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Research paper

Assessing the influence of allometry on sexual and non-sexual traits: An example in *Cicindelidia trifasciata* (Coleoptera: Cicindelinae) using geometric morphometrics

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ABSTRACT

Based on a quantitative mathematical revolution, the study of morphology has had an important emphasis by developing statistical shape analysis. This made possible the combination of multivariate statistical methods and new ways to visualize a morphological structure. Patterns of allometry (shape influence on size) in sexual and non-sexual traits were examined in adults of *Cicindelidia trifasciata* Fabricius collected in north Chilean wetland, using geometric morphometric techniques. Abdomen, mandible and wing shapes were analyzed using 16, 12 and 19 morphological landmarks. Sexual and non-sexual traits differences were found after a principal component analysis, however, most of them were ascribable to sexual size dimorphism. A multivariate regression analysis of shape on size of the abdomen, mandible and wing shapes showed high levels of allometry in *C. trifasciata*. Static allometry in the sexual traits of *C. trifasciata* is a common pattern, being the size an important trait that plays an important role during the sexual selection in this species. These differences raise the question of whether sexual dimorphism of sexual traits may be modulated by natural selection.

1. Introduction

The subfamily Cicindelinae comprises almost 3000 known species (Zettel & Wiesner 2018), from which a big percentage inhabit the Neotropic, that is the second richest region worldwide after the Oriental region (Cassola & Pearson 2001; Roig-Juñent & Flores 2001). Its systematics has been thoroughly studied using morphological and molecular characters (Ball et al. 2011; Gough et al. 2019; Vogler and Pearson and Cassola 2005). The members of this group are those mainly used as biological indicators in conservation and biodiversity studies (Carroll & Pearson 1998; Pearson 1988; Pearson & Cassola 1992; Ricketts et al. 1999; Selness 1999).

In Chile, there are seven species distributed in four genera: *Picnochile* Motschoulsky, 1856; *Tetracha* Hope, 1838; *Cicindelidia* Rivalier, and *Cylindera* Westwood, 1831 (Wiesner, 1992). One of the members of the genus *Cicindelidia* is the species *Cicindelidia trifasciata* Fabricius, was recognized as the subspecies *peruviana* from Chile (Peña & Barría 1973) recorded in several localities of central Peru (Lima, Chorrillos and Chilca) (Mandl 1958, 1974).

Only a few descriptive studies have been conducted on Chilean adult Cicindelinae (Peña & Barría 1973; Varas Arangua 1921), their larval instars (Cekalovic 1981; Cekalovic & Reyes 1985) and there are no records about morphological variation regarding sexual dimorphism and even less information regarding the use of mathematical tool to analyze shape variation on the group.

In previous studies in insects, females are on average larger than males, resulting in an adaptive advantage for females that includes increased fecundity and parental care e.g. mole crickets (Forrest 1987); flower longhorns (Møller & Zamora-Muñoz 1997); and common fruit fly (Reeve & Fairbairn 1999). However, in some species males are longer in size but lightweight than females e.g. darkling beetle (Cepeda-Pizarro et al. 1996). No work has been performed on the quantitative evaluation of sexual shape dimorphism in Cicindelinae species or any of the other species existing in Chile or worldwide the only information about sexual shape

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dimorphism was reported in the genus *Ceroglossus* (Benítez et al., 2010a; Benítez et al., 2013a; Benítez et al., 2011; Benítez et al., 2013c; Benítez et al., 2010b). Nevertheless, other tiger beetle's species also have some studies that improve the combination of phylogeographical questions with DNA and morphological analysis to identify sexual dimorphism and geographical variation (Jaskuła et al. 2016).

