

Scaling of Limb Proportions in Monitor Lizards (Squamata: Varanidae)

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ABSTRACT.— The lengths and diameters of the limb segments of 105 monitor lizards from 22 species were measured on preserved museum specimens in order to determine whether limb proportions vary in relation to snout-vent length (used as an indicator of overall body size). Scaling exponents (slopes of allometric equations) were estimated for log-transformed species' mean values, using both conventional nonphylogenetic statistics as well as the method of phylogenetically independent contrasts. Both methods gave essentially the same results. All limb segment lengths and diameters scale with exponents exceeding 1.0; thus, larger species of monitors tend to have larger limbs relative to their snout-vent length. Foot length, however, decreases relative to total hindlimb length in larger species. Measures of limb segment diameters scale with greater exponents than do limb lengths; thus, larger species also tend to have relatively thicker limbs. The empirical results on limb shape are consistent with predictions derived from biomechanical models.

Much attention has been paid to the allometry of animals and how they overcome various physical "problems" associated with large body size (e.g., Alexander, 1982, 1985; Jungers, 1984, 1985; McMahon, 1984; Schmidt-Nielsen, 1984; Preuschoft and Demes, 1985; Hildebrand, 1988; Biewener, 1990; Demes, 1991; Bertram and Biewener, 1992; Preuschoft et al., 1994). For isometric animals, body mass scales with the cube of the linear body dimensions whereas the cross-sections of muscles, bones, and tendons—and, therefore, the forces that can be exerted or sustained by these tissues—increase only with the square of the linear body dimensions. Large mammals "solve" this problem by deviating from geometric similarity; they have relative larger leg muscles and greater bone cross-sectional areas (Alexander et al., 1979, 1981; Alexander, 1985).

Large mammals also show increased lever arms of their muscles ("inlevers") and generally keep the legs in a straighter position than do smaller mammals (e.g., Biewener, 1990). With straighter limbs the directions of the ground reaction forces—the forces that are exchanged between substrate and feet—can be chosen in a way that the lines of action of these forces pass close by the limb joints. Then, the "outlevers"—the distances between joints and line of action of the ground reaction force—are short, so that the torques at the limb joints, which are given by the magnitude of the ground reaction force multiplied by the outlevers, are low. To keep a joint in equilibrium, muscles around the joint must be active, so that the torque produced by these muscles, which is given by muscle force

multiplied by arm of lever (inlever), has the same magnitude as the torque that results from the ground reaction force. As outlevers are shortened relative to inlevers, less muscle force is necessary to keep the joints in equilibrium. On the other hand, longer outlevers relative to inlevers allow limbs to be moved more quickly (e.g., Hildebrand, 1988).

In comparison with mammals, relatively little attention has been paid to the allometry of lizards, the other major extant group of terrestrial tetrapods. Although no lizard has ever been as large as the largest terrestrial mammals (references in Garland et al., 1993), the body mass of extant lizards spans a range from <1 g to >100 kg (MacLean, 1975; Pough, 1980; Auffenberg, 1981; Raxworthy, 1991), and extinct forms were larger still (e.g., Hecht, 1975). Therefore, pronounced size-related changes can also be expected in the morphology of lizards.

The degree of sprawling of the limbs may differ among species of lizards and in the same individual at different locomotor speeds (e.g., Urban, 1965), but even such large lizards as the Komodo dragon (*Varanus komodoensis*) exhibit a basically sprawling limb posture. In lizards of all sizes the sprawling limb posture necessarily leads to long outlevers, unless the limbs are short. Therefore, pronounced size-related changes in the shape of the limbs can be expected (Christian, 1995): larger lizards should have relatively stronger limbs than do smaller lizards. Because the strength of a limb is reflected in the diameters of its segments, which increase with increasing bone diameters as well as with increasing muscle mass, large lizards

should have relatively thicker limb segments than do smaller lizards. With a sprawling limb posture a reduction of the outlevers at the limb joints could be morphologically achieved either by reducing the total limb length or by reducing the lengths of certain limb segments relative to body length. The hands and feet should be relative short in large lizards, because they are placed in a plantigrade way, at least at moderate speeds (e.g., Padian and Olsen, 1984), so that the outlevers at wrist and ankle joints are long (see Discussion). Relatively short limbs, however, would probably have negative effects on aspects of locomotor performance, such as maximal sprint running speed or jumping ability (e.g., Coombs, 1978; Losos, 1990; Garland and Janis, 1993; Garland and Losos, 1994; Preuschoft et al., 1994; Christian, 1995). For an arbitrary sample of lizards from different phylogenetic groups that rely on their limbs for terrestrial locomotion, Christian (1995) observed a negative allometry of total limb length. In addition, ontogenetic studies of several lizard species also indicate that a negative allometry of total hindlimb length is the more common pattern (Pounds et al., 1983; Garland, 1985; Witten, 1985; Losos et al., 1989).

As an empirical test of the predictions of biomechanical models, we focus here on monitor lizards (Varanidae) from Australia and southeast Asia (Green and King, 1993). This family contains species of very different body sizes, ranging from about 10 cm to >1 m in snout-vent length (SVL). As noted by Pianka (1994, p. 395), "*Varanus* are morphologically conservative but vary widely in size, making this genus a model system for understanding the evolution of body sizes." Similarly, Houston (1978) remarked that Australian monitors "tend to be much more uniform structurally" than are Australian agamids, and Greer (1989) commented that "all varanids look more or less alike, differing only in details." Varanids have sometimes been viewed as relatively homogeneous in terms of behavior and ecology as well, but this perspective now seems difficult to support (e.g., Shine, 1986; Auffenberg, 1988; Losos and Greene, 1988; Greer, 1989; James et al., 1992; Green and King, 1993; Pianka, 1994), and quantitative comparisons of the phenotypic diversity or rates of evolution of different clades of lizards (cf. Garland, 1992) have yet to be performed. In any case, we hoped that the biomechanical reasons behind morphometric variation in the Varanidae should be relatively apparent, and not greatly obscured by adaptation to varying selective factors.

