Shape of Western Australian dragon lizards (Agamidae)

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Abstract. For 41 species of Western Australian agamid lizards, we found that most appendage lengths vary isometrically, so shape is largely independent of size. Of the three methods we used to quantitatively remove the effects of size on shape, the two that use principal component analysis (PCA; Jolicoeur, 1963; Somers, 1986; 1989) provided similar results, whereas regression residuals (against body length) provided a different interpretation. Somers' size-free PCA approach to remove the size-effects was the most useful because it provided 'size-free' scores for each species that were further analysed using other techniques, and its results seemed more biologically meaningful. Some, but not all, of the variation in size-free shape for these lizards could be related to phylogeny, retreat choice and performance traits.

Introduction

The obvious differences in head and limb dimensions (shape) among species of Western Australian (WA) dragon lizards (Agamidae; subsequently referred as dragons) are probably related to performance traits, behaviour and preferred habitat (Losos, 1990; Garland and Losos, 1994; Miles, 1994; Malhotra and Thorpe, 1997; Vanhooydonck and Van Damme, 1999; Kohlsdorf et al., 2001; Melville et al., 2001; Herrel et al., 2002). Some of the variation in shape might be accounted for by differences in body size, and some may reflect ancestry (phylogenetic inertia).

Body size and shape are often complexly inter-related (Mosimann, 1970; LaBarbera, 1989; Hews, 1996; Malhotra and Thorpe, 1997), therefore to properly understand the relationship between variations in body shape and habitat it is necessary to quantitatively account for effects of body size. Three approaches to remove the effects of size on shape are ratios, regression residuals, and principal component analysis (PCA). Humphries et al. (1981) argued

that ratios should not be used for a variety of reasons. Many authors have used residuals of morphological characteristics regressed against a body dimension (e.g. snout-to-vent length) to remove the effects of size before assessing the relationship between 'size-free' shape and habitat use (e.g. Malhotra and Thorpe, 1997; Vanhooydonck and Van Damme, 1999; Herrel et al., 2001, 2002; Kohlsdorf et al., 2001). A major disadvantage of using regression residuals is that a single morphological character (e.g. snout-to-vent length) is assumed to represent size.

Jolicoeur (1963) suggested that the first principal component of the correlation matrix for logarithmic-transformed data was a better expression of size than the choice of any single body dimension (e.g. mass or snout-to-vent length) for regression. Implicit in Jolicoeur's (1963) approach is that the logarithms of shape variables are more variable than the logarithms of the size variable and that shape is independent of size; i.e., the first principal component (size) accounts for the majority of variance. However, this may not be true for all data sets. Jolicoeur's (1963) PC method has the advantage over bivariate regression in that many variables can be simultaneously interpreted as size, and a judgment as to which single variable equates with 'size' does not have to be made. However, Mosimann (1970) and Sprent (1972) suggested that interpreting the first principal component as size was arbitrary.

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Somers (1986) used a method that constrained PCA to extract a first component that represented only size, then amended his method (Somers, 1989) to account for comments by Sundberg (1989) and Rohlf and Bookstein (1987). Somers' revised approach also provides 'size-free' residual values for each variable, which can be used in subsequent analyses. Somers (1986) argued that conventional PCA did not completely isolate variation in isometric size from shape.

This study had three objectives. First, we examined the extent to which variation in head, limb and tail dimensions of Western Australian dragons are correlated with a single measure of 'size' (body length) and deviate from isometry. Second, we examined differences in shape for agamids after the effects of size have been removed using residuals from regression of head, limb and tail dimensions with body length, conventional PCA (Jolicoeur, 1963), and Somers' (1986, 1989) size-free PCA. Thirdly, we examined variation in size-free shape in the context of phylogeny, habitat and performance traits for these Western Australian dragons.

Materials and methods

Measurements

Morphological measurements were made for adult males of 41 species of Western Australian dragon lizards (subsequently referred to as dragons) in the Western Australian Museum collection. One species of *Rankinia* (classified as *Ctenophorus*; see Melville et al., 2001), *Caimanops*, *Moloch*, *Chlamydosaurus*, *Amphibolurus* and *Chelosania*, two *Pogona*, four *Tympanocryptis* and *Lophognathus* [also described as *Amphibolurus* (Houston, 1998) and *Gemmatophora* (Storr et al., 1983)], 10 *Diporiphora* and 17 *Ctenophorus* species were measured. *Pogona minor* has three subspecies in Western Australia, *P. m. minor*, *P. m. minima* and *P. m. mitchelli*, that have been recognized as separate species (Cogger, 1992). There are obvious morphological differences among these subspecies, so for the purposes of this analyse these subspecies have been treated as separate 'species', taking the total to 43 'species'.

