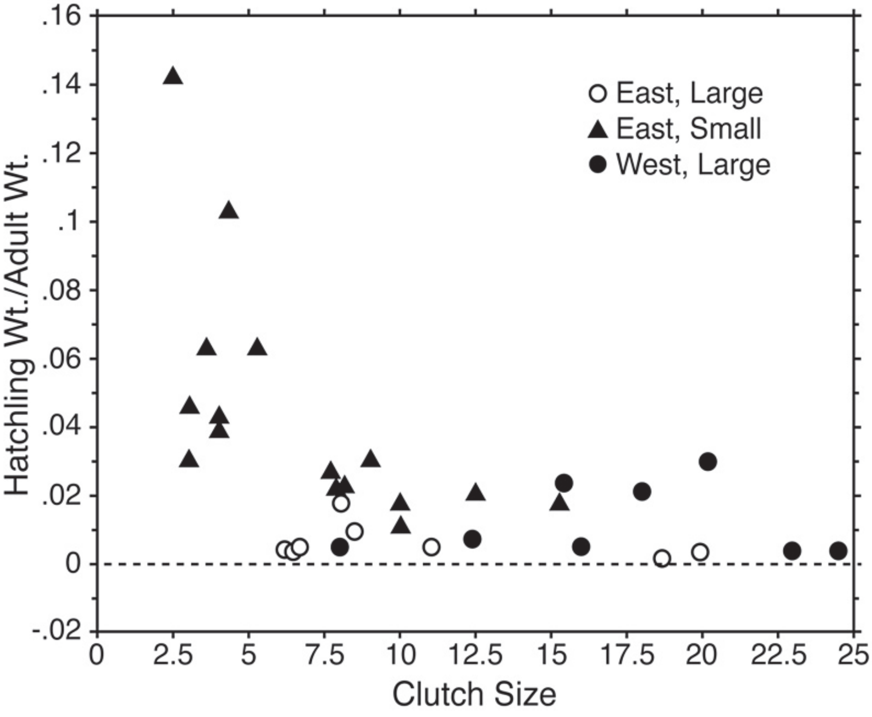

Fig. 4. Size dependency of reproductive investment in varanid lizards (data from Tab. 3).

The resulting fecundity disadvantage from increased investment per offspring could be one reason why small monitors are restricted to areas east of Wallace's Line. Most small monitor species may have no choice but to produce relatively large offspring in order for them to survive to adulthood. Small species also exhibit higher relative clutch masses than large species. In a comparative sense, we note that large monitors that occur east of Wallace's Line exhibit the same pattern in producing fewer eggs than do Afro-Asian species of similar size. The implications may well be different, however, in that hatchlings of species such as *V. komodoensis, V. salvadorii* and *V. varius* are as large as adult individuals of many species of *Odatria*.

Although scant data on lifespans are available, large monitor species almost certainly live longer than do smaller species. Longer life expectancies would translate into higher lifetime fecundities, which could offset heavier juvenile mortality. If small monitors did exist west of Wallace's Line, they would almost certainly suffer heavier mortality there than they do east of Wallace's Line. These could well be factors contributing to the biogeographic patterns detailed above.

Our general conclusion is that neither phylogenetic constraints nor dispersal limitation can adequately explain the absence of small monitor species on lands west of Wallace's Line, or their failure to evolve in African and Asian deserts, woodlands and wet forests, or on the islands of the Sunda Shelf and the Philippines. We suggest that predatory interactions rather than competitive exclusion is the most likely explanation for the restricted distribution of small monitor species, while also embracing the concept that the unique abundance of small lizard prey species contributes to the richness of the Australian monitor fauna.

Acknowledgements

We wish to thank Ben Aller, Wolfgang Böhme, Dale McGinnity, Robert Mendyk and Vincent den Breejen for allowing us to include reproductive data for several monitor species in Tab. 3, and the late Mark Bayless for his ever-cheerful assistance in locating obscure literature. We also thank the Deutsche Forschungsgemeinschaft for supporting this symposium, and the Academic Senate, University of California, Santa Barbara (SSS) and the Denton A. Cooley Centennial Professorship, University of Texas (ERP), for travel support.