In monitors, because of the reasons given above, we predicted size-dependent changes in the lengths of limb segments, in particular a decrease of foot and hand length compared to

the length of the rest of hindlimb and forelimb, respectively. We also predicted a positive allometry of segment diameters compared to segment lengths. Scaling effects in limb posture, inlevers, and muscle composition can also be expected in monitors but are not examined in the present study.

MATERIALS AND METHODS

Studied Animals.—We studied 22 species of monitor lizards, using preserved adult specimens in the collections of the Museums and Art Galleries of the Northern Territory, Darwin, and the Australian Museum, Sydney (Table 1). Five specimens represented each species, except for *V. komodoensis* (two specimens), *V. glauerti* (three specimens), and *V. kingorum* (three specimens).

Morphometric Measurements.—All lengths and diameters were measured with a ruler or a caliper and recorded to the nearest 0.5 mm. Upper arm length was measured from the shoulder joint to the elbow joint, the forearm length from the elbow joint to the center of the carpus, hand length from the center of the carpus to the tip of the longest toe (claw excluded), upper leg length from the hip joint to the knee joint, lower leg length from the knee joint to the center of the tarsus, and foot length from the center of the tarsus to the tip of the longest toe (claw excluded). Before taking these measurements, the joints were located by bending and extending the limbs in different ways. Forelimb length was then computed as the sum of upper arm length, forearm length, and hand length; hindlimb length was calculated as the sum of upper leg length, lower leg length, and foot length. At the site of the largest crosssection of upper arm, forearm, upper limb, and lower limb (which was always approximately at the middle of the segment), the largest diameter and the diameter perpendicular to the largest diameter were measured. Under the assumption of an elliptic crosssection with these diameters as major axes, the crosssectional area was then calculated. The square root of the crosssectional area is referred to as 'diameter' of the segment.

Snout-vent length (SVL) was used instead of body mass as the reference for computing allometric relationships. The latter is more difficult to obtain from preserved specimens, because it depends more on the condition of the animal and is altered by preservation. Also, in many specimens the body cavity had been cut open and in some the intestines had been partly removed.

As a consequence of the preservation, the diameters of the limb segments may have changed more or less depending on the size of the specimen, thereby leading to a bias in the data for the diameters (see Lee, 1982, for anurans). In

TABLE 1. Limb proportions (mm) means, N = 5 except for *kingorum* (N = 3), *glauerti* (N = 3), and *komodoensis* (N = 2), of 22 species of *Varanus* lizards.

Species	Snout-vent length	Upper arm length	Upper arm diam.	Fore-arm length	Fore-arm diam.	Hand length	Fore-limb length	Upper leg length	Upper leg diam.	Lower leg length	Lower leg diam.	Foot length	Hind-limb length
<i>brevicauda</i>	90	7.3	3.5	6.1	3.5	9	22.4	8.5	4.4	7.1	3.5	10.4	26
<i>gilleni</i>	149	12.6	5.3	10.5	5.1	15.2	38.3	13.7	7.4	12.7	5.9	20	46.4
<i>primordius</i>	107.6	9.4	3.65	8.4	3.5	10.4	28.2	10	5.4	9	4.2	13.8	32.8
<i>acanthurus</i>	230	21.6	12	19.4	10.7	24.8	65.8	26.8	16.4	22	12.8	33.2	82
<i>kingorum</i>	97.7	9	3.8	7.7	3.6	10.5	27.2	9.5	5.4	9.3	3.8	14.5	33.3
<i>mitchelli</i>	272	23.1	10.5	21.3	9.3	29.8	74.2	32.8	15.9	26	12.1	41.4	100.2
<i>scalaris</i>	219	18.2	10	17.8	9.4	25.3	61.3	25.7	14	20.6	10.7	33.3	79.6
<i>tristis</i>	272	25.8	12.6	24.2	11.2	30.4	80.4	32.6	18.8	30.3	14.5	41.6	104.5
<i>glauerti</i>	196	21	7.2	17.8	6.7	23.7	62.5	24	10.1	21.7	7.7	34	79.7
<i>storri</i>	129	11.2	5.5	9.7	5.5	15.4	36.3	13.3	8	11.9	6.1	18.2	43.4
<i>semiremex</i>	252	21.4	9.1	18	8.4	25.6	65	24.2	12.8	21.8	9.7	35.4	81.4
<i>glebopalma</i>	300	34.8	11.9	28.5	10.8	32.1	95.4	41.4	19.4	38.2	13.8	48.8	128.4
<i>indicus</i>	399	41.2	19.8	39.4	18.8	49.8	130.4	48.4	26.9	46.4	21	66.6	161.4
<i>mertensi</i>	394	38.8	17.4	33.6	16.1	47	119.4	49.8	26.4	46	20.9	64.6	160.4
<i>spenceri</i>	414	39.6	21.9	38.4	21.2	50	128	58.2	30.9	52.2	23.9	57.8	168.2
<i>rosenbergi</i>	444	43.4	25.3	42	24.7	51.8	137.2	57	34.4	54.8	26.7	69	180.8
<i>gouldii</i>	454	42.2	24.5	40	22.5	48	130.2	54.4	33.7	54.4	26.7	66.4	176.2
<i>panoptes</i>	595	62.6	33.6	61.4	31.7	68.4	192.4	75.4	48.2	77.4	40.1	88.2	241
<i>giganteus</i>	680	68.6	31.6	69.2	26.8	78.4	216.2	86	42.7	85	30.4	101	272
<i>varius</i>	568	61	33.1	60	30.3	74	195	75	42.8	73	33.1	98	246
<i>komodoensis</i>	1000	101	75.7	103	64.2	135	339	122	97	121	61.1	148	391
<i>eremius</i>	157	13.6	6	12.5	5.5	15.4	41.5	18.4	8.9	17.8	7.6	22	58.2

the absence of data for living specimens, we have no way to test for this possible bias. Also, the location of the joints is more difficult to determine in large monitors with thick limbs, but this possible increase in measurement error with the size of the studied animals should not lead to an important bias with respect to body size.

