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Head morphology in three species of tiger beetles (Coleoptera: cicindelidae): a geometric morphometric study

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Abstract
Tiger beetles are one of the world's most studied groups of insects. They are similar in body shape and proportions and have a well-sclerotized head with large protruding eyes that make it wider than the pronotum. Despite body shape being a fundamental metric of animal diversity, the current state of detailed data on tiger beetles' external morphology needs to be improved. Geometric morphometrics is increasingly used in entomology, representing a powerful tool to capture subtle differences that can aid in taxonomic decisions. Broad literature data provide evidence for the effectiveness of geometric morphometrics in quantifying the differences in size and shape between the sexes in coleopteran species. In contrast, most of the available morphological studies on tiger beetles rely on traditional morphometrics. Here, we examined and compared the head morphology in three species of tiger beetles belonging to the genus *Calomera*, widely distributed in Turkey, using geometric morphometrics to reveal putative intra- and interspecific differences. While there remain many gaps in our understanding of the processes that contribute to shape differences in closely related species, our study is the first to demonstrate the existence of variations in head shape and size in Anatolian tiger beetles using geometric morphometrics. Additionally, our findings revealed significant differences in shape and size across all three studied species, also showing that head size significantly differs between males and females. This study aims to contribute to the discussion on interspecific and intersexual differences in cicindelids by proposing a methodological approach that could represent a valuable investigative tool.

Keywords: Calomera, *geometric morphometrics*, *head*, *tiger beetles*

Introduction

Tiger beetles (Coleoptera: Cicindelidae) are a large group within Adephaga encompassing about 2800 described species distributed around the globe, except Antarctica and isolated oceanic islands (Cassola & Pearson 2000; Pearson & Vogler 2001; Duran & Gough 2020). Tiger beetles have been historically considered a subfamily of Carabidae, known as Cicindelinae. However, since 2020, several studies have revealed that tiger beetles are a monophyletic clade sister to Carabidae, leading to their recognition as the family Cicindelidae (Duran & Gough 2020).

Although the larvae and adults have different lifestyles and distinct ecological niches, both are predators and share the same habitat preferences, being highly specialized (Jaskuła & Płóciennik 2020). These characteristics of wide distribution and high habitat specificity make cicindelids an excellent

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model in conservation biology (Cassola & Pearson 2000; Zhao et al. 2019; Jaskuła & Płóciennik 2020).

Although tiger beetles are one of the world's most studied groups of insects (Pearson 1988; Pearson & Vogler 2001, 2017), their taxonomy needs to be updated and fully clarified. Indeed, results from morphological and molecular data are often inconsistent (Vogler & Pearson 1996; Putchkov & Cassola 2005; Chou & Yeh 2019; Duran & Gough 2019; Beutel et al. 2020), and this is partially due to the use of a small number of morphological characters used to delineate these taxa (Laroche et al. 2023). The morphological traits commonly used for species delineation in tiger beetles include the colour and maculation patterns on their dorsal surface and the distribution of hairs on their head and body (Laroche et al. 2023). Body shape is a fundamental metric of animal diversity since similarities and differences in morphological traits may relate to gender, geographical location, phylogenetic relationship and ecological features (Lorenz et al. 2017). Still, the current state of detailed data on tiger beetles' external morphology needs to be improved.

Tiger beetles are often remarkably similar in body shape and proportions and have a well-sclerotized head with large protruding eyes that make it wider than the pronotum (Vogler & Pearson 1996; Pearson & Vogler 2001; Acciavatti 2011; Acal et al. 2024). The shape of the head is of taxonomic value and is a key character that differentiates tiger beetles from all other Adephaga (Pearson 1988; Pearson & Vogler 2001; Uniyal & Bhargav 2007; López-López & Vogler 2017; Assmann et al. 2018). However, despite its importance in classifying tiger beetles, head shape has not been thoroughly investigated.

For many years, traditional morphometrics has been applied to entomological investigations, and it is recognized as a valuable tool in systematics and taxonomy (Tatsuta et al. 2018; Csősz et al. 2021; Galindo-Malagón et al. 2022). With the emergence of sophisticated and powerful statistical tests, morphological analyses have transformed from being purely descriptive to incorporating quantitative methods over the years (Lorenz et al. 2017 and references therein). Geometric morphometric analysis is a method that focuses on comparing organisms by summarizing their morphological data both numerically and graphically. This approach enables the examination of relationships across multiple dimensions using multivariate techniques (Daly 1985; Lorenz et al. 2017). Broad literature data provide evidence for the effectiveness of geometric morphometrics in quantifying the differences in size and shape among coleopteran species (Benítez et al. 2010; Benitez et al. 2013; Lemic et al. 2014; Mikac et al. 2016). This method has also been effectively applied to study morphological variations, sexual dimorphism and phylogenetic relationships (Rodrigues et al. 2005; Dujardin et al. 2014; Lorenz et al. 2017).