Only few studies about sexual dimorphism on the genus *Cicindelidia* have been carried out. Kritsky and Simon (Kritsky & Simon 1995) used conventional morphometrics methods and found that male mandibles were generally smaller than those of females. *Cicindelidia nigrocoerulea* is the only species where males have longer mandibles. On the other hand, Jaskuła (2005) conducted biometric studies on *Cicindela hybrida hybrida*, concluding that females were larger (total body length) and wider (maximum elytron width) than males, whereas the right mandible length was bigger in males. Obviously, these methods of linear morphometrics do not generate a clear view of the morphological changes. In the last few years the revolution of the multivariate statistics and geometric morphometrics has facilitate for researcher the way to analyze the phenotype particularly for morphologically cryptic species (Zúniga-Reinoso & Benítez 2015). Geometric morphometrics can accurately quantify the shape and size of an insect organism rather than simply provide rudimentary measurements of mass and length (Adams & Funk 1997; Benítez et al. 2011; Benítez et al. 2010b; Bogdanović et al. 2009; Gidaszewski et al. 2009; Kaliontzopoulou et al. 2010; Lemic et al. 2014). This technique has been especially useful to quantify the differences in size and shape between sexes of a coleopteran species as demonstrated in many studies (Benítez et al. 2013c; Benítez et al. 2010b; Lemic et al. 2014; Lemic et al. 2016; Mikac et al. 2016; Nair et al. 2019; Vesović et al. 2019). Together with sexual dimorphism it is extremely important to also examine whether allometry (described as relationship of body size to shape, anatomy, physiology and finally behavior (Calder 1984; McMahon et al. 1983) contributes to the sexual dimorphism found. The following article aim to identify the influence of allometric variation on sexual shape dimorphism in the *C. trifasciata* in order to evaluate the relationship between shape variation and sex differentiation, based on sexual and non-sexual morphological traits.

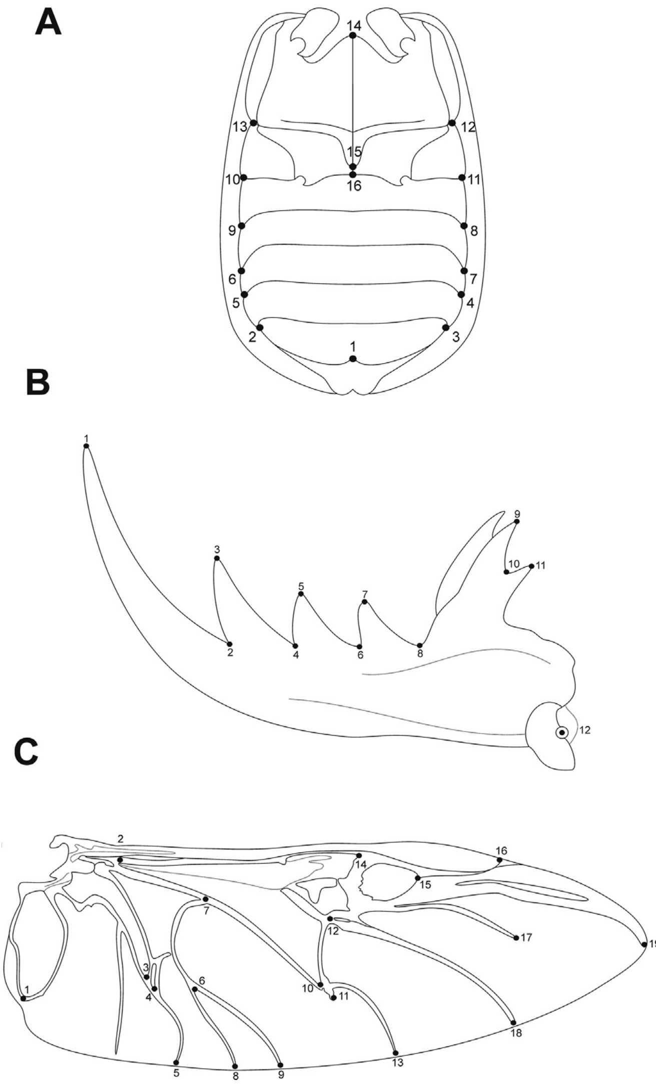

Fig. 1. Representation of morphological landmarks identified in the A- abdomen, B- mandible and C- hind wings of *Cicindelidia trifasciata*.

