

Size-free shape differences between male and female Western Australian dragon lizards (Agamidae)

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Abstract. Examination of size-free body shape for males and females of 41 species of Western Australian dragon lizards (Agamidae) indicate that males generally have a proportionally longer head, and females a proportionally longer abdomen. Principal component and cluster analyses show that size-free body shape differences between males and females are neither uniform nor consistent within the Agamidae, or the genus *Ctenophorus*. This inconsistency is problematic when linking morphological characteristics with performance traits, use of space, or preferred habitat for species. We recommend that male and female dragons are treated separately in morphological analyses, but acknowledge that this increases the complexity of analyse and interpretations.

Introduction

Differences between sexes in overall body size and/or shape are common in many animals (Shine, 1979, 1989; Fitch, 1981; Brana, 1996). For some reptiles, males have a proportionally larger head and females have a proportionally longer body (lacertid lizards: Brana, 1996; goannas: Thompson and Withers, 1997; Thompson, 2002). The larger abdomen of females is possibly related to reproduction (egg carrying), and the larger head of males to combat or intersexual dietary differences (Brana, 1996). Recent research on reptiles has related variation in proportional appendage lengths to locomotory performance (Losos, 1990; Garland and Losos, 1994; Miles, 1994; Bonine and Garland, 1999; Irschick and Jayne, 1999), use of space (Jaksic et al., 1980; Pianka, 1986; Melville and Swain, 1999) and preferred habitat (Williams, 1972, 1983; Losos, 1992; Beutell and Losos, 1999; Vanhooydonck and van Damme, 1999). In some of these investigations, only one sex has been examined on

the presumption that species are sexually dimorphic (e.g. Bauwens et al., 1995; Kohlsdorf et al., 2001). In other studies, the sexes have been treated separately, presuming that the morphological differences between sexes were too great to justify combining the data (e.g. Malhotra and Thorpe, 1997; Vanhooydonck and Van Damme, 1999; Herrel et al., 2002), or, morphometrics were measured for both sexes and the data combined where there were no differences (e.g. Garland, 1985). Or differences between sexes were presumed to be minimal without testing for difference, and the 'average shape' of both sexes was used in the analysis (e.g. Moermond, 1979; Bonine and Garland, 1999; Melville and Swain, 2000).

If differences in body shape between sexes are minimal for a species, and less than between species being examined, then ignoring sexual differences is likely to have a minimal impact on the analyses. However, if sexes differ significantly in body shape and these differences are greater than differences between species, and the direction of sex differences is inconsistent between species, then combining data for both sexes could affect the outcome and interpretation of the analysis. This study examined size-free morphological differences (shape) between sexes of Western Australia agamid lizards (subsequently referred to as dragons) to: a) determine the extent of differences; b) examine

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whether there were systematic differences either within Agamidae or the genus *Ctenophorus*, and c) to see whether females generally have a proportionally longer abdomen and males a proportionally longer head, as is the case for lacertid lizards and goannas.

Methods

We measured 41 species of Western Australian agamids, 17 of which were from the genus *Ctenophorus* (we considered *Rankinia adelaidensis* to be a *Ctenophorus*, see Melville et al., 2001), ten *Diporiphora*, four *Tympanocryptis* and *Lophognathus*, two species of *Pogona*, and one species of *Moloch*, *Caimanops*, *Chlamydosaurus* and *Chelosania*. *Pogona minor* has three sub-species in Western Australia, *P. m. minor*, *P. m. minima* and *P. m. mitchelli*, which have in the past been recognized as separate species (Cogger, 1992). There are obvious morphological differences among these sub-species (see Thompson and Withers, 2005b) so for the purpose of this analyse these three sub-species have been treated separately, taking the total number of species examined to 39. Means for *Ctenophorus yinnietharra* were included in the principal components analysis (PCA) and cluster analysis, but the sample for each sex was too small to compared means using a *t*-test or in the discriminant analysis.

For each specimen, its museum acquisition number was ascertained, sex was determined by the examination of gonads, and measurements made of 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 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; fig. 1). BL, SVL and Tail were measured with a ruler to the nearest millimetre; all other measurements were made with vernier calipers to the nearest 0.1 millimetre after positioning the body as shown in figure 1. We did not measure specimens that were contorted or poorly preserved, or had tails or limbs broken. Only adult specimens were measured.

