Sexual Shape and Size Dimorphism in Carabid Beetles of the Genus Ceroglossus: is Geometric Body Size Similar Between Sexes Due to Sex Ratio?

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Insects in many species vary greatly in the expression of secondary sexual traits, resulting in sexual dimorphism, which has been proposed to be a consequence of differences in sexual selection. In this study, we analyze the occurrence of sexual shape dimorphism and the correlation between geometric body size in males and females and sex ratio in the genus *Ceroglossus* (Coleoptera: Carabidae) using geometric morphometrics and randomization analysis. Our results show a positive relationship between the centroid size of males and females and sex ratio. However, we also observed a trend to maintain a "similar" body shape between sexes and species due to characteristics associated with sexual selection of the group in which the scarcity of outstanding morphological characters does not restrict reproduction capacity. The trend in sexual proportions was found to be near 1:1 for the eight species. We propose that the observed differences between sexes associated with the sex ratio are due to an energy cost caused by sexual selection; nevertheless, since proportions are similar for all the species, it is really not relevant to generate more conspicuous structures for a stronger male-male competence.

Key words: *Ceroglossus*, geometric morphometric, sex ratio, sexual dimorphism, centroid size

INTRODUCTION

Sexual dimorphism is one of the most generalized and notable sources of phenotypic variation in animals and plants, and is hence of great interest in evolutionary biology (Fairbairn and Preziosi, 1996). Generally, dimorphism is correlated with differential mating success for sexual selection, which is reinforced by the visibility of primary sexual traits (Moore, 1990; Mead and Arnold, 2004). However, both theoretical and empirical studies have demonstrated that sexual dimorphism reflects the net effect of both natural and sexual selection. Sexual size dimorphism (SSD) in male body size is considered to be one of the major determinants of mating success in many species (Eberhard, 1979; Brock et al., 1982; Emlen, 1996; Fincke et al., 1997). Because larger males are generally more aggressive and more competitive than smaller males, larger males often attain greater reproductive success through intrasexual selection (Andersson, 1994). The direction and degree of sexual differences in body size vary greatly among different animal taxa (Andersson, 1994; Shreeves and Field, 2008). This phenomenon has inspired a large number of studies devoted to explaining the evolutionary mechanisms underlying intra-species patterns of SSD (Hurlbutt, 1987; Fairbairn, 1997; Colwell, 2000). In contrast, sexual shape dimorphism (SShD) has been much less widely investigated (Lande, 1980; Lande and Arnold, 1985; Fairbairn et al., 2007; Gidaszewski et al., 2009). Most studies to consider SShD have discussed it as a diagnostic trait for different purposes, such as sex identification or the analysis of ontogeny (O'Higgins et al., 1990; Valenzuela et al., 2004; Pretorius, 2005; Taylor, 2006). Insects in many species vary greatly in the expression of secondary sexual traits (Andersson, 1994). In some species, variation in the expression of such traits is discontinuous, resulting in the co-occurrence of two or more discrete phenotypes within members of a single sex (Gross, 1996). The discrete expression of secondary sexual traits has attracted particular attention, as it is thought to reflect alternative adaptations to heterogeneous social conditions (Mockzek and Emlen, 2000).

Occasionally, variation in male morphology is dimorphic and two or more distinct male shapes co-occur in populations, with scarce or missing intermediate shapes (Zimmerer and Kallman, 1989; Danforth, 1991; Emlen, 1997). Male-

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biased sex ratios may provide additional evidence for sexual selection as the cause of dimorphism (Kumano et al., 2010; Wong-Muñoz et al., 2011). Species with low dimorphic variation can be especially revealing to researchers, as they generally imply morphological specializations for alternative behavioral or ecological situations. Thus, for optimal detection, it is recommended to use more complex measurement techniques, which include, for example, geometrical shape (Gidaszewski et al., 2009; Benítez et al., 2011). Many beetle species express secondary sexual characters, such as horn-like outgrowths from their thorax and head, disproportionately enlarged mandibles, or elongated front legs.