For each specimen, its museum acquisition number and sex (by examination of gonads) were noted and we measured snout-to-vent length (SVL), tail length (tip of the tail to vent; Tail), body length (vent to shoulder; BL), total length (TL = SVL + Tail), head length (tip of the snout to rear of tympanic opening; HL), head depth (greatest depth of the skull; HD), head width (greatest width of skull; HW), neck length [SVL − (BL + HL); Neck], upper fore-limb length (UFL), lower fore-limb length (LFL), forefoot length (Ffoot), upper hind-limb length (UHL), lower hind-limb length (LHL) and hind-foot length (Hfoot). BL, SVL and Tail were measured with a ruler to the nearest millimetre, and all other measurements were made with vernier calipers to the nearest 0.1 of a millimetre, after positioning the body as shown in figure 1. Every effort was made to measure 10 adult males for each species, but this was not always possible. We did not measure specimens that were contorted or poorly preserved, or had broken tails or limbs.

Shape analysis

To compare 'size-free' shape of Western Australian agamids we used three different methods; residuals from regression, PCA, and size-free PCA. If all three approaches removed the same 'size' effect, then the grouping/placement of species in morphometric space as an expression of body shape should be very similar using PC axes 2 and 3 from PCA, and PC axes 1 and 2 from Somers size-free scores, and PC axes 1 and 2 from regression residuals. For the analysis that used regression residuals, we considered three different variables to representative of overall size; SVL, TL and BL. BL was selected because SVL and TL incorporate HL and Neck; the ratios between these and BL vary among species, and this could confound the analysis. Also, dragons often have the tail tip missing, and this compromises accurate measurement of TL (although we excluded individuals that obviously had the tip of their tail missing, it was not always possible to know if the tip of the tail had been lost and the wound healed).

All data were logarithmically transformed (base 10) to minimize variance between different-sized specimens and to obtain a near linear relationship between variables. Allometric relationships of limb and head dimensions with $\log_{10}$ BL were determined by regressing log-transformed appendage lengths using both linear and reduced major axis regression models. We tested whether the slopes for the least squares regression and reduced major axis equations differed from isometry (Rayner, 1985). $\log_{10}$ transformed, non-standardised residuals from the least squares regression of the eleven body and appendage dimensions (HL, HD, HW, Neck, UFL, LFL, Ffoot, UHL, LHL, Hfoot and Tail) with BL were analysed by PCA, using the correlation matrix.

All $\log_{10}$ transformed appendage and body dimensions were analysed by conventional PCA using the correlation matrix. If the first PC axis represents size, then the second and third PC axes should represent variations in body shape [although some authors will argue that PC 1 will include shape and following PC axes will include size and shape; see Sundberg (1989)]. In addition, appendage lengths were analysed after Somers (1986, 1989) to obtain 'size-free' scores. These 'size-free' scores were $\log_{10}$ transformed and subjected to PCA. PC axes 1 and 2 from this analysis should represent variations in body shape. We rewrote Somers'
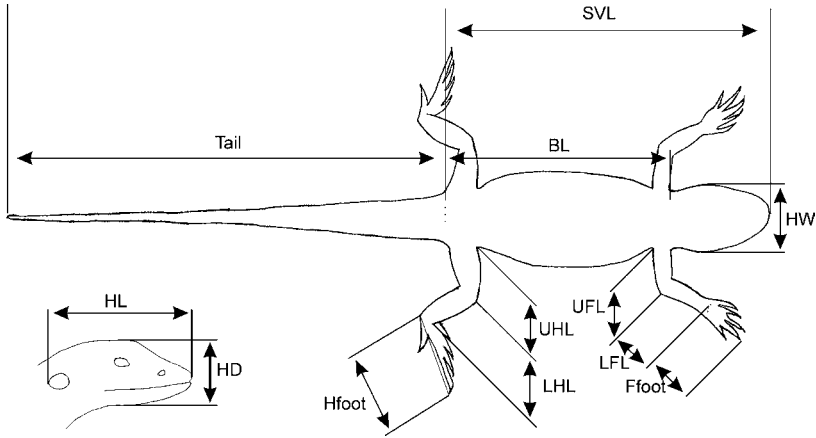
Figure 1. Morphological measurements for dragons.

(1986, 1989) software in Visual Basic. Copies of this software are available from either author.

Ideally, effects of phylogeny should be accounted for before examining links between body shape and preferred habitat. However, a multivariate approach controlling for phylogenetic effects is not currently available that could be applied to these data. The independent contrasts method of Garland et al. (1992, 1993) does not provide 'phylogenetically-free' values for each species and the alternative methods such as autocorrelation (Rohlf, 2001) and PVR (Diniz-Filho et al., 1998) require reasonably accurate estimates of branch lengths, which are not available for Western Australian dragons. Even if a multivariate approach was available, an incorrect phylogenetic tree or branch lengths renders the analysis valueless. Until the phylogenetic tree provided by Melville et al. (2001) is confirmed by further research it must be treated with caution. We have therefore compared the dendrogram from a cluster analysis of size-free variables with the phylogeny for agamids prepared by Melville et al. (2001). We used cluster analysis by Ward's method using squared Euclidean distance. This also acted as a useful check on the robustness of PCA to define appropriate groups based on appendage lengths.

Results

Allometry of body and appendage length

Of the slopes and intercepts from least squares and reduced major axis regression equations for $\log_{10}$ appendage lengths with $\log_{10}$ BL (table 1) for the 43 species of dragons, only the slope from the least squares regression equations for LFL with BL differed significantly from 1.0; all other body and appendage lengths varied iso-

metrically. Slopes for eight of the reduced major axis regressions differed slightly (but significantly) from isometry (table 1). Thus, shape is not completely independent of size, and it is necessary to quantitatively remove the effects of size from shape.

