

## Comparative Morphology of Western Australian Varanid Lizards (Squamata: Varanidae)

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**ABSTRACT** Varanid lizards, which vary considerably in body mass both interspecifically and intraspecifically, are generally considered to be morphologically similar. However, significant and non-isometric variation in the relative appendage dimensions for 17 species of Western Australian goannas suggest that these lizards are not morphologically conservative. The first and second canonical variates clearly distinguish the two subgenera *Odatria* and *Varanus*, and species are generally sexually dimorphic. The morphological variation observed among these 17 species of goanna is associated with foraging mode and ecology. However, no single or small group of morphological dimensions discriminates phylogenetic groups, sexes, or ecological groups, and body size is an important component in these analyses. *J. Morphol.* 233:127–152, 1997. © 1997 Wiley-Liss, Inc.

The morphology of a lizard is largely determined by its ancestry, ecological niche, body size, and development (Peters, '83; Calder, '84; Schmidt-Nielsen, '84). In addition, some species of reptile are also sexually dimorphic in body shape or size (Vitt and Cooper, '85; Shine, '92). The lizard family Varanidae provides an excellent opportunity to study the interrelationships of body size and shape with ecology. Varanidae consists of only a single extant genus, *Varanus*, and contains about 45 species. The mass range of *Varanus* is more than three orders of magnitude, ranging from  $\approx 20$  g (*V. brevicauda*; personal observations) to  $\approx 54$  kg (*V. komodoensis*; Auffenberg, '81). There are a variety of ecological specializations, including tree climbing, rock scampering, and swimming. Nevertheless, a numbers of authors (Shine, '86; Greer, '89; King and Green, '93b; Pianka, '95) have suggested that their body form is conservative compared with the variation in other families of lizards.

The genus *Varanus* is considered to be monophyletic (Baverstock et al., '93), and thus comparison of varanid species is not complicated by higher level phylogenetic differences. Baverstock et al. ('93) summarized the phylogeny of *Varanus* and suggested four clades based on immunogenetic and karyotypic studies: an Asian clade, an African

clade, an Australian/S.E. Asian clade of large goannas (subgenus *Varanus*), and a clade of Australian pygmy goanna (subgenus *Odatria*). Nearly all of the members of the *Varanus* clade (except *V. komodoensis* and *V. salvadorii*) and all of the members of the *Odatria* clade are found in Australia; *V. eremius* probably belongs to the *Odatria* group, although it was initially placed outside these clades (Pianka, '95). Morphometric examination of the 18 species/subspecies of goanna found in Western Australia allows a comparison of the *Varanus* and *Odatria* subgenera.

Others (e.g., Snyder, '54; Collette, '61; Ballinger, '73; Laerm, '74; Moermond, '79; Pianka, '86; Losos, '90a–c; Miles, '94) have suggested that there are morphological characteristics that can be associated with habitat and performance traits. Pianka ('68, '69, '70a,b, '71, '82, '86, '94) provides most of the limited ecological and behavioral data, and some additional general information on their ecology is provided by Storr et al. ('83) and Wilson and Knowles ('92). Greer ('89) groups all Australian goannas into four broad ecological categories (ground, rocky outcrop, arboreal, and aquatic/arboreal). The only obvi-

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ous morphological adaptation of any of these groups is the laterally compressed tail and dorsal placement of the nostrils for the semi-aquatic species *V. mertensi*.

*Varanus*, being a speciose genus of lizard with a very wide range in body size, provides an ideal opportunity to explore variation in body size and shape as these may relate to differences in phylogeny, ecology, and habitat, although the present lack of a rooted phylogenetic tree for Varanidae limits our capacity to account for lower order phylogenetic effects. The objectives of this study were to examine the allometry of Western Australian goanna morphology and to determine whether there are size or shape differences among these goannas which are associated with species ecology, habitat, or phylogeny, particularly comparing the subgenera *Varanus* and *Odatria*.

#### MATERIALS AND METHODS

##### Measurements

Various morphological dimensions (width, depth, and length) were measured for 17 species (including two subspecies of *Varanus panoptes*; see Results for a list of species) of goanna specimens from the Western Australian Museum (WAM). Unfortunately, the number of specimens of *V. kingorum* in the WAM collection was too small to enable any meaningful analysis and so this species was not included in the study. The nomenclature used for *V. gouldii* and *V. panoptes* is that of Storr ('80). It is our view that the use of the alternative names as suggested by Bohme ('91) will lead to further confusion until the taxonomy of both species is further clarified.

Total length (TL), snout-to-vent length (SVL), tail length (TAIL), head length (HL), neck length (NECK), head width (HW), head depth (HD), fore-limb length (FLL), upper fore-limb length (UFL), lower fore-limb length (LFL), hind-limb length (HLL), upper hind-limb length (UHL), lower hind-limb length (LHL), and thorax-abdomen length (TA) were measured (Fig. 1). All measurements were made to  $\pm 1$  mm, after positioning the body in the approximate shape shown in Figure 1. The recommendation of Reymont et al. ('84) was adopted in selecting 12 measurements (since 10 is considered optimal). Only dimensions likely to show minimal shrinkage after preservation (i.e., not soft tissue) were included. The sex of each goanna was determined by examination of the gonads.

##### Body size

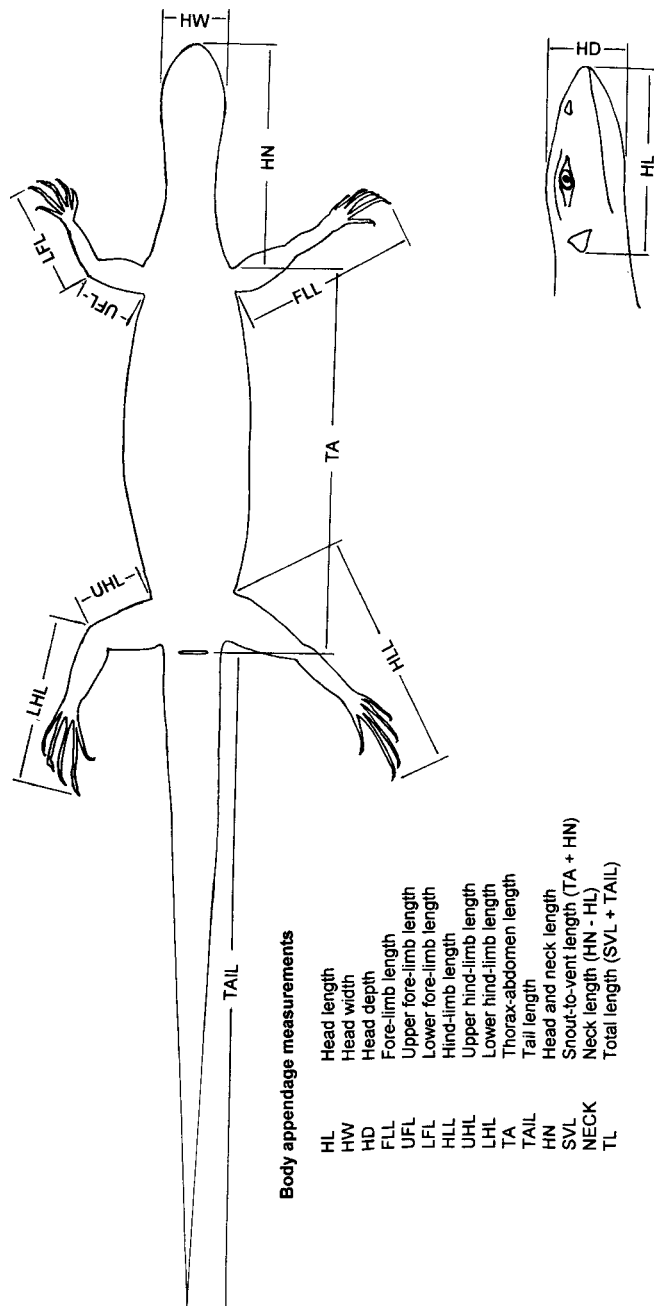
To determine whether SVL, TL, or TA best characterized "body size," the ratio of any particular dimension to either TL, SVL, or TA was compared by analysis of variance (ANOVA) for adult specimens, using the minimum SVL adopted for each species to account for effects of growth on changing body proportions, to best discriminate between species (Bookstein, '91: pp. 83–87). Both raw and logarithmically transformed data were analyzed in this fashion.

The overall best separation of species by TL, SVL, or TA determined that TA was the best index of "body size." The highest number of significant *F*-ratio values was obtained for the body dimension divided by TL, when logarithmically transformed (Table 1). However, during the measurement of goannas, it was apparent for numerous individuals that the end of their tail had been broken. Where the end of the tail had obviously been broken off the measurement was not used, but for many individuals it was not possible to determine if a small tip of the tail had been broken off. Therefore, as the *F*-ratios for values of the logarithmically transformed appendage length divided by logarithmically transformed TA were generally only slightly less than those for TL (when TL was the higher; Table 1), we chose TA as the best measure of overall body size to subsequently discriminate between the relative appendage dimensions of the various species, and TA was used to determine the relative appendage proportion dimension for each species.

An outline of the body shape was obtained by scanning a photograph of an adult of each species. These body outlines were adjusted to the same relative TA using Corel Draw (V6.0), to enable a visual inspection of relative body proportions (Fig. 2).

##### Isometric similarity

The extent of isometric similarity among goanna species was determined by examining slopes of the regression lines for the means of each species of logarithmically transformed body appendage dimensions with the logarithmically transformed TA, i.e., untransformed relationships, appendage (mm) =  $aTA^b$ . If the body proportions are isometrically similar, then  $b = 1.0$  (or, statistically,  $b$  is not significantly different from 1.0).



**Body appendage measurements**

- |      |                                |
|------|--------------------------------|
| HL   | Head length                    |
| HW   | Head width                     |
| HD   | Head depth                     |
| FLL  | Fore-limb length               |
| UFL  | Upper fore-limb length         |
| LFL  | Lower fore-limb length         |
| HLL  | Hind-limb length               |
| UHL  | Upper hind-limb length         |
| LHL  | Lower hind-limb length         |
| TA   | Thorax-abdomen length          |
| TAIL | Tail length                    |
| HN   | Head and neck length           |
| SVL  | Snout-to-vent length (TA + HN) |
| NECK | Neck length (HN - HL)          |
| TL   | Total length (SVL + TAIL)      |

Fig. 1. Measurements for goannas.

TABLE 1. F-ratio values determined by ANOVA for relative appendage dimensions of goannas divided by TL, SVL, or TA\*

Variables	Denominators					
	TL	SVL	TA	logTL	logSVL	logTA
TAIL	102.1	110.4	118.4	<u>198.0</u>	120.3	108.3
HL	<u>86.8</u>	34.1	33.9	<u>188.6</u>	188.2	150.3
HW	<u>91.6</u>	30.2	24.3	<u>71.1</u>	60.5	71.6
HD	<u>48.0</u>	13.7	12.1	49.5	42.4	<u>50.6</u>
FLL	30.1	31.8	55.9	<u>195.6</u>	167.4	<u>154.4</u>
UFL	24.0	43.5	70.0	<u>199.3</u>	195.9	<u>213.1</u>
LFL	39.3	37.2	59.6	<u>260.4</u>	231.0	<u>214.5</u>
HLL	35.2	71.2	85.8	<u>265.1</u>	226.8	184.1
UHL	34.7	68.4	86.7	<u>256.2</u>	257.9	254.6
LHL	47.5	90.9	105.6	<u>384.7</u>	<u>335.4</u>	287.4
NECK	28.3	54.3	82.9	<u>156.1</u>	154.6	<u>165.5</u>

\*The highest *P*-value is underlined.

### Sexual dimorphism

Possible morphological differences between sexes were determined separately for each species, using discriminant analysis of the logarithmically transformed data for HL, HW, NECK, UFL, LFL, UHL, LHL, TAIL, and TA for each specimen. Stepwise discriminant analysis was then used to determine which dimensions contributed most to sexual dimorphism.

Analysis of covariance (ANCOVA) was also used to determine whether any single variable (logHL, logHW, logFLL, logHLL, or logNECK with logTA as the covariate to remove the effect of size) could be used to separate sexes, for each species.

### Body appendage dimensions

Logarithmically transformed body appendage dimensions were regressed against the logarithmically transformed TA for the various species, and standardized residual values were used to examine the extent that relative appendage dimension was not explained by size. ANOVA was used to examine differences between species for these standardized residuals, and *t*-tests were used to determine if the residual appendage dimensions of individual species differed significantly from zero.

### Morphometric analysis

In our analyses to determine the extent to which morphological characteristics categorized individuals by their correct species or species by their correct subgenus, we have been heavily influenced by the view of Bookstein et al. ('85: p. 27) that size ought not to be removed from observed measures as it

often explains meaningful covariance in the morphological variance, and the comments of Klingenberg ('96), who reports that Burnaby's ('66: p. 35) procedure to eliminate the effects of growth only works when all groups share a common allometric pattern. For groups that differ in their size vectors, as we know goannas do (unpublished observations), removing all size vectors from the data may leave non-meaningful variation (Humphries et al., '81). Canonical variate analysis using the within groups covariance matrix (SPSS-PC) was used to determine the interrelationships among all species of goannas for the logarithmically transformed data (Reyment et al., '84). Eigenvalues >1.0 were used to indicate which canonical variate functions were significant; confidence limits in all tests were  $P < 0.05$ .

## RESULTS

### Body and appendage dimensions

For the 17 species (and 2 subspecies) of Western Australian goanna that were examined, there was a predominance of sexually mature individuals with only a small number of juveniles and subadults for each species. Mean values for the linear dimensions of each species are given in Table 2 along with the range in SVL.

Table 3 summarizes the appendage dimensions in proportion to TA, our estimate of body size, for adult individuals of each of the 17 goanna species. Our estimate of minimum SVL for adults of each species is included in Table 3. Table 4 summarizes the standardized residuals (from regression analysis of those log-transformed measurements against logTA) for each appendage measurement for the 17 goanna species. In general, if a species has one short appendage (e.g., HL), then the other appendages are also short (e.g., *V. brevicauda*); or if one appendage is long, then the other appendages are also long (e.g., *V. glauerti*). There are highly significant intercorrelations between residuals of all length measurements, except HW and HD, for all individual specimens (Table 5).