Statistical Analyses.—Allometric scaling relationships were estimated using \log_{10} transformed mean values for each of the 22 species presented in Table 1. Least squares linear regressions were fitted in the usual way. In addition, we computed reduced major axis (RMA) slopes, which are equivalent to the least squares slopes divided by the Pearson product-moment correlation coefficient, or simply the standard deviation (SD) of the dependent variable (e.g., log limb length) divided by the SD of the independent variable (log SVL). Because the correlation coefficients for all scaling relationships were high (r ranged from 0.986 to 0.996), these two alternate estimates of the slopes were always quite similar. However, because the functional relationship between two variables will tend to be underestimated by least squares regression when measurement error exists in the independent variable, the RMA estimates should generally be considered more reliable (e.g., LaBarbera, 1989; Harvey and Pagel, 1991; Riska, 1991).

Deviations from isometry (a scaling exponent

of 1.0) were tested by inspection of 2-tailed 95% confidence intervals on least squares regression slopes and by using the t -statistic for RMA slopes described in Clarke (1980) with degrees of freedom computed from his equation 5.1.

Conventional statistical methods, such as those described in the preceding two paragraphs, assume that the data points are independent (and identically distributed). Mean values for a series of species generally cannot be assumed to be independent in the statistical sense, because they have evolved as part of a hierarchical phylogeny. Several statistical methods have been developed to incorporate estimates of hierarchical phylogenetic topologies and estimates of branch lengths between speciation events (reviews in Harvey and Pagel, 1991; Garland et al., 1993). Of the available procedures, Felsenstein's (1985) method of phylogenetically independent contrasts is the best understood and displays statistical performance that is at least as good as other alternatives (Grafen, 1989; Martins and Garland, 1991; Garland et al., 1992; Garland and Adolph, 1994; Diaz-Uriarte and Garland, 1996). Therefore, we also estimated scaling exponents using phylogenetically independent contrasts, as implemented in the PD TREE computer program (version 2.0), first described in Garland et al. (1993).

An estimate of phylogenetic relationships was obtained from Baverstock et al. (1993; see Fig. 1). Thus, the implicit model of evolutionary

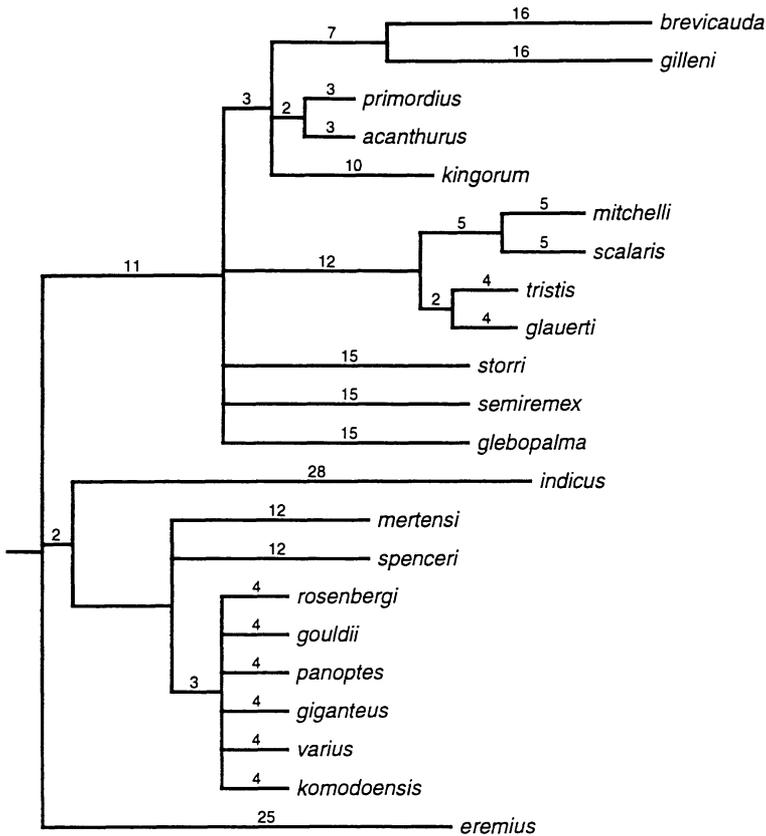


FIG. 1. Hypothesis of phylogenetic relationships of species of varanid lizards included in the present study, taken from Fig. 2 of Baverstock et al. (1993; some branch lengths were estimated by eye).

change is that amount of evolution of the morphometric traits we measured is roughly proportional to change in the albumin molecule. The statistical adequacy of the branch lengths was checked as described in Garland et al. (1992; see also Diaz-Uriarte and Garland, 1996), and no transformations of branch lengths were judged to be necessary. The phylogeny shown in Fig. 1 contains several unresolved nodes (polytomies). Such uncertainty about the true, presumably bifurcating, branching pattern leads to uncertainties in implementing independent contrasts procedures. Following Purvis and Garland (1993), we computed all $N - 1 = 21$ independent contrasts from the 22-species phylogeny for obtaining estimates of scaling exponents (see formulas in the appendices of Garland et al., 1992). For hypothesis testing, we bracketed the degrees of freedom between $N - 1 = 20$ (where N = the number of independent contrasts) and $p - 1 = 10$, where p = the number of nodes in the working phylogeny, including the root (see Purvis and Garland, 1993).