Size and shape

For regression residuals, PC axis 1 accounted for 47.6% of the variance; component scores ranged from -0.12 to -0.39 and all had the same sign (table 2). These results suggested that residuals from regression of appendage lengths with BL did not remove all the effect of size-related shape changes. PC axis 2 accounted for 19.5% of variance and component scores ranged from -0.33 to 0.55. In the scattergram of PC axes 1 and 2 (fig. 2A) *Moloch horridus* and *C. kingii* were separated from all other species on PC axis 1. Two groups of *Ctenophorus* spp. are apparent, and *Diporiphora* spp. and *Tympanocryptis* spp. are more dispersed than in the PCA analysis (see below).

Conventional PC axis 1 ('size') accounted for 89.4% of the total variance in the PCA (table 2). Component scores for PC 1 were all similar in magnitude (between 0.25 and 0.30) and positive (table 2), suggesting that this PC axis primarily accounted for size (Jolicoeur and Mosimann, 1960). PC axis 2 accounted for 6.2% of the variance, and PC axis 3, for 2.1% of

Table 1. Slope and elevation for least squares regression, and reduced major axis for $\log_{10}$ appendage lengths with $\log_{10}$ BL for 43 Western Australian agamid species.

Appendages	Least squares regression		Reduced major axis regression	
	Slope $\pm 1\,\bar{s}$	Intercept $\pm 1\,\bar{s}$	Slope	Intercept
$\log_{10}$ Tail	0.95 ± 0.152	0.59 ± 0.253	**1.36**	-0.08
$\log_{10}$ HW	1.03 ± 0.059	-0.57 ± 0.099	**1.10**	-0.68
$\log_{10}$ HD	1.10 ± 0.059	-0.83 ± 0.098	**1.17**	-0.94
$\log_{10}$ HL	1.05 ± 0.060	-0.46 ± 0.100	**1.12**	-0.57
$\log_{10}$ UFL	1.06 ± 0.039	-0.72 ± 0.065	**1.09**	-0.77
$\log_{10}$ LFL	**1.13 ± 0.037**	-0.88 ± 0.061	**1.15**	-0.92
$\log_{10}$ Ffoot	0.97 ± 0.055	-0.57 ± 0.092	1.03	-0.67
$\log_{10}$ UHL	1.07 ± 0.069	-0.57 ± 0.115	**1.16**	-0.71
$\log_{10}$ LHL	0.95 ± 0.079	-0.36 ± 0.132	1.08	-0.57
$\log_{10}$ Hfoot	0.79 ± 0.112	0.03 ± 0.186	1.07	-0.43
$\log_{10}$ Neck	1.07 ± 0.054	-0.32 ± 0.089	**1.13**	0.41

Slopes significantly different from isometry ($\alpha = 0.05$) are in bold.
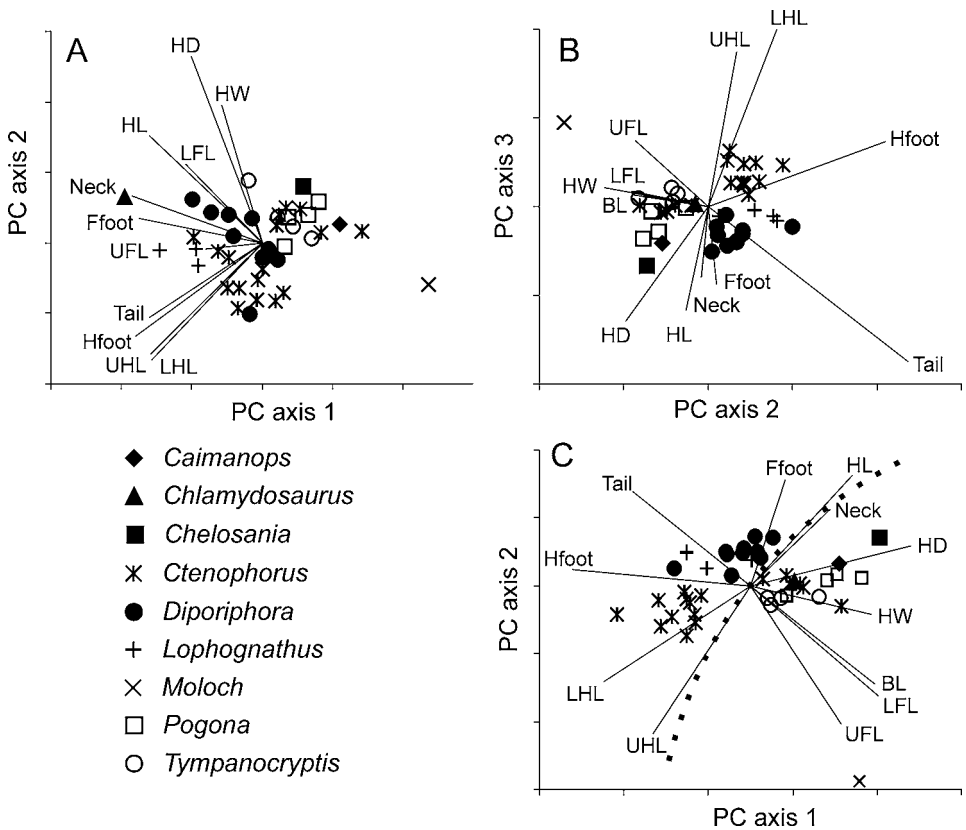

Figure 2. Scattergrams representing the grouping of all 43 species of Western Australian dragons in morphometric space based on body shape variations using three alternative methods for removing the effects of size: A = size removed using regression residuals, B = size removed using Jolicoeur's method, C = size removed using Somers' method.