### Discriminant classification of individuals by species

Canonical variate analysis, using a within groups covariance matrix, correctly classified 81.3% of the 562 individual goannas to species, using the logarithmically transformed values of HL, HD, HW, NECK, UFL,

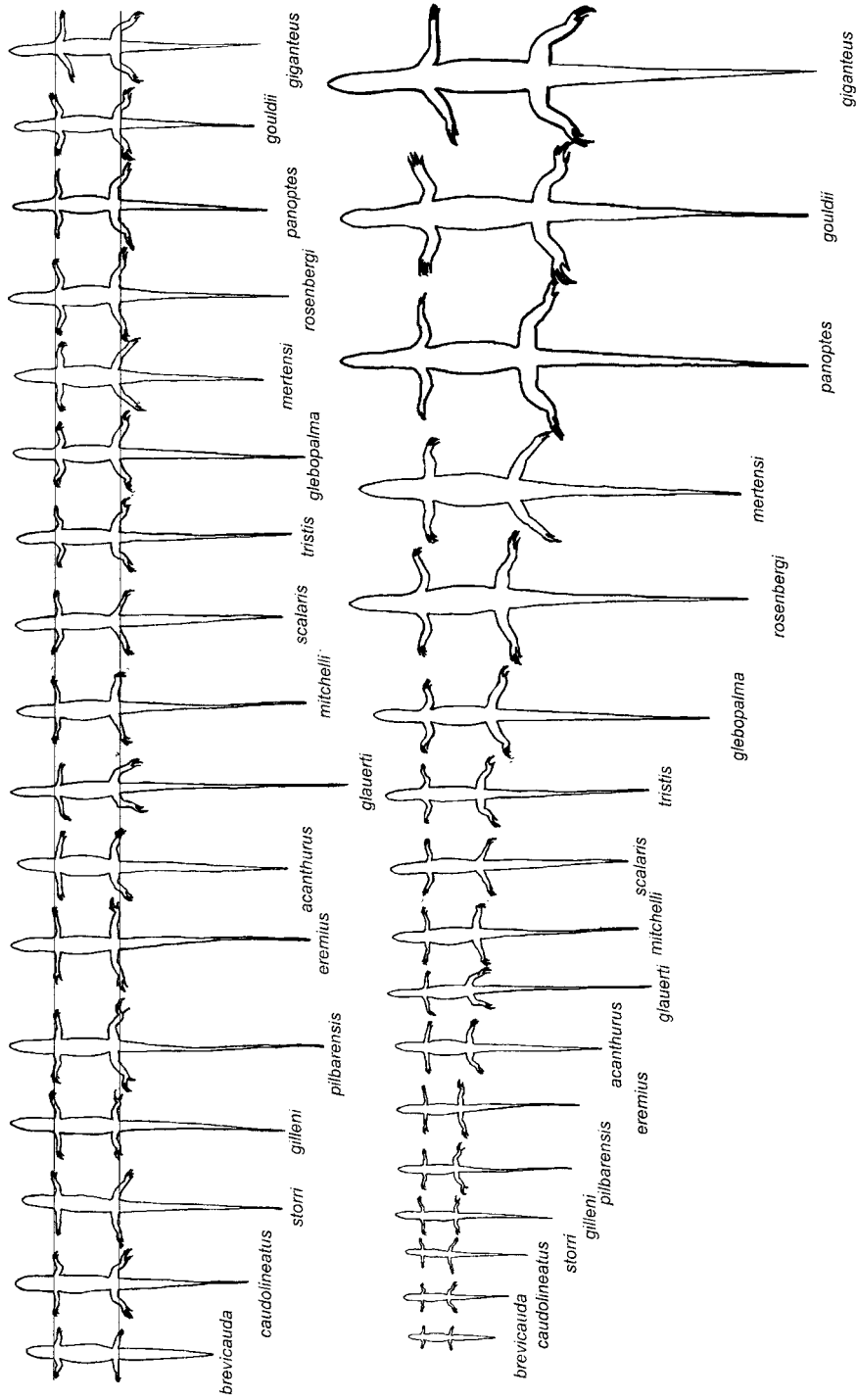


Fig. 2. Artist's drawing of goannas scaled to the same TA (**top**) and arranged in ascending order based on TA (**bottom**).

TABLE 2. Number of specimens examined, maximum and minimum SVL, and the mean ( $\pm$ SD) for other body appendage dimensions (mm) for 17 species of goannas

Varanus	N	Mini- SVL	Maxi- num SVL	SVL	HL	NECK	HW	HD	FDL	UFL	LFL	HLL	UHL	LHL	TA	TAIL
brevicauda	40	51	126	99.1 $\pm$ 16.3	17.1 $\pm$ 2.2	14.9 $\pm$ 2.7	8.9 $\pm$ 1.4	6.2 $\pm$ 1.3	19.7 $\pm$ 2.6	5.7 $\pm$ 1.2	15.6 $\pm$ 1.9	23.5 $\pm$ 3.2	7.3 $\pm$ 1.3	17.4 $\pm$ 2.1	66.9 $\pm$ 12.5	85.5 $\pm$ 25.7
caudo-																
lineatus	67	73	131	106.8 $\pm$ 10.0	19.3 $\pm$ 1.8	20.6 $\pm$ 3.0	10.5 $\pm$ 1.2	6.6 $\pm$ 0.8	25.6 $\pm$ 3.1	7.5 $\pm$ 1.1	19.4 $\pm$ 2.5	33.1 $\pm$ 3.6	10.9 $\pm$ 1.6	24.2 $\pm$ 2.5	67.6 $\pm$ 7.0	106.9 $\pm$ 52.5
storri	24	92	134	114.5 $\pm$ 12.7	23.4 $\pm$ 2.6	20.9 $\pm$ 2.7	12.0 $\pm$ 1.8	7.8 $\pm$ 2.4	29.6 $\pm$ 3.7	9.5 $\pm$ 1.5	22.5 $\pm$ 2.7	40.2 $\pm$ 4.7	12.7 $\pm$ 1.9	29.7 $\pm$ 3.2	70.7 $\pm$ 9.4	151.2 $\pm$ 72.4
gillemi	26	103	175	134.6 $\pm$ 21.1	23.0 $\pm$ 2.9	26.6 $\pm$ 4.2	12.2 $\pm$ 2.0	7.5 $\pm$ 1.5	31.3 $\pm$ 4.9	8.9 $\pm$ 1.5	23.2 $\pm$ 3.5	39.6 $\pm$ 6.7	11.7 $\pm$ 2.0	29.0 $\pm$ 4.3	84.3 $\pm$ 14.4	163.7 $\pm$ 46.5
pilbarensis	10	67	180	137.4 $\pm$ 31.9	26.9 $\pm$ 5.5	29.7 $\pm$ 7.2	12.9 $\pm$ 2.5	7.4 $\pm$ 1.7	39.6 $\pm$ 9.9	12.8 $\pm$ 3.2	28.4 $\pm$ 6.4	52.6 $\pm$ 13.6	18.0 $\pm$ 4.9	38.0 $\pm$ 9.9	79.2 $\pm$ 20.7	215.1 $\pm$ 93.8
eremius	54	68	185	139.4 $\pm$ 23.7	26.7 $\pm$ 3.8	25.5 $\pm$ 6.1	13.0 $\pm$ 2.2	9.3 $\pm$ 1.6	33.9 $\pm$ 5.4	10.5 $\pm$ 2.1	24.9 $\pm$ 3.9	51.5 $\pm$ 8.4	15.8 $\pm$ 2.7	37.6 $\pm$ 5.7	86.8 $\pm$ 5.2	229.0 $\pm$ 63.0
scalaris	56	72	268	170.6 $\pm$ 34.5	29.9 $\pm$ 4.7	35.7 $\pm$ 7.6	14.0 $\pm$ 2.8	10.3 $\pm$ 2.1	41.6 $\pm$ 8.0	12.4 $\pm$ 3.1	31.9 $\pm$ 5.6	55.5 $\pm$ 10.6	18.1 $\pm$ 3.9	41.9 $\pm$ 7.5	104.7 $\pm$ 22.5	181.5 $\pm$ 119.2
acanthurus	36	90	220	178.6 $\pm$ 30.6	31.9 $\pm$ 4.1	35.7 $\pm$ 6.9	15.6 $\pm$ 2.0	10.7 $\pm$ 1.8	44.8 $\pm$ 7.8	13.8 $\pm$ 2.7	34.4 $\pm$ 6.1	62.2 $\pm$ 12.8	19.8 $\pm$ 4.3	45.5 $\pm$ 7.8	111.2 $\pm$ 21.5	226.1 $\pm$ 132.5
mitchelli	23	118	253	193.3 $\pm$ 39.8	33.8 $\pm$ 5.7	41.3 $\pm$ 8.6	13.1 $\pm$ 2.4	9.9 $\pm$ 2.2	46.0 $\pm$ 9.2	13.1 $\pm$ 2.6	36.2 $\pm$ 7.4	63.7 $\pm$ 11.8	20.2 $\pm$ 4.3	48.3 $\pm$ 8.9	117.6 $\pm$ 26.9	303.7 $\pm$ 116.6
glauerti	28	90	239	199.6 $\pm$ 35.8	37.5 $\pm$ 5.7	48.8 $\pm$ 9.8	15.9 $\pm$ 2.7	9.3 $\pm$ 1.9	53.7 $\pm$ 10.4	18.2 $\pm$ 4.2	40.9 $\pm$ 8.0	72.5 $\pm$ 13.3	25.6 $\pm$ 5.0	53.7 $\pm$ 10.1	116.0 $\pm$ 23.5	369.1 $\pm$ 174.3
tristis	53	68	290	208.7 $\pm$ 51.4	37.5 $\pm$ 7.6	46.7 $\pm$ 12.0	17.2 $\pm$ 3.6	11.8 $\pm$ 2.8	54.4 $\pm$ 12.5	17.1 $\pm$ 4.5	41.7 $\pm$ 9.7	76.9 $\pm$ 18.2	24.5 $\pm$ 6.2	56.7 $\pm$ 13.1	124.8 $\pm$ 31.7	353.8 $\pm$ 111.7
p. panoptes	12	143	510	252.0 $\pm$ 122.0	47.5 $\pm$ 16.9	53.8 $\pm$ 26.6	21.7 $\pm$ 8.7	15.7 $\pm$ 6.6	68.5 $\pm$ 33.0	23.2 $\pm$ 12.1	52.5 $\pm$ 26.9	96.5 $\pm$ 48.3	31.8 $\pm$ 17.8	72.3 $\pm$ 6.4	153.1 $\pm$ 81.0	251.7 $\pm$ 160.5
gouldii	76	107	590	277.3 $\pm$ 106.7	48.0 $\pm$ 14.4	56.4 $\pm$ 24.0	22.3 $\pm$ 7.1	16.5 $\pm$ 5.4	72.5 $\pm$ 26.5	23.7 $\pm$ 8.9	55.2 $\pm$ 21.2	104.5 $\pm$ 38.4	34.7 $\pm$ 13.8	77.8 $\pm$ 29.5	171.7 $\pm$ 67.9	374.1 $\pm$ 184.9
glebopalma	31	152	397	297.9 $\pm$ 49.1	51.1 $\pm$ 6.9	82.6 $\pm$ 15.8	23.2 $\pm$ 3.7	16.4 $\pm$ 2.7	79.8 $\pm$ 13.6	30.2 $\pm$ 5.0	59.3 $\pm$ 9.3	115.9 $\pm$ 20.4	43.8 $\pm$ 8.3	89.6 $\pm$ 13.1	166.8 $\pm$ 27.4	428.1 $\pm$ 246.3
rosenbergi	38	150	422	319.2 $\pm$ 65.5	58.2 $\pm$ 10.3	66.8 $\pm$ 14.7	28.1 $\pm$ 5.3	21.1 $\pm$ 4.5	84.2 $\pm$ 17.3	28.2 $\pm$ 6.3	67.7 $\pm$ 14.3	116.8 $\pm$ 22.6	40.9 $\pm$ 9.1	89.7 $\pm$ 17.4	193.7 $\pm$ 42.1	423.3 $\pm$ 170.3
mertensi	26	150	460	320.6 $\pm$ 78.0	49.6 $\pm$ 9.4	76.1 $\pm$ 21.9	24.6 $\pm$ 3.5	17.1 $\pm$ 3.1	78.3 $\pm$ 21.0	25.6 $\pm$ 7.3	61.3 $\pm$ 16.9	111.3 $\pm$ 29.3	37.6 $\pm$ 11.6	85.2 $\pm$ 21.6	193.8 $\pm$ 50.6	435.0 $\pm$ 143.5
p. rubidus	17	141	535	350.8 $\pm$ 132.9	61.0 $\pm$ 17.3	77.7 $\pm$ 32.9	26.9 $\pm$ 8.5	21.1 $\pm$ 6.7	100.4 $\pm$ 39.0	34.2 $\pm$ 15.0	75.8 $\pm$ 30.0	147.1 $\pm$ 57.9	48.9 $\pm$ 20.8	110.2 $\pm$ 44.4	216.6 $\pm$ 83.2	564.0 $\pm$ 218.1
giganteus	25	159	660	442.2 $\pm$ 124.3	82.0 $\pm$ 20.1	114.2 $\pm$ 36.0	34.0 $\pm$ 9.1	25.1 $\pm$ 7.9	130.0 $\pm$ 37.7	43.4 $\pm$ 13.0	97.1 $\pm$ 26.1	174.4 $\pm$ 48.9	60.1 $\pm$ 18.3	129.0 $\pm$ 35.7	245.1 $\pm$ 68.9	467.4 $\pm$ 306.6

LFL, UHL, LHL, TA, and TAIL (Table 6). The analysis correctly classified 100% of the individuals of *V. glauerti*, *V. glebopalma*, and *V. brevicauda*. The order of all 18 species/subspecies in Table 6 has been arranged according to morphological affinity using the misclassification of species from the canonical variate analysis and the data in Tables 3 and 4. *V. acanthurus* was the most misclassified species of the subgenus *Odatria*, being miscategorized as six other species (including one subgenus *Varanus*). *V. gouldii* was the most misclassified of the subgenus *Varanus*, being miscategorized as seven other species (including three subgenus *Odatria*). Although the classification of individuals into their correct species was not always 100%, we considered the discrimination sufficient to justify further examination of the canonical variate analysis.

The first three canonical variates had eigenvalues >1.0 and accounted for 89.7% of the total variance in morphology for all species measured, whereas the fourth and subsequent canonical variates had eigenvalues <1.0 (Table 7). The first and second canonical variates clearly separated the two subgenera, *Odatria* and *Varanus* (Fig. 3; this figure shows males and females separately, because there is sexual dimorphism). TAIL was the measurement most highly correlated with the first canonical variate (Table 7), but residual TAIL was significantly correlated with all other variables except HD and HW (Table 5). The first canonical variate does not seem to be a pure indicator of size, although there is a general size effect especially when considering the subgenera separately. That is, the mean TA of each species does not rank strictly in accordance with the first canonical variate score, although there is a general trend for small species to a negative first canonical variate score and large species to a positive score. The second canonical variate correlated best with HD (Table 7; Fig. 3). The third canonical variate does not separate the species into the two subgenera (Fig. 4); it is correlated best with NECK (Table 7).

Because the first two canonical variates clearly separated the subgenera *Odatria* and *Varanus*, as proposed by Mertens ('42) and supported by Baverstock et al. ('93), we analyze these subgenera separately below.

Subgenus *Odatria*

TAIL correlated best with the first canonical variate (Table 7) for the *Odatria* group.