In coleopterans of the genus *Ceroglossus* (Carabidae), a phenomenon occurs which is absolutely contrary to that described above. *Ceroglossus* Solier is an endemic genus to *Nothofagus* forests of the extreme south of South America, with eight species described: *C. chilensis* (Eschscholtz, 1829), *C. darwini* (Hope, 1837), *C. speciosus* Gerstaecker, 1858, *C. magellanicus* Géhin, 1885, *C. buqueti* (Laporte, 1834), *C. suturalis* (Fabricius, 1775), *C. ochsenii* (Germain, 1895) and *C. guerini* (Germain, 1895). They are all diurnal predators of smaller organisms and have an accentuated chromatic polymorphism, which appears to be associated with environmental differences (Jiroux, 2006). Studies of shape in *Ceroglossus chilensis* have demonstrated that the similarity of males and females is directly associated with sex ratio in this species (Benítez et al., 2010b). Morphological sexual dimorphism is much reduced, and only visible under a microscope. However, in terms of geometric morphometrics, the differences are visible in two body regions: the abdomen of females, variation in which has been reported to have adaptive value due to the presence of eggs; and changes in the pronotum of the thorax in males, which has been attributed to intrasexual competition in this species (Benítez et al., 2008, 2010a, b, 2011b). These characters, which exhibit little sexual dimorphism and are related to the relative proportions of the sexes, are analyzed in this study to provide an objective explanation of the morphological similarities of males and females. The purpose of this study is to evaluate whether the pattern associated with the minimum shape differentiation between males and females in *Ceroglossus* is directly related to sex ratio, as an indirect evaluation of sexual selection effect.

MATERIALS AND METHODS

Data acquisition and sex ratio differentiation

We studied the eight species of *Ceroglossus* of central-south Chile, which were collected in several expeditions using pitfall traps.

We collected more than 1000 individuals, from which we used a random selection of 100 individuals per species (fewer in two species (*C. speciosus* and *C. darwinii*), see Table 1). The sex of individuals was determined by observation of the carenae of the antennae present in the 5th antennal segment (Benítez et al., 2010a, b) using an optical microscope. With this information, we determined the sex ratio or proportion between female and male (i.e., females over males), and differences between the observed value and the equal proportion of each species.

Shape analysis

The geometric analysis considered exclusively variation in shape, and it was performed using a photograph in ventral view of males and females with an Olympus X-715 digital camera; using the methodology described by Alibert et al. (2001), we digitized 22 landmarks (LMs, anatomical homologous points) on every picture, by TpsDig 2.12 (Rohlf, 2008) (Fig. 1). All analyses were then run using
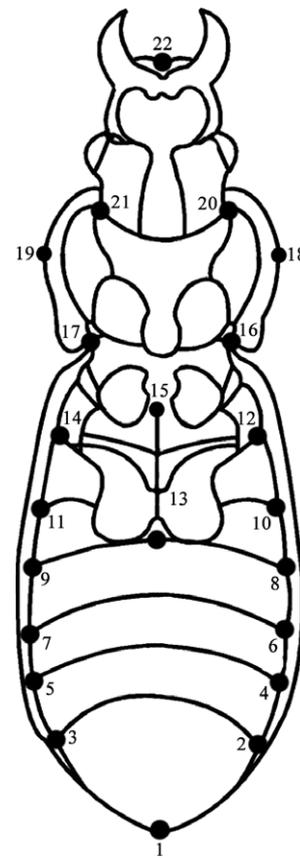
Fig. 1. *Ceroglossus.* Indication of 22 landmarks in the ventral view.

Table 1. Male-female sex ratios determined by the presence of antennal carenae in males, and mean values of centroid size for the eight species of *Ceroglossus*. *F: Female, **M: Male.

Specie	Male	Female	n	Sex Ratio	Centroid size F*	Centroid size M**	dif CS F-M
Ceroglossus buqueti	47	53	100	0.128	944.4181064	909.2698213	35.14828508
Ceroglossus chilensis	37	63	100	0.703	1167.568346	1101.135569	66.43277624
Ceroglossus guerini	44	56	100	0.273	1179.364186	1142.759059	36.60512694
Ceroglossus ochseni	47	56	103	0.191	1063.871009	1049.717203	14.15380591
Ceroglossus magellanicus	51	49	100	−0.039	1121.927193	1128.174488	−6.247295406
Ceroglossus suturalis	44	56	100	0.273	1058.024992	999.5277901	58.49720218
Ceroglossus darwinii	18	22	40	0.222	945.5537985	907.7180855	37.83571307
Ceroglossus speciosus	2	2	4	0	838.6989833	960.333728	−121.6347447

MorphoJ software version 1.05c (Klingenberg, 2011).