Table 2. Eigenvalues, explained variance, component scores and component loadings for PC axes from the three alternative methods of analysis for 43 species of Western Australian agamids. For PCA, PC1 represents 'size'; 'size' has been removed for residuals and size-free PCA.

	PCA			Residuals		Size-free PCA	
	PC 1	PC 2	PC 3	PC 1	PC 2	PC 1	PC 2
Eigenvalue	10.73	0.74	0.25	5.24	2.14	5.17	3.10
% of Var.	89.38	6.19	2.11	47.63	19.45	43.04	25.79
Cum. % Var.	89.38	95.57	97.68	47.63	67.08	43.04	68.84
Component score coefficients (eigenvectors)							
$\log_{10}$ BL	0.295	−0.225	0.033	−	−	0.298	−0.292
$\log_{10}$ Tail	0.250	0.597	−0.440	−0.333	−0.221	−0.282	0.281
$\log_{10}$ HW	0.285	−0.310	0.053	−0.120	0.407	0.290	−0.084
$\log_{10}$ HD	0.291	−0.248	−0.325	−0.209	0.550	0.382	0.120
$\log_{10}$ HL	0.298	−0.065	−0.295	−0.333	0.317	0.244	0.330
$\log_{10}$ UFL	0.293	−0.218	0.187	−0.167	−0.019	0.216	−0.411
$\log_{10}$ LFL	0.296	−0.227	0.045	−0.228	0.233	0.305	−0.327
$\log_{10}$ Ffoot	0.299	0.026	−0.221	−0.366	0.073	0.083	0.315
$\log_{10}$ UHL	0.296	0.087	0.441	−0.330	−0.329	−0.234	−0.440
$\log_{10}$ LHL	0.289	0.205	0.505	−0.328	−0.346	−0.351	−0.287
$\log_{10}$ Hfoot	0.266	0.530	0.184	−0.374	−0.276	−0.426	0.047
$\log_{10}$ Neck	0.302	−0.021	−0.201	−0.387	0.138	0.189	0.229
Component loadings							
$\log_{10}$ BL	0.965	−0.194	0.017	−	−	0.678	−0.514
$\log_{10}$ Tail	0.818	0.515	−0.221	−0.762	−0.324	−0.640	0.494
$\log_{10}$ HW	0.933	−0.267	0.027	−0.275	0.595	0.659	−0.148
$\log_{10}$ HD	0.952	−0.213	−0.163	−0.477	0.804	0.869	0.211
$\log_{10}$ HL	0.975	−0.056	−0.148	−0.762	0.464	0.554	0.581
$\log_{10}$ UFL	0.960	−0.188	0.094	−0.383	−0.028	0.491	−0.723
$\log_{10}$ LFL	0.971	−0.196	0.023	−0.521	0.341	0.694	−0.576
$\log_{10}$ Ffoot	0.981	0.023	−0.111	−0.838	0.107	0.189	0.553
$\log_{10}$ UHL	0.969	0.075	0.222	−0.756	−0.481	−0.532	−0.773
$\log_{10}$ LHL	0.947	0.177	0.254	−0.751	−0.506	−0.797	−0.504
$\log_{10}$ Hfoot	0.871	0.457	0.093	−0.857	−0.403	−0.969	0.082
$\log_{10}$ Neck	0.988	−0.018	−0.101	−0.887	0.201	0.430	0.403

the variance. PC axes 2 and 3 explained 78.2% of the remaining variance, after 'size' was accounted for [(100 × (6.19 + 2.11)/10.6%)]. If PC axis 1 completely removed the effects of just size, then a scattergram of PC axes 2 and 3 (fig. 2B) would group the 43 species in morphometric space based on size-free body shape. PC axis 2 was loaded heavily with positive values for tail and Hfoot, and negatively for HW, HD and fore-limb length, whereas PC axis 3 was loaded positively for hind-limb length and negatively for HD, HL, Neck and Ffoot (fig. 2B). *Moloch horridus* was clearly different to all other dragons, being differentiated by a shorter head, tail and hind feet, and the second longest fore limbs. All but one *Diporiphora* spp. clus-

tered closely; *D. superba* was separated from other *Diporiphora* mostly on PC axis 2, which was heavily loaded on tail and hind foot length. Three of the four *Pogona* spp., three of the four *Lophognathus* spp. and three of the four *Tympanocryptis* spp. also clustered closely. *Pogona m. minima*, *L. norrisi* and *T. cephala* were all separated from other species of their respective genera, on PC axis 2. *Chlamydosaurus kingii* was close to the centroid for the entire group, despite being clearly the largest of the Western Australian agamids and having some major morphometric (shape) specialisations (e.g. long neck, which was not an influencing factor for PC axis 2). *Ctenophorus* spp. were clearly divided into two groups mostly by PC axis 2.