Data analysis

We tested differences in the ratio of HL/BL (using individual scores) for males and females for all species to see if males had a longer head, and females had a longer abdomen, as Brana (1996) reported for lacertid lizards. This analysis was undertaken using raw morphometric scores. We also used a discriminant classification analysis using only the HL and BL variables for each species to determine the percentage of individuals correctly classified according to their sex.

For many Western Australian dragons, males can attain a larger size than females. Although appendage lengths for male Western Australian dragons generally vary isometrically with BL (Thompson and Withers, 2005b). We removed the effects of body size on shape with size-free analysis (Somers, 1986, 1989; Thompson and Withers, 2005b) of the pooled means for all species, so that only size-free shape was considered when comparing sexes for a species.

A discriminant analysis was performed separately for each species on size-free data (BL, HW, HW, HL, UFL, LFL, Ffoot, UHL, LHL Hfoot and Neck) to determine the extent to which sexes could be differentiated by body shape variables. Consistently high loadings for either sex on the same variable(s) would indicate those aspects of body shape that were useful discriminators across all agamid species for separating sexes. A principal component analysis (PCA) was performed on means for size-free morphometric variables of males and females of all species to examine the similarity of males and females for a species in morphometric space compared with differences among species. The same species-mean PCA was repeated separately for the 17 *Ctenophorus* spp., again to examine the closeness of males and females for a species in morphometric space compared with differences among species within the genus. Size-free data (after Somers) for all species were also subjected to cluster analysis by Ward's method using squared Euclidean distance.

Results

The ratio of HL/BL differed significantly between sexes for 28 of the 38 species of agamid lizards (table 1). In all 28 cases, the ratio of BL/HL was higher for females than males (table 1) indicating that either males had a proportionally longer head, or females a proportionally longer abdomen, or both. When only BL and HL were used in the discriminant analysis, all individuals were only correctly classified according to their sex for *L. longirostris*; for all other species the percentage correctly classified varied from as low as 54 to 90% (table 1).

The discriminant analysis for each species using all morphological variables was able to classify all individuals into their correct sex for 25 of the 38 species, although differences between sexes were statistically significant for a lesser number of species. This imperfect classification for the other 13 species was obviously a function of small sample sizes and considerable variability in appendage dimensions among individ-

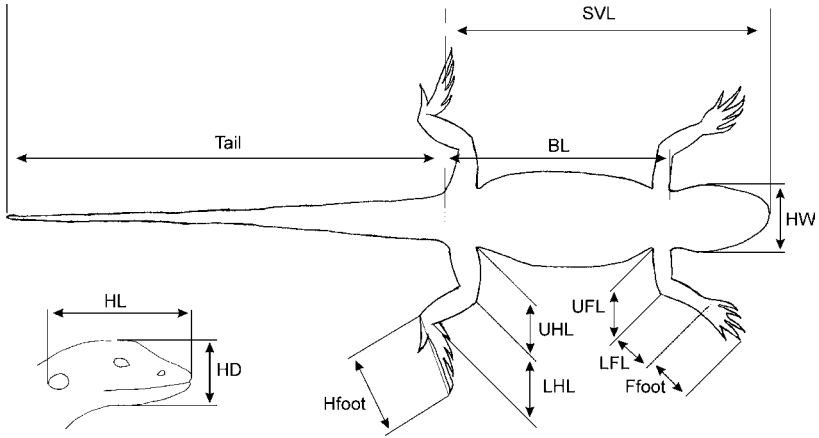


Figure 1. Morphological measurements for dragons.

uals for many species. Standardised discriminant function coefficients for each of the variables indicated that there was no one or small group of morphological variables that was predominant in separating sexes for all species, nor was there a clear pattern within any genus.

A scattergram of PC axes 1 and 2 for males and females of all 38 species (fig. 2) clearly showed that no grouping of appendages consistently separated sexes (i.e. males were not all toward the positive end of PC axes 1 or 2). However, within genera, all male *Tympanocryptis* spp. were positively placed on PC axis 1, three of the four male *Lophognathus* spp. were negatively placed on PC axis 1, and nine of the ten male *Diporiphora* spp. were positively placed on PC axis 1 compared with their respective females. It was evident that morphological differences between sexes for some species in morphometric space were greater than differences between some species. When PC axis 1 was plotted against PC axis 2 for the 17 *Ctenophorus* spp. (fig. 3) the same lack of pattern was evident, and differences in morphometric space between sexes for some species was greater than differences between some species. The dendrogram for males and females for *Ctenophorus* spp. in figure 4 shows substantial differences in the clustering of males and females for each of the species.