Zusammenfassung

Obwohl Varaniden und Säuger in vielen Teilen der Welt eine gewisse Gleichrangigkeit erreicht haben, nutzen sie hierfür ganz andere metabolische Strategien und sensorische Mechanismen und werden deshalb in Bezug auf ihre Lebensweise als konvergent mit kleinen räuberischen Säugern eingestuft. Es erscheint deshalb gerechtfertigt, dass auf Teilen der Inselwelt Südostasiens und in Australien kleine Waranarten ökologische Nischen von Katzen, Musteliden (Marderartigen) und Viverriden (Schleichkatzen) besetzen, die in anderen Teilen der Welt von eben diesen Säugern besetzt sind. Die Anzahl großer Waranarten (>1,3 m GL) ändert sich nicht wesentlich beim Überschreiten der Wallace-Linie, die eine Verbreitungsgrenze für nahezu alle kleinen, carnivoren, placentalen Säuger darstellt, aber die Zahl kleiner Waranarten (<1,2 m GL) steigert sich östlich dieser Linie abrupt. Wir diskutieren hier alternative Hypothesen dieser Verbreitungsverhältnisse, die nach unserer Ansicht von phylogeographischen Einschränkungen oder einem besonderen Typ ökologischer Wechselwirkungen herrühren könnten. Eine ältere Begründung dieser Erscheinung kann nicht ausgeschlossen werden, ist aber einem direkten Vergleich nicht zugänglich. Kleine Waranarten können, wie bekannt, mit Dasyuriden, räuberischen Beutlern, koexistieren, aber offensichtlich nicht mit placentalen Carnivoren (dieser Punkt unterliegt gegenwärtig infolge der eingeschleppten Katzen und Füchse in Australien einem ungewollten Test). Da Juvenile von Großwaranarten ganz offensichtlich in Gegenwart placentaler Carnivoren westlich der Wallace-Linie überleben können, vermuten wir, dass eher Jagdstrategien als der Wettbewerb um Ressourcen die beobachteten Verhältnisse beinflusst hat. Von Großwaranen werden große Gelege produziert, und ihre Nachkommen entwachsen schnell dem gefährlichen Größenstadium, während Kleinwarane kleine Gelege produzieren und stets einer großen Mortalität durch räuberische Mammalier unterliegen. Daraus schließen wir, dass sie nicht mit placentalen, carnivoren Säugern über evolutionäre Zeiträume koexistieren können.

Schlüsselwörter: Squamata: Varanidae; konkurrierende carnivore Säuger; Indo-Australien: Wallace-Linie.

References

Ali, J.R., Hall, R. & S.J. Baker (2001): Paleomagnetic data from a Mesozoic Philippine Sea Plate ophiolite on Obi Island, eastern Indonesia. . – J. Asian Earth Sciences 19: 535-546.

Ast, J. C. (2001): Mitochondrial DNA evidence and evolution in Varanoidea (Squamata). – Cladistics 17: 211-226.

Auffenberg, W. (1981): The Behavioral Ecology of the Komodo Monitor. Gainesville, University Presses of Florida.

Baverstock, P. R., King, D., King, M., Birrell, J. & M. Krieg (1993): The evolution of species of the Varanidae: Microcomplement fixation analysis of serum albumins. – Austral. J. Zool. **41**: 621-638.

Böhme, W. & T. Ziegler (2007): Notes on the distribution, diet, hemipenis morphology and systematics of *Varanus spinulosus* Mertens, 1941. – Mertensiella (this volume).

Card, W. & A. G. Kluge (1995): Hemipeneal skeleton and varanid lizard systematics. – J. Herpetol. **29**: 275-280.

Corbett, G. B. & J. E. Hill (1992): The Mammals of the Indomalayan Region. Oxford: Oxford Univ. Press.

De Buffrénil, V., Ineich, I. & W. Böhme (2004): Comparative data on epiphyseal development in the family Varanidae. – J. Herpetol. **37**: 328-335.

Dickman, C. R. (1996): Overview of the impacts of feral cats on Australian native fauna. – Austral. Nature Conservation Agency.

Estes, R. (1983): The fossil record and early distribution of lizards. Pp. 365-398, in: Rhodin, A. G. J. & K. Miyata (eds.): Advances in Herpetology and Evolutionary Biology. Museum of Comparative Zoology, Harvard University Press.

Flannery, T. F. (1989): Mammals of the South-West Pacific and Moluccan Islands. Sydney, Reed Books.

— (1995): Mammals of New Guinea, 2nd ed. Ithaca, Cornell Univ. Press.

Fuller, S., Baverstock, P. & D. King (1998): Biogeographic origins of goannas (Varanidae): a molecular perspective. – Mol. Phyl. Evol. **9**: 294-307.

Hall, R. (1998): The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. Pp. 99-131, in: Hall, R. & J. D. Holloway (eds.): Biogeography and Geological Evolution of SE Asia. Leiden, Backhuys Publishers.

— (2002): Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions and animations. – J. Asian Earth Sci. **20**: 353–434.

— & J. D. Holloway (Eds.) (1998): Biogeography and Geological Evolution of SE Asia. – Leiden, Backhuys Publishers.

