The relationship between size-free body shape and choice of retreat for Western Australian *Ctenophorus* (Agamidae) dragon lizards

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Abstract. We examined the relationship between body shape and choice of retreat for males of 17 species of Western Australian *Ctenophorus* dragon lizards, accounting for body size by using Somers' (1986, 1989) size-free principal component analysis. *Ctenophorus* species group strongly in size-free morphometric space (shape) based on the nature of their natural retreat (i.e. burrows, no burrows and rocks). Those species that dig their own burrow as a retreat have short tails and hind limbs, whereas that those do not generally retreat to a burrow have longer lower hind limbs and hind feet. Three of the four species that retreat to crevices or under rocks have a dorso-ventrally flattened head and body, and relatively long upper fore-limbs. The fourth rock-retreat species (*C. caudicinctus*) does not have a dorso-ventrally flattened head and body; its body shape is intermediate between those species in the three ecological groups.

Introduction

Numerous studies have grouped Australian agamid lizards (dragons) on various ecological and/or morphological attributes (Storr, 1965, 1966, 1967; Pianka, 1971a; Storr et al., 1983; Wilson and Knowles, 1988; Greer, 1989; Witten, 1993; Houston, 1998). Melville et al. (2001) argued that the three ecological groups represented evolutionary stable alternatives that arose early in the history of *Ctenophorus*. They did not, however, examine whether species in these three ecological groups shared similar morphological characteristics.

The extent to which different morphologies function best in particular habitats or are associated with particular performance traits, and are favoured by natural selection, has been the subject of considerable study (Moermond, 1979; Losos and Sinervo, 1989; Losos, 1990a, b, c). Losos (1990a, b, c) examined this theme with *Anolis* lizards, reporting that when body size was controlled for, morphological, be-

haviural (foraging mode) and performance traits (locomotor patterns, speed), and ecology evolved synchronously, with morphologically-similar species having similar performance abilities, ecology and behaviour (see also Bauwens et al., 1995; Vitt et al., 1997; Melville and Swain, 2000). Reviews by Garland and Losos (1994), Losos and Miles (1994) and Miles (1994) supported and developed the notion of synchronous evolution and interaction among morphology, performance, behaviour and fitness attributes being influenced by habitat, such that the morphology of species occupying similar habitats and behaviours are likely to converge. However, the relationship between morphology and habitat may not always be clear (see Miles, 1994). A recent analysis by Vanhooydonck and Van Damme (1999) indicated that morphological differences among species with different habitat use were not as evident when genealogical relationships among lacertid species were accounted for.

Our study had two objectives. First, we examined the extent to which variation in head, limb and tail dimensions deviate from isometry for Western Australian *Ctenophorus* spp. (subsequently referred to as dragons). Second, we examined the association of their size-free shape with phylogeny and choice of retreats.

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Materials and methods

Morphological measurements (width, length and depth) were made for adult males of 16 species of Western Australian *Ctenophorus* dragon species and *Rankinia adelaidensis* (classified as *Ctenophorus*; Melville et al., 2001) from the Western Australian Museum collection.

For each specimen, its museum acquisition number, sex (by examination of gonads), 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 the rear of tympanic opening; HL), head depth (greatest depth of 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), fore-foot length (Ffoot), upper hind-limb length (UHL), lower hind-limb length (LHL) and hind-foot length (Hfoot) were measured (fig. 1). BL, SVL and Tail were measured with a ruler to the nearest millimetre, and all other measurements were taken with vernier calipers and measured to the nearest 0.1 millimetre. We did not measure contorted or poorly preserved specimens.

Data analysis

We first tested whether the slopes for the least squares regression and reduced major axis (RMA) equations differed from isometry for all morphometric variables against BL (Rayner, 1985). Since all variables were isometric, we obtained 'size-free' body and limb dimensions using a Visual Basic V.6 program for Somers' (1986, 1989; see Thompson and Withers, 2005) size-free principal components analysis (PCA) that constrained the PCA to extract a first component that was defined as size. 'Size-free' residuals were then $\log_{10}$ transformed and subjected to conventional PCA.