2. Materials and methods

2.1. Sampling

The study was conducted around the Lluta River wetland in the north of Chile near the border with Peru. The specimens were collected during the summer in 2018 in five different location across the Lluta River wetland. In order to not perturb the environment only 100 specimens of *C. trifasciata* (50 females and 50 males) were collected using interceptions nets. The sex was determined using the tarsal adhesive setae, which is located at the first three tarsal of the prothoracic tarsus of male (Pearson 1988; Stork 1980). The material collected was preserved in alcohol (70%) until processing. Sampled specimens were stored at the entomological collection from the Universidad de Tarapacá, Facultad de Ciencias Agronómicas Arica, Chile.

2.2. Morphometrics analyses

The specimens were analyzed using a two-dimensional morphometric approach. Ventral side of abdomen, mandible and wings of every specimen were photographed using a Sony DSC HX200V digital camera. Abdomen, mandible and wing shapes were taken using 16, 12 and 19 landmarks, respectively (Fig. 1). Landmarks were digitized using the software tpsDig2 (Rohlf 2013). In order to avoid problems withing the landmarking procedure a repetition of the landmarking process was conducted comparing in with the original landmarking process, combining these two datasets, a measurement error was calculated using a Procrustes ANOVA were the MS values of the individuals were compared with the error.

Geometric morphometric analyses were performed using MorphoJ software, version 1.06d (Klingenberg 2011). Shape information was extracted with a Procrustes fit analysis from all landmark configurations (Rohlf & Slice 1990). This superimposition method eliminates non-shape information caused by scale, orientation and size, by standardizing each specimen to a unit centroid size (Dryden & Mardia 1998). A Principal Component Analysis (PCA) based on the covariance matrix of the individual shape was performed in order to analyze shape space and shape raw variation (Jolliffe 2002). This result may be influenced by changes in size during development (allometry), therefore, in order to correct the results of the size influence a multivariate regression was performed in order to discard if the sexual shape influences are affected by allometry (Benítez et al. 2013b). Using the covariance matrix of the residual of the regression an additional PCA was performed to analyze the data out of the allometric effect.

3. Results

The measurement error was discarded from the data after the comparison of the three set of digitized landmarks, the results of the Procrustes ANOVA showing that the mean square for individual variation exceeded the error in the three datasets (Table 1).

The PCA calculated for the abdomen showed that the first three PCs accounted for 64,5% of the total shape variation (PC1 = 31,256%; PC2 = 21,158%; PC3 = 12,443%), for the mandible the shape variation was higher for the first three PCs accounting for the 68,11% (PC1 = 32,705%; PC2 = 21,649%; PC3 = 13,815%) at the contrary to these two traits the variation for the wing at the first three PCs was lower, accounting for the 46,1% of the wing shape variation (PC1 = 24,630%; PC2 = 12,822%; PC3 = 8686%). The scatterplot of variation for the three PCA's showed clear differences between sexual dimorphism at two of the three structures analyzed (Fig. 2A, C & D), nevertheless the variation showed a notorious influence by the centroid size of the first component of variation (allometric component).

In order to discard the allometric influence of the shape the multivariate regression showed for the abdomen and mandible an allometric influence of the 15,1% and 14,4% respectively (Fig. 3A and B) and for the wings the allometric influence was lower than the other structures with a shape predicted by size only in a 1,8% (Fig. 3C). Using the residual of the multivariate regression the PCA for the three structures showed a notorious variation where the influence of the allometry was principally involved and describe the sexual shape dimorphism (Fig. 2B, D, F).