TABLE 3. Body appendage ratios for the adult individuals for each of the 17 species of goanna<sup>1</sup>

Varanus	Minimum adult SVL (mm)	TAIL/TA	HL/TA	HW/TA	HD/TA	NECK/TA	FLL/TA	UFL/TA	LFL/TA	HLL/TA	UHL/TA	LHL/TA
brevicauda	90	1.34 ± 0.109	0.25 ± 0.024	0.13 ± 0.015	0.09 ± 0.012	0.22 ± 0.036	0.29 ± 0.031	0.09 ± 0.012	0.23 ± 0.024	0.35 ± 0.035	0.11 ± 0.016	0.26 ± 0.028
caudolineatus	100	1.93 ± 0.158	0.28 ± 0.021	0.15 ± 0.014	0.10 ± 0.010	0.30 ± 0.032	0.38 ± 0.038	0.11 ± 0.016	0.28 ± 0.027	0.49 ± 0.042	0.16 ± 0.020	0.36 ± 0.032
storri	100	2.55 ± 0.269	0.33 ± 0.022	0.17 ± 0.017	0.11 ± 0.031	0.30 ± 0.028	0.42 ± 0.032	0.13 ± 0.015	0.32 ± 0.021	0.56 ± 0.041	0.18 ± 0.017	0.41 ± 0.029
eremius	130	2.76 ± 0.232	0.31 ± 0.018	0.15 ± 0.010	0.10 ± 0.008	0.30 ± 0.034	0.39 ± 0.029	0.12 ± 0.017	0.28 ± 0.021	0.59 ± 0.038	0.18 ± 0.016	0.43 ± 0.027
gillessi	130	2.08 ± 0.157	0.27 ± 0.019	0.14 ± 0.010	0.09 ± 0.008	0.31 ± 0.022	0.37 ± 0.027	0.10 ± 0.011	0.27 ± 0.023	0.47 ± 0.047	0.14 ± 0.013	0.34 ± 0.027
pilbarensis	130	2.95 ± 0.436	0.33 ± 0.033	0.16 ± 0.015	0.09 ± 0.011	0.37 ± 0.035	0.49 ± 0.088	0.16 ± 0.031	0.35 ± 0.054	0.66 ± 0.109	0.23 ± 0.044	0.47 ± 0.066
scalaris	150	2.38 ± 0.167	0.28 ± 0.020	0.13 ± 0.012	0.10 ± 0.010	0.34 ± 0.034	0.39 ± 0.026	0.12 ± 0.013	0.30 ± 0.023	0.53 ± 0.042	0.17 ± 0.016	0.40 ± 0.028
acanthurus	160	2.63 ± 0.418	0.28 ± 0.023	0.14 ± 0.013	0.09 ± 0.009	0.32 ± 0.029	0.40 ± 0.033	0.12 ± 0.010	0.31 ± 0.027	0.56 ± 0.058	0.18 ± 0.024	0.41 ± 0.044
tristis	200	2.93 ± 0.212	0.29 ± 0.015	0.13 ± 0.009	0.09 ± 0.006	0.38 ± 0.030	0.43 ± 0.032	0.14 ± 0.012	0.33 ± 0.021	0.61 ± 0.048	0.20 ± 0.015	0.45 ± 0.026
mitchelli	200	2.73 ± 0.141	0.27 ± 0.013	0.13 ± 0.013	0.08 ± 0.010	0.34 ± 0.038	0.38 ± 0.022	0.11 ± 0.010	0.30 ± 0.020	0.53 ± 0.045	0.17 ± 0.015	0.40 ± 0.023
glauerti	200	2.78 ± 0.282	0.31 ± 0.016	0.13 ± 0.008	0.08 ± 0.007	0.42 ± 0.035	0.46 ± 0.035	0.16 ± 0.016	0.35 ± 0.023	0.62 ± 0.019	0.22 ± 0.019	0.46 ± 0.026
p. panoptes	200	2.17 ± 0.414	0.29 ± 0.030	0.13 ± 0.015	0.09 ± 0.017	0.34 ± 0.039	0.44 ± 0.032	0.15 ± 0.017	0.33 ± 0.027	0.62 ± 0.058	0.22 ± 0.027	0.47 ± 0.037
glebopalma	300	3.26 ± 0.318	0.30 ± 0.012	0.14 ± 0.007	0.10 ± 0.005	0.50 ± 0.029	0.48 ± 0.025	0.18 ± 0.011	0.35 ± 0.014	0.70 ± 0.025	0.26 ± 0.017	0.49 ± 0.023
rosenbergi	300	2.45 ± 0.107	0.30 ± 0.015	0.14 ± 0.010	0.11 ± 0.009	0.35 ± 0.038	0.43 ± 0.036	0.14 ± 0.013	0.45 ± 0.021	0.60 ± 0.046	0.21 ± 0.019	0.46 ± 0.031
gouldii	300	2.33 ± 0.139	0.27 ± 0.014	0.13 ± 0.009	0.09 ± 0.008	0.33 ± 0.030	0.42 ± 0.026	0.14 ± 0.015	0.32 ± 0.019	0.60 ± 0.038	0.20 ± 0.016	0.45 ± 0.026
mertensi	300	2.34 ± 0.276	0.25 ± 0.015	0.12 ± 0.009	0.09 ± 0.007	0.39 ± 0.041	0.40 ± 0.028	0.13 ± 0.011	0.32 ± 0.021	0.58 ± 0.044	0.20 ± 0.017	0.44 ± 0.020
p. rubidus	300	2.63 ± 0.187	0.26 ± 0.021	0.12 ± 0.008	0.09 ± 0.006	0.37 ± 0.029	0.47 ± 0.046	0.16 ± 0.021	0.36 ± 0.026	0.70 ± 0.050	0.23 ± 0.021	0.52 ± 0.029
giganteus	400	2.59 ± 0.216	0.33 ± 0.021	0.14 ± 0.011	0.10 ± 0.009	0.47 ± 0.045	0.53 ± 0.035	0.18 ± 0.013	0.40 ± 0.027	0.71 ± 0.058	0.25 ± 0.026	0.52 ± 0.039
r with TA - all species (P)		0.22 (0.37)	0.18 (0.47)	-0.54 (0.02)	0.01 (0.97)	0.61 (0.01)	0.59 (0.01)	0.64 (0.01)	0.69 (0.01)	0.67 (0.01)	0.68 (0.01)	0.73 (0.01)
r with TA, Odatria (P)		0.70 (0.01)	0.01 (0.99)	-0.49 (0.11)	-0.28 (0.38)	0.84 (0.01)	0.50 (0.10)	0.61 (0.04)	0.58 (0.05)	0.61 (0.03)	0.66 (0.02)	0.62 (0.03)
r with TA, Varanus (P)		0.97 (0.01)	-0.31 (0.55)	0.04 (0.94)	0.15 (0.77)	0.76 (0.08)	0.80 (0.05)	0.77 (0.07)	0.37 (0.47)	0.88 (0.02)	0.78 (0.07)	0.87 (0.03)

<sup>1</sup>Correlation coefficients are for proportional appendage length with TA; values are means ± SE.

TABLE 4. Species standardized residual appendage deviations from the regression line of all *Varanus* species with TA<sup>1</sup>

Varanus	Mean TA (mm)	HL	NECK	HW	HD	FLL	UFL	LFL	HLL	UHL	LHL	TAIL
brevicauda	66.90	-1.58 ± 0.82	-1.72 ± 1.17	-1.30 ± 0.99	-0.63 ± 0.88	-2.01 ± 0.87	-1.65 ± 0.91	-1.76 ± 0.96	-2.33 ± 0.77	-2.07 ± 0.96	-2.36 ± 0.91	-2.27 ± 0.39
caudolineatus	67.54	-0.68 ± 0.63	-0.03 ± 0.65	0.10 ± 0.91	-0.26 ± 0.80	-0.24 ± 0.75	-0.25 ± 0.78	-0.30 ± 0.91	-0.39 ± 0.57	-0.12 ± 0.71	-0.47 ± 0.61	-0.72 ± 0.38
storri	70.71	0.64 ± 0.56	-0.20 ± 0.62	1.02 ± 0.93	0.96 ± 1.04	0.46 ± 0.59	0.71 ± 0.69	0.49 ± 0.58	0.49 ± 0.56	0.43 ± 0.69	0.48 ± 0.59	0.49 ± 0.49
gilleni	84.27	-0.88 ± 0.61	-0.01 ± 0.56	-0.21 ± 0.62	-0.94 ± 0.67	-0.54 ± 0.58	-0.74 ± 0.59	0.75 ± 0.72	-0.84 ± 0.62	-1.12 ± 0.59	-0.91 ± 0.59	-0.67 ± 0.42
pilbarensis	79.20	1.04 ± 0.93	1.07 ± 0.67	1.02 ± 1.02	-0.45 ± 0.72	1.72 ± 1.29	1.63 ± 1.13	1.43 ± 1.28	1.37 ± 1.11	1.54 ± 1.09	1.21 ± 0.97	1.05 ± 0.69
eremius	86.85	0.19 ± 0.51	-0.52 ± 0.56	0.12 ± 0.69	0.56 ± 0.60	-0.17 ± 0.68	-0.08 ± 0.76	-0.43 ± 0.79	0.57 ± 0.55	0.25 ± 0.57	0.49 ± 0.59	0.66 ± 0.38
scalaris	104.71	-0.28 ± 0.60	0.18 ± 0.63	-0.68 ± 0.80	0.02 ± 0.73	-0.17 ± 0.64	-0.38 ± 0.67	-0.09 ± 0.77	-0.28 ± 0.61	-0.24 ± 0.59	-0.16 ± 0.63	-0.03 ± 0.36
acanthurus	111.17	-0.20 ± 0.79	-0.24 ± 0.65	-0.10 ± 0.91	-0.06 ± 0.82	-0.12 ± 0.70	-0.19 ± 0.57	-0.05 ± 0.75	-0.06 ± 0.63	-0.14 ± 0.74	-0.10 ± 0.78	0.45 ± 0.75
mitchelli	117.61	-0.14 ± 0.58	0.26 ± 0.79	-0.89 ± 0.91	-1.08 ± 0.87	-0.35 ± 0.59	-0.77 ± 0.74	-0.11 ± 0.70	-0.22 ± 0.77	-0.35 ± 0.70	-0.10 ± 0.69	0.56 ± 0.41
glauerti	115.96	0.53 ± 0.71	1.26 ± 0.66	-0.23 ± 0.64	-1.45 ± 0.81	0.88 ± 0.72	1.00 ± 0.59	0.92 ± 0.67	0.64 ± 0.69	0.96 ± 0.74	0.63 ± 0.59	1.89 ± 0.45
tristis	124.83	0.36 ± 0.77	0.53 ± 0.61	0.04 ± 0.86	-0.15 ± 0.69	0.43 ± 0.78	0.26 ± 0.74	0.48 ± 0.72	0.49 ± 0.87	0.25 ± 0.60	0.47 ± 0.69	0.79 ± 0.44
p. panoptes	153.10	1.10 ± 1.22	0.12 ± 0.88	0.71 ± 1.43	0.75 ± 1.50	0.61 ± 0.81	0.67 ± 0.77	0.61 ± 0.82	0.55 ± 0.83	0.36 ± 0.77	0.63 ± 0.83	-0.22 ± 0.81
gouldii	171.75	0.14 ± 0.97	-0.54 ± 0.66	0.01 ± 0.83	0.30 ± 0.96	0.06 ± 0.82	0.08 ± 0.91	-0.02 ± 0.78	0.22 ± 0.80	0.12 ± 0.84	0.23 ± 0.81	-0.28 ± 0.51
166.81	0.61 ± 0.34	1.72 ± 0.36	0.42 ± 0.47	0.22 ± 0.45	0.81 ± 0.43	1.38 ± 0.40	1.38 ± 0.40	0.63 ± 0.43	0.87 ± 0.37	1.35 ± 0.34	0.65 ± 0.36	1.02 ± 0.44
rosenbergi	193.66	0.59 ± 0.42	-0.43 ± 0.67	0.99 ± 0.61	1.09 ± 0.59	0.03 ± 0.62	0.09 ± 0.58	0.40 ± 0.53	-0.08 ± 0.53	0.08 ± 0.53	0.12 ± 0.58	-0.20 ± 0.38
mertensi	193.77	-0.72 ± 0.72	0.28 ± 0.64	-0.21 ± 0.74	-0.44 ± 0.67	-0.51 ± 0.57	-0.42 ± 0.57	-0.41 ± 0.60	-0.41 ± 0.51	-0.42 ± 0.46	-0.21 ± 0.44	-0.51 ± 0.57
p. rubidus	216.60	-0.12 ± 0.86	-0.37 ± 0.54	-0.15 ± 0.67	0.46 ± 0.59	0.45 ± 0.72	0.34 ± 0.70	0.32 ± 0.67	0.53 ± 0.57	0.26 ± 0.53	0.56 ± 0.53	-0.14 ± 0.36
giganteus	245.10	1.73 ± 0.65	0.97 ± 0.53	0.95 ± 0.76	0.66 ± 0.79	1.32 ± 0.57	0.88 ± 0.70	1.21 ± 0.69	0.73 ± 0.74	0.58 ± 0.74	0.70 ± 0.74	-0.03 ± 0.58

<sup>1</sup>Species are ranked according to increasing TA.

The logarithmically transformed residuals for TAIL are significantly and positively correlated with UHL and LHL ( $r = 0.79$  and  $0.87$ , respectively), suggesting that the length of the hind appendages is the primary determinant in separating species on the first canonical variate (Fig. 5). NECK is the measurement most highly correlated with the second canonical variate (Table 7). The first canonical variate is not a pure size indicator as the species mean TA is not strictly ranked in accordance with the first canonical variate. The third canonical variate (Fig. 6) has the strongest negative correlation with TA (although relatively weak,  $r = -0.24$ ); it separates *V. caudolineatus* from *V. gilleni*, and *V. glebopalma* from *V. glauerti* (which are closely aligned on the first and second canonical variates), and *V. mitchelli* from *V. scalaris* and *V. tristis* (which are closely associated by the second canonical variate). There is considerable overlap in "morphological space" for individuals of most species of the *Odatria* clade based on the first three canonical variates (Figs. 5, 6). Nevertheless, *V. brevicauda* is clearly separated from the other species, primarily by the first canonical variate, while *V. glebopalma* and *V. glauerti* form an overlapping group toward the other end of this axis. *V. eremius* is separated from most of the other species by the second canonical variate, overlapping slightly with *V. storri* and *V. acanthurus*, and to a much lesser extent with *V. mitchelli* (Fig. 5). *V. caudolineatus* and *V. gilleni* form a group located between the majority of the *Odatria* species and *V. brevicauda*, being separated from the other species primarily by the first canonical variate.

#### Subgenus *Varanus*

The highest correlation with the first canonical variate for the subgenus *Varanus* is HL (Table 7). However, Tabachnick and Fidell (1989: p. 539) suggest that correlations lower than 0.30 cannot be interpreted adequately, although the interpretation of HL as the primary discriminator is in accordance with the univariate data (Tables 3, 4), which indicate that *V. mertensi* and *V. giganteus* have the smallest and largest relative HL for this group. The second canonical variate is most strongly correlated ( $r = 0.29$ ) with NECK, indicating that *V. giganteus* and *V. mertensi* have relatively longer necks than the other species (Fig. 7), a result concordant with data in Tables 3 and 4. Eigenvalues are  $<1.0$  for subsequent functions



TABLE 5. Correlation coefficients (r) between residual appendage lengths for all specimens\*

	HW	HD	NECK	FLL	UFL	LFL	HLL	UHL	LHL	TAIL
HL	<u>0.80</u>	<u>0.48</u>	<u>0.60</u>	<u>0.89</u>	<u>0.85</u>	<u>0.91</u>	<u>0.80</u>	<u>0.64</u>	<u>0.86</u>	<u>0.62</u>
HW		<u>0.64</u>	<u>0.39</u>	<u>0.75</u>	<u>0.77</u>	<u>0.74</u>	<u>0.71</u>	<u>0.64</u>	<u>0.70</u>	<u>0.36</u>
HD			-0.18	<u>0.25</u>	<u>0.29</u>	<u>0.26</u>	<u>0.33</u>	<u>0.06</u>	<u>0.35</u>	-0.09
NECK				<u>0.77</u>	<u>0.75</u>	<u>0.76</u>	<u>0.70</u>	<u>0.76</u>	<u>0.67</u>	<u>0.74</u>
FLL					<u>0.95</u>	<u>0.98</u>	<u>0.94</u>	<u>0.83</u>	<u>0.93</u>	<u>0.73</u>
UFL						<u>0.93</u>	<u>0.92</u>	<u>0.82</u>	<u>0.89</u>	<u>0.72</u>
LFL							<u>0.91</u>	<u>0.75</u>	<u>0.91</u>	<u>0.73</u>
HLL								<u>0.80</u>	<u>0.99</u>	<u>0.82</u>
UHL									<u>0.76</u>	<u>0.71</u>
LHL										<u>0.81</u>

\*Values underlined are  $P < 0.05$ .

and are therefore not considered to be significant. Figure 7 suggests that the morphology of both *V. mertensi* and *V. giganteus* is appreciably different from that of the other species in this clade, with both species being separated from the others primarily by the first canonical variate. There is considerable overlap in the morphology of *V. rosenbergi*, *V. panoptes*, and *V. gouldii* (Fig. 7). *V. p. panoptes* and *V. p. rubidus* are separated by *V. rosenbergi* (Fig. 7).