RESULTS

Species' mean values of all measured variables are given in Table 1. Table 2 presents estimates of scaling exponents based on conventional, nonphylogenetic analyses. For isometric scaling, all exponents would be 1. This is not the case for any of the examined characters of the limbs; all scaling exponents are significantly greater than 1 ($P < 0.05$), whether judged by least squares regressions or reduced major axis slopes. For the RMA slopes, which ranged from 1.081 to 1.260 (Table 2), t statistics (not shown) ranged between 3.13 and 7.71, as compared with a critical value of approximately 2.119 for 16.1 degrees of freedom (df) at $P = 0.05$. Fig. 2 illustrates the deviations from isometry for the total lengths of both hind- and forelimbs and for the diameters of the stylopodia (upper arm and upper leg).

Using the method of phylogenetically independent contrasts we also find that scaling exponents for all characters exceed unity (Table 3). For the RMA estimates of slopes, which

TABLE 2. Allometric equations for limb proportions of 22 species of varanid lizards (data from Table 1).

Character	$\log a \pm 95\% \text{ CI}$	$b \pm 95\% \text{ CI}$	$r^2 (\%)$	SEE	CV	RMA
Hindlimb length	-0.755 ± 0.126	1.133 ± 0.051	99.1	0.0325	7.30	1.138
Upper leg length	-1.294 ± 0.149	1.147 ± 0.061	98.7	0.0383	8.61	1.154
Lower leg length	-1.455 ± 0.164	1.198 ± 0.067	98.6	0.0422	9.49	1.207
Foot length	-1.010 ± 0.142	1.074 ± 0.058	98.7	0.0364	8.17	1.081
Upper leg diameter	-1.748 ± 0.180	1.227 ± 0.073	98.4	0.0464	10.41	1.237
Lower leg diameter	-1.796 ± 0.203	1.199 ± 0.082	97.9	0.0521	11.70	1.212
Forelimb length	-0.813 ± 0.100	1.115 ± 0.041	99.4	0.0257	5.76	1.118
Upper arm length	-1.250 ± 0.133	1.092 ± 0.054	98.9	0.0342	7.67	1.098
Forearm length	-1.475 ± 0.124	1.168 ± 0.051	99.1	0.0319	7.16	1.173
Hand length	-1.175 ± 0.116	1.093 ± 0.047	99.2	0.0297	6.68	1.097
Upper arm diameter	-1.945 ± 0.212	1.246 ± 0.086	97.9	0.0544	12.23	1.260
Forearm diameter	-1.883 ± 0.238	1.208 ± 0.097	97.1	0.0612	13.75	1.226

SEE = standard error of estimate of least squares linear regression in \log_{10} units.

CV = $230.26 \times \text{SD}$ of residuals from least squares linear regression equations of log-transformed data, which approximates a coefficient of variation (see Garland, 1984).

RMA = reduced major axis slope.

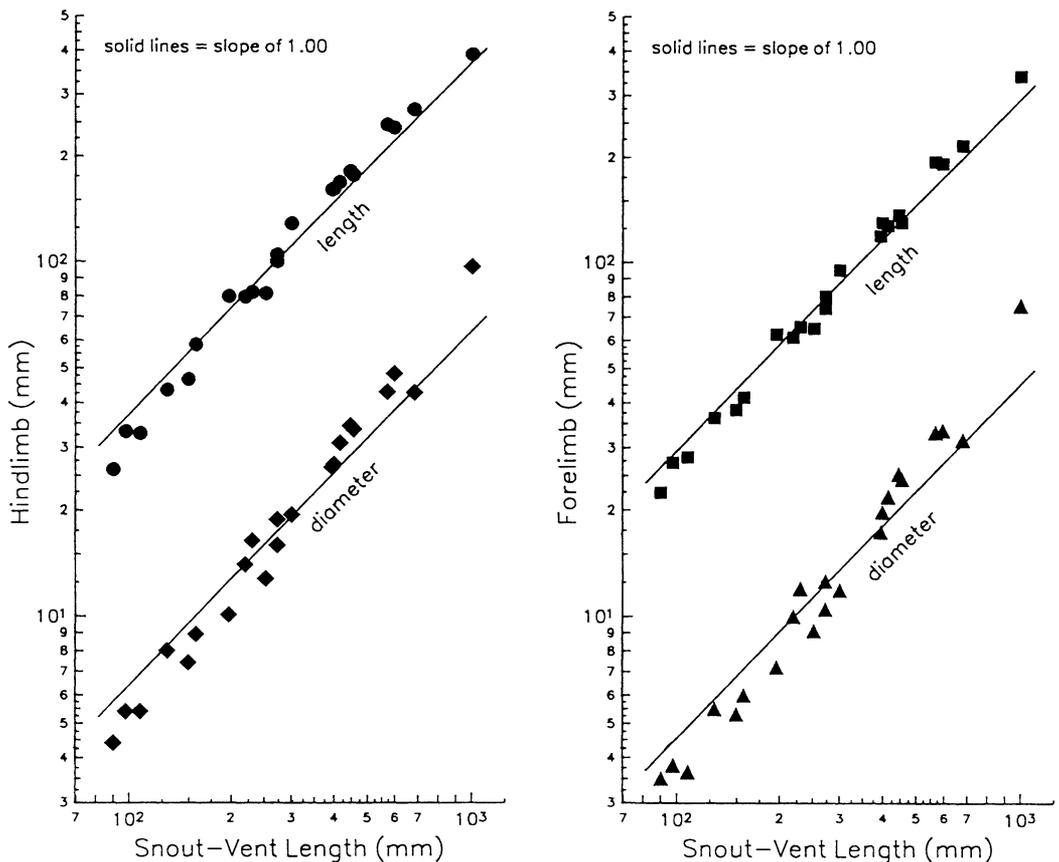


FIG. 2. Allometry of total limb lengths and of upper limb segment diameters for both hind- (A) and forelimbs (B). Solid lines have slopes of 1.0 and pass through the antilog of the mean of the log snout-vent length for all 22 species. Note that limb proportions do not scale as predicted by these lines of isometry; rather, larger species have relatively longer and thicker limbs (see Tables 2 and 3 for actual slopes).