Discussion

The simplistic analysis of HL/BL ratios suggested that many Western Australian agamid species are sexually dimorphic, males either have a proportionally larger head and/or females have a proportionally longer abdomen. It might then have been expected that the sign for the discriminant function coefficients for BL would have been the opposite of that for HL for most species in the discriminant analysis for each species, but this was not the case. Discriminant analysis of BL and HL generally correctly classified 60-80% of the individuals. The multivariate discriminant analysis for each species using all morphometric measures showed that many species are sexually dimorphic, but variables other than BL or HL often made a greater contribution to separating sexes. The multivariate approach generally correctly classified 90-100% of individuals, which was expected because more variables were utilised. However, there was no systematic pattern for size-free shape differences between male and female Western Australian dragons. Even when only the *Ctenophorus* spp. were considered, there was no consistent pattern for morphological differences between sexes. *Ctenophorus* spp. separated into three groups in morphometric space that were linked with their retreats (Thompson and Withers, 2005a), but there was no obvious pattern in the separation of sexes in these eco-

Table 1. Mean BL/HL ($\pm 1 s$) ratio for males and females of Western Australian agamids, two-tailed t -test results (including df and P -values) for differences between males and females based on a ratio BL/HL and the percentage of individuals whose sex was correctly predicted with a discriminant analysis using BL and HL.

Species	Sex	Mean for BL/HL \pm SE	N	t -test value	DF	P	% correct from discrim. analysis
<i>R. adalaidensis</i>	M	2.39 \pm 0.049	9	-4.630	17.0	0.000	58
	F	2.69 \pm 0.042	10				
<i>C. amphibolurooides</i>	M	2.36 \pm 0.031	7	-3.807	10.5	0.003	90
	F	2.77 \pm 0.104	10				
<i>D. arnhemica</i>	M	2.28 \pm 0.042	8	-1.721	6.3	0.068	77
	F	2.49 \pm 0.116	6				
<i>D. bennettii</i>	M	1.88 \pm 0.039	10	-2.299	8.0	0.028	83
	F	2.12 \pm 0.098	7				
<i>D. bilineata</i>	M	2.22 \pm 0.042	9	-0.540	14.0	0.597	69
	F	2.25 \pm 0.036	7				
<i>C. brunnea</i>	M	2.28 \pm 0.056	10	-2.315	12.0	0.020	83
	F	2.53 \pm 0.095	4				
<i>T. butleri</i>	M	2.30 \pm 0.057	11	-1.854	17.0	0.081	70
	F	2.44 \pm 0.038	8				
<i>C. caudicinctus</i>	M	2.13 \pm 0.030	10	-3.246	7.4	0.014	81
	F	2.43 \pm 0.087	7				
<i>T. cephalo</i>	M	2.30 \pm 0.060	9	-2.826	15.0	0.013	76
	F	2.54 \pm 0.062	8				
<i>C. clayi</i>	M	2.50 \pm 0.057	8	-4.220	16.0	0.001	83
	F	2.78 \pm 0.037	10				
<i>C. cristatus</i>	M	2.45 \pm 0.040	8	-3.046	15.0	0.008	83
	F	2.63 \pm 0.043	9				
<i>C. femoralis</i>	M	2.72 \pm 0.029	9	-0.751	16.0	0.232	78
	F	2.77 \pm 0.048	9				
<i>C. fordi</i>	M	2.50 \pm 0.027	9	-2.632	16.0	0.018	83
	F	2.63 \pm 0.041	9				
<i>L. gilberti</i>	M	1.99 \pm 0.045	8	-2.236	13.0	0.043	66
	F	2.17 \pm 0.072	7				
<i>M. horridus</i>	M	4.13 \pm 0.106	10	-3.041	18.0	0.007	65
	F	4.55 \pm 0.084	10				
<i>C. nuchalis</i>	M	2.77 \pm 0.059	7	0.224	15.0	0.826	54
	F	2.74 \pm 0.071	10				
<i>C. isolepis</i>	M	2.30 \pm 0.057	11	-1.854	17.0	0.041	68
	F	2.44 \pm 0.038	8				
<i>C. kingii</i>	M	1.97 \pm 0.062	9	-3.816	15.0	0.002	77
	F	2.27 \pm 0.041	8				
<i>T. lineata</i>	M	2.61 \pm 0.046	10	-1.493	14.1	0.079	65
	F	2.75 \pm 0.083	10				
<i>L. longirostris</i>	M	1.95 \pm 0.036	6	-4.257	11.0	0.001	100
	F	2.26 \pm 0.061	7				
<i>C. maculatus</i>	M	2.54 \pm 0.051	8	-1.562	14.0	0.141	69
	F	2.65 \pm 0.055	8				
<i>D. magna</i>	M	2.11 \pm 0.031	9	-2.333	13.9	0.036	78
	F	2.32 \pm 0.084	12				
<i>P. minima</i>	M	2.49 \pm 0.039	9	-0.137	14.0	0.893	64
	F	2.50 \pm 0.056	7				