Size-free data for the 17 species were also subjected to cluster analysis. Ward's method for cluster analysis using squared Euclidean distance was used to group species based on size-free data. This acted as a useful check on the robustness of PCA to define appropriate groups based on body and appendage lengths. The dendrogram from the cluster analysis was matched with the phylogeny for *Ctenophorus* prepared by Melville et al. (2001). Ideally, the effects of phylogeny should be accounted for before examining links between body shape and preferred habitat. However, a multivariate approach controlling for phylogenetic effects that could be applied to these data was not available. Garland et al.'s (1992, 1993) independent contrasts method does not provide 'phylogenetically-free' values for each species, and 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. Even if a multivariate approach was available, an incorrect phylogenetic tree or poorly resolved branch lengths render the analysis doubtful.

Results

Allometry of body and appendage length

Slopes and intercepts from least squares and reduced major axis regression equations for $\log_{10}$ head, tail and appendage lengths with $\log_{10}$ BL are presented in table 1. None of the eleven slopes from the least squares regression method differed significantly from isometry; however, four of the slopes determined by reduced major axis did differ significantly from 1.0 (table 1).

Retreats

Retreats for the 17 species are shown in table 2. Four species are associated with rocks and primarily retreat to crevices under rocks, six species dig their own burrows and seven species do not dig their own burrow unless it is for the purpose of laying eggs. There is a strong pattern of relationship between the nature of the retreat with the dendrogram from the cluster analysis for size-free morphometric data (fig. 2A). Species that dig their own burrow clearly separate morphologically from the non-burrowing *Ctenophorus*, among which *C. maculatus*, *C. fordi* and *C. femoralis* form a cohesive group. Two species that retreat to rock crevices (*C. ornatus* and *C. yinnietharra*) form a sub-group within the species that do not dig their own holes. The saxicolous *C. caudicinctus* and *C. rufescens*, which are much less dorso-ventrally depressed, are grouped with those species that do not dig their own burrow, but are not closely grouped with *C. ornatus* and *C. yinnietharra*.

Shape PCA

Component scores for PC axis 1 for size-free residuals vary between −0.34 and 0.33 (table 3) and are positive and substantial for BL, HW, HD, HL, LFL and Neck, and negative and substantial for Tail, UHL, LHL and Hfoot. All but two component loadings were greater than 0.5 for PC axis 1, and PC axis 1 explained 66.7% of variance in size-free residuals. For PC axis 2, component scores are positive and substantial
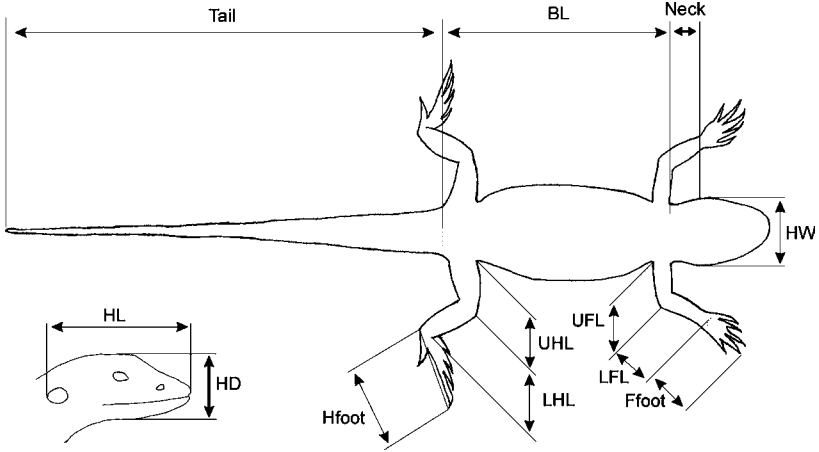
Figure 1. Morphological measurements for dragons.