Once the Cartesian x-y coordinates were obtained for all landmarks, the shape information was extracted with a full Procrustes fit (GPA, Rohlf and Slice, 1990; Dryden and Mardia, 1998), taking into account the object symmetry of the structure. Procrustes superimposition is a procedure that removes information regarding size, position, and orientation so as to standardize each specimen according to centroid size. The symmetry of the structure eliminates reflection by including the original and mirror image of all configurations in the analysis and simultaneously superimposing them all (Klingenberg et al., 2002).

We analyzed the shape variation in the entire dataset with principal component analysis (PCA) based on the covariance matrix of symmetric and asymmetric components of shape variation. The first of these is the average of left and right sides and represents the shape variation component, whereas the asymmetric component represents the individual left-right differences (Klingenberg et al., 2002).

Differences between locations were assessed using canonical variate analysis (CVA), a multivariate statistical method used to find the shape characters that best distinguish multiple groups of specimens. Because of the lack of specimens for *Ceroglossus speciosus*, we ran the analysis only for the other seven species. Finally, to examine the differences in shape among species and the amount of symmetric variation and asymmetry we used Procrustes ANOVA to assess studies on object symmetry (Klingenberg and McIntyre, 1998; Klingenberg et al., 2002; Klingenberg and Monteiro, 2005). To avoid the assumption of having an equal and independent variation at all points, we performed a MANOVA test to evaluate symmetric components and asymmetry.

Centroid size and sex ratio relationship

The relationship between minimal differentiation in body centroid size, calculated as the average difference of centroid size between females and males, and sex ratio were determined via regression analysis. Centroid size corresponds to a geometrical measure of the size of the measured object, defined as the square root of the sum of the squared distance between each landmark and the centre of gravity of the measured object (Zelditch et al., 2004). The significance of this relationship was evaluated in EcoSim 7.72 software (Gotelli and Entsminger, 2010). In this software we fit

a standard linear regression to the data and then we used the randomization approach (30,000 random matrices, random number seed = 12345) to test the null hypothesis that the slope was equal to 0 (a significance level of $P = 0.05$ was assumed in this study).

RESULTS

The morphological variation among beetles determined by Procrustes ANOVA indicates that variation in size and symmetric shape among species and sexes is highly significant (Table 2). The PCA plot for the symmetric component (individual variation) and asymmetric component shows

Table 2. Procrustes ANOVA for both centroid size (CS) and shape (SH) of *Ceroglossus*, characterized by object symmetry (symmetric component). Sums of squares (SS) and mean squares (MS) are in units of Procrustes distances (dimensionless). The df of shape represents the landmarks and object symmetry variation (2k-4 = 40/2 = 20) where k is the number of landmarks. Sexual dimorphism (SD): The small differentiation in sexual shape dimorphism is due to life history, and even in the complete samples it is small.