For PCA on Somers' size-free data, PC axis 1 accounted 43.0% of the variance and component scores range from −0.43 to 0.38 with a mixture of positive and negative values; PCA 2 accounted for 25.8% of variance (table 2). When PC axes 1 and 2 are considered together (fig. 2C), component loads for PC axes 1 and 2 are more evenly distributed and have similar levels of influence on the distribution of species in morphometric space then for either of the other two methods. The placement of species in morphometric space is more like that using PCA than regression residuals, i.e. *Diporiphora* spp., *Pogona* spp., *Tympanocryptis* spp. and *Lophognathus* spp. were all grouped except for a single species in each genus, two groups of *Ctenophorus* spp. were apparent, and the single species of *Caimanops* and *Chelosania* were placed in morphometric space close to *Pogona* spp.

Phylogeny

The primary separation of species into two groups by cluster analysis concurs with the results of the size-free PCA; the dotted line on the PC scattergram (fig. 2C) separates the 43 species in a similar fashion to the first primary separation of species in the cluster analysis dendrogram (fig. 3), primarily on PC axis 1. Those species with relatively long tails, hind-feet and LHL were grouped together, and those species with relative long upper limbs (but not fore-feet) and long bodies were grouped together.

There is only a partial alignment between the phylogeny (fig. 4; Melville et al., 2001) and the cluster analysis dendrogram (fig. 3), suggesting that factors other than phylogeny influence body shape. *Moloch horridus* separated first from the other agamids in the phylogeny and was the most morphologically different species, but *Chelosania brunnea*, which also branched off early from other Agamidae is morphologically similar to *Caimanops amphiboluroides* and a number of other species. *Caimanops amphiboluroides* is phylogenetically closest to *Diporiphora* spp. but is morphologically placed with other species. In general, the major clus-

tering divisions only partially reflect the phylogeny, suggesting that factors other than phylogeny have influenced shape.

Habitat

For *Ctenophorus* spp., there were two groups that corresponded to burrowers and non-burrowers (fig. 3). Species that retreat to rock crevices are within the group that that do not dig their own burrow. *Lophognathus* spp. which also do not dig burrows, are closely aligned with the non burrowing *Ctenophorus* spp. Individual species separated from others in their genus by the PC axes 1 and 2 scattergram (fig. 2A, B, C) are also separated in the cluster analysis, i.e. *L. norrisi* with *Diporiphora*; *P. minima* with *Tympanocryptis*; *C. nuchalis* with *Pogona*; and *T. cephala* with *Pogona*.

Discussion

There is little effect of body size on shape in Western Australian dragons. The three alternative methods that we used to account for size placed species differently in morphometric space. Conventional PCA (Jolicoeur, 1963) and size-free (Somers, 1986, 1989) produced the most similar results, as might be expected (because both are based on the PCA). Regression residuals against BL yielded the most different result, although some aspects of a general pattern were evident in all three methods.

Most of the agamid species clustered together with congeners in the scattergrams that purport to describe body shape, and there was considerable morphological overlap among genera, suggesting that size-free body shape of Western Australian agamids was not influenced by phylogeny (compare figs. 3 and 4). If phylogeny was a major determinant of body shape, then it would be expected that the various genera would be clearly separated in the cluster analysis.

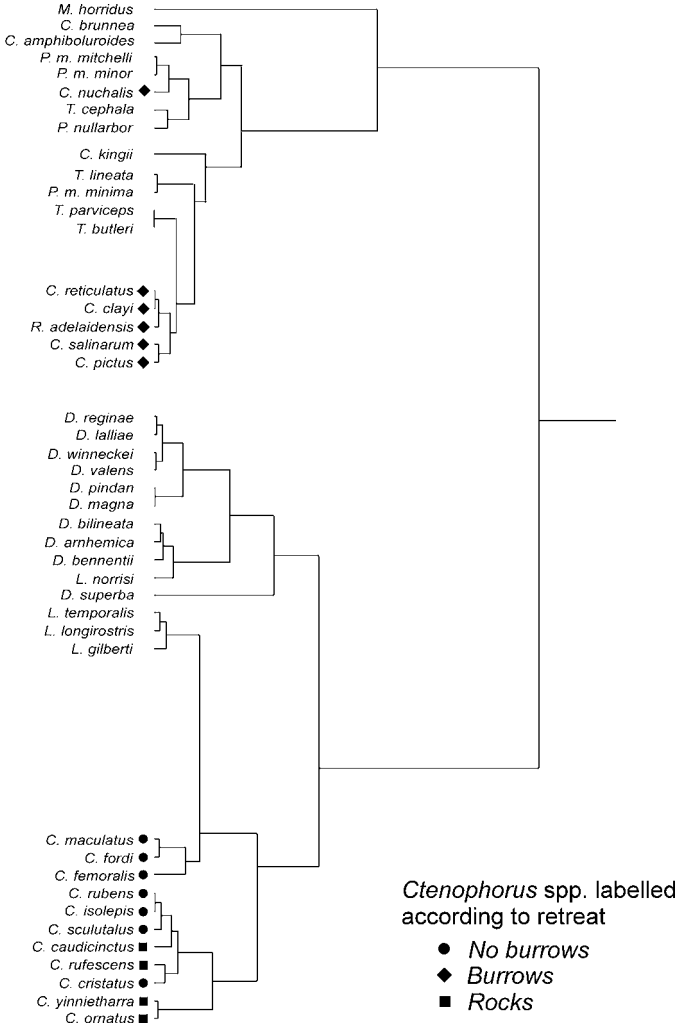Given that *Ctenophorus* spp. grouped morphologically according to choice of retreat