Sexual dimorphism

The specimens measured in the WAM collection were predominantly male (Table 8). There was significant sexual dimorphism for most species in body shape, as determined by a discriminant analysis for all specimens of each species (that were able to be sexed) using a combination of logarithmically transformed appendage dimensions (Table 8). The

combined standardized canonical discriminant function coefficients that separated the sexes for all species of goannas are shown in Table 9.

Stepwise discriminant analysis was subsequently used to determine which variable(s) contributed most to the separation of sexes. *F*-values were insufficient to isolate significant individual variables for some species. However, logHL and logTA correctly classified 82.5% of *V. caudolineatus* (standardized canonical discriminant function coefficients [scdfc] - 1.346logTA + 1.790logHL); logNECK correctly classified 69.7% of *V. brevicauda*; logUFL correctly classified 75.5% of *V. eremius*; logUFL correctly classified 73.1% of *V. glauerti*; logTAIL, logUFL, and logUHL correctly classified 100% of *V. glebopalma* (scdfc 1.109logTAIL - 1.396logUFL + 1.665logUHL); logHD and logUHL correctly classified 68.1% of *V. gouldii* (scdfc 3.913logHD -

TABLE 6. Proportion of individuals correctly allocated to species using canonical variate analysis (logarithmically transformed variables of HL, HW, HD, NECK, UFL, LFL, UHL, LHL, and TA) for *Odatria* and *Varanus* subgenera

Varanus/ subspecies	Species no.	Predicted species/subspecies																% Correct			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16		17	18	
<i>glauerti</i>	1	<u>24</u>																			100.0
<i>glebopalma</i>	2		<u>24</u>																		100.0
<i>pilbarensis</i>	3			<u>7</u>	<u>1</u>								<u>1</u>								77.8
<i>mitchelli</i>	4				<u>18</u>	<u>3</u>		<u>1</u>													85.7
<i>tristis</i>	5			<u>2</u>	<u>5</u>	<u>39</u>	<u>1</u>		<u>2</u>					<u>1</u>		<u>1</u>					76.5
<i>eremius</i>	6					<u>46</u>	<u>3</u>	<u>2</u>	<u>1</u>												88.5
<i>acanthurus</i>	7				<u>3</u>	<u>2</u>	<u>2</u>	<u>12</u>	<u>1</u>	<u>7</u>						<u>1</u>					42.9
<i>storri</i>	8			<u>1</u>				<u>1</u>	<u>15</u>	<u>1</u>	<u>1</u>	<u>1</u>									78.9
<i>scalaris</i>	9							<u>4</u>		<u>36</u>									<u>1</u>		87.8
<i>gilleni</i>	10									<u>1</u>	<u>23</u>	<u>1</u>									92.0
<i>caudolineatus</i>	11			<u>1</u>							<u>9</u>	<u>45</u>									81.8
<i>brevicauda</i>	12												<u>38</u>								100.0
<i>mertensi</i>	13				<u>2</u>									<u>21</u>	<u>1</u>	<u>1</u>					84.0
<i>p. rubidus</i>	14													<u>13</u>	<u>3</u>	<u>1</u>	<u>1</u>				64.3
<i>gouldii</i>	15					<u>1</u>	<u>1</u>		<u>2</u>					<u>2</u>	<u>6</u>	<u>45</u>	<u>5</u>	<u>8</u>			64.3
<i>rosenbergi</i>	16													<u>3</u>	<u>2</u>	<u>27</u>	<u>2</u>				79.4
<i>p. panoptes</i>	17													<u>2</u>		<u>2</u>	<u>6</u>				60.0
<i>giganteus</i>	18													<u>1</u>					<u>18</u>		94.7

TABLE 7. Pooled within group correlations between discriminant variables and canonical discriminant functions for all 17 species, and separately for the *Odatria* and *Varanus* subgenera

Variables	All species			Subgenus <i>Odatria</i>			Subgenus <i>Varanus</i>		
	Function 1	Function 2	Function 3	Function 1	Function 2	Function 3	Function 1	Function 2	Function 3
logNECK	0.408	0.205	0.332	0.418	0.342	-0.148	0.136	0.286	0.304
logTA	0.289	0.270	0.154	0.258	0.147	-0.239	0.074	0.117	0.236
logUFL	0.449	0.280	0.225	0.424	0.217	0.024	0.170	0.121	0.323
logHW	0.354	0.312	0.157	0.296	0.116	-0.030	0.146	0.122	0.175
logHL	0.463	0.348	0.186	0.423	0.127	-0.203	0.220	0.136	0.232
logTAIL	0.494	0.094	0.101	0.556	0.076	-0.218	0.124	0.115	0.311
logUHL	0.461	0.257	0.172	0.459	0.164	0.034	0.142	0.100	0.310
logHD	0.350	0.389	0.051	0.260	-0.021	-0.064	0.149	0.046	0.213
logLHL	0.482	0.300	0.121	0.487	0.079	-0.122	0.136	0.118	0.340
logLFL	0.422	0.300	0.228	0.410	0.228	-0.183	0.159	0.128	0.288
Eigenvalue	12.977	4.172	1.813	15.14	2.31	1.11	4.15	1.34	0.66
% Variance	61.38	19.73	8.58	74.83	11.41	5.50	63.70	20.59	10.04
Wilks' lambda	0.012	0.061	0.173	0.038	0.13	0.27	0.186	0.436	0.721
Chi-square	2.424	1.525	959	1,226	777	496	279	137	54
df	144	120	98	90	72	56	36	24	14
P	<0.0001	<0.0001	<0.0001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

3.140logUHL); logTA, logLHL, and logTAIL correctly classified 94.4% of *V. mertensi* (scdfc  $9.032\log\text{TA} - 12.889\log\text{LHL} + 4.375\log\text{TAIL}$ ); logHD and logTA correctly classified 100% of *V. pilbarensis* (scdfc  $-4.578\log\text{TA} + 4.784\log\text{HD}$ ); logLFL, logLHL, logUHL, and logUHL correctly classified 90.0% of *V. p. panoptes* (scdfc  $-30.234\log\text{LFL} + 12.606\log\text{LHL} - 4.117\log\text{LFL} + 21.948\log\text{UHL}$ ); and logTA, logHL, logLHL, and logTAIL correctly classified 94.7% of *V. storri* (scdfc  $5.381\log\text{TA} - 4.833\log\text{HL} - 2.927\log\text{LHL} + 2.426\log\text{TAIL}$ ). No single logarithmically transformed variable could separate the sexes for each of the species (Table 10). Where a significant difference existed between sexes, males had proportionally longer appendages or, alternatively, the TA of the females was proportionally longer than for males.

#### Isometry

Although all body appendage dimensions are significantly and positively correlated with TA, only HL, HD, and TAIL scaled isometrically with TA for all species (i.e., the slope b was not significantly different from 1.0; Table 10). For *Odatria*, FLL as well as HL and HD scale isometrically with TA. The smaller sample size and hence higher standard error of the slope for the subgenus *Varanus* probably account for the higher number of appendage dimensions that scale isometrically with TA (Table 10). The residual body appendage dimensions, other

than HD, are significantly correlated; all of the significant correlations were positive, i.e., any goanna species with a relatively long (or short) appendage dimension also had relatively long (or short) other appendages (except HD; Table 4).

#### Grouping of species based on the relative length of appendages

Figures 8–11 show the relative appendage sizes as a proportion of TA for each *Varanus* species/subspecies. ANOVA for the standardized residual values (from the regression with logTA) of appendage dimensions showed a significant difference between species for HL ( $F_{17,624} = 37.52, P < 0.001$ ), HW ( $F_{17,624} = 19.74, P < 0.001$ ), HD ( $F_{17,623} = 23.57, P < 0.001$ ), NECK ( $F_{17,624} = 46.49, P < 0.001$ ), FLL ( $F_{17,624} = 37.59, P < 0.001$ ), UFL ( $F_{17,624} = 34.73, P < 0.001$ ), LFL ( $F_{17,624} = 29.03, P < 0.001$ ), HLL ( $F_{17,624} = 50.25, P < 0.001$ ), UHL ( $F_{17,624} = 43.05, P < 0.001$ ), LHL ( $F_{17,624} = 46.27, P < 0.001$ ), and TAIL ( $F_{17,545} = 117.51, P < 0.001$ ). Those relative appendage dimensions for which the residuals were significantly different from 0 are circled in Figures 8–11.

A visual inspection of Figures 8–11 when interpreted in conjunction with Tables 2–4 indicates the following:

1. *V. brevicauda* has a relatively shorter head, neck, fore- and hind-limbs, and tail than any other species (Tables 3, 4; Figs. 8–11).

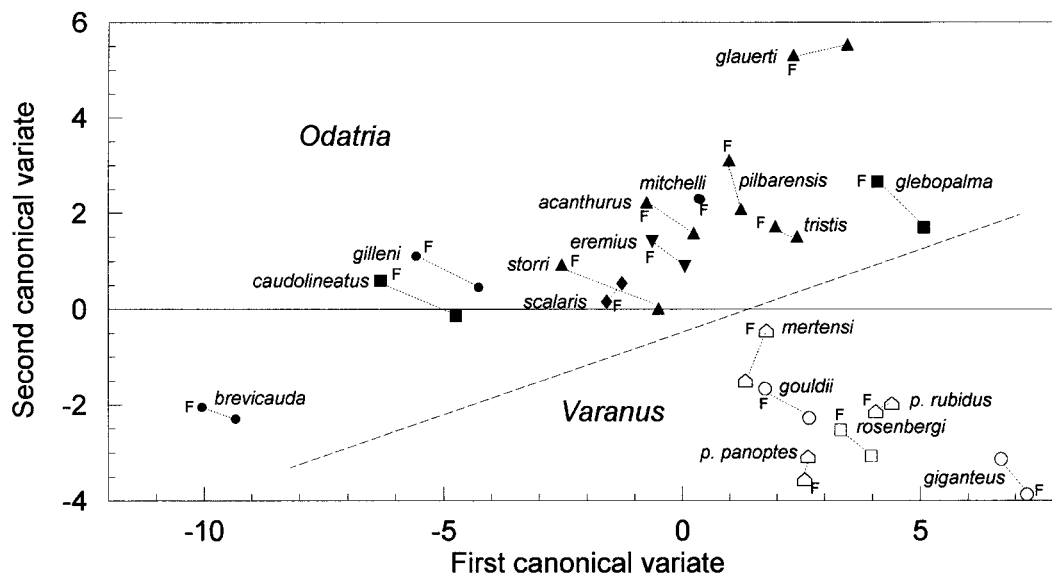


Fig. 3. The first and second canonical variates for morphometrics of Western Australian goannas, based on logarithmically transformed data for different sexes. The values marked with an F are for females of each species. The first standardized canonical vector for the data not separated by sex is:  $-3.505\log TA - 0.517\log HD + 2.291\log HL - 0.277\log HW - 0.776\log LFL + 1.497\log LHL - 0.182\log NECK + 0.285\log UFL + 0.187\log UHL + 1.414\log TAIL$ . The second standardized canonical vector is:  $-0.004\log TA + 1.156\log HD + 1.994\log HL - 0.638\log HW + 0.418\log LFL + 1.649\log LHL - 0.631\log NECK - 0.097\log UFL - 0.409\log UHL - 3.203\log TAIL$ .

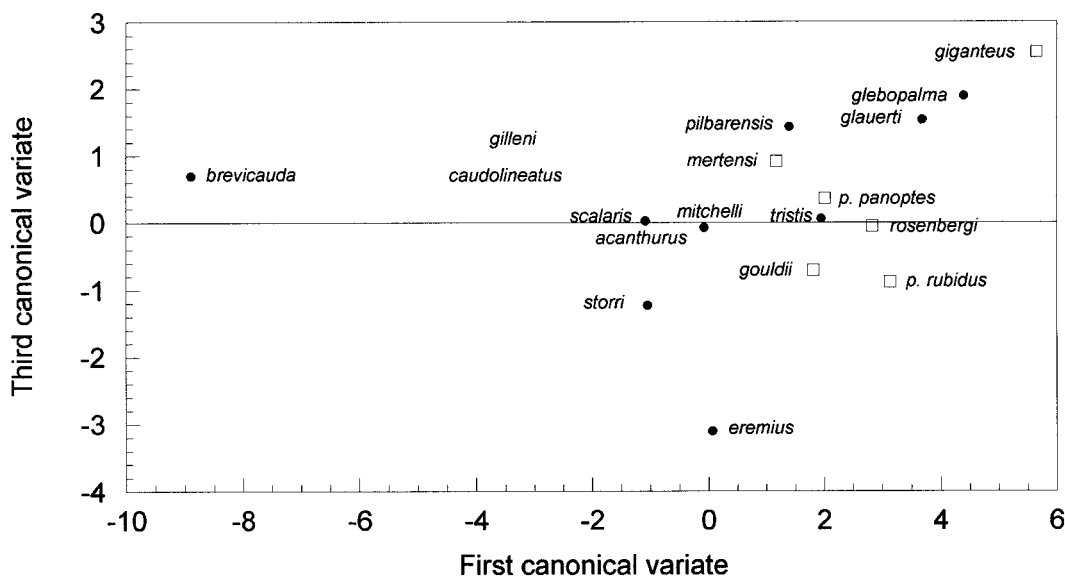


Fig. 4. The first and third canonical variates for Western Australian goannas based on logarithmically transformed data. See Figure 3 for the first canonical vector. The third canonical vector is:  $-0.627\log TA - 1.496\log HD + 0.840\log HL + 0.501\log HW + 2.253\log LFL - 3.186\log LHL + 2.246\log NECK + 0.673\log UFL + 0.160\log UHL - 1.146\log TAIL$ .