Table 1. Slope and elevation for least squares and reduced major axis regressions for $\log_{10}$ head, tail and appendage lengths with $\log_{10}$ BL for 16 species of *Ctenophorus* spp. and *R. adelaidensis*.

Appendages	Least squares regression		Reduced major axis regression	
	Slope $\pm$ se	Intercept $\pm$ se	Slope	Intercept
$\log_{10}$ Tail	0.87 $\pm$ 0.212	0.71 $\pm$ 0.347	1.20	0.17
$\log_{10}$ HW	1.00 $\pm$ 0.066	-0.50 ± 0.108	1.03	-0.55
$\log_{10}$ HD	0.96 $\pm$ 0.116	-0.62 ± 0.189	1.06	-0.78
$\log_{10}$ HL	0.95 $\pm$ 0.061	-0.31 ± 0.101	0.98	-0.36
$\log_{10}$ UFL	1.03 $\pm$ 0.076	-0.68 ± 0.125	**1.07**	-0.75
$\log_{10}$ LFL	0.99 $\pm$ 0.049	-0.67 ± 0.081	1.01	-0.70
$\log_{10}$ Ffoot	0.88 $\pm$ 0.064	-0.44 ± 0.105	**0.92**	-0.50
$\log_{10}$ UHL	1.05 $\pm$ 0.137	-0.52 ± 0.224	**1.18**	-0.72
$\log_{10}$ LHL	0.95 $\pm$ 0.154	-0.31 ± 0.253	1.12	-0.59
$\log_{10}$ Hfoot	0.85 $\pm$ 0.195	-0.03 ± 0.319	1.13	-0.50
$\log_{10}$ Neck	1.00 $\pm$ 0.052	-0.23 ± 0.086	**1.02**	-0.26

Bold slope values are significantly different from isometry, $\alpha = 0.05$.

for UFL and Ffoot (fig. 2B) and negative and substantial for tail, HD and neck, although only two component loadings are greater that 0.5. PC axis 2 explained 14.7% of variance in size-free residuals. PC axis 3 only explained 6.6% of the variance and its eigenvalue was less than one, so we do not considered it or subsequent PC axes. PC axis 1 of size-free residuals separates those species that dig a burrow from those that do not, and PC axis 2 separates those that retreat to rocks and rock crevices from those that do not dig their own burrow (fig. 2B).

There was a high concurrence with the groupings of species in the scattergram of PCA 1 and 2 using Somers' size-free residuals (fig. 2B)

with the dendrogram from the cluster analysis (fig. 2A).

Discussion

All body appendages scaled isometrically (using least squares regression) for Western Australian *Ctenophorus* spp., and only four were non-isometric by RMA, so non-isometry is not a major analytical (methodological) issue.

Our PC analysis of size-free residuals indicated that Western Australian *Ctenophorus* spp. fall into two very obvious groups (on PC 1) — those that dig burrows and those that do not. Within the group that do not dig burrows there

Table 2. Retreats for 17 species of *Ctenophorus*.

Species	Retreat type	Source
R. adelaidensis	No burrow/burrows	Wilson and Knowles, 1988; Greer, 1989
C. caudicinctus	Rocks	Bradshaw, 1965; Storr, 1967; Wilson and Knowles, 1988; pers. obs.
C. clayi	Burrows	Storr, 1966; Wilson and Knowles, 1988; Greer, 1989
C. cristatus	No borrow/burrows	Wilson and Knowles, 1988; Greer, 1989; pers. obs.
C. femoralis	No burrow	Wilson and Knowles, 1988; Greer, 1989
C. fordi	No burrow	Wilson and Knowles, 1988; Greer, 1989; pers. obs.
C. isolepis	No burrow	Pianka, 1971b; Wilson and Knowles, 1988; Greer, 1989; pers. obs., — burrows near Bungalbin Hill sand plain)
C. maculatus	No burrow	Wilson and Knowles, 1988; Greer, 1989; pers. obs.
C. nuchalis	Burrows	Pianka, 1971a; Storr, 1966; Wilson and Knowles, 1988; Greer, 1989; pers. obs.
C. ornatus	Rock crevices	Bradshaw, 1965; Wilson and Knowles, 1988; Greer, 1989; pers. obs.
C. pictus	Burrows	Wilson and Knowles, 1988; Greer, 1989
C. reticulatus	Burrows	Storr, 1966; Wilson and Knowles, 1988; Greer, 1989; pers. obs.
C. rubens	No burrow	Wilson and Knowles, 1988; Greer, 1989
C. rufescens	Rocks crevices	Wilson and Knowles, 1988
C. salinarum	Burrows	Storr, 1966; Greer, 1989
C. scutulatus	No burrow/burrow	Wilson & Knowles, 1988; Greer, 1989; pers. obs.
C. yinnietharra	Rock crevices, hollow logs, burrows	Storr, 1981; Wilson and Knowles, 1988