Figure 3. Dendrogram of Western Australian dragons from the cluster analysis based on size-free body dimensions.

(Thompson and Withers, 2005), we considered whether the remaining 26 species of Western Australian agamids also grouped in the same manner by choice of retreats. To test this, we used discriminant analysis of PC scores for size-free shape of *Ctenophorus* spp. to separate them into three groups based on their choice of retreat, and used the discriminant function to derive component scores for the other 26 non-*Ctenophorus* spp. If the body dimensions for *Ctenophorus* spp. that were associated with choice of retreat also influenced the choice of retreat in the non-*Ctenophorus* spp., then these other species should be placed in morphometric space in the appropriate groups with *Ctenophorus* spp. However, this was not the case, suggesting that the body shape characteristics that are predisposed to grouping *Ctenophorus* spp. based on their choice of retreats are different to those for the remaining Western Australian dragons.

Species morphological groupings and habitat

Moloch (Thorny devil). *Moloch horridus* is a slow-moving, ant-eating specialist (mostly *Iridomyrmex* spp.) that uses its cryptic shape and colour rather than speed to avoid predation (Pianka and Pianka, 1970; Withers and
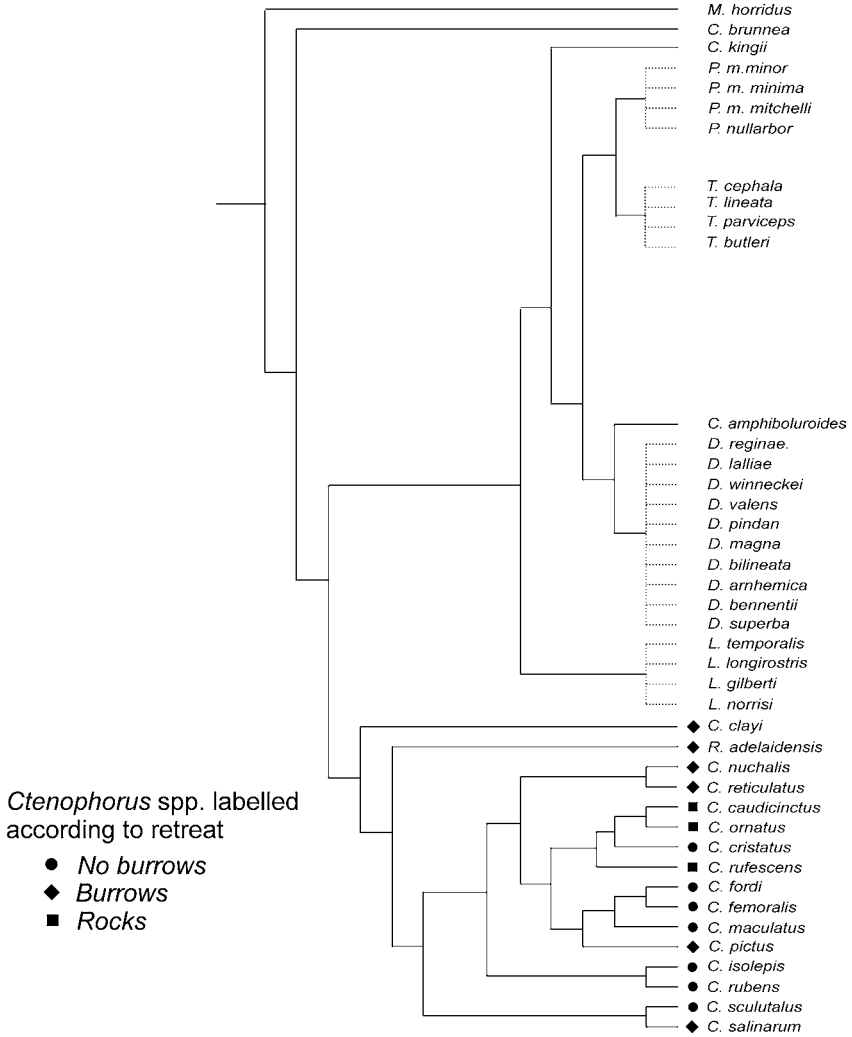
Figure 4. Phylogenetic placement of Western Australian dragons based on Melville et al. (2001), with the extra species added shown as half-tone and dotted.