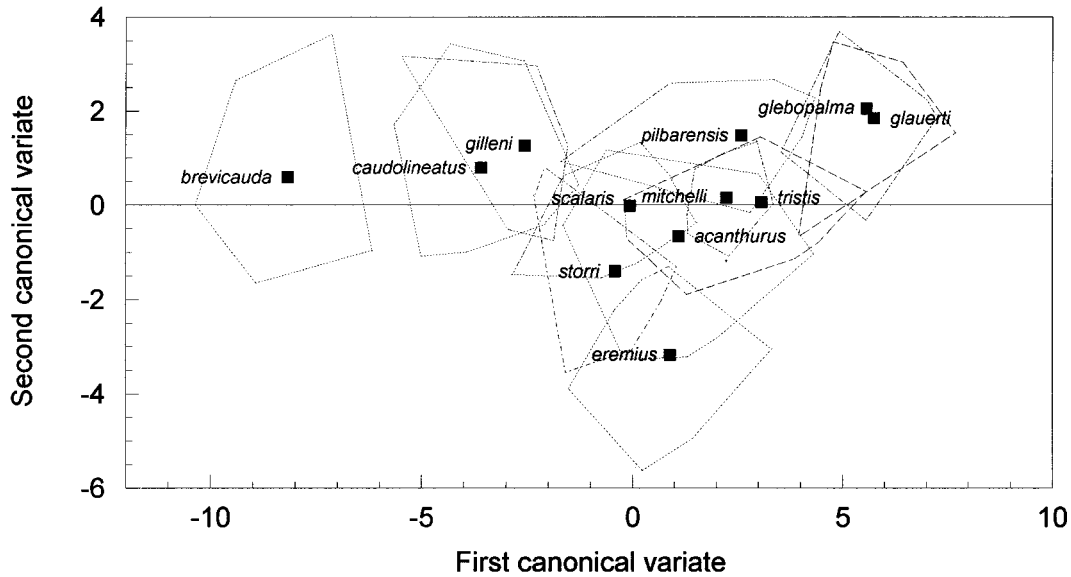


Fig. 5. The first and second canonical variates for morphometrics of the *Odatria* clade of goannas based on logarithmically transformed data showing the extreme values for different individuals as a convex polygon. The first standardized canonical vector is:  $-2.231\log\text{TA} - 0.866\log\text{HD} + 0.947\log\text{HL} + 0.034\log\text{HW} - 0.466\log - \text{LFL} + 0.878\log\text{LHL} + 0.091\log\text{NECK} + 1.698\log\text{TAIL} + 0.139\log\text{UFL} + 0.195\log\text{UHL}$ . The second standardized canonical vector is:  $-0.024\log\text{TA} - 1.419\log\text{HD} - 0.031\log\text{HL} + 0.486\log\text{HW} + 1.875\log\text{LFL} - 2.430\log - \text{LHL} + 1.606\log\text{NECK} - 0.785\log\text{TAIL} + 0.659\log\text{UFL} + 0.319\log\text{UHL}$ .

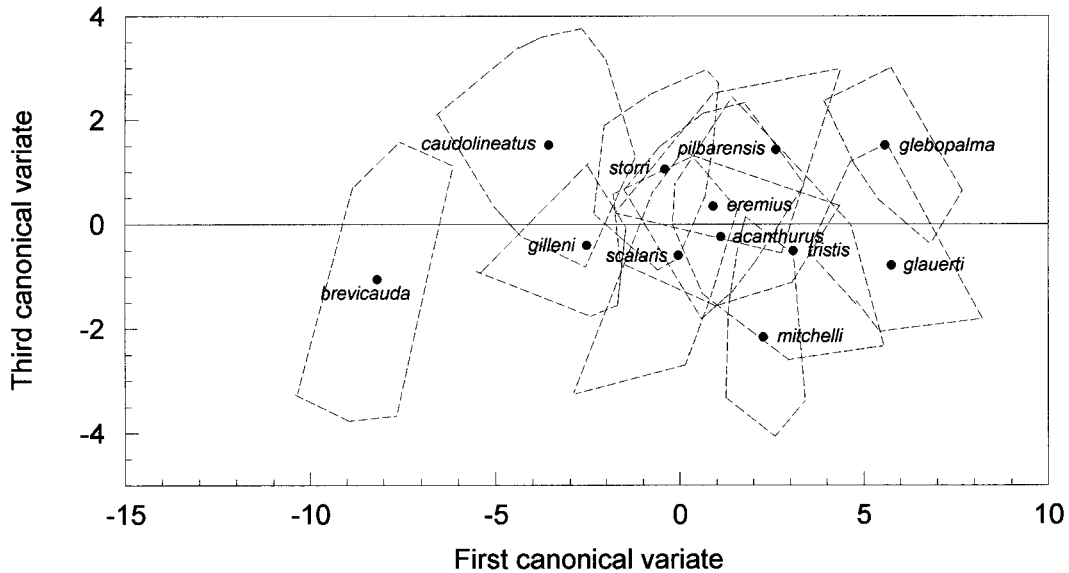


Fig. 6. The first and third canonical variates for the *Odatria* clade of goannas based on logarithmically transformed data showing the extreme values for different individuals as a convex polygon. The first standardized canonical vector is:  $-2.231\log\text{TA} - 0.866\log\text{HD} + 0.947\log\text{HL} + 0.034\log\text{HW} - 0.466\log\text{LFL} + 0.878\log - \text{LHL} + 0.091\log\text{NECK} + 1.698\log\text{TAIL} + 0.139\log\text{UFL} + 0.195\log\text{UHL}$ . The third standardized canonical vector is:  $-1.316\log\text{TA} + 0.550\log\text{HD} - 2.618\log\text{HL} + 1.375\log\text{HW} - 0.499\log\text{LFL} + 0.706\log\text{LHL} + 0.062\log\text{NECK} - 0.725\log\text{TAIL} + 1.051\log\text{UFL} + 1.468\log\text{UHL}$ .

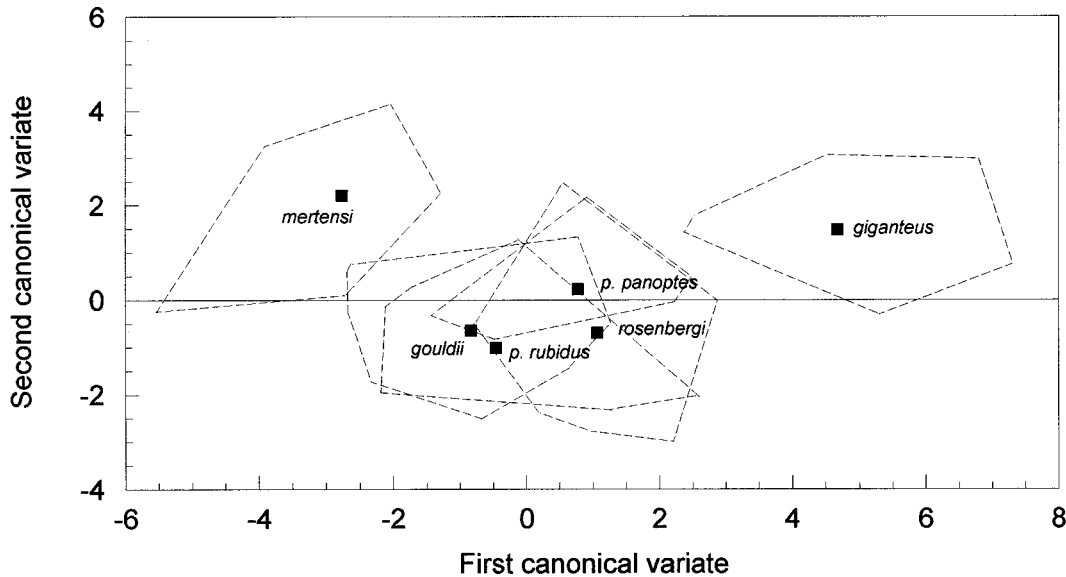


Fig. 7. The first and second canonical variates for the *Varanus* clade of goannas based on logarithmically transformed data showing the extreme values for different individuals as a convex polygon. The first standardized canonical vector is:  $-5.541\log\text{TA} - 0.261\log\text{HD} + 7.390\log\text{HL} - 1.122\log\text{HW} + 1.017\log\text{LFL} - 1.274 - \log\text{LHL} - 1.044\log\text{NECK} + 0.413\log\text{TAIL} + 0.323\log\text{UFL} + 0.219\log\text{UHL}$ . The second standardized canonical vector is:  $-0.399\log\text{TA} - 2.160\log\text{HD} - 0.116\log\text{HL} + 1.593\log\text{HW} - 0.473\log\text{LFL} - 1.514\log\text{LHL} + 4.873\log\text{NECK} - 0.739\log\text{TAIL} - 0.345\log\text{UFL} - 0.600\log\text{UHL}$ .

2. *V. glebopalma*, *V. giganteus*, *V. glauerti*, and *V. pilbarensis* have an appreciably longer neck (0.6 SD above the mean) than other species, whereas *V. giganteus*, *V. pilbarensis*, and *V. p. panoptes* have an appreciably longer head (0.6 SD above the mean). The head length of *V. gilleni* and *V. mertensi* is appreciably shorter (0.6 SD below the mean) than for all other species, except *V. breviceauda*. The head of *V. storri*, *V. pilbarensis*, *V. rosenbergi*, *V. giganteus*, and *V. p. panoptes* is appreciably wider (0.5 SD above the mean) than for other species, while that of *V. mitchelli* and *V. scalaris* is appreciably narrower (0.5 SD below the mean) than for all other species, except *V. breviceauda*. The head depth for *V. storri*, *V. rosenbergi*, *V. p. panoptes*, *V. giganteus*, and *V. eremius* is appreciably deeper (0.5 SD above the mean) than for other species, while that of *V. glauerti*, *V. mitchelli*, *V. gilleni*, and *V. breviceauda* is appreciably shallower (0.5 SD below the mean) than that of other species (Tables 3, 4; Fig. 8).
3. The fore-limb lengths of *V. pilbarensis*, *V. giganteus*, *V. glebopalma*, and *V. glauerti* are appreciably longer (0.6 SD above the mean) than for other species, while for *V. mertensi* and *V. gilleni* the fore-limb is generally shorter (0.3 SD below the mean) than for other species, except *V. breviceauda* (Tables 3, 4; Fig. 9).
4. The hind-limbs of *V. pilbarensis*, *V. glebopalma*, and *V. glauerti* are appreciably longer (0.6 SD above the mean) than for other species, while *V. gilleni* has appreciably shorter hind-limbs (0.6 SD below the mean) than other species, except *V. breviceauda* (Tables 3, 4; Fig. 10).
5. The tail length of *V. glauerti*, *V. pilbarensis*, and *V. glebopalma* is appreciably longer (0.8 SD above the mean) than for all other species. *V. caudolineatus* and *V. gilleni* have an appreciably shorter tail than any other species (0.5 SD below the mean), except *V. breviceauda* (Tables 3, 4; Fig. 11).

#### DISCUSSION

Morphometrics is the study of covariances of biological form. Bookstein ('91) has suggested that, for many biological investigations, the most effective way to analyze the form of an organism is to record the geomet-

TABLE 8. Determination of morphological differences for male and female goannas of 18 species/subspecies using discriminant analysis, based on logarithmically transformed morphometric data

Varanus	Sex		% Predicted correctly	Eigenvalue	Wilks' lambda score	Chi-square	Group centroids			Pooled within group correlations between discriminating variables and canonical discriminant functions									
	M	F					M	F	logHL	logHW	logHD	logNECK	logUFL	logLFL	logUHL	logLHL	logTAIL	logTA	
brevicauda	18	14	90.6	1.67	0.375	<0.01	1.10	-1.42	0.126	0.290	0.160	0.322	0.160	0.202	0.025	0.204	0.091	0.014	
caudolineatus	33	19	86.5	1.09	0.478	<0.01	0.78	-1.35	0.608	0.296	0.391	0.290	0.255	0.292	0.407	0.489	0.349	0.133	
storri	10	8	100.0	12.9	0.072	0.01	3.03	-3.79	0.139	0.128	0.154	-0.002	0.055	0.094	0.087	0.158	0.141	-0.005	
gilleni	12	9	100.0	10.2	0.089	<0.01	-2.63	3.51	-0.076	-0.039	-0.043	-0.016	-0.009	-0.016	-0.094	0.003	0.008	0.053	
pilbarensis	6	2	100.0	29.3	0.033	0.11	-2.70	8.11	-0.047	-0.116	-0.159	0.057	-0.150	-0.070	-0.056	-0.065	-0.031	-0.053	
eremius	30	17	76.6	0.4	0.700	0.16	0.48	-0.85	0.574	0.335	0.412	0.293	0.651	0.513	0.631	0.625	0.347	0.375	
scalaris	23	10	87.9	0.9	0.518	0.07	-0.62	1.42	0.231	0.128	0.142	0.144	0.154	0.235	0.228	0.218	0.155	0.302	
acanthurus	13	6	100.0	5.7	0.149	0.01	1.54	-3.33	-0.015	0.043	0.058	-0.096	-0.087	-0.032	-0.005	-0.029	-0.047	-0.147	
mitchelli	11	8	94.7	2.5	0.283	0.13	-1.28	1.77	0.171	0.120	0.145	0.256	0.295	0.243	0.206	0.272	0.220	0.228	
glauerti	17	5	94.4	1.8	0.357	0.12	0.69	-2.36	0.271	0.155	0.202	0.266	0.374	0.198	0.248	0.231	0.349	0.169	
tristis	20	23	76.7	0.2	0.813	0.68	0.50	-0.44	0.220	0.149	0.306	0.052	0.235	0.120	0.037	0.199	0.257	0.015	
p. panoptes	5	3	100.0	38.3	0.025	0.09	4.15	-6.92	-0.132	-0.078	-0.059	-0.151	-0.381	-0.123	-0.198	-0.095	-0.161	-0.157	
gouldii	43	24	79.1	0.7	0.573	<0.01	-0.64	-1.14	0.367	0.372	0.417	0.371	0.361	0.337	0.274	0.330	0.309	0.293	
glebopalma	17	4	100.0	8.1	0.110	<0.01	1.31	-5.57	0.457	0.348	0.335	0.472	0.377	0.486	0.600	0.466	0.376	0.457	
rosenbergi	19	11	86.7	0.8	0.560	0.20	0.65	-1.13	0.214	0.203	0.276	0.217	0.394	0.266	0.233	0.319	0.205	0.161	
mertensi	10	8	100.0	4.4	0.186	0.05	-1.77	2.21	0.187	0.145	0.171	0.144	0.171	0.177	0.166	0.183	0.272	0.216	
p. rubidus	11	2	76.9	0.6	0.616	0.96	0.31	-1.70	0.107	0.054	0.116	0.004	0.196	0.117	0.154	0.088	0.128	0.112	
giganteus	9	7	100.0	8.5	0.105	0.03	-2.41	3.10	0.066	0.059	0.071	0.035	0.052	0.049	0.092	0.053	0.052	0.055	

TABLE 9. Standardized canonical discriminant function coefficients for distinguishing sex differences in goannas<sup>1</sup>

Varanus	Standardized canonical discriminant function coefficients									
	logHL	logHW	logHD	logNECK	logUFL	logLFL	logUHL	logLHL	logTAIL	logTA
<i>brevicauda</i>	-0.413	1.753	0.321	0.796	0.282	1.578	-0.696	-0.225	-0.313	-2.558
<i>caudolineatus</i>	2.027	-0.420	0.620	-0.098	0.118	-0.454	-0.135	0.157	-0.189	-1.274
<i>storri</i>	4.891	0.139	-0.309	-0.452	-0.820	2.244	1.359	2.581	-2.657	-6.936
<i>gilleni</i>	-6.460	1.092	-1.528	0.564	0.623	0.560	-2.874	3.555	0.328	4.291
<i>pillbarensis</i>	-2.900	1.693	-11.818	—	—	9.962	—	-8.150	—	12.345
<i>eremius</i>	0.792	-0.591	-0.270	-0.088	0.312	-0.018	-0.070	2.140	-0.920	-0.763
<i>scalaris</i>	-0.989	-1.073	-0.644	-1.406	-1.686	3.125	0.957	-0.093	-2.796	4.705
<i>acanthurus</i>	0.444	2.300	3.452	-0.323	2.481	-1.715	0.059	-1.506	1.783	-5.880
<i>mitchelli</i>	-5.146	-2.763	0.417	2.262	1.117	1.636	-1.716	3.741	0.063	0.721
<i>glauerti</i>	-0.434	0.048	2.129	1.740	2.428	-0.869	-0.025	-2.553	1.755	-3.176
<i>tristis</i>	-0.269	0.144	1.762	-0.355	0.241	-0.323	-1.168	1.925	0.762	-2.454
<i>p. panoptes</i>	3.885	-3.773	5.498	-13.988	—	22.842	—	—	—	-14.258
<i>gouldii</i>	4.811	0.652	2.116	0.407	0.805	2.401	-2.943	-0.629	-0.076	-7.176
<i>glebopalma</i>	-0.510	0.759	-0.491	-0.299	-1.972	0.151	2.475	-0.633	1.667	0.299
<i>rosenbergi</i>	0.110	-1.079	1.479	-0.296	1.430	1.484	0.184	2.279	-1.010	-4.162
<i>mertensi</i>	-1.277	3.770	1.057	-0.109	2.009	-4.147	-2.073	-15.058	7.900	8.664
<i>p. rubidus</i>	4.407	-4.348	3.792	-3.570	-0.036	8.533	—	-12.456	1.616	2.114
<i>giganteus</i>	13.114	1.534	2.654	-15.436	-3.288	-18.469	10.620	-18.608	23.612	4.721