is a subgroup (PC 2 axis) that retreat either under rocks or into rock crevices. The remainder species in this group retreat to various locations, such as log hollows, depressions in the ground and under bushes. Only *Ctenophorus caudicinctus* seems to not fit any group (despite it clearly being a rock-crevice dweller), and is close to the origin for PC axes 1 and 2. This suggests that this species has a 'generalist' shape, not particularly adapted to burrowing or rock-dwelling.

Ctenophorus associated with rocks

Greer (1989) reported that *C. caudicinctus*, *C. decresii*, *C. fionni*, *C. ornatus*, *C. rufescens*, *C. vadnappa* and *C. yinnietharra* are associated with rocks; of these only *C. caudicinctus*, *C. ornatus*, *C. rufescens* and *C. yinnietharra* are included in this study (i.e. occur in Western Australia). Cluster and PCA of size-free residuals closely grouped *C. ornatus* and *C. yinnietharra*. These two species are closer to *C. rufescens* in the PCA than *C. caudicinctus*, but *C. rufescens* is grouped with *C. caudicinctus* in the cluster analysis. *Ctenophorus ornatus* and *C. yinnietharra* retreat to rock crevices and have a dorso-ventrally flattened profile (i.e. shallowest

heads) that enables them to squeeze into narrow horizontal spaces. *Ctenophorus rufescens* is morphologically close to *C. ornatus* and *C. yinnietharra* although it is not as dorso-ventrally flattened as these two species. This species also retreats to rock crevices. This species group is consistent with Storr et al.'s (1983) *C. (Amphibolurus) decresii* group, which they describe as 'moderately large rock-dragons with more or less depressed heads and bodies'. Why the morphology of *C. caudicinctus* differs from the other saxicolous species is not clear, but it may become more evident with a detailed examination of micro-habitat use by saxicolous species.