4. Discussion

Sex based differences in *C. trifasciata* body shape were detected using geometric morphometric procedures. The following results confirmed the influence of allometry of sexual and non-sexual traits shape in *C. trifasciata*. The analyzed traits (mandible and abdomen: sexual; wings: non-sexual) shown high levels of allometry based shape dimorphism and confirm a highly sexual size dimorphism (SSD) product of the influence of centroid size. Several previous studies shown the allometry influence in sexual dimorphism in insects as an adaptive characteristic (Benítez et al. 2010b; Fairbairn 2013; Gidaszewski et al. 2009; Shingleton et al. 2007; Stern & Emlen 1999). For *C. trifasciata* this variation was particularly noticeable in the abdomen by the expansion of the landmark (LM) 1,2 and 3 where females had a wider abdomen shape than males, with particularly expanded and thick section of the abdominal shape. In the mandibles the main differentiation was located at the LM 9 and LM 10. The main difference was observed at the base of the mandible where wider and longer mandibles were present in males than in females. Also, the expansion of LM 5 and LM2 allow females a wider mandible than males have, which can be clearly related with predatory capacity of female sex. Finally, the wing shape analyses shown variation in between sexes, which occurs in longer wings in female than in males but significant differences in structural morphology were not observed. This species is well-known for its incredible dispersal flight capacity and has even been found on offshore oil platforms in the Gulf of Mexico and it seems that there are no differences between flight capabilities between sexes of this species.

It's generally known, larger females could have an advantage over smaller females, such as fecundity and parental care (Andersson 1994; Stillwell & Davidowitz 2010). In addition, the males of some species such as *C. hybrida hybrida* have larger jaws and a with greater distance between their bases, which means greater length between the ends of these organs when the jaws are fully open, which in turn allows them to catch and hold to larger females during mating (Jaskuła, 2005).

Sexual selection on males particularly due to fecundity selection on females are particularly the major sources of selection on the election of larger size organism (e.g. insects). Larger males' preference in sexual selection, is driven principally for insects by the mating success by male—male competition or the female choice and could be improved depending the groups by the nuptial gifts (Andersson 1994).

Those considerations suggest that inferring and quantifying sexual dimorphism require the tools that allows the correlation between shape and size, in order to quantify the relationship at the different traits specifically (Benítez et al. 2013a; Outomuro et al. 2016). Our results showed that the static allometry in the sexual traits of *C. trifasciata* is common pattern and the size is indeed a very important trait that plays an important role during the sexual selection in this species. Carabids particularly have a strong sexual selection that can be correlated with the population sex ratio (Benítez et al. 2013a). Nevertheless, sexual selection hypotheses, normally proposed to explain the dimorphism in insects do not consider if differences may be due to SSD or to allometric processes

Table 1
Measurement Error Procrustes ANOVA for both centroid size and shape of *Cicindelidia trifasciata*, Sums of squares (SS) and mean squares (MS) are in units of Procrustes distances (dimensionless). Abdomen (A), Mandible (M), Wing (W).

Centroid size					
Effect	SS	MS	df	F	P (param.)
Individual (A)	5,060,037	0,153,334	33	3,83	<.0001
Error 1 (A)	1,360,126	0,040,004	34		
Individual (M)	0,445,709	0,013,506	33	9,91	<.0001
Error 1 (M)	0,046,349	0,001363	34		
Individual (W)	37,782,851	1.144.935	33	6,66	<.0001
Error 1 (W)	5,847,098	0,171,973	34	0,17	1,0000

Shape							
Effect	SS	MS	df	F	P (param.)	Pillai tr.	P (param.)
Individual (A)	0,17,029,957	0,0001,843,069	924	5,33	<.0001	18,11	<0001
Error 1 (A)	0,03,290,319	3,45622E-05	952				
Individual (M)	0,06,492,717	9,83745E-05	660	4,94	<.0001	15,05	<.0001
Error 1 (M)	0,01,353,005	1,98971E-05	680				
Individual (W)	0,05,945,019	5,29859E-05	1122	3,01	<.0001	27,37	<.0001
Error 1 (W)	0,02,034,105	1,75961E-05	1156	0,8	10.000	6,95	10.000