<sup>1</sup>Missing values failed the tolerance test.

ric locations of landmark points. Then, the measurement of shape configurations of landmark locations can be reduced to multiple vectors of shape coordinates. Therefore, the study of covariance of landmark configurations (triangles) can then be undertaken independent of size. However, the nature of the available data (measurements for preserved museum specimens) and the focus on appendage lengths do not enable use of this multiple vector approach in this study. Rather, canonical variate analysis, ratios, and residuals from regression equations of appendage dimensions with TA have been

used here to analyze the size shape of goannas. Some authors have been critical of the use of ratios in the analysis of body shape. Reyment et al. ('84) criticized the use of ratios since 1) the ratio will not be constant for organisms of the same species by virtue of the almost universal occurrence of differential growth rates; 2) ratios contain only two variables and this affords a poor appreciation of contrast between forms with multidimensionality; and 3) to compound two characters into a ratio implies that only one contrast of the form is studied. These criticisms have been addressed here in that mul-

TABLE 10. Slope (b) of the regression line for appendage dimension and logTA using only values of adults for each of the 18 species/subspecies of goanna\*

	HL	NECK	HW	HD	FLL	UFL	LFL	HLL	UHL	LHL	TAIL
<i>All Species (n = 18)</i>											
Slope	<b>0.98</b>	1.27	0.88	<b>0.99</b>	1.18	1.29	1.19	1.25	1.32	1.27	<b>1.10</b>
±SE	0.048	0.077	0.037	0.047	0.059	0.082	0.049	0.070	0.088	0.066	0.146
P	NS	<0.05	<0.05	NS	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	NS
r <sup>2</sup>	0.97	0.94	0.98	0.97	0.97	0.94	0.98	0.97	0.94	0.96	0.77
<i>Odatria (n = 12)</i>											
Slope	<b>1.01</b>	1.54	0.84	<b>0.88</b>	<b>1.23</b>	1.38	1.24	1.36	1.48	1.35	1.59
±SE	0.084	0.128	0.069	0.087	0.123	0.178	0.105	0.152	0.191	0.147	0.236
P	NS	<0.05	<0.05	NS	NS	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
r <sup>2</sup>	0.94	0.94	0.94	0.90	0.90	0.86	0.94	0.88	0.86	0.90	0.81
<i>Varanus (n = 6)</i>											
Slope	<b>1.61</b>	<b>1.18</b>	<b>0.97</b>	<b>1.13</b>	1.50	1.54	1.41	1.45	1.46	1.42	<b>1.60</b>
±SE	0.290	0.33	0.228	0.248	0.20	0.24	0.16	0.154	0.162	0.132	0.693
P	NS	NS	NS	NS	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	NS
r <sup>2</sup>	0.88	0.77	0.81	0.85	0.94	0.90	0.94	0.96	0.96	0.96	0.58

\*P-values for the t-value testing the difference of the slope from 1.0 (isometry) and the coefficient of determination between the logarithmically transformed appendage length and logTA are also given. NS, not significant.

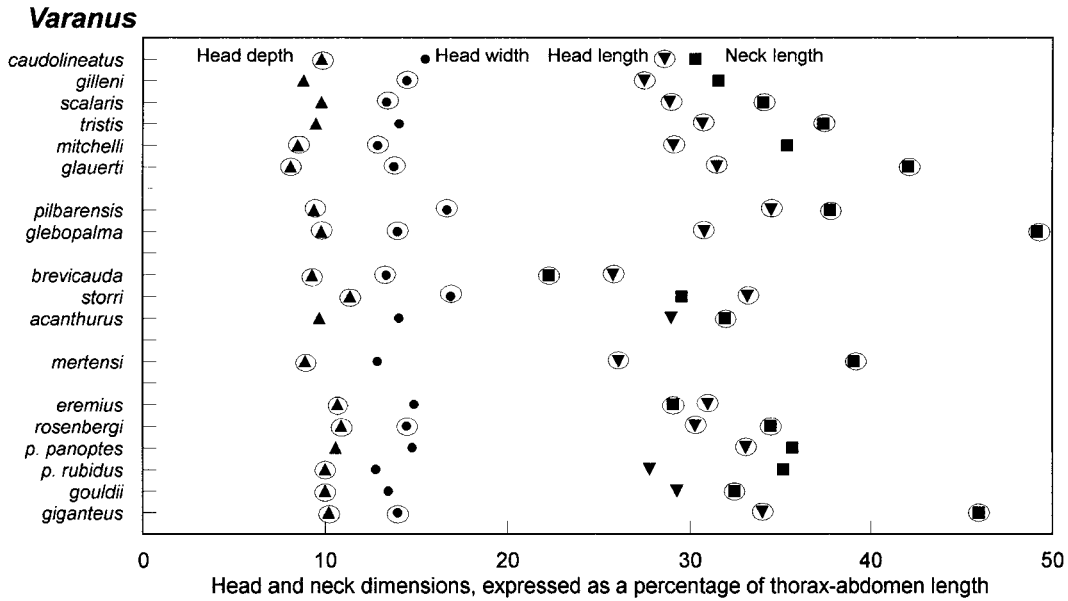


Fig. 8. Head and neck dimensions expressed as a percentage of TA, with species arranged by habitat utilization; a value enclosed in circle represents a mean

residual value from the regression equation with logTA that is significantly different from the mean for all species.

tiple ratios have been used in comparison of body forms, and they have been used in conjunction with a suite of other approaches, most often as collaborating data. Juveniles

and subadult specimens were not included in the calculation of appendage dimension ratios, thereby minimizing proportional variation due to non-isometric growth.

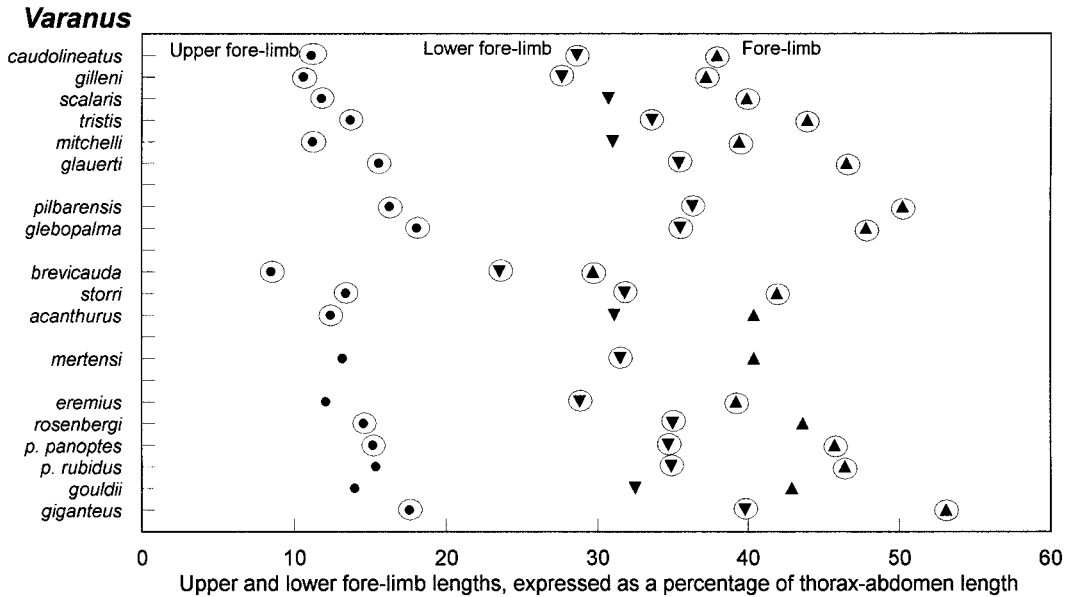


Fig. 9. Upper and lower fore-limb lengths as a percentage of TA, with species arranged by habitat utilization; a value enclosed in circle represents a mean

residual value from the regression equation with logTA that is significantly different from the mean for all species.



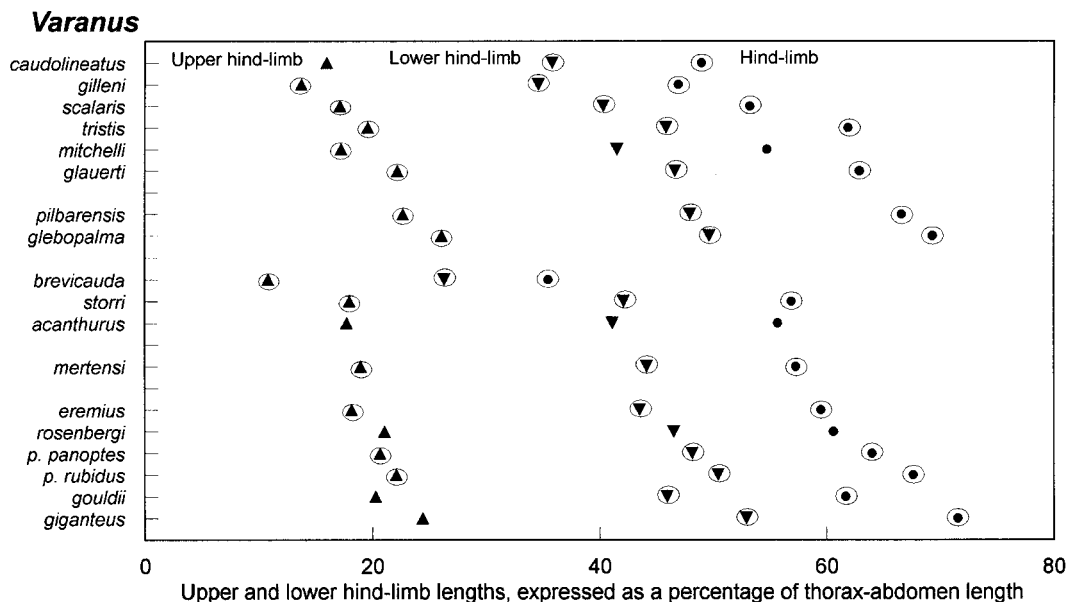


Fig. 10. Upper and lower hind-limb lengths as a percentage of TA, with species arranged by habitat utilization; a value enclosed in circle represents a mean residual value from the regression equation with logTA that is significantly different from the mean for all species.

Size, phylogeny, habitat or ecological niche, growth, and sex are all related to body proportions (Peters, '83; Calder, '84; Schmidt-Nielsen, '84; Miles, '94). There is no estab-

lished and rooted phylogenetic tree for varanids (Baverstock et al., '93) and it has therefore not been possible to properly account for phylogenetic effects in the analysis

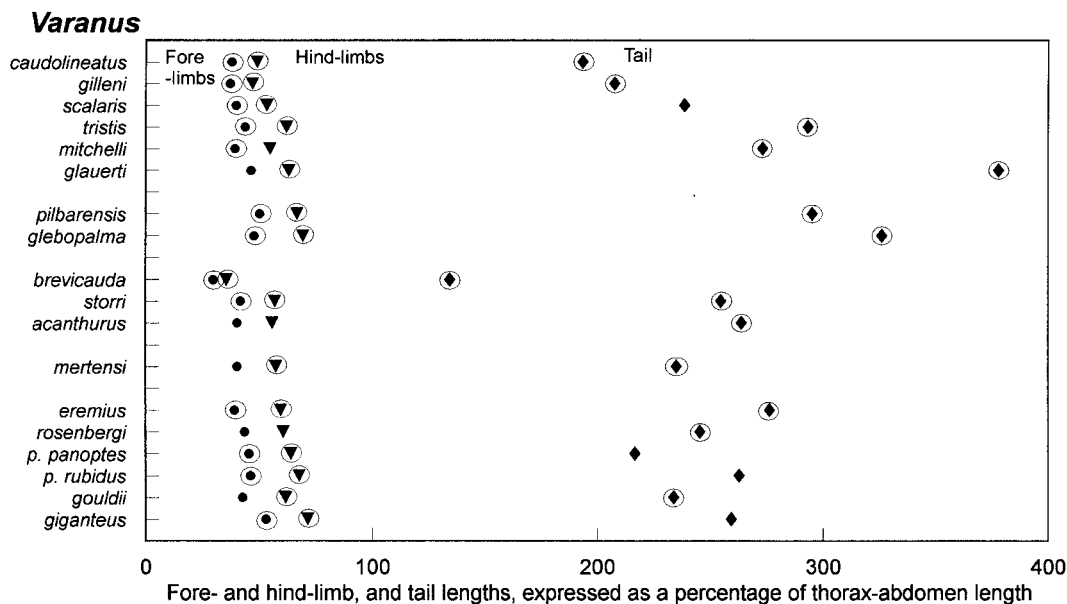


Fig. 11. Fore- and hind-limbs, and tail lengths as a percentage of TA, with species arranged by habitat utilization; a value enclosed in circle represents a mean residual value from the regression equation with logTA that is significantly different from the mean for all species.

of morphology of these goannas, other than at the subgeneric level. The basic ecology is also not known for many Western Australian goanna species, and so inferences drawn from this ecomorphological analysis of *Varanus* must therefore be considered preliminary.

#### *Phylogenetic patterns of morphology*

The first and second canonical variates clearly separate the two goanna subgenera *Odatria* and *Varanus*, consistent with the phylogeny of King and King ('75) and Baverstock et al. ('93). Our morphological grouping of species also provides supporting evidence that those species not included in the immunogenetic and karyotypic studies of King and King ('75), Holmes et al. ('75), and Baverstock et al. ('93) (e.g., *V. pilbarensis*, *V. storri*, *V. glebopalma*) have been correctly classified by King and Green ('93a) and Pianka ('95). The present analysis indicates that the *Odatria* clade, with generally smaller species, is nevertheless morphologically different (in shape) from the *Varanus* clade, with generally larger species. The two variables that are best correlated with the first and second canonical functions separating the two clades were logTAIL and logHD, respectively.

The first canonical variate is often interpreted as "size," but this is not necessarily so (see Klingenberg, '96). From our morphometric analysis, it is clear that the first canonical variate is not just a pure size indicator for Western Australian goannas. Figure 3 indicates a general size effect (e.g., the smallest *V. brevicauda* and largest *V. glebopalma* being at either end of the first canonical variate scale) but *V. pilbarensis*, *V. acanthurus*, *V. mitchelli*, and *V. scalaris* are all out of "size" sequence (based on TA) for the subgenus *Odatria*. The overlap of the two subgenera *Odatria* and *Varanus* on the first canonical variate is also not "size" related. Similarly, the first canonical variates for the two subgenera when considered separately (Figs. 5, 7) are not a pure size indicator.