— & M. E. J. Wilson (2000): Neogene sutures in eastern Indonesia. – J. Asian Earth Sci. **18**: 781-808.

HECHT, M. (1975): The morphology and relationships of the largest known terrestrial lizard, *Megalania prisca* Owen, from the Pleistocene of Australia. – Proc. Royal Soc. Victoria **87**: 239-250.

HERMES, N. (1981): Mertens' water monitor feeding on trapped fish. – Herpetofauna **13**: 34.

HILL, K.C., & R. HALL (2003): Mesozoic-Cenozoic evolution of Australia's New Guinea margin in a west Pacific context. Pp. 265-290, in: HILLIS, R .R. & R. D. MULLER (eds.): Evolution and Dynamics of the Australian Plate. – Geol. Soc. America, Special Paper 372.

HORN, H.-G. (1999): Evolutionary efficiency and success in monitors: A survey on behavior and behavioral strategies and some comments. In: HORN, H.-G. & W. BÖHME (eds.): Advances in Monitor Research II. Mertensiella **11**: 167-180.

— (2004): *Varanus salvadorii*. Pp. 234-243, in: Pianka, E. R. & D. R. King (eds.): Varanoid Lizards of the World. Bloomington, Indiana University Press.

HUGALL, A. R. & M. S. Y. LEE (2004): Molecular claims of Gondwanan age for Australian agamid lizards are untenable. – Mol. Biol. Evolution 21: 2102-2110.

JERISON, H. J. (1973): Evolution of the Brain and Intelligence. New York, Academic Press.

KEAST, A. (1972): Australian mammals: zoogeography and evolution. Pp. 427-515, in: KEAST, A., ERK, F. C. & B. GLASS (eds.): Evolution, Mammals, and Southern Continents. Albany, State Univ. New York Press.

KING, M. & D. KING (1975): Chromosomal evolution in the lizard genus *Varanus* (Reptilia). – Austal. J. Biol. Sci. **28**: 89-108.

KING, D., KING, M. & P. BAVERSTOCK (1991): A new phylogeny of the Varanidae. Advances in Monitor Research. Mertensiella **2**: 211-219.

MCLOUGHLIN, S. (2001): The breakup history of Gondwana and its impact on pre-Cenozoic floral provincialism. – Aust. J. Bot. **49**: 271-300.

METCALFE, I., SMITH, J. M. B., MORWOOD, M. & I. DAVIDSON (Eds.) (2001): Faunal and Floral Migrations and Evolution in SE Asia-Australasia. Lisse, A.A. Balkema Publishers.

MOLNAR, R. (2004): The long and honorable history of monitors and their kin. Pp. 10-67 in: PIANKA, E. R. & D. R. KING (eds.): Varanoid Lizards of the World. Bloomington, Indiana University Press.

— & E. R. PIANKA (2004): Pp. 68-76 in: Pianka, E. R. & D. R. King (eds.): Varanoid Lizards of the World. Bloomington, Indiana University Press.

NICHOLS, G. & R. HALL (1999): History of the Celebes Sea basin based on its stratigraphic and sedimentological record. – J. Asian Earth Sci. **17**: 47-59.

NORTHCUTT, R.G. (1984): Anatomical organization of the optic tectum in reptiles. Pp. 547-600, in: VANEGAS, H. (ed.): Comparative Neurology of the Optic Tectum. New York, Plenum.

NOWAK, R.M. (1999): Walker's Mammals of the World, 6th ed. Baltimore, Johns Hopkins University Press.

PEARSON, R. (1972): The Avian Brain. Academic Press, London and NewYork.

PEPIN, D. J. (1999): The origin of monitor lizards based on a review of the fossil evidence. In: HORN, H.-G. & W. BÖHME (eds.): Advances in Monitor Research II. Mertensiella **11**: 11-42.

PIANKA, E. R. (1969): Habitat specificity, speciation, and species density in Australian desert lizards. –Ecology **50**: 498-502.

— (1994): Comparative ecology of *Varanus* in the Great Victoria desert. – Austral. J. Ecol. **19**: 395-408.

— (1995): Evolution of body size: Varanid lizards as a model system. – Amer. Natural. **146**: 398-414.

— (2004a): *Lanthanotus borneensis*. Pp. 535-538, in: PIANKA, E. R. & D. R. KING (eds.): Varanoid Lizards of the World. Bloomington, Indiana University Press.

— (2004b): Evolution of Body Size and Reproductive Tactics. Pp. 549-555 in: Pianka, E. R. & D. R. King (eds.): Varanoid Lizards of the World. Bloomington, Indiana University Press.