logical groups (e.g. males were not displaced in one consistent direction on a PC axis). Based on a phylogeny for Agamidae (Melville et al., 2001), there is no apparent relationship been

the morphological characteristics that separate sexes and their phylogenetic placement (e.g. males for sister species are not displaced in one consistent direction on a PC axis).

Table 1. (Continued).

Species	Sex	Mean for BL/HL \pm SE	N	<i>t</i> -test value	DF	<i>P</i>	% correct from discrim. analysis
<i>P. minor</i>	M	2.27 \pm 0.040	9	-5.745	18.0	0.000	90
	F	2.58 \pm 0.036	11				
<i>P. mitchelli</i>	M	2.25 \pm 0.042	9	-4.242	16.0	0.001	89
	F	2.46 \pm 0.025	9				
<i>L. norrisi</i>	M	2.05 \pm 0.039	9	-2.946	11.9	0.013	72
	F	2.30 \pm 0.076	9				
<i>C. ornatus</i>	M	2.55 \pm 0.057	6	-1.823	10.0	0.049	75
	F	2.69 \pm 0.057	6				
<i>T. parviceps</i>	M	2.50 \pm 0.049	10	-1.076	18.0	0.296	65
	F	2.58 \pm 0.055	10				
<i>C. pictus</i>	M	2.40 \pm 0.046	10	-1.466	17.0	0.080	79
	F	2.52 \pm 0.071	9				
<i>D. pindan</i>	M	2.24 \pm 0.061	8	-2.275	15.0	0.038	65
	F	2.43 \pm 0.057	9				
<i>D. reginae</i>	M	2.54 \pm 0.046	9	-2.920	15.0	0.011	82
	F	2.82 \pm 0.087	8				
<i>C. reticulatus</i>	M	2.58 \pm 0.060	9	-3.902	17.0	0.001	79
	F	2.94 \pm 0.067	10				
<i>C. rubens</i>	M	2.18 \pm 0.036	9	-4.337	16.0	0.001	89
	F	2.41 \pm 0.039	9				
<i>C. rufescens</i>	M	2.48 \pm 0.070	10	-0.510	15.0	0.618	69
	F	2.54 \pm 0.077	7				
<i>C. salinarum</i>	M	2.33 \pm 0.060	9	-2.926	16.0	0.010	83
	F	2.62 \pm 0.078	9				
<i>C. scutulatus</i>	M	2.59 \pm 0.030	9	-4.255	14.1	0.001	84
	F	2.85 \pm 0.053	10				
<i>D. superba</i>	M	2.73 \pm 0.044	9	-2.577	16.0	0.020	78
	F	2.88 \pm 0.036	9				
<i>D. winneckei</i>	M	2.64 \pm 0.062	10	-3.592	17.0	0.002	79
	F	2.95 \pm 0.060	9				

So what does this lack of a pattern in shape with sex mean for analyses that relate body shape or limb appendage length with locomotory performance, use of space and preferred habitat? For some species (e.g. *C. rufescens*, *C. cristatus*, *D. winneckei*), morphological differences between sexes are small enough to suggest that data for both sexes can be combined in an analysis and inferences about associations between shape and performance or ecological attributes would probably be applicable for either sex. However, where there are significant differences in body shape between sexes (e.g. *D. pindan*, *D. reginae*, *C. brunnea*), then it is probably inappropriate to combine data for sexes, as this would provide an 'average' for the species (and with an uneven number of males and females in the sample, the placement of species in

morphometric space will be biased toward the sex with the higher sample size). Here, sexes need to be analysed and reported separately. It therefore seems prudent to accept that differences in morphology exist between sexes, and to treat each sex separately, acknowledging that this will lead to a more complex analysis and interpretation of the data. For example, a cluster analysis performed on the logarithmically transformed size-free data for the male and female *Ctenophorus* spp. produced quite different dendrograms (fig. 4). Because body shape of males and females differ, and differences are neither uniform nor systematic, then males of the species cluster differently to the females in morphometric space. The most noticeable species in this respect is *Ctenophorus pictus*, where males and females have been placed in