#### *Sexual dimorphism*

The sex of varanids is reported as being difficult to determine from external morphometric characteristics or scalation (Green and King, '78; King and Green, '93b), although Auffenberg ('81), Yadav and Rana ('88), and Auffenberg et al. ('91) report differences in cloacal scales for sexes of *V. bengalensis*

and *V. komodoensis*, and Yadav and Rana ('88) and Auffenberg ('94) report that body micropores can be used to distinguish the sexes for *V. bengalensis*. Adult males are generally larger than females (Shine, '86; Auffenberg, '94; Pianka, '94), but this is not a useful discriminator for juvenile and small-adult specimens. Using a suite of logarithmically transformed appendage lengths, it was possible to correctly determine the sex of a number of species of *Varanus* with a relatively high level of accuracy (Tables 8, 9), although no single character or set of characters was a useful discriminator for all species of the genus. There were significant differences in logarithmically transformed appendage lengths between sexes for some of the dimensions commonly used (HL, HW, NECK, FLL, and HLL) when the effects of TA were removed for some species (Table 11). In all cases, the appendage length was proportionally longer in males than females, or alternatively, the TA was proportionally longer in females than males. For most species, there was little separation between the sexes when the first and second canonical variates were plotted (Fig. 3). The greatest separation of sexes with the first and second canonical variates was for *V. caudolineatus*, *V. gilleni*, and *V. storri*. Generally, the males were displaced to the more positive value on the first canonical variate and negatively on the second canonical variate, suggesting that males have longer tails and deeper heads. It might be speculated that fighting between males (Thompson et al., '92; Horn et al., '94) may have resulted in the evolution of relatively larger heads and longer limbs or, alternatively, females have evolved relatively longer bodies to maximize fecundity. However, there appears to be no sexual dimorphism in the number of presacral vertebrae for goannas (Greer, '89; p. 208) and so the vertebrae are presumably more elongate in females. Female *V. gilleni* and *V. caudolineatus* appear to be morphologically more similar to each other than to males of their own species (Fig. 3). If these two species are closely related and the sexual dimorphism evolved prior to the evolution of separate species, then this might explain the close morphological affinity of the sexes of sister species. There also appears to be an appreciable difference between male and female *V. storri*, which may account for their morphological overlap with other species (Table 2).

TABLE 11. F-values and significance levels for sexual differences for selected body dimensions\*

<i>Varanus</i>	df	log HL	log HW	log FLL	log HLL	log NECK
<i>brevicauda</i>	1,30	4.69	19.87	4.28	9.70	8.20
<i>caudolineatus</i>	1,60	<u>50.69</u>	<u>4.85</u>	<u>21.99</u>	<u>23.20</u>	<u>5.09</u>
<i>storri</i>	1,20	<u>38.04</u>	<u>12.43</u>	<u>8.32</u>	<u>25.38</u>	0.26
<i>gilleni</i>	1,19	<u>32.47</u>	<u>13.81</u>	<u>4.04</u>	1.33	4.33
<i>pilbarensis</i>	1,6	0.00	3.10	0.37	0.56	0.86
<i>eremius</i>	1,46	6.64	0.05	5.88	2.71	0.00
<i>scalaris</i>	1,44	<u>3.88</u>	7.31	1.26	1.03	5.01
<i>acanthurus</i>	1,24	<u>13.01</u>	<u>9.68</u>	<u>6.70</u>	<u>8.49</u>	<u>0.16</u>
<i>mitchelli</i>	1,18	2.09	2.21	1.89	2.00	0.24
<i>glauerti</i>	1,23	3.47	0.01	4.15	0.62	1.58
<i>tristis</i>	1,42	4.21	2.06	1.26	1.67	0.45
<i>p. panoptes</i>	1,7	7.53	1.55	1.61	0.40	0.04
<i>gouldii</i>	1,69	<u>23.79</u>	<u>9.63</u>	<u>7.36</u>	0.00	<u>13.11</u>
<i>glebopalma</i>	1,25	1.93	0.01	0.39	0.07	2.38
<i>rosenbergi</i>	1,30	2.27	0.36	2.33	4.70	0.41
<i>mertensi</i>	1,16	0.40	4.63	2.87	0.08	2.09
<i>p. rubidus</i>	1,10	0.00	0.62	0.51	0.40	1.70
<i>giganteus</i>	1,18	0.02	0.04	1.25	1.86	1.24

\*Values are F-ratios and P-values. Values underlined are  $P < 0.05$ .

### Isometry and shape

There is considerable conservatism in the general body morphology of the family Varanidae. King and Green (193b) describe Australian goannas as having long and slender necks, long bodies with strong, muscular tails, and well-developed, pentadactyl limbs with a strong claw on each digit. They went on to indicate that Australian goannas are medium to large in size. Greer (1989: p. 195) indicates that, although there is a huge variation in body size, "all varanids look more or less alike, differing only in details such as relative lengths of snouts and tails, shape and spyness of the tail, and the position of the nostrils on the snout." A similar view was expressed by Shine (1986). Pianka (1995) suggests that *Varanus* is morphologically conservative, despite species varying in mass by five orders of magnitude. Although we concur with the generalizations that goannas are morphologically similar despite their considerable variation in body size, we address here the quantitative question: Are goanna species isometric?

In the absence of changes in basic body physiology or mechanics, the shape of an organism must alter with size to preserve functional equivalence, both in ontogeny and phylogeny (Huxley, '32; Gould, '66; Schmidt-Nielsen, '75, '79; Sweet, '80; McKinney, '90; Losos, '90a; Swartz and Biewener, '92). There are, however, several examples in which shape does not vary among members of a

size series (Meunier, '59; Sweet, '80), a phenomenon termed "geometric similarity" (Gould, '69; Gunther, '75). Considering the comments of other researchers on morphological conservatism in *Varanus* (Shine, '86; Greer, '89; Pianka, '95), with which we concur, varanids might be expected to approach geometric similarity. To have isometric or geometric similarity, changes in appendage lengths of goannas would need to be proportional to changes in body length; i.e., interspecific variations in appendage dimensions would scale with  $TA^{1.0}$  since we use TA as a linear measure of body size. The relationship between appendage dimensions and TA appears to be generally linear for most measurements (Figs. 12, 13), but the 18 species/subspecies of goanna measured are not geometrically similar for all measures; only HL, HD, and TAIL were consistently isometric for most species. HL, HD, and FLL were isometric for the subgenus *Odatria*, while HD, NECK, and TAIL were isometric for the subgenus *Varanus* (Table 10). Limb dimensions of the larger species are generally proportionally larger than for the smaller species, as changes in appendage dimensions (residuals) are significantly and positively correlated with changes in TA. The scaling exponent with TA varies from about 0.88 for HW to 1.32 for UHL for the combined 18 species/subspecies (Table 10). Even for a single limb, the upper and lower proportions vary with TA for different-sized species. This general lack of isometry, and body proportions which are correlated with size in goannas, are in accord with the generally accepted dogma of non-isometric body scaling (Ricklefs et al., '81; McKinney, '90; Losos, '90a,c; Swartz and Biewener, '92). However, there are no comparable morphometric analyses for other groups of lizards to indicate whether goannas are nevertheless very morphologically similar (as we and others suggest) or whether goannas are in fact just as morphologically variable as other families of lizards.

### Habitat and morphology of species based on relative appendage length

Variations in appendage length of *Varanus* that are not correlated with body size or growth nor found in sister taxa may, as suggested by King (1991), be related to their habitat and niche utilization, or performance traits. This view is supported by Laerm (1974) for basilisk lizards (*Basiliscus* spp.) and Losos and Sinervo (1989) and Losos

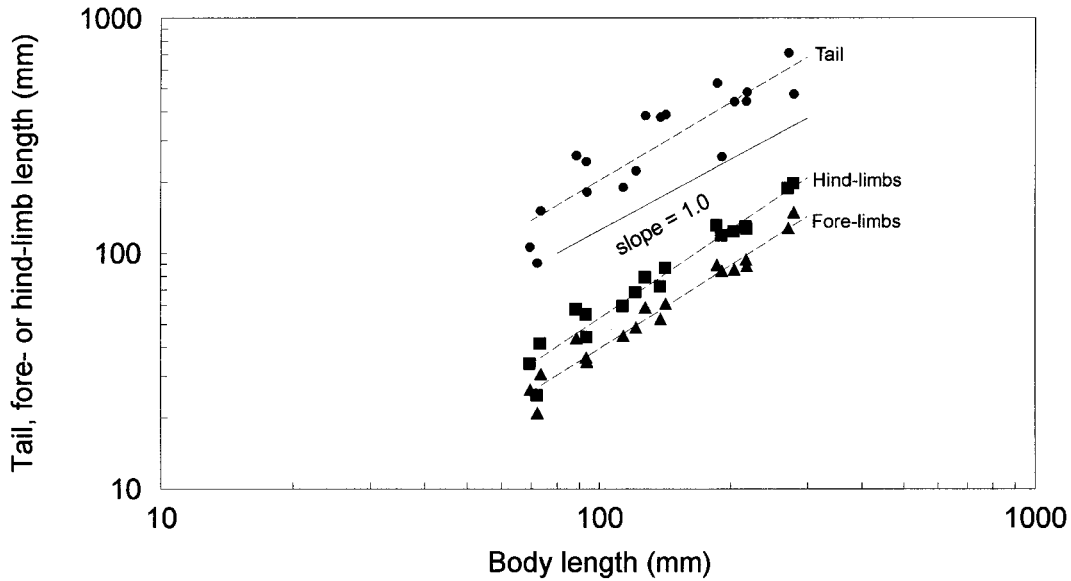


Fig. 12. The relationship between the logarithmically transformed dimensions of tail, fore- and hind-limbs, and TA for 17 species of goannas.

('90a-c) for *Anolis* lizards. Consequently, some morphological attributes of goannas are likely to correspond to various ecological and environmental variables, as suggested by Collette ('61), Moermond ('79), Ricklefs et al. ('81), Pianka ('86), and Losos ('90a) for

other lizards. With few exceptions (Arnold and Bennett, '88; Losos, '90a; Miles, '94), the assumption that similar morphological characteristics among species grouped by habitat or niche are based on common functions or performance attributes has seldom been

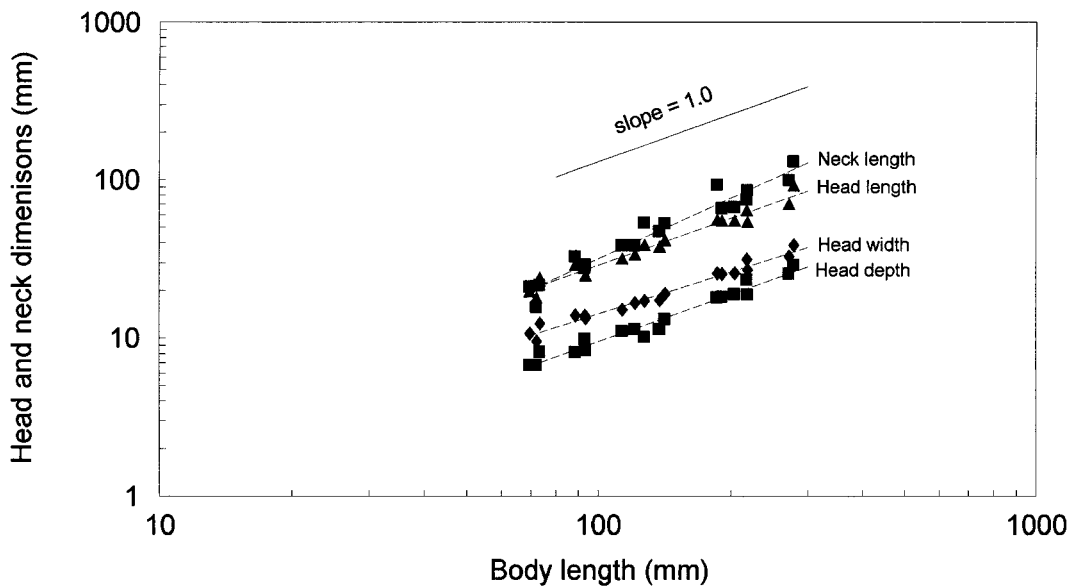


Fig. 13. The relationship between the logarithmically transformed dimensions of head and neck and TA for 17 species of goannas.

tested. Unfortunately, little is known of the habitat, foraging areas and retreats, or locomotor performance attributes of many Western Australian goannas.

To evaluate possible links between morphological features and habitats, the goannas measured in this study have been classified into four broad categories (widely foraging terrestrial, sedentary terrestrial, arboreal/rock scamperers, and semiaquatic; Table 12) according to the best available data for habitat and ecology. Discriminant analysis of the goanna morphometrics by habitat and ecology classified 82% of the individuals into the correct habitat/ecology group. The first canonical variate had an eigenvalue of 2.0 and accounted for 74% of total variance, whereas the second had an eigenvalue of 0.6 and accounted for a further 22% of the total variance. On the first canonical variate, the widely foraging goannas of the subgenus *Varanus* are clearly separated as a group from the odatrians (Fig. 14). However, the widely foraging odatrian *V. eremius* was closer to this group than to the other odatrians. The dimension best correlated with the first canonical variate was logHD. Many of the odatrians clustered together, but the second canonical variate separated the sedentary *V. breviceuda* and to a lesser extent the arboreal/rock scampering *V. glauerti* and *V. glebopalma*, and the semiaquatic *V. mertensi*. The second canonical variate was best correlated with logNECK.

#### Widely foraging terrestrial goannas

Varanid lizards are generally considered to be large, widely foraging, active, terres-

trial lizards, corresponding to our category of widely foraging terrestrial goannas. The species we place in this category are *V. panoptes*, *V. gouldii*, *V. rosenbergi*, *V. giganteus*, and *V. eremius*.

Of the goannas in the subgenus *Varanus*, *V. panoptes*, *V. gouldii*, and *V. rosenbergi* are the most similar morphologically, with *V. giganteus* and *V. mertensi* having higher and lower first canonical variates (Fig. 7). A surprising result of this morphological study is the considerable difference between the two subspecies of *V. panoptes*, although it is noted that there was appreciable overlap in the morphological space of *V. panoptes*, *V. gouldii*, and *V. rosenbergi* based on the first two canonical variates (Fig. 7). The *V. p. panoptes* has a head that is longer, wider, and deeper, and a neck that is longer than *V. p. rubidus*; however, limb and tail lengths are very similar. These two subspecies might reasonably have been expected to be more similar in appendage dimensions than when compared with other species. There is considerable overlap in the morphological shape of *V. gouldii*, *V. panoptes*, and *V. rosenbergi* (Tables 3, 4; Fig. 7) as might be expected for these three species, which are all medium-to-large-sized, widely foraging, terrestrial, and carnivorous predators of the subgenus *Varanus* (Pianka, '70a, '82; Green and King, '78; King and Green, '79; Shine, '86) (personal observations). Perhaps a revision of the taxonomy of the *gouldii/panoptes/rosenbergi* complex may explain these differences between the two subspecies of *V. panoptes* and the misclassification of *V. gouldii* (Table 6) for other species. If, e.g., *V. gouldii* was

TABLE 12. General habitat and foraging groups for Western Australian *Varanus*<sup>1</sup>

Habitat type/ foraging mode	<i>Varanus</i>	Reference
Widely foraging terrestrial	<i>eremius</i>	Thomson and Hosmer, '63; Pianka, '68, '82
	<i>rosenbergi</i>	Green and King, '78; King, '80
	<i>panoptes</i>	Shine, '86
	<i>gouldii</i>	Zietz, '14; Thomson and Hosmer, '63; Pianka, '70a, '82, '94; Shine, '86
Sedentary terrestrial	<i>giganteus</i>	Zietz, '14; Cogger, '65; Brunn, '80; Pianka, '82, '94; King et al., '89
	<i>breviceuda</i>	Pianka, 70b, '94; James, '94, '96
	<i>storri</i>	Zietz, '14; Peters, '73; Stirnberg and Horn, '81
Arboreal/rock scamperers	<i>acanthurus</i>	Thomson and Hosmer, '63; Brunn, '82
	<i>caudolineatus</i>	Pianka, '69, '94; Thompson, '93
	<i>gilleni</i>	Zietz, '14; Thomson and Hosmer, '63; Martin, '75; Delean, '80; Pianka, '82
	<i>pillbarensis</i>	Pianka, '95; Kendrick (personal communication)
	<i>scalaris</i>	Pianka, '95
	<i>mittchelli</i>	Shine, '86
	<i>glauerti</i>	Sweet (personal communication); Pianka, '95
	<i>tristis</i>	Pianka, '71, '82, '94; Brunn, '82; Fitzgerald, '83
	<i>glebopalma</i>	Sweet (personal communication); Horn and Schurer, '78; Swanson, '79
Semiaquatic	<i>mertensi</i>	Hermes, '81; Shine, '86

<sup>1</sup>Data from a variety of specific references as listed, plus more general descriptions of habitat type selected as reported in Storr et al. ('83), Greer ('89), Cogger ('92), Wilson and Knowles ('92), and personal observations.