Dickman, 1995; Pianka et al., 1996, 1998). Its distinctive limb dimensions (shortest tail and neck, and the narrowest and shortest head, second longest fore limbs but shortest fore feet) probably account for its atypical movement pattern with lower fore and hind limbs that swing forward in a pendulum-like fashion, while the upper fore and hind limbs remain horizontal (Clemente, 2001). This dragon represents an extreme in body shape that is presumably linked with its slow movement but high endurance (unpublished data) and its ecology (e.g. sedentary,

sit-and-wait predator that eats highly mobile prey).

Chlamydosaurus (Frilled lizard). *Chlamydosaurus kingii* has the deepest and second widest head, longest neck, and third longest head (behind *D. bennettii* and *L. gilberti*), the longest fore limbs and fore feet, and longest upper hind limbs, of all Western Australian agamids. This dragon, which uses a bipedal gait as its normal mode of movement, does not separate from the other Western Australian dragons on the first two PC axes, as the combination of its size-free

body appendage dimensions was not consistent with either of these first two PC shape axes loadings. However, it was separated from the other agamids in the scattergram of PC axes 1 and 2 based on regression residuals (fig. 2A). This indicates that where a single species shape is appreciably different to that of all other species, but the combination of variation in body and appendage dimensions that sets it apart from the other species are not common with at least a couple of other species, then it will not always be separated from the other species along PC axes that account for most of the variance. This highlights one of the problems with PCA; that is, the grouping of species is based on sets of variables that differ in some uniform manner. Where a single species is morphologically different from all other species, as is *C. kingii*, this species will not always be set apart from the other species, as the set of morphological characteristics that differentiates it from other species are not common to any of the other species.

The frilled lizard is an unusual reptile as it forages slowly using a bipedal gait. For most dragons, the centre of gravity is in front of their hind limbs when moving, making it difficult to retain the bipedal gait at low speeds. The very erect posture of *C. kingii*, its long neck and large head, make it possible for this dragon to keep its centre of gravity over its hind feet and to move bipedally (Shine and Lambeck, 1989). The large frill extending from its neck behind the head could potentially entangle its fore-feet when it runs quadrupedally if it had a 'normal' length neck. The frill under the chin forms a 'V', and along the midline probably would not tangle with the fore-feet, however, it might with the more laterally displaced feet; a question that will only be resolved with more research. Presumably to minimise interference between its frill and fore feet, it has the longest neck and fore limbs of all dragons examined. The potential entanglement of the frill and fore feet when moving quadrupedally might also account for its bipedal movement,

which largely avoids the problem. It might be expected that lizards have relatively large heads because of battles between males over females (Carothers, 1984; Vitt and Cooper, 1985; Hews, 1996; Anderson and Vitt, 1990; Gvozdik and Van Damme, 2003), or because they predate on large prey items, including small vertebrates. Shine and Lambeck (1989) and Griffiths and Christian (1996) reported that *C. kingii*'s diet consists mostly of Isoptera and Orthoptera; suggesting that the large head may have evolved for other reasons. There is some anecdotal evidence to suggest that males fight (G. Bedford, pers. comm.), which perhaps accounts for the large head. It appears that its unusual morphology is closely aligned with a performance trait and not a preferred habitat (it spends more than 90% of its time in the trees, Shine and Lambeck, 1989).

Ctenophorus. Greer (1989), Houston (1998), Storr (1965, 1966, 1967), Storr et al. (1983) and Witten (1993) grouped various species of *Ctenophorus* using different characteristics. For example, Greer (1989) used shelter whereas Storr et al. (1983), Houston (1998) and Witten (1993) used mostly morphometric characteristics. Greer (1989) categorised *Ctenophorus* into three clear ecological groups; those that are associated with rocks, those that dig burrows, and those that shelter in vegetation. We concur with this grouping of *Ctenophorus* spp. on our morphological analysis (see Thompson and Withers, 2005).

Diporiphora. *Diporiphora* are relatively small dragons with a very long tail, between 230-370% of SVL. Some species are semi-arboreal (Greer, 1989), although climbing is mostly restricted to spinifex, shrubs and small trees. *Diporiphora superba* differs appreciably from other *Diporiphora* species in having the shallowest and shortest head, most elongate tail, longest upper fore limbs, and longest fore and hind feet. Wilson and Knowles (1988) suggested that this species is almost exclusively arboreal, dwelling in the foliage of slender-leaved *Acacia* (which may account for its appreciably

slender body form), that provides an advantage when moving on very thin pliable branches. The remaining species cluster into two groups; *D. bilineata*, *D. arnhemica* and *D. bennettii*, and *D. reginae*, *D. lalliae*, *D. pindan*, *D. magna*, *D. valens* and *D. winneckei*. Storr (1979) reported that *D. winneckei* and *D. pindan* were so alike that it was hard to believe they were more than races of the same species, yet our morphological analysis does not indicate a high level of similarity between these two species. Insufficient is known about comparative habitat use or performance traits of *Diporiphora* spp. to draw conclusions about possible links between their morphology, habitat and possibly performance traits.