TABLE 3. Estimates of allometric scaling exponents for limb proportions, using phylogenetically independent contrasts. * 95% confidence interval on slope computed using 20 degrees of freedom. † 95% confidence interval on slope computed using 10 degrees of freedom. SEE = standard error of estimate of least squares linear regression through origin. RMA = reduced major axis slope; see text for significance tests. t_{20} = test statistic for t distribution assuming 20 degrees of freedom. t_{10} = test statistic for t distribution assuming 10 degrees of freedom.

Character	b ± 95% CI*	± 95% CI†	r ² (%)	SEE	RMA	t ₂₀	t ₁₀
Hindlimb length	1.087 ± 0.077	± 0.082	97.7	0.0100	1.100	2.81	1.99
Upper leg length	1.122 ± 0.089	± 0.095	97.2	0.0116	1.138	3.45	2.44
Lower leg length	1.108 ± 0.088	± 0.093	97.2	0.0114	1.123	3.10	2.19
Foot length	1.048 ± 0.091	± 0.097	96.7	0.0118	1.065	1.55	1.10
Upper leg diameter	1.270 ± 0.146	± 0.156	94.3	0.0190	1.308	5.03	3.56
Lower leg diameter	1.183 ± 0.172	± 0.184	91.2	0.0223	1.239	3.23	2.28
Forelimb length	1.102 ± 0.068	± 0.073	98.3	0.0088	1.112	3.64	2.57
Upper arm length	1.075 ± 0.084	± 0.090	97.2	0.0110	1.090	2.30	1.63
Forearm length	1.128 ± 0.077	± 0.082	97.9	0.0099	1.140	4.04	2.86
Hand length	1.104 ± 0.084	± 0.089	97.4	0.0109	1.118	3.09	2.19
Upper arm diameter	1.304 ± 0.164	± 0.175	93.2	0.0213	1.350	5.15	3.64
Forearm diameter	1.209 ± 0.181	± 0.193	90.7	0.0234	1.269	3.49	2.47

ranged from 1.065 to 1.350, all exponents differ significantly from a slope of 1 based on 20 df, with the exception of foot length (critical value for t with 15.5 df [using Clarke's (1980) formula 5.1] = approximately 2.125). Under the maximally conservative assumption of only 10 df (critical value for t with 8.7 df = approximately 2.27), most exponents remain significantly different from unity, except those for the scaling of total hindlimb length, lower leg length, foot length, upper arm length, and hand length (see Table 3).

The diameters increase more rapidly with increasing SVL than do the lengths of the segments (see Tables 2 and 3). Also, the diameters of the stylopodia increase more than do the diameters of the zeugopodia (forearm and lower limb).

The slight increase of the total limb lengths with SVL is attributable to similar increases of the lengths of all three limb segments, although the foot length increases somewhat less. Thus, the ratio of foot length divided by the sum of upper leg length plus lower leg length decreases with increasing log SVL (Fig. 3). This decrease is statistically significant ($P < 0.05$) in a two-tailed test in the nonphylogenetic analysis and also in the analysis with phylogenetically independent contrasts with 20 df, but not in the latter analysis if only 10 df are used ($r = -0.626$ and $r = -0.395$, respectively, in a regression against log SVL). We might reasonably have employed a one-tailed test—in which the decrease is significant in all of the analyses—because we expected the foot length to decrease relative to the total limb length (see Discussion). However, a shift towards cursoriality with a relative increase of the length of distal limb segments in large species could not be excluded

a priori (cursorial mammals tend to have relatively long distal limb segments, e.g., Coombs, 1978). The scaling exponent for hand length is similar to the exponent for total forelimb length.

A principal component analysis (Table 4) using residuals from log-log regressions on SVL reveals that in both the nonphylogenetic and the phylogenetic analyses most characters load heavily on the first factor, which accounts for about 40% of the overall variance. This means that, after removing variation related to overall body size (as indexed by SVL), much of the remaining variation is attributable to general variation in limb size. Principal component II accounts for about 1/3 of the overall variation, and contrasts the lengths of the limb segments with their diameters, thus indicating variation in limb stoutness. Hand length loads by far the most heavily on factor III (11–12% of the overall variation), showing that relative hand length is not tightly coupled to other characters.

DISCUSSION

Among species of monitor lizards, limb length does not scale isometrically with SVL nor are limb proportions geometrically similar in monitors of different body sizes. Total limb length as well as limb segment lengths and diameters are greater relative to SVL in larger species. Or, equivalently, SVL decreases relative to limb length.

Relatively shorter limbs in large monitors would reduce the outlevers at the limb joints so that less muscle force would be necessary to keep the joints in equilibrium (see Introduction), but should also negatively affect locomotor performance (Coombs, 1978; Losos, 1990; Garland and Janis, 1993; Garland and Losos, 1994). Direct measurements of performance

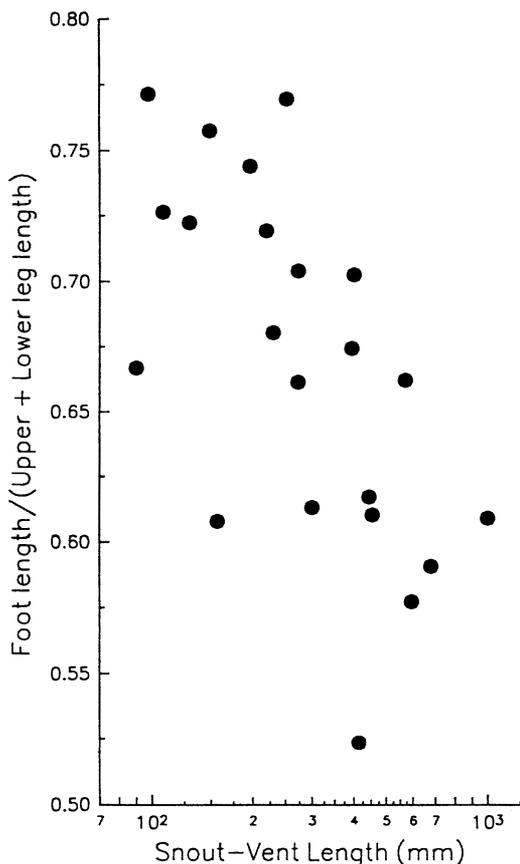


FIG. 3. Ratio of foot length divided by the sum of upper leg length plus lower leg length decreases with increasing log snout-vent length.