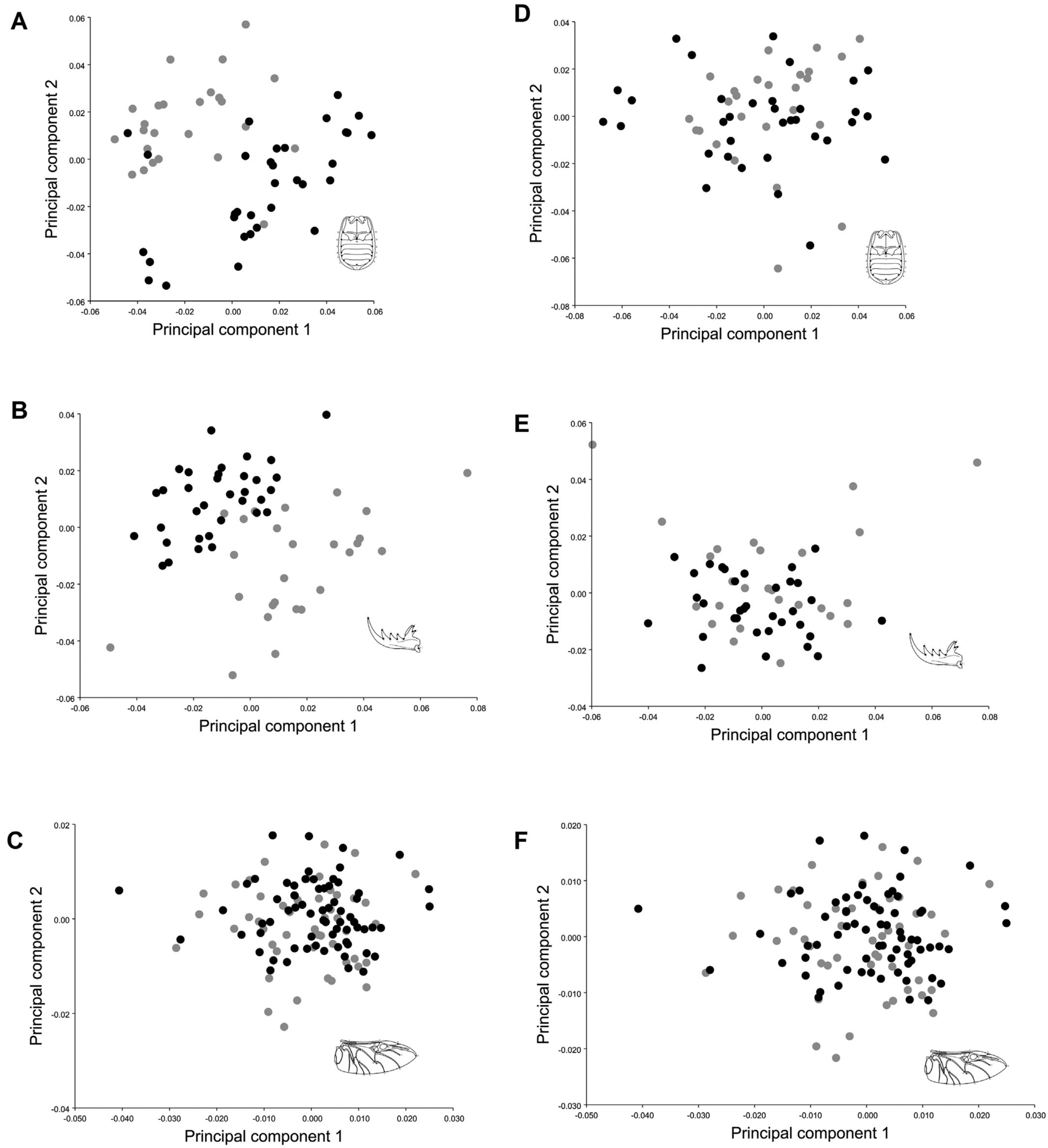

Fig. 2. Principal component analysis (PCA) showing the complete variation between male and females in *Cicindelidia trifasciata*. A: Abdomen with allometric effect, B: Abdomen corrected by size, C: Mandible with allometric effect, D: Mandible corrected by size, E: Wing with allometric effect, F: Wing corrected by size *Each point represents a shape variable for individuals *of Cicindelidia trifasciata*; black: Males purple: Females.