— & D. R. King (Eds.) (2004): Varanoid Lizards of the World. Bloomington, Indiana University Press.

Polhemus, D. & J. T. Polhemus (1998): Assembling New Guinea: 40 million years of island arc accretion as indicated by the distributions of aquatic Heteroptera (Insecta). Pp. 327-340 in: Hall, R. & J. D. Holloway (eds.): Biogeography and Geological Evolution of SE Asia. Leiden, Backhuys Publishers.

Röll, B. & H.-G. Horn (1999): The structure of the eye of the monitor lizard *Varanus griseus caspicus* (Reptilia, Varanidae). In: Horn, H.-G. & W. Böhme (eds.): Advances in Monitor Research II. Mertensiella **11**: 291-306.

Sanmartin, I. & F. Ronquist (2004): Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. – Syst. Biol. 53: 216-243.

Schulte, J. A. II, Melville, J. & A. Larson (2003): Molecular phylogenetic evidence for ancient divergence of lizard taxa on either side of Wallace's Line. – Proc. Roy. Soc. London, Biol. Sci **270**: 597-603.

Schwenk, K. (1995): Of tongues and noses: Chemoreception in lizards and snakes. – Trends Ecol. Evol. **10**: 7-12.

— & G. P. Wagner (2001): Function and the evolution of phenotypic stability: connecting pattern to process. – Amer. Zool. **41**: 552-563.

Shine, R. (1986): Food, habitats and reproductive biology of four sympatric species of varanid lizards in tropical Australia. – Herpetologica **42**: 336-360.

Sprackland, R. G. (1991): Taxonomic review of the *Varanus prasinus* group with descriptions of two new species. – Mem. Qld. Mus. **30**:561-576.

Storr, G. (1964): Some aspects of the geography of Australian reptiles. – Senck. Biol. **45**: 577-589.

Strahan, R. (Ed.) (1989): The Complete Book of Australian Mammals. Sydney, Angus & Robertson.

Sweet, S. S. (1999): Spatial ecology of *Varanus glauerti* and *V. glebopalma* in northern Australia. In: Horn, H.-G. & W. Böhme (eds.): Advances in Monitor Research II. Mertensiella **11**: 317-366.

— (2007): Comparative Spatial Ecology of Two Small Arboreal Monitors in Northern Australia. – Mertensiella (this volume).

— & E. R. Pianka (2003): The lizard kings. – Natural History **112**(9): 40-45.

Ten Donkelaar, H. J. (1998): Reptiles. Pp. 1315-1523, in: Nieuwenhuys, R., Ten Donkelaar, H. J. & C. Nicholson (eds.): The Central Nervous System of Vertebrates. Berlin, Springer.

Thompson, G. G. & E. R. Pianka (2001): Allometry of clutch and neonate sizes in monitor lizards (Varanidae: *Varanus*). Copeia **2001**: 443-458.

Tsellarius, A. Y. & Y. G. Menshikov (1994): Indirect communication and its role in the formation of social structure in *Varanus griseus* (Sauria). – Russ. J. Herpetol. **1**: 121-32;443-458.

Ulinski, P.S. (1990): Nodal events in forebrain evolution. – Netherlands J. Zool. **40**: 215-240.

Veevers, J. J., Powell, C. M. & S. R. Roots (1991): Review of sea floor spreading around Australia. I. Synthesis of the patterns of spreading. – Austal. J. Earth Sci. **38**: 373-389.

Weisrock, D. W., Macey, J. R., Ugurtas, I. H., Larson, A. & T. J. Papenfuss (2001): Molecular phylogenetics and historical biogeography among salamandrids of the 'true' salamander clade: rapid branching of numerous highly divergent lineages in *Mertensiella luschani* associated with the rise of Anatolia. – Mol. Phyl. Evol. **18**: 434-448.

WROE, S. (2002): A review of terrestrial mammalian and reptilian carnivore ecology in Australian fossil faunas, and factors influencing their diversity: the myth of reptilian domination and its broader ramifications. – Austral. J. Zool. **50**: 1-24.

—, ARGOT, C. & C. DICKMAN (2004): On the rarity of big fierce carnivores and primacy of isolation and area: tracking large mammalian carnivore diversity on two isolated continents. Proceedings Royal Society of London, Biol. Sci. **271:** 1203-1211.

Authors: SAMUEL S. SWEET, Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106-9610, USA; e-mail: sweet@lifesci.ucsb.edu. ERIC R. PIANKA, The University of Texas Austin, Integrative Biology C 0930, One University Station, Austin, Texas 78712 – 0253, USA; e-mail: pianka@mail.utexas.edu