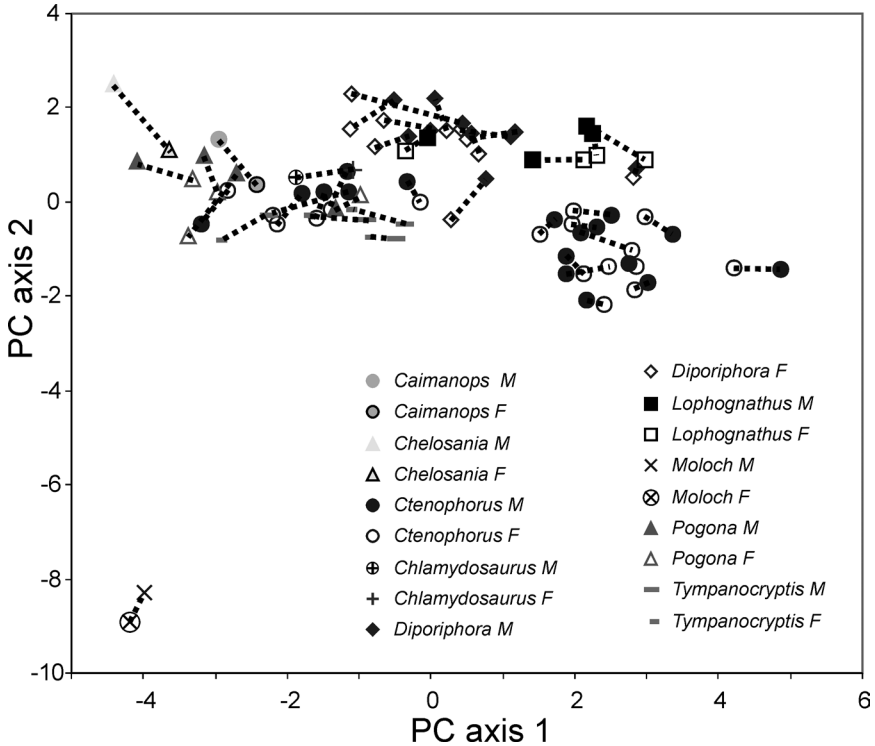


Figure 2. Scattergram of PC axes 1 and 2 for males and females of Western Australian dragon lizards. Dotted lines join males and females for each species.

different clusters based on their body shape. It then becomes problematic linking species morphology with performance traits or habitat use, although it is possible that males and females for a species might differ in performance or habitat use.

Significant and inconsistent morphological differences between sexes leads to two questions: why are there these differences, and do these differences relate to differences in performance traits (e.g. sprint speed), activity patterns, use of space or preferred habitat? For example, male Western Australian *Ctenophorus* spp. divide into three groups based on preferred retreat in a PCA base on size-free shape variables (Thompson and Withers, 2005a). Female *C. fordi* and *C. caudicinctus* are morphologically closer than their respective males to species that retreat to rock crevices (fig. 3). Is this difference reflected in how female *C. fordi*

and *C. caudicinctus* use the available natural environment?

There is a rapidly growing body of literature on sexual dimorphism in head size for lizards (see Carothers, 1984; Anderson and Vitt, 1990; Brana, 1996; Herrel et al., 1996, 1999; Hews, 1996; Gvozdik and Van Damme, 2003). Brana (1996) argued that there was strong evidence for sexual selection on female body size because of the association between female abdomen size and fecundity. Gvozdik and Van Damme (2003) reported that males with larger heads won more male–male interactions, and succeeded in grasping a female faster than did males with a smaller head, and concluded that male reproductive success both through intra- and inter-sexual competition would lead to males having relatively larger heads. Our data suggest that a comparison of head and body length between sexes for lizards may be a little simplistic, as these two variables were able