Ctenophorus that do not dig burrows

Ctenophorus femoralis, *C. fordi*, *C. isolepis*, *C. maculatus* and *C. rubens* are collectively known as the *maculatus* group (Storr, 1965; Greer, 1989; Houston, 1998). These species plus *C. cristatus* and *C. scutulatus* are grouped in the PCA (fig. 2B), but form two separate groups in the cluster analysis (fig. 3). *Ctenophorus maculatus*, *C. fordi* and *C. femoralis* are grouped in the cluster analysis. We concur with Storr (1965) that *Ctenophorus rubens* and *C. isolepis*
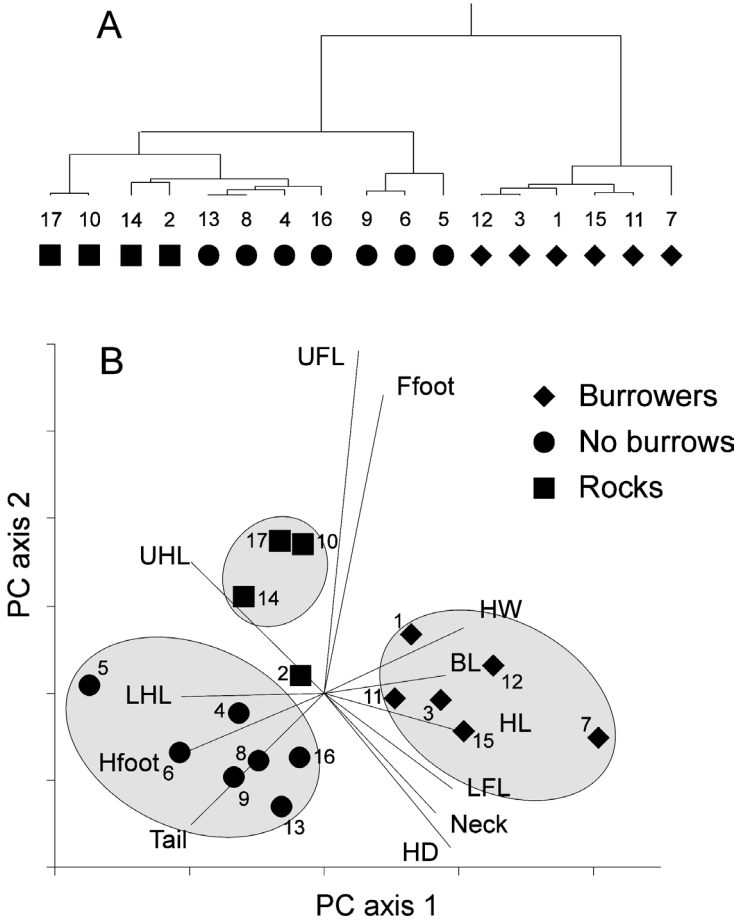
Figure 2. A. Dendrogram from the cluster analysis for all 16 species of *Ctenophorus* spp. of Western Australian agamid lizards and *R. adelaidensis*; B. Scattergram of PC axes 1 and 2 for all 16 species of *Ctenophorus* spp. of Western Australian agamid lizards and *R. adelaidensis* showing the influence of how each head, tail and body dimensions places species in morphometric space. 1 = *R. adelaidensis*, 2 = *C. caudicinctus*, 3 = *C. clayi*, 4 = *C. cristatus*, 5 = *C. femoralis*, 6 = *C. fordi*, 7 = *C. nuchalis*, 8 = *C. isolepis*, 9 = *C. maculatus*, 10 = *C. ornatus*, 11 = *C. pictus*, 12 = *C. reticulatus*, 13 = *C. rubens*, 14 = *C. rufescens*, 15 = *C. salinarum*, 16 = *C. scutulatus*, 17 = *C. yinnietharra*.

are morphologically similar; Storr (1965) initially described *C. rubens* as a subspecies of *C. isolepis*.

The morphological placement of *C. scutulatus* and *C. cristatus* with the *maculatus* group of dragons is not in accordance with the classification of these lizards by Greer (1989), who recorded them as dig-burrowers (see below). Pianka (1971c) reported these two species as being closely related and having distributions that overlap in the Goldfields region of Western Australia. Both species forage in open spaces, especially around *Acacia*. Greer (1989) reported