abilities are essential for determining the ecological or evolutionary significance of morphological variation (reviews in Garland and Carter, 1994; Garland and Losos, 1994). Unfortu-

nately, we know of no published comparative data on the locomotor abilities of varanid lizards (see also Garland, 1993). Table 5 presents preliminary data for maximal sprint speeds of some monitors. Data for three species (*V. gilleni*, *mertensi*, *tristis*) were obtained on a laboratory photocell-timed racetrack as described in Garland (1985), except that the track was doubled in length for the latter two species. As maximal sprint speed generally increases ontogenetically in lizards (Garland, 1985; Losos et al., 1989; Garland and Losos, 1994), the datum for *Varanus gilleni* is not comparable to those for the other species. We also recognize that measurements of speed taken in the field by chasing animals on feet or with automobiles can be highly unreliable, but the data presented in Fig. 4 are the only such data presently available. Even not considering the datum for *Varanus gilleni*, Fig. 4 suggests that maximal sprint speed does not decrease with increasing body size among species of monitors, as would be expected if large monitors had relatively short limbs, which they do not (Figs. 2, 3).

The increase of foot length with increasing SVL is significantly lower than is the increase of the rest of the hindlimb (although this is not statistically significant with 10 df—see Tables 2 and 3). The foot of a monitor (which is at least at moderate speeds placed plantigrade on the ground) is exposed to bending moments along its length. All joints must be balanced against the ground reaction force by muscle forces (Preuschoft, 1970, 1971). One way to reduce force and energy requirements is shortening of the segments of the foot. Also, the mass moments of inertia of the limbs should be kept low to allow quick accelerations of the limbs during locomotion. Distal masses contribute more to the mass moment of inertia of a limb than do

TABLE 4. Principal component analysis of residuals from least squares regressions on snout-vent length. Values are component correlations with factors. Values > 0.423 are in boldface; this is the two-tailed critical value at $P = 0.05$ for 20 degrees of freedom.

	Nonphylogenetic			Independent contrasts		
	I	II	III	I	II	III
Upper leg length	0.582	0.527	-0.323	0.638	0.437	-0.412
Lower leg length	0.634	0.579	-0.390	0.600	0.604	-0.431
Foot length	0.352	0.714	0.349	0.527	0.628	0.209
Upper leg diameter	0.808	-0.499	-0.092	0.724	-0.650	-0.088
Lower leg diameter	0.748	-0.453	-0.340	0.703	-0.546	-0.367
Upper arm length	0.490	0.726	0.058	0.495	0.793	0.060
Forearm length	0.701	0.516	0.033	0.554	0.622	0.113
Hand length	0.549	0.061	0.770	0.568	0.149	0.764
Upper arm diameter	0.694	-0.676	0.122	0.719	-0.653	0.157
Forearm diameter	0.705	-0.661	0.116	0.758	-0.619	0.125
Eigenvalue	4.087	3.269	1.129	4.030	3.516	1.182
% of variance explained	40.9	32.7	11.3	40.3	35.2	11.8
Cumulative % explained	40.9	73.6	84.9	40.3	75.5	87.3

TABLE 5. Maximal sprint running speeds of varanid lizards. (Estimated values.) Speeds and body dimensions represent single fastest individual where available. * F = captive animals filmed after release and chase on outdoor asphalt pavement surface, P = photocell-timed racerack in laboratory, SF = timed with stopwatch in field while being chased by human on foot or in automobile. † N = nature, NS = nature (sand), P = pavement, animals filmed running across a parking lot, R = rubberized.

Species	Snout-vent length (mm)	Body mass (g)	Speed (km/h)	Distance (m)	T _b	N of indiv. tested	Method*	Substrate*	Source
<i>Varanus gilgii</i> (juvenile)	81	5.5	9.14	0.5	36	1	P	R	this study
<i>Varanus tristis</i>	218	114	14.5	0.5	36	1	P	R	this study
<i>Varanus gouldii</i>		(700)	34	10-40	?	>8	SF	NS	T. Garland, unpubl.
							SF	NS	G. DuBois, pers. comm.
<i>Varanus salvator</i>	355	749	17.2	1	32	4	F	N	D. King, pers. comm.
<i>Varanus exanthematicus</i>	410	1310	14.0	1	32	3	F	P	R. L. Marsh, pers. comm.
<i>Varanus mertensi</i>	423	1320	16.5	1.5	36	1	F	P	R. L. Marsh, pers. comm.
<i>Varanus panoptes</i>	(550)	(6000)	22	5	?	1	SF	R	this study
<i>Varanus komodoensis</i>		(20,000)	(28)	?	?	>11	SF	N	this study
									Auffenberg, 1978, 1981

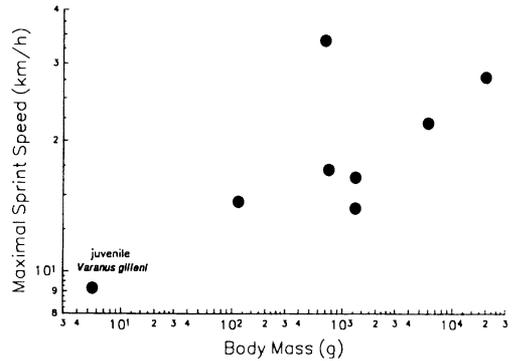


FIG. 4. Estimates of maximal sprint running speed in relation to body mass for eight species of varanid lizards.