		SS	MS	df	F	P
CS						
C.buqueti	SD	29327.9274	29327.9274	1	21.31	<.0001
C. chilensis	SD	89127.40958	89127.40958	1	41.95	<.0001
C. darwinii	SD	15292.74005	15292.74005	1	3.77	0.0585
C. guerinii	SD	4910.093733	4910.093733	1	5.06	0.0268
C. magellanicus	SD	954.610139	954.610139	1	0.5	0.4808
C ochsenii	SD	82267.25411	82267.25411	1	23.59	<.0001
C. suturalis	SD	34617.26862	34617.26862	1	25.84	<.0001
SH						
C.buqueti	SD	0.00969912	0.000484956	20	21.07	<.0001
C. chilensis	SD	0.00935952	0.000467976	20	26.51	<.0001
C. darwinii	SD	0.00844987	0.000422494	20	13.27	<.0001
C. guerinii	SD	0.00591792	0.000295896	20	24.05	<.0001
C. magellanicus	SD	0.0086548	0.00043274	20	27.88	<.0001
C ochsenii	SD	0.00759301	0.000379651	20	23.35	<.0001
C. suturalis	SD	0.00873229	0.000436615	20	35.26	<.0001
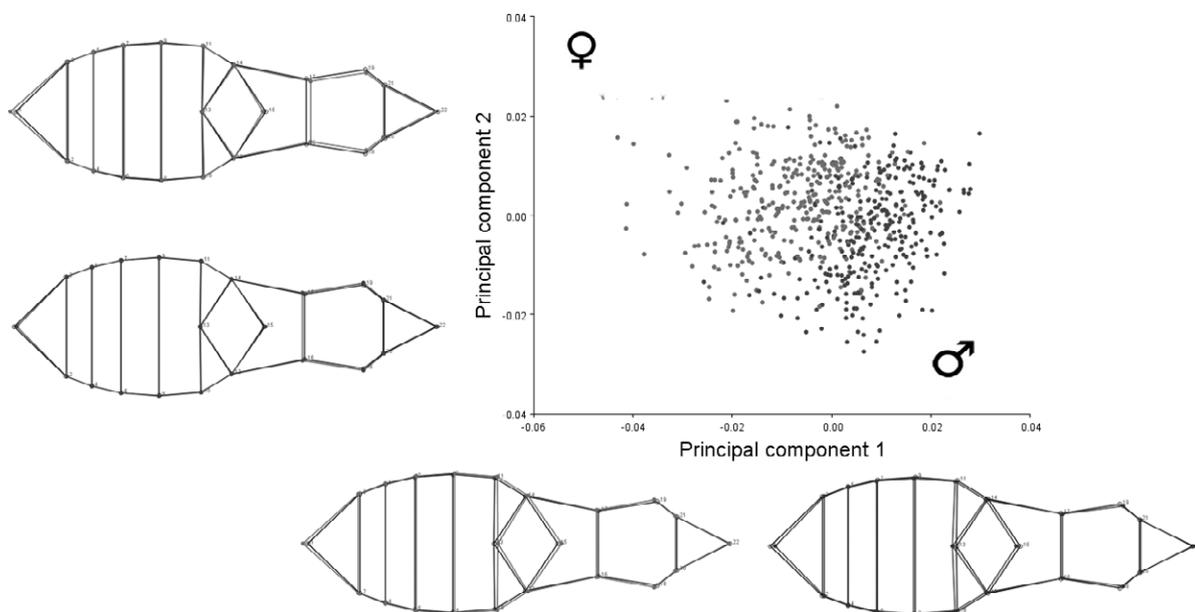
Fig. 2. Principal component analysis (PCA) showing the complete variation between male and females (symmetric component) in genus *Ceroglossus*. *Each point represents a shape variable for individuals of *Ceroglossus*; each grid is the main shape of PC1 and PC2 in ventral view.

some differences among the seven species analyzed. The first three PCs account for 53.48% (symmetric component: PC1 + PC2 + PC3= 27,678% + 15.56% + 10.25%) of the total shape variation and provide a reasonable approximation of the total amount of variation, with the other PC components, accounting each for no more than 8% of the variation. The first two PCs account for 72.08% (Asymmetric component PC1 + PC2 = 54.89% + 17.19%) of the total shape variation, and each of the other PCs accounts for no more than 8% of the variation (Fig. 2). However, to determine whether there were large differences in the eigenvalues, covariance matrices were developed per sex for each species and evaluated separately by means of PCAs, resulting in a maximum of 25% for the value of the first three eigenvalues (*C. darwinii* was the only exception with 34%) in each species (Fig. 3).

In the ventral view, the landmarks with greatest variation were numbers 4, 5, and 7, indicating that males have a less robust abdomen than females; this is related to a wider proepisternum in males and wider abdominal sternites in females. MANOVA tests, for both symmetric and asymmetric components confirm these results (sex: Pillay = 2.86, $P <$ 0.0001; species: Pillay = 0.71, $P < 0.0001$ and sex: Pillay = 0.64, $P < 0.0001$; species: Pillay = 0.09, $P < 0.0001$, respectively).

The morphological variability in the whole sample was analyzed and displayed with CVA analyses and determined by Procrustes distances (Table 3), being highly significant for assessing differences among species and sexual dimorphism.