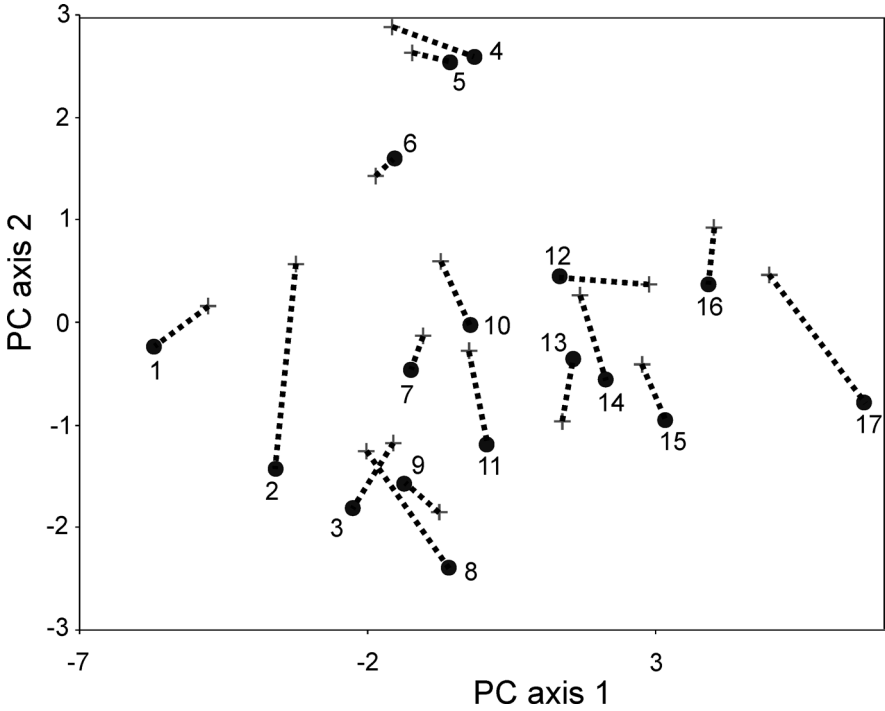


Figure 3. Scattergram of PC axes 1 and 2 for males and females for all 17 species of *Ctenophorus* spp. Males filled circles and females are crosses, dotted lines join males and females for each species. 1 = *C. femoralis*, 2 = *C. fordi*, 3 = *C. maculatus*, 4 = *C. ornatus*, 5 = *C. yinnietharra*, 6 = *C. rufescens*, 7 = *C. cristatus*, 8 = *C. rubens*, 9 = *C. isolepis*, 10 = *C. caudicinctus*, 11 = *C. scutulatus*, 12 = *Rankinia adalaidensis*, 13 = *C. pictus*, 14 = *C. clayi*, 15 = *C. salinarum*, 16 = *C. reticulatus*, 17 = *C. nuchalis*.

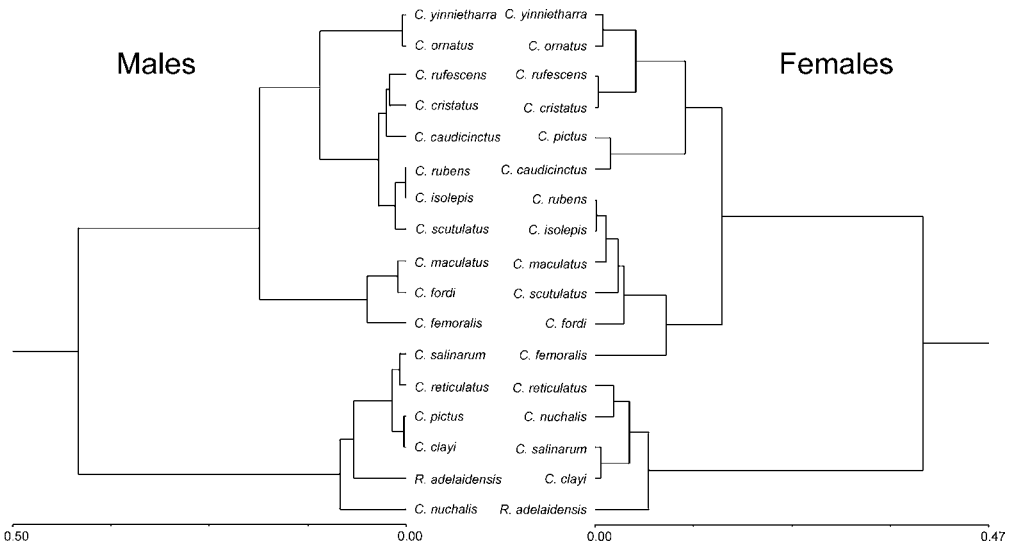


Figure 4. Comparison of the dendrograms for male and female *Ctenophorus* spp. based on log₁₀ transformed size-free shape variables. Species are aligned for *C. yinnietharra*.

to correctly classify fewer individuals according to their sex than when a suite of morphological variables. A combination of head and limb dimensions, for example, might contribute to the dominance of one male over another, or provide greater access to mating success with females, than just relative head size.

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