Lophognathus/Amphibolurus. This group is part of the *Amphibolurus* assemblage (Greer, 1989), and comprises moderate-size lizards that are mostly terrestrial, but will readily climb into trees and will flee up trees to avoid capture. The genus has been modified a number of times and has included *Physignathus* (Storr, 1974), *Gemmatophora* (Storr et al., 1983) and *Amphibolurus* (Greer, 1989). Compared with other agamids, *Lophognathus* has a relatively long head, jaw and tail. *Lophognathus gilberti*, *L. longirostris* and *L. temporalis* are morphologically similar relative to other dragons (they group together in both the PC and cluster analyse). It is unclear whether *L. norrisi* belongs to *Lophognathus* or *Amphibolurus*. Early taxonomic classification of *L. norrisi* suggested it was different to the other three species; Witten and Coventry (1984) originally classified it as *Amphibolurus norrisi*; Cogger (1992) and Aplin and Smith (2001) still use this name. Witten and Coventry (1984) reported that *L. norrisi* is morphologically intermediate between *Amphibolurus muricatus* and *A. nobbi*. In our analysis *L. norrisi* differs morphologically from the other three *Lophognathus* spp. and is clustered with *Diporiphora*. Of the four species we examined in this genus, *L. norrisi* has the shortest tail, fore feet, and hind limbs and feet, and the widest head, but details of the ecology of

these fast and often bipedal, mostly terrestrial agamids (Blamires, 1998, 1999; Blamires and Christian, 1999; Christian et al., 1999; Thompson and Thompson, 2001) are inadequate to draw conclusions about relationships between body shape and habitat or performance traits.

Tympanocryptis. *Tympanocryptis* are generally easily distinguished from other dragons by their small size, squat body, short tail that narrows quickly after the pelvis, and an ear opening that is difficult to detect (Storr, 1964). Greer (1989) reported two subgroups, the *T. parviceps* group (*T. parviceps*, *T. butleri*) and the *T. lineata* group (*T. lineata*, *T. cephala*, *T. intima*, *T. uniformis*). Our morphometric analysis concurs with the grouping of *T. parviceps* and *T. butleri*. In our cluster analysis, *T. cephala* is morphologically different to all the other species, having the largest head, long fore limbs and fore feet. Insufficient information is available about the performance traits, ecology or habitat of *T. cephala* compared with other species in this genus to draw conclusions on why its morphology might be different.

Pogona. *Pogona* consist of a number of subspecies and species including; *P. barbata*, *P. brevis*, *P. henrylawsoni*, *P. microlepidota*, *P. m. minima*, *P. m. minor*, *P. m. mitchelli*, *P. nullarbor* and *P. vitticeps* (Greer, 1989; Storr, 1982; Witten, 1994). Only *P. microlepidota*, *P. m. minima*, *P. m. minor*, *P. m. mitchelli* and *P. nullarbor* occur in Western Australia. We did not measure *P. microlepidota* due to insufficient specimens.

Cogger (1992) reported *P. m. minima*, *P. m. minor* and *P. m. mitchelli* as separate species, whereas Storr et al. (1983) described them as subspecies of *P. minor*. Cogger (1992) reported that the distributions for *P. m. minor*, *P. m. minima* and *P. m. mitchelli* overlap, whereas Storr (1982) reported them as allopatric. To add to the confusion, Storr (1982) reported *P. m. minima* as being found only on the Abrolhos Islands, whereas Cogger (1992) described the geographic distribution of *P. m. minima* as overlapping with *P. m. minor* in most of the south-

west corner of Australia. Based on the taxonomic confusion, it might be expected that *P. m. minor*, *P. m. minima* and *P. m. mitchelli* might be more similar to each other than to *P. nullarbor*, but in the cluster analysis *P. m. minima* was most separated from the others. *Pogona m. minima* has the longest tail, fore and hind limb length and smallest head of the four species. Few data exist to indicate if *Pogona* spp. occupy different habitats. All are semi-arboreal/terrestrial and are found in scrub and woodlands on a range of soil types (Chapman and Dell, 1985)

Caimanops and *Chelosania.* *Caimanops* and *Chelosania* are monotypic genera, with *C. amphiboluroides* being restricted to central Western Australia and *C. brunnea* being restricted to the wet-dry tropics of northern Western Australia and Northern Territory. *Caimanops amphiboluroides* was previously placed in *Diporiphora* (Storr, 1974) and should therefore be expected to be morphologically similar to other *Diporiphora*. However, our cluster analysis clearly separates *C. amphiboluroides* from *Diporiphora*. Greer (1989) reported *C. amphiboluroides* to be semi-arboreal, found mostly in the mulga and *Acacia* shrublands on red soil. *Chelosania brunnea* is one of the least known of the Australian dragons, being found in the far north of Western Australia and Northern Territory. Commonly referred to as the Australian chameleon, it is a slow, deliberate moving, almost exclusively arboreal species (Greer, 1989). *Caimanops amphiboluroides* is grouped with *C. brunnea* in both the PCA and cluster analyses. Both these species have comparatively narrower heads and shorter upper and lower hind limbs and feet than other agamids, except *M. horridus*. The shorter hind limbs are probably an adaptation to their arboreal lifestyle (Losos, 1990; Miles, 1994), as it would enable these species to manoeuvre on narrow branches and possibly trade-off sprint speed on the ground for this increased agility in vegetation as suggested by Losos et al. (1993). These two species provide additional evidence of morphological adaptations that relates to their habitat.

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