The *Ceroglossus* species showed values of sex ratio between −0.039 and 0.703; however the species did not exhibit sex ratios greater than 2:1 (Table 1). The randomization approach of regression analysis indicated a positive relationship between minimal differentiation in centroid size between males and females (i.e., mean centroid size differences) and sex ratio ($P = 0.0055$; $r = 0.65$) (Fig. 4). This result is congruent with the distributions of shape for females and males and their positive correlation with sex ratio.

DISCUSSION

Our results show a positive relationship of the minimal male-female differentiation in geometric body size (i.e., mean centroid size differences) and sex ratio, which are consistent with the commonly observed pattern described in literature (e.g., Kumano et al., 2010; Wong-Muñoz et al., 2011). We propose that differences observed between sexes associated with the sex ratio are attributable to an energy cost (behavioural cost) caused by sexual
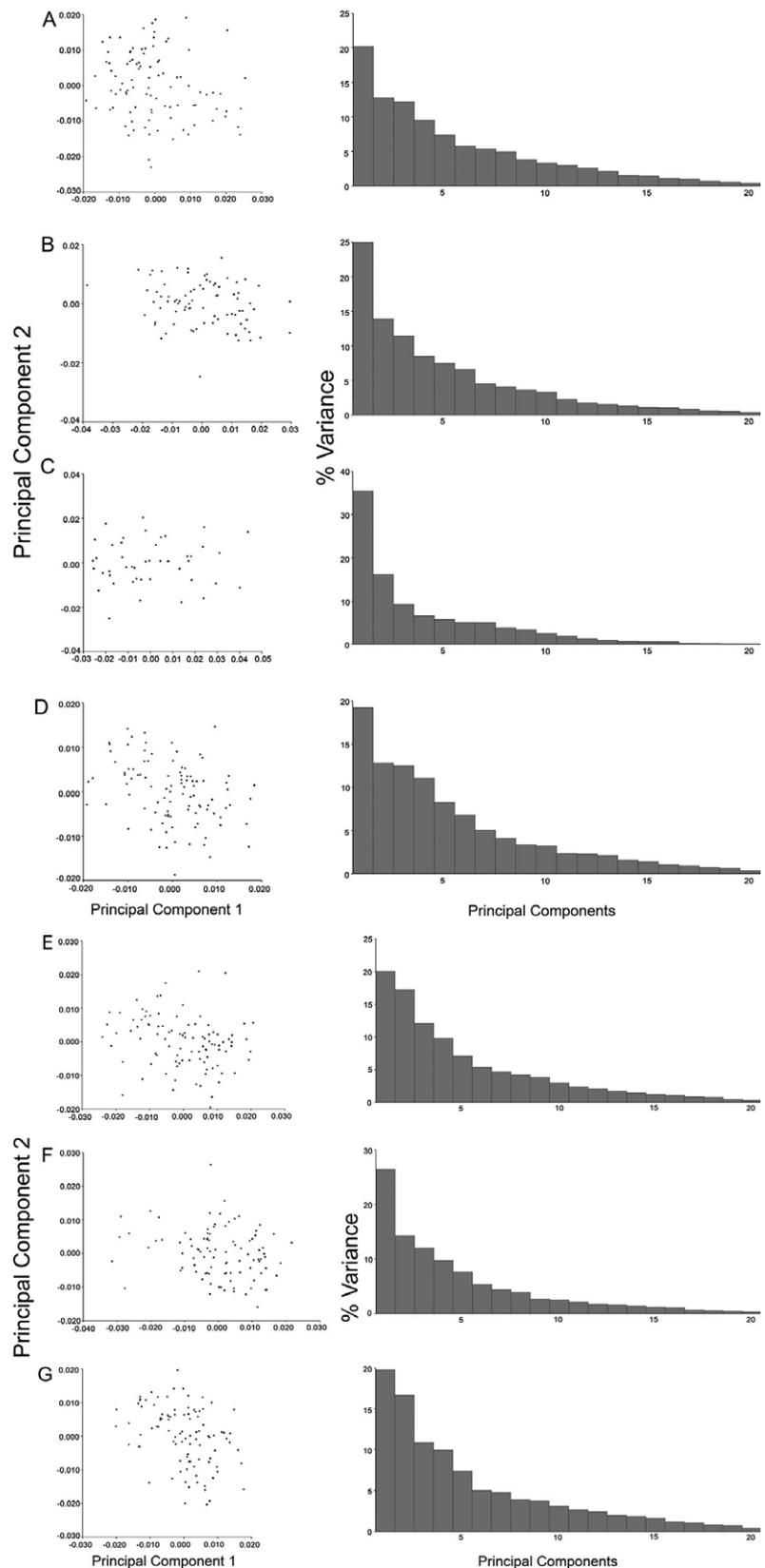
Fig. 3. Principal component analysis (PCA) (PC1 vs. PC2) and % variance of all principal components characterized by eigenvalues individually for each species. **(A)** *C. buqueti*, **(B)** *C. chilensis*, **(C)** *C. darwinii*, **(D)** *C. guerinii*, **(E)** *C. magellanicus*, **(F)** *C. ochsenii*, **(G)** *C. suturalis*. *Each point represents a shape variable for female and male individuals of *Ceroglossus* in ventral view.