that *C. cristatus* and *C. scutulatus* dig burrows, which would place them in the 'dig-burrowers' group. However, extensive discussions with a number of Western Australian herpetologists who have regularly caught these two dragon lizards, and our own experiences, indicate that (in Western Australia at least), there is no evidence that either species digs or retreats to a burrow in the ground; rather they retreat to hollow logs or sleep in the open. Body shape for these two species appears to be more related to taxa that are fast moving, terrestrial lizards that prefer open areas in which to forage.
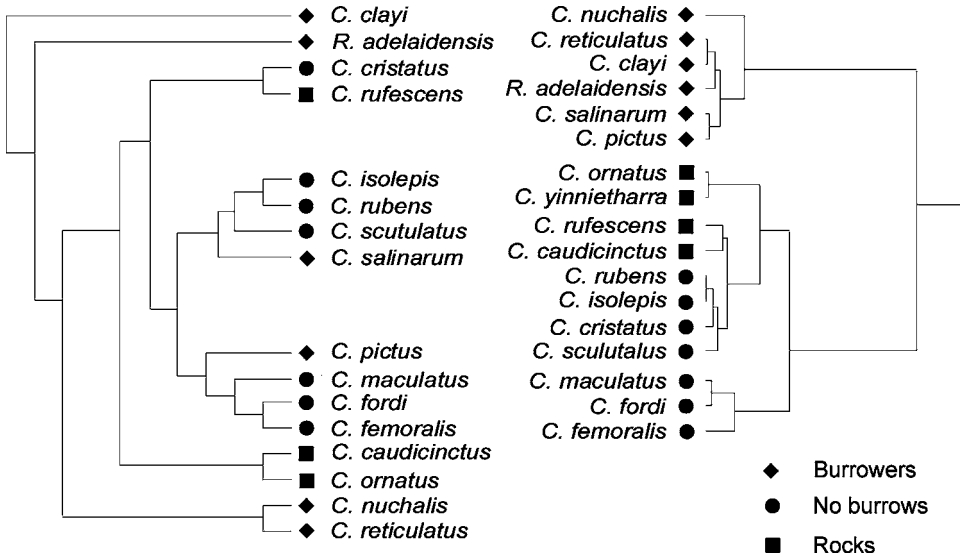
Figure 3. Phylogenetic placement of Western Australian agamid species based on Melville et al. (2001; left side) showing retreat types compared with the cluster analysis (right side) of the same species.

Ctenophorus that dig burrows

Greer's (1989) 'dig-burrowers' include *C. clayi*, *C. gibba*, *C. cristatus*, *C. nuchalis* (*inermis*), *C. mckenziei*, *C. pictus*, *C. reticulatus*, *C. salinarum* and *C. scutulatus*. Houston (1998) places *C. pictus* and *C. salinarum* in the '*pictus*' group, and *C. clayi*, *C. gibba*, *C. maculosus*, *C. nuchalis* and *C. reticulatus* in the '*reticulatus*' group. Storr et al. (1983) grouped *C. scutulatus* and *C. mckenziei*, but made another group with the sole occupant of *C. cristatus*, and placed *C. reticulatus*, *C. nuchalis*, *C. clayi*, *C. pictus* and *C. salinarum* in the '*reticulatus*' group. Greer (1989) suggested that, within the '*reticulatus*' group, *C. nuchalis* and *C. reticulatus* are closely related, as are *C. cristatus*, *C. scutulatus* and *C. mckenziei*, and *C. pictus* and *C. salinarum*. Based on our cluster analysis, *C. reticulatus*, *C. clayi* and *R. adelaidensis* form one morphological group, and *C. pictus* and *C. salinarum* form another; *C. nuchalis* is morphologically different but is still in the *Ctenophorus* group that digs a burrow. Our data indicate that this group has relatively short tails, short upper fore and upper and lower hind limbs and hind feet, but there is no evidence to support Storr's (1966) argument

that this group have shorter heads or shorter lower fore limbs or feet. Compact hind limbs may provide an advantage in digging holes, as the hole need not be as wide and muscles contracting over short levers (limbs) are generally stronger than those that contracting over long levers, providing a strength advantage for digging holes in confined spaces.

There is considerable taxonomic confusion over *R. adelaidensis* (see Aplin and Smith, 2001; Melville et al., 2001) that has lead to misidentification in the field and different views on their retreats (Houston, 1998). The specimens that we measured (and are labelled as *R. adelaidensis* in WAM) group with those species that dig their own burrows.

Species with tails between 200-285% of BL dig their own burrows, those with tails between 300-385% of BL retreat to rocks and those with tails longer than 360% of BL do not dig their own burrows. Species that dig their own burrows have UHL less than 34% of BL, LHL less than 38% of BL and Hfoot less than 50% of BL; hind limb lengths for all other species are proportionally longer.

Table 3. Eigenvalues, variance and component scores and loadings for PC axes 1, 2 and 3 for size-free residuals for 16 species of *Ctenophorus* and *R. adelaidensis*.