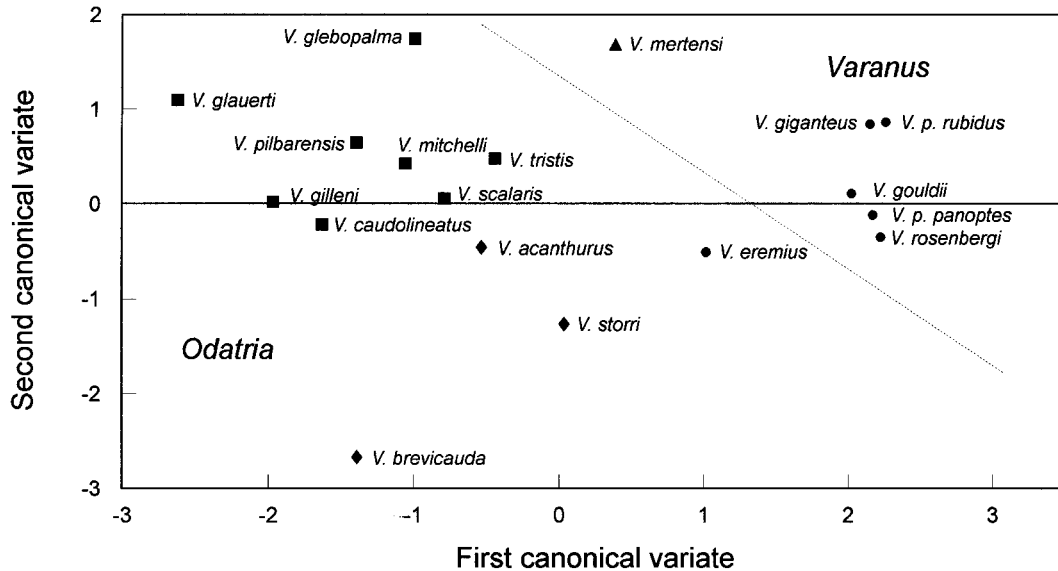


Fig. 14. The first and second canonical variates for goannas classified by habitat and ecology: circles, widely foraging terrestrial; diamonds, sedentary terrestrial; squares, arboreal/rock scamperers; triangle, semiaquatic. The first standardized canonical vector is:  $-0.280\log TA + 0.840\log HD + 2.961\log HL - 0.192\log HW - 2.970\log$

$LFL + 5.251\log LHL - 2.879\log NECK - 1.900\log TAIL - 0.471\log UFL - 0.072\log UHL$ . The second standardized canonical vector is:  $-0.788\log TA - 1.374\log HD - 2.321\log HL + 0.950\log HW - 1.649\log LFL - 4.046\log LHL + 2.726\log NECK - 0.972\log TAIL - 0.591\log UFL - 0.454\log UHL$ .

subsequently divided into more than one species (it already has two subspecies), this would alter the basis of the canonical variate analysis and may reduce the degree of misclassification.

*V. giganteus*, the largest Australia goanna, differs appreciably from the other widely foraging terrestrial species (Tables 3, 4; Fig. 7). Head length is the primary characteristic that separates the five species in this subgenus (Table 7; Fig. 7), with *V. giganteus* having the longest relative head length. In addition to head length, *V. giganteus* has a longer neck, wider head, and longer forelimbs than any of the other species in the *Varanus* clade (Tables 3, 4). *V. giganteus*, *V. rosenbergi*, and *V. p. panoptes* have relatively wider and deeper heads than other goanna species. However, there is no evidence to suggest that their foraging behavior or prey, a possible factor in influencing head dimensions, differs from those of *V. gouldii* or *V. p. rubidus*, and so differences in head dimensions in this category are difficult to interpret from an ecological perspective.

*V. eremius* is a small, widely foraging terrestrial odatrian goanna (Pianka, '68, '94;

Storr et al., '83) which differs from the other *Odatria* (except for *V. brevicauda*) by its relatively short neck (Table 4; Fig. 5). In this respect, *V. eremius* is morphologically similar to the widely foraging terrestrials *V. gouldii*, *V. rosenbergi*, and *V. p. rubidus* of the subgenus *Varanus*, although it clearly falls within the odatrian group (Fig. 3).

#### *Sedentary terrestrial goannas*

We place *V. acanthurus*, *V. storri*, and *V. brevicauda* in a sedentary terrestrial category rather than the widely foraging terrestrial category, but only for *V. brevicauda* are there substantial morphological differences.

*V. acanthurus* is the most generalized odatrian species measured here; its body appendages appear to deviate least from the regression lines for all body dimensions with TA (Table 4) for the *Odatria* group. This is also supported by the data in Table 6, showing that *V. acanthurus* is the odatrian most often incorrectly classified. *V. acanthurus* is a ground-dwelling monitor that retreats to rock crevices or holes under medium-sized boulders (Storr et al., '83; Dryden et al., '90) (personal observations). The most morphologically similar species to *V. acanthurus* is

*V. baritji* from the Northern Territory of Australia (King and Horner, '87), which has a similar ecological niche (Sweet, personal communication).

Storr et al. ('83) report *V. storri* to be very like, but smaller than, *V. acanthurus*. However, our morphological analysis indicates that *V. storri* has a relatively longer, wider, and deeper head than *V. acanthurus* and appreciably longer limbs (Table 4). As little is known of the ecology or the preferred habitat of *V. storri* (possibly under rocks and large objects lying on the ground; Sweet, personal communication), it is not possible to infer a relationship between its gross morphology and habitat use.

*V. breviceauda* is the smallest and most morphologically different goanna measured (Table 4; Figs. 3–6, 8–11). This species, relative to its thorax-abdomen length, has the shortest head and neck, narrowest head, shortest fore- and hind-limbs, and shortest tail. However, Greer ('89: p. 208) reports that *V. breviceauda* has more presacral vertebrae than any of the other goannas measured and so this might reflect an evolutionary pressure for relative elongation of the body length per se. James ('96) reports that 73% of *V. breviceauda* movements in a pit-trapping program were less than 20 m and that these goannas were very seldom seen surface-active, a view supported by Pianka ('94). The relatively short limbs and short head of *V. breviceauda*, and the evidence of James ('96), suggest that this terrestrial goanna is not widely foraging and may catch most of its prey by using a sit-and-wait strategy or by searching in burrows located within a relatively small home range. Vitt and Congdon ('78) suggest that widely foraging lizards have a relatively low clutch mass, whereas the sit-and-wait foragers have a relatively high relative clutch mass. A relatively high clutch mass can also be associated with a larger abdominal cavity (Shine, '92). Although James ('96) concluded that the absolute clutch size of two eggs for *V. breviceauda* was consistent with that predicted from correlations between SVL and clutch size in other goannas, a few *V. breviceauda* were recorded with clutches of 4 and 5. If, however, *V. breviceauda* had a relatively large clutch mass for its body size, due to the size of its eggs, then this goanna's morphology would support the established dogma that taxa with relatively smaller limbs, tails, and heads have relatively larger volumes

available in their body cavity to carry eggs and are generally sit-and-wait foragers (Vitt and Congdon, '78; Shine, '92). At a casual glance, *V. primordius* appears to be a similar size and have a similar morphology to *V. breviceauda*. A comparative analysis of these two small goannas' morphology and ecology might assist in explaining why the morphology of *V. breviceauda* is appreciably different from the rest of the genus.

#### *Arboreal/rock scampering goannas*

This category includes a continuum of scampering goannas from typically arboreal species (*V. scalaris*, *V. gilleni*) to typically saxicolous species (*V. pilbarensis*, *V. glebopalma*), with *V. caudolineatus*, *V. tristis*, *V. mitchelli*, and *V. glauerti* being found in both trees and rocks. Within this category, morphology seems to be related more to body size or performance traits than habits. *V. mitchelli*, *V. tristis*, and *V. scalaris* have a fairly generalized odatrian morphology, like *V. acanthurus* and *V. storri*, which are generalized sedentary terrestrial goannas. *V. glebopalma*, *V. pilbarensis*, and *V. glauerti* have relatively long appendages and a flattened head. In contrast, *V. caudolineatus* and *V. gilleni* have relatively short appendages.

*V. scalaris* is morphologically very similar to *V. acanthurus*, having a relatively similar length head and neck, head depth and fore- and hind-limb length. It, however, has a narrower head and shorter tail. Little is known of its ecology or behavior other than it is arboreal (Sweet, personal communication). The larger species, *V. tristis*, appears to be a "stretched" version of *V. acanthurus*, with all dimensions being slightly longer, except it has a shallower head (Table 4). Pianka ('71) reports *V. tristis* as moving from tree to tree as it mostly climbs in search of prey. Baverstock et al. ('93) report that *V. scalaris* and *V. tristis* are closely related; this, together with their preference for arboreal habitats, would explain their similar body shape. The high degree of morphological similarity between these two arboreal species and a terrestrial species (*V. acanthurus*) is unexpected. Baverstock et al. ('93) indicate that *V. acanthurus* is more closely related to *V. gilleni* and *V. breviceauda* (and two goannas not measured in this study, *V. kingorum* and *V. primordius*). The generalized body form of *V. acanthurus* may simply indicate that it is similar to the ancestral form of the subgenus *Odatria*, and this may

account for the similarity in body shape between *V. acanthurus*, *V. scalaris*, and *V. tristis*.

*V. mitchelli*, which is grouped with *V. acanthurus*, *V. scalaris*, and *V. tristis* on the first and second canonical variates, differs markedly on the third canonical variate (Fig. 6). Table 4 indicates that *V. mitchelli* has a relatively longer neck but narrower and shallower head, and shorter limbs than *V. acanthurus*, or alternatively it has a relatively longer body and similar-sized appendages. *V. mitchelli*'s relative appendage lengths are similar to those of *V. scalaris*, having proportionally the same head and neck length, head width, and fore- and hind-limb length. It differs from *V. scalaris* in that it has a much shallower head. *V. mitchelli*, *V. tristis*, and *V. scalaris* are all known to be arboreal (Pianka, '71; Storr et al., '83; Shine, '86), whereas *V. acanthurus* is a ground monitor retreating to rock crevices or holes under medium-sized boulders (Storr et al., '83; Dryden et al., '90) (personal observations). The most noticeable difference between *V. acanthurus* and these three arboreal monitors is that *V. acanthurus* has an appreciably shorter neck (Table 4), which might suggest that small-to-medium-sized arboreal species of goannas have longer necks compared with similar-sized terrestrial species. The relative neck length of these three arboreal species is, however, not as long as those of the rock scampering/arboreal *V. pilbarensis*, *V. glebopalma*, and *V. glauerti*. Additional arboreal species (e.g., *V. prasinus*) need to be measured before a more conclusive statement is possible.

*V. glebopalma*, *V. glauerti*, and *V. pilbarensis*, from the *Odatria* clade, have similarly long tails, long necks, and long FLL, although *V. glebopalma* differs from *V. pilbarensis* and *V. glauerti* in having a proportionately longer neck, and *V. pilbarensis* has a proportionately longer HLL than *V. glebopalma* and *V. glauerti* (the large *V. giganteus* from the *Varanus* clade also has a long NECK, HL, FLL, and HLL; see below). The long heads and necks of *V. glebopalma*, *V. glauerti*, and *V. pilbarensis* may be associated with searching for prey in rock or tree cervices in the medium (and large)-sized goannas. The longer hind-limbs of *V. glebopalma* and *V. pilbarensis* may be a specialization that separates these "rock scramblers" from *V. glauerti*, which is primarily arboreal (this suggestion is supported by the longer HLL of the sometimes rock-dwelling, widely foraging, but never arboreal, *V. giganteus* of the *Varanus* clade). Losos and Sinervo ('89)

report that species of *Anolis* lizards with longer hind-limbs run faster on thicker rods and that their speed is more affected on thinner rods than short-legged lizards. Similarly, very long hind-limbs may be disadvantageous for medium-sized arboreal goannas, if they impede movement on narrow branches or in tree hollows.

*V. caudolineatus* and *V. gilleni* are two small, arboreal goannas from central inland Western Australia. They are, as Pianka ('69) suggests, morphologically similar with comparatively short heads, tails, and hind-limbs. However, they can be morphologically separated, with *V. gilleni* having a shallower head and slightly shorter fore- and hind-limbs. The relatively shorter limbs and shallower head may enable *V. gilleni*, the larger of the two pygmy goannas, to move more freely in tree hollows (Pianka, '69) (personal observations). These two small, arboreal goannas, however, do not conform with the slender body, long tail, long hind-toes pattern suggested by Snyder ('54), Ballinger ('73), Ricklefs et al. ('81), and Pianka ('86) for arboreal species. Behavioral observations of *V. caudolineatus* suggest that this goanna seldom jumps from a tree to the ground, even when fleeing a predator, which generally fits Moermond's ('79) category of "runners and crawlers" having more equally proportioned fore- and hind-limbs than the jumpers. Arboreal species may need to be further subdivided into jumpers (slender body, long tail, long hind-toes) and runners and crawlers (shorter fore- and hind-limbs) before links can be drawn between their morphology and habitat-performance traits.

Arboreal lizards have been described as having a slender body, long tail, and long hind-toes (Snyder, '54; Ballinger, '73; Ricklefs et al., '81; Pianka, '86), a hypothesis supported by the body form of *V. glauerti*, although it is not supported by the body shape of *V. caudolineatus*, *V. gilleni*, *V. scalaris*, and *V. tristis*. Moermond ('79) asserts that for *Anolis* lizards, jumpers tend to have longer tails, a view generally supported by Pianka ('86). It would be interesting to quantify the extent to which *V. glebopalma*, *V. glauerti*, and *V. pilbarensis* jump from rock to rock, tree to tree, or tree to ground compared with other goannas, as this may be linked with the length of their tail and hind-limbs and may be a performance trait that separates these three species from other arboreal species such as *V. scalaris* and *V. tristis*. The total TA of *V. tristis* and *V. glauerti* is similar; they are closely related (Baver-



stock et al., '93) and from the limited data available they both are arboreal. It is therefore surprising that their relative appendage lengths are appreciably different (Table 4). This paradox is only likely to be resolved with a better understanding of their behavior and their microhabitat.

#### *Semiaquatic goannas*

*V. mertensi* has the narrowest and shallowest head, and shortest limbs and tail, of members the *Varanus* clade. *V. mertensi* is the only semiaquatic goanna of this clade that was measured here. *V. mitchelli*, of the subgenus *Odatria*, is sometimes seen in water but is mostly arboreal (Shine, '86); it also has short limbs. This may suggest a link between semiaquatic habits and appendage length. Measurement of other semiaquatic varanids would obviously assist in the interpretation of these variations in body appendage length.

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