proximal masses. Therefore, the necessity to reduce the mass moments of inertia of the swinging limb entails a reduction of the mass of the lower leg muscles. Because these muscles move and control the joints of the foot, the torques inside the foot must be limited to a rather low level. This leads to functional advantages in forms with short foot length. This argument has been developed by Preuschoft and Witte (1993) to explain the short toes of hominoids in comparison to all other hominoids. The same trend was expected for the forelimb, but examination of Tables 2 and 3 indicates that the scaling of the hand did not differ markedly from the scaling of the rest of the arm. Of course, limb length and shape may be related to other functions in addition to locomotion. The hand, in particular, can play an important role in climbing, burrowing, mating, and other activities (e.g., Auffenberg, 1978, 1981, 1988; Losos and Greene, 1988; Green and King, 1993). The principal component analysis of SVL residuals supports the idea that the scaling of hand length has been influenced by other selective factors: variation in hand length is to a high degree uncoupled from variation in the other measured characters (Table 4).

As expected (see Introduction), the diameters of the limb segments increase considerably more with SVL than do the segment lengths. Because the upper and lower limbs of lizards consist mainly of muscles, the increase of diameters of these segments can be attributed to an increase in muscle mass. This increased muscle mass can be considered as necessary to cope with the high torques about the limb joints caused by the rather sprawling limb posture exhibited by monitors of all sizes. In mammals—aside from size-dependent internal changes, e.g., of the inlevers, which can also be expected for monitors—large size is accompanied by changes in limb

posture (see Introduction). Therefore, muscle mass does not need to increase so much with size. Accordingly, data collected by Alexander et al. (1981) for a sample of mammals from different phylogenetic groups show a scaling exponent for muscle mass (about 1.05 vs. body mass) of the limbs that is three times the scaling exponent of the limb bone lengths (about 0.35) as expected for geometrically similar limbs (Alexander, 1985). Alexander's data indicate that, in the legs of mammals, average diameters scale with about the same exponent as does leg length (the scaling exponent of the bone diameters is also similar to the scaling exponent of the bone lengths; Alexander, 1985).

In lizards, the over-proportional increase of the limb segment diameters in relation to their lengths suggests—compared to mammals—a low limit to the body size that can be attained for fast animals with a sprawling limb posture. First, limbs that were excessively massive would be uneconomical and would negatively affect locomotor performance both by increasing total body mass, and thereby the total mass that has to be carried by the limbs, and by increasing the inertia that has to be overcome during accelerations of the body. Second, the high moments of inertia of massive limbs would oppose quick movement of the limbs and would make locomotion energetically expensive (see, e.g., Steudel, 1990a,b; Witte et al., 1991; Myers et al., 1993; Preuschoft et al., 1994). Finally, the limb diameter cannot be increased infinitely without physically restricting the maximal excursions of the limb.

It should be mentioned here that a comparison of the scaling exponents in monitor lizards with simple scaling concepts, such as elastic similarity (e.g., McMahon, 1984), does not seem to be worthwhile. Such scaling models usually start from an assumption of geometrically similar scaling of length variables, and that is clearly not the case in monitors. Moreover, the results shown in Tables 2 and 3 indicate a considerably greater difference between the scaling exponents for segment diameters and lengths in the stylopodia (upper arm and upper leg) than in the zeugopodia (forearm and lower leg).

The apparently greater difference between the scaling exponents of diameter and length in stylopodia as compared to zeugopodia could be interpreted as a proximal shift of the limb mass. A proximal concentration of the limb mass has been observed in cursorial mammals and is interpreted as a means to reduce the moments of inertia (Hildebrand, 1985; Witte et al., 1991; Preuschoft et al., 1994).

According to Christian et al. (1994a, b), a sprawling limb posture combined with long and strong hindlimbs and considerably shorter and

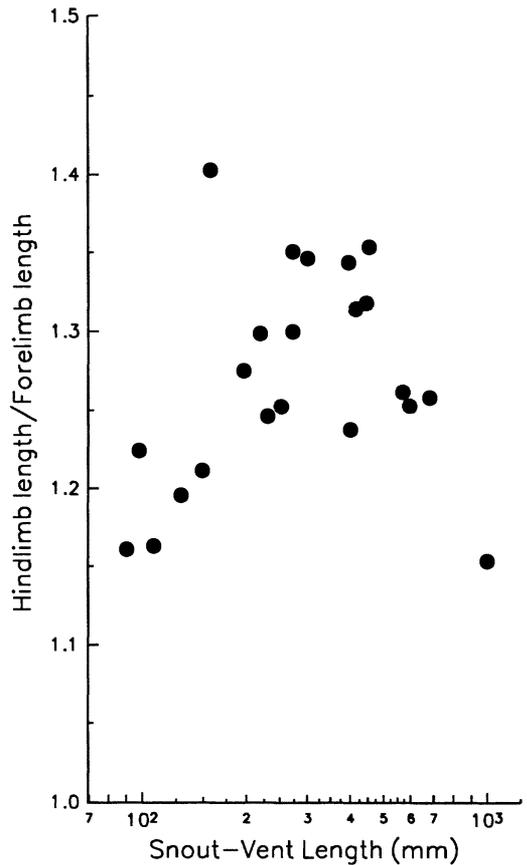


FIG. 5. Ratio of hindlimb length divided by forelimb length in relation to snout-vent length for the 22 species of varanid lizards listed in Table 1.