(Benítez et al. 2013b; Gidaszewski et al. 2009). Future work will focus on combining geometric morphometrics visualization of sexual traits to gain a better understanding of how *C. trifasciata* phenotypes have changed over space and time during evolutionally selection. Therefore, research suggests that geometric morphometrics techniques provides a powerful graphic visualization to detect slightly morphological variation providing the necessary detail to differentiate the sexual shape dimorphism in sexual and non-sexual traits in *C. trifasciata*. Abdomen and mandibles have shown clear sexual differences. There were no clear differences in wing shape as a trait, which is not surprise for species which does not use flying for courtship or searching places for laying eggs.

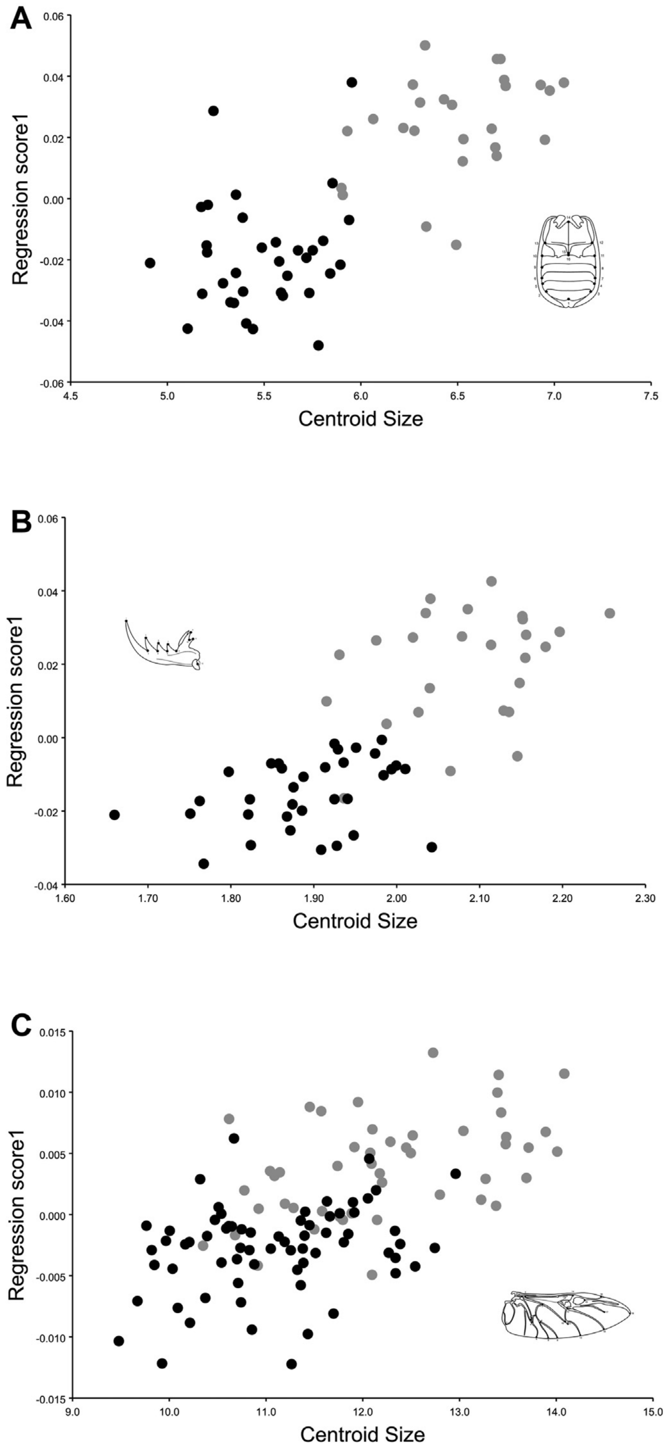

Fig. 3. Multivariate regression analysis of shape as a dependent variable (y-axis Regression scores 1) and size (x-axis centroid size) as an independent variable of the A: Abdomen, B: Mandible, C: Wing.

Finally, these differences raise the question of whether sexual dimorphism of sexual traits may be modulated by natural selection.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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