Table 3. Pairwise comparisons by the canonical variate analysis performed among the seven species and sex. Results are reported as Procrustes distance, after 10,000 permutation runs *All *P* values were significant (< 0.001).

Species/Sex	C.buqu, f	C.buqu, m	C.chil, f	C.chil, m	C.darw, f	C.darw, m	C.guer, f	C.guer, m	C.mage, f	C.mage, m	C.ochs, f	C.ochs, m	C.sutu, f
C.buqu, m	0.0202												
C.chil, f	0.0207	0.0287											
C.chil, m	0.03	0.0238	0.0215										
C.darw, f	0.0234	0.0336	0.0151	0.0301									
C.darw, m	0.031	0.028	0.0262	0.0192	0.0272								
C.guer, f	0.0222	0.0167	0.0226	0.0184	0.028	0.0231							
C.guer, m	0.0309	0.0199	0.0337	0.0229	0.0363	0.0215	0.0155						
C.mage, f	0.0184	0.0235	0.0139	0.0202	0.0195	0.0229	0.0174	0.0248					
C.mage, m	0.0283	0.0206	0.0256	0.0115	0.0331	0.0196	0.0154	0.016	0.0188				
C.ochs, f	0.019	0.0209	0.0225	0.0251	0.0276	0.0288	0.0127	0.0222	0.0171	0.0211			
C.ochs, m	0.0274	0.0196	0.0325	0.0232	0.0365	0.0242	0.0167	0.0122	0.0237	0.016	0.0178		
C.sutu, f	0.0214	0.0207	0.028	0.0274	0.0322	0.0317	0.0142	0.0226	0.0229	0.0242	0.0126	0.0181	
C.sutu, m	0.0317	0.0228	0.039	0.0299	0.042	0.0299	0.0216	0.0143	0.0297	0.0227	0.0233	0.0106	0.019
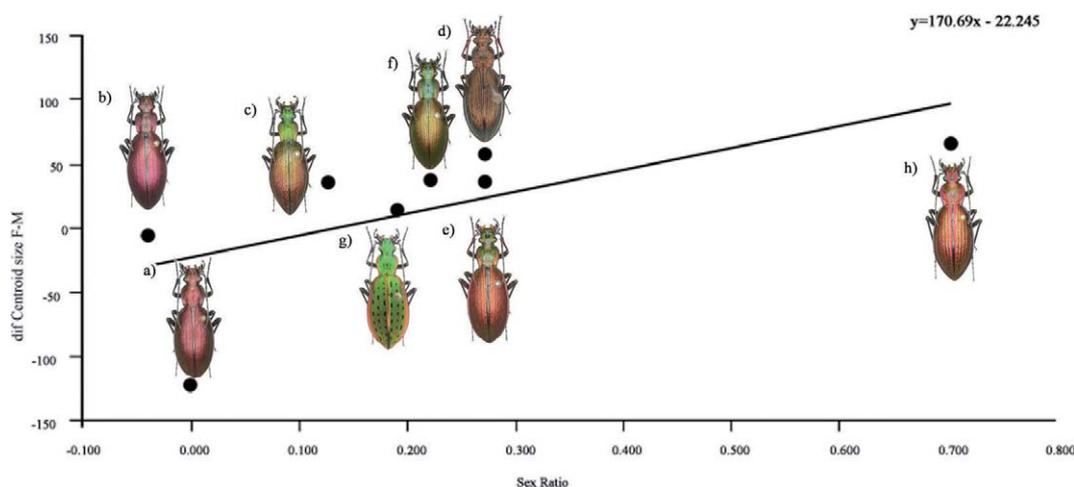
Fig. 4. Relationship between sex ratio and average centroid size differentiation F–M, for the eight species of genus *Ceroglossus*. a) *C. speciosus*, b) *C. magellanicus*, c) *C. buqueti*, d) *C. suturalis*, e) *C. guerinii*, f) *C. darwinii*, g) *C. ochsenii*, h) *C. chilensis*). The black line shows the standard linear regression fit to the data. The p-value is the result of randomization analysis (30,000 random matrices, random number seed = 12345) to test the null hypothesis that the slope is equal to 0.