	PC axis 1	PC axis 2	PC axis 3
Eigenvalues	8.01	1.76	0.79
% of variance	66.73	14.68	6.59
Cum. % variance	66.73	81.41	88.00
Component score coefficients (eigenvectors)			
$\log_{10}$ LHL	−0.341	−0.006	−0.131
$\log_{10}$ Hfoot	−0.339	−0.111	−0.022
$\log_{10}$ Tail	−0.316	−0.240	−0.171
$\log_{10}$ UHL	−0.316	0.240	−0.124
$\log_{10}$ UFL	0.081	0.627	−0.418
$\log_{10}$ Ffoot	0.142	0.547	0.395
$\log_{10}$ Neck	0.265	−0.220	−0.430
$\log_{10}$ BL	0.288	0.033	−0.487
$\log_{10}$ HD	0.300	−0.285	0.275
$\log_{10}$ LFL	0.304	−0.175	−0.243
$\log_{10}$ HL	0.310	−0.066	0.222
$\log_{10}$ HW	0.333	0.120	0.028
Component loadings			
$\log_{10}$ LHL	−0.966	−0.008	−0.116
$\log_{10}$ Hfoot	−0.960	−0.147	−0.019
$\log_{10}$ Tail	−0.894	−0.319	−0.152
$\log_{10}$ UHL	−0.894	0.319	−0.111
$\log_{10}$ UFL	0.229	0.832	−0.372
$\log_{10}$ Ffoot	0.402	0.726	0.351
$\log_{10}$ Neck	0.749	−0.292	−0.383
$\log_{10}$ BL	0.814	0.043	−0.433
$\log_{10}$ HD	0.850	−0.378	0.245
$\log_{10}$ LFL	0.860	−0.233	−0.217
$\log_{10}$ HL	0.876	−0.088	0.197
$\log_{10}$ HW	0.942	0.159	0.025

Shape-habitat-phylogenetic linkages

For the Caribbean *Anolis* lizards there is a well established relationship between habitat use and general morphology, with similar anole communities having evolved independently at least four times in the West Indies (Williams, 1983; Losos and Sinervo, 1989; Losos, 1992; Irschick et al., 1997). Vanhooydonck and Van Damme (1999) reported for lacertid lizard (using a non-phylogenetic analysis) that there was morphological similarity among species based on habitat use, with ground-dwelling species from open habitats having longer femurs, tibiae and humeri than other groups, and cursorial species having relatively high heads and trunks compared with climbing species. However, a phylogenetic analysis of the same data failed to establish

these same clear relationships between habitat use and morphology (Vanhooydonck and Van Damme, 1999). Studies of other lizards have not always shown the same strong pattern of association between habitat and morphology (Jaksic et al., 1980; Miles, 1994). Without branch lengths and a multivariate phylogenetic method for comparing species, it was not possible to undertake a phylogenetic analysis of morphological differences among *Ctenophorus* species to quantitatively resolve whether differences in morphology are clearly linked with retreat choice. However, our less rigorous descriptive analysis suggests that retreat choice is strongly linked with body shape. Based on the phylogeny of Melville et al. (2001; fig. 3) species that diverged first dig their own burrows (*C. clayi*, *R. adelaidensis*, *C. nuchalis*, *C. reticulatus*). Of the four species that diverged next, three use rock crevices as retreats (*C. caudicinctus*, *C. ornatus* and *C. rufescens*), and *C. cristatus* is a widely-foraging, fast moving dragon that does not live in rocky areas or dig retreats. For those species that diverged most recently, most do not dig their own burrow. Two species appear to have 'reverted' to digging burrows and are morphologically similar to burrow-diggers. Vitt et al. (1997) reported that reptiles are capable of relatively rapid changes in morphology to accommodate a shift in habitat, and our data suggest that the body shape of *Ctenophorus* and choice of retreat are plastic, and relatively independent of phylogeny.

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