weaker forelimbs is well suited to small animals that rely primarily on sprinting, frequent accelerations, and the ability to walk and run on different substrates, but which rely less on stamina. Many small lizards (e.g., most New World iguanians) fit this description. Monitor lizards, however, depend relatively heavily on stamina, rather than acceleration, during their normal foraging activities (Auffenberg, 1981, 1988; Losos and Greene, 1988; Green and King, 1993). Therefore, monitors would be expected to have not very much different fore- and hindlimb proportions. This prediction is generally supported by the data shown in Table 1 and illustrated for the limb lengths in Fig. 5 (also Garland, unpublished data). Especially small monitor lizards do not exhibit very much difference in size between fore- and hindlimbs (the average ratio between hindlimb length and forelimb length is below 1.2 for the five smallest species in Fig. 5—in most agamids and iguanids this ratio exceeds 1.3 and is above 1.5 in many species; Garland, unpubl. data). On the other hand, the large

komodo dragon, despite its size and relatively equal-sized fore- and hindlimbs, sometimes uses ambush and sprinting to capture prey (Auffenberg, 1981; Losos and Greene, 1988).

We conclude that large monitors solve the force problems associated with a rather sprawling limb posture by having relatively more massive limbs as compared to smaller monitors. This suggests an upper size limit for animals with high locomotor performance and a sprawling limb posture. Data on limb posture, muscle and bone properties, the scaling of locomotor performance, and behavior under natural conditions (cf. Garland, 1993) will be required in order to draw a more complete picture of the evolution of varanid limb proportions.

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APPENDIX

List of the museum numbers of the specimens of *Varanus* lizards studied in the Australian Museum (AM), Sydney, Australia, and in the Museums and Art Galleries of the Northern Territory (NTM), Darwin, Australia (for some specimens a museum number was not available): *V. breviceauda*—NTM R 7153, NTM R 7154, NTM R 7155, NTM R 7599, NTM R 14983. *V. gillemi*—NTM R 203, NTM R 1579, NTM R 1784, NTM R 1972, NTM R 9773. *V. primordius*—NTM R 3398, NTM R 3449, NTM R 5853, NTM R 8345, NTM R 9271. *V. acanthurus*—NTM R 3379, NTM R 8937, NTM R 8939, NTM R 12706, NTM R 16395. *V. kingorum*—NTM R 7288, NTM R 8687, NTM R 8688. *V. mitchelli*—NTM R 2299, NTM R 2300, NTM R 3065, NTM R 5268, NTM R 8614. *V. scalaris*—NTM R 3555, NTM R 5269, NTM R 6532, NTM R 7658, NTM R 8740. *V. tristis*—NTM R 443, NTM R 1533, NTM R 7944,

NTM R 7996, NTM R 8588. *V. glauerti*—NTM R 972, NTM R 8674, AM R 123850. *V. storri*—NTM R 1064, NTM R 1065, NTM R 2098, NTM R 8922, NTM R 8925. *V. semiremex*—NTM R 843, NTM R 2107, AM R 93739, AM R 97998, AM R 107537. *V. glebopalma*—NTM R 896, NTM R 2252, NTM R 2411, NTM R 8673, NTM R 17941. *V. indicus*—AM R 9312, AM R 9544, AM R 12968, AM R 25391, AM R 134953. *V. mertensi*—NTM R 41, NTM R 3727, NTM R 3728, NTM R 7543, NTM R 8259. *V. spenceri*—NTM R 1082, NTM R 3842, NTM R 3843, NTM R 8592, NTM R 9317. *V. rosenbergi*—AM R 95810, AM R 120944, AM R 123331, AM R 123333, AM R 133750. *V. gouldii*—AM R 60216, AM R 94674, AM R 112855, AM R 123636, AM R 123637. *V. panoptes*—AM R 40647, AM R 75333, AM R 97508, AM R 100499. *V. giganteus*—NTM R 1657. *V. varius*—AM R 96478, AM R 104940, AM R 113960, AM R 123425. *V. komodoensis*—AM R 106 933.

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Patterns of Dominance in the Small Scincid Lizard *Lampropholis guichenoti*

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ABSTRACT.— We observed captive groups of six to ten scincid lizards (*Lampropholis guichenoti*) to investigate dominance patterns and to quantify and describe site defence. Most groups exhibited too few social interactions to determine social structure; however, in one group of nine *L. guichenoti*, a “modified” despotic social structure was formed with two lizards dominant over all of the others. Body size and sex influenced position within the social structure, with males tending to dominate females and larger lizards tending to dominate smaller ones. In general males were more aggressive than females. A “neck-arch” was used as the common assertion display and was seen significantly more frequently in males than females. Aggressive behavior did not decrease with time and thus may be involved in the maintenance of dominance as well as its establishment.

Agonistic behavior resulting in displacement of lizards from basking or shelter sites was rare (observed in only one of 20 groups). When such behavior occurred, it generally consisted of displacement of smaller males by larger, more dominant males. Large males also tended to be found with females under shelter more often than were smaller males. The scarcity or absence of active site defence in *L. guichenoti* may be due to their small body size (and hence, the fact that suitable sites for basking and shelter are unlikely to be in short supply) and the apparent lack of fixed home ranges in this species.

Territoriality is the social structure most commonly reported in the lizard species studied to date under natural conditions (Heatwole and Taylor, 1987). In captivity, however, particularly when animals are crowded, territoriality commonly breaks down into a hierarchical social structure (e.g., Carpenter, 1960, 1961; Bratts-

trom, 1974). This breakdown of territoriality has also been seen to occur in some natural, high-density populations (e.g., Milstead, 1970; Tinkle, 1967). Territoriality is uncommon in the Scincidae (Stamps, 1977). Most skinks are active foragers, spending much of their time on or near the ground or even beneath the leaf litter. Hence, visibility is likely to be poor and detection of intruders consequently difficult. Under these circumstances, defence of a home range would require active patrolling and significant expenditure of time and energy. In most skinks

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