selection. Nevertheless, since proportions are similar for all the species (i.e., < 1:2), it is not relevant to generate more conspicuous structures for stronger male-male competence, as is the case in other insects (e.g., Mockzeck and Emlen, 2000; Danforth, 1991; Emlen, 1997, 2008). In general, this relation was associated with different sizes, thus evaluation of the shape as a secondary character of dimorphism revealed that this attribute is directly correlated with the different types of sex ratio in these beetles, and potentially with sexual selection.

Sexual selection vs. sex ratio hypothesis

In the past few decades, a number of hypotheses have been proposed to explain sexual dimorphism in insects (Fairbairn, 1997; Wiklund and Forsberg, 1991; Walker and Rypstra, 2001; Esperk, 2007). The most solidly grounded hypothesis is the connection of sexual selection with natural selection, along with environmental variation, although male-male competition (Saito and Mori, 2005; Emlen, 2008), and the segregation of sexes due to limited resources (Saito & Mori, 2005) have produced notable selective differentiation.

Large males and pronounced forms often have advantages in male-male competition and female choice (Thornhill and Alcock, 1983). On the other hand, the fact that there are females larger than males and with elongated shape of the abdomen is suggestive of natural selection acting on female fecundity and being stronger than the action of sexual selection on males (Ridley, 1983; Wiklund and Karlsson, 1988).

In our results the proportion farthest from 1:1 was associated with more disparate body shapes, even though the entire group had minimum variation in sex ratio, which is a life history character of this group. The correlation between shape, species, and sex may be related to energetic costs in metabolic development, since when males are in greater proportion they require showier attributes to be chosen as partners by females (Wong-Muñoz et al., 2011). Species with similar proportions, such as *C. magellanicus* 49:51 (Table 1), either did not show significant differences, or the differences associated with centroid size were not very large (Table 2). However, a sexual shape dimorphism pattern can be observed, as in the other species (Fig. 3). Our hypothesis

is that since males and females have similar morphology, the chance of a sexual encounter is 50%. Field observations of the reproductive behavior of various species of *Ceroglossus* are consistent with the results presented here (Jaffrézic and Rataj, 2006). There were only matched couples between sexes, and the reproductive activities of the group were completely matched with no need for strong male-male competition. In such cases, the probability of a male having a sexual companion is almost 1; it is not necessary for males to generate showy sexual attributes, thus enabling them to avoid greater energetic cost. Another important character in this genus is that they are apterous, implying limited variability, which in turn is expected to limit the search for sexual partners (Lailvaux and Irschick, 2006). The evolutionary development of minimal variation in morphological attributes associated with shape appears to be directly associated with the capacity of organisms to avoid energetic loss in the generation of structures, and the incorporation of this energy in reproduction and better fitness (Emlen, 2001; Iguchi, 2006; Simmons and Emlen, 2008).

The use of geometric morphometrics plus multivariate statistical techniques provides a graphic visualization of the morphological variation of individuals. The correlation of morphological similarity with sex ratio appears to indicate the importance of the relation between corporal and reproductive development (similar shape/similar sex ratio), in both favorable and unfavorable situations. Finally, these differences between sexes raise many questions, such as how morphological variation and sexual dimorphism may be modulated behaviorally as a result of natural selection.

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