In contrast, most of the available morphological studies on tiger beetles rely on traditional morphometrics (Kritsky & Simon 1995; Satoh et al. 2003; Franzen & Heinz 2005; Jaskuła 2005; Franzen 2007; Ball et al. 2011; Young 2015; Jaskuła et al. 2016), while only a few have been conducted using geometric morphometrics (Jones & Conner 2018; Doğan Sarıkaya et al. 2020; Espinoza-Donoso et al. 2020) leaving the potential of this analytical method highly underexploited. Additionally, cicindelids are the most thoroughly studied group of insects in terms of niche overlaps, with an extensive literature mainly focusing on microhabitat usage and the partitioning of foraging habitats (spatial, seasonal or temporal) (Hoback et al. 2000; Brosius & Higley 2013).

On these bases, here we investigated the head morphology in three species of tiger beetles belonging to the genus *Calomera* Motschulsky, 1862. The three considered species, *Calomera fischeri fischeri* (Adams, 1817), *Calomera littoralis mandli* (Mandl, 1967) and *Calomera caucasica* (Adams, 1817) are widely distributed in Turkey, especially in sparsely vegetated areas with open and sandy riverbanks (Cassola 1999; Franzen & Gebert 2003; Avgın 2006; Özgökçe et al. 2006; Avgın & Özdikmen 2007).

By performing landmark-based geometric morphometrics, we examined and compared head morphology to reveal putative interspecific differences. To the best of our knowledge, no previous study has investigated the morphological parameters of heads in these species.

The evolution of sexual size dimorphism (SSD) probably arises from adaptive advantages, which include greater fecundity and better parental care or increased mating success in female-biased and male-biased SSD, respectively (Stillwell et al. 2010 and references therein). Although there are large variations, species exhibiting female-biased SSD, which is the most common pattern among insects, tend to have females that are more sensitive to environmental conditions (Rohner et al. 2017 and references therein). Research on sexual dimorphism in cicindelids is scarce (Kritsky & Simon 1995; Jaskuła 2005; Jones & Conner 2018; Espinoza-Donoso et al. 2020; Doğan Sarıkaya et al. 2020; Jaskuła et al. 2021; da Silva et al. 2023; Acal et al. 2024), and for the genus *Calomera* in particular, only three reports are available (Jaskuła et al. 2016, 2019; Talarico et al. 2024).

Therefore, to determine whether there are significant differences between sexes, we also compared the shape and size of males and females in the selected species.

Materials and methods

Data collection and landmark digitizing

All specimens were collected by entomological hand net in May and August of 2016 from sparsely vegetated areas with open, sandy soils around Hirfanlı Dam Lake located at Kırşehir, Turkey, and then preserved in 70% ethanol (Figures 1, 2). Specimens of both sexes were identified by dissecting the genitalia. For each specimen, the head was observed and photographed under a stereomicroscope (Leica S6D) equipped with a camera (Leica MC 170 hD camera), and 12 landmarks on the head were digitized once for each image using TPSdig2.31 (Figure 3). The landmark coordinates of 90 specimens (16 females and 15 males of *Calomera caucasica*, 15 females and 16 males of *Calomera fischeri fischeri*, 15 females and 13 males of *Calomera littoralis mandli*) were used for the head shape analyses (Table I). Further analyses of landmark configurations were done using MophoJ v. 1.07a (Klingenberg 2011).

Geometric morphometrics and statistical analysis

Geometric morphometrics was used because it allows us both to analyse the shape differences with statistical approaches and to display the shape changes quantitatively, accurately and clearly (Rohlf & Marcus 1993). First, generalized Procrustes analysis (GPA) superimposed the specimens into a common coordinate system and mathematically eliminated the effects of digitizing position, orientation and scale (Rohlf & Slice 1990). To compare the size both between the sexes and among taxa, the centroid size (CS) (square root of the sum of the square distances between each landmark and the centroid) (Bookstein 1986) was computed. CS is the measure of size used almost universally in geometric morphometrics (Klingenberg 2016).

Figure 1. Photographs of three species of *Calomera* and sandy shorelines of Hirfanlı Dam Lake. (a) *Calomera fischeri fischeri*, (b) *Calomera caucasica*, (c) *Calomera littoralis mandli* (photos by Y. Koçak).

Figure 2. Hirfanlı Dam Lake in Kırşehir Province, Turkey (satellite image from: https://www.google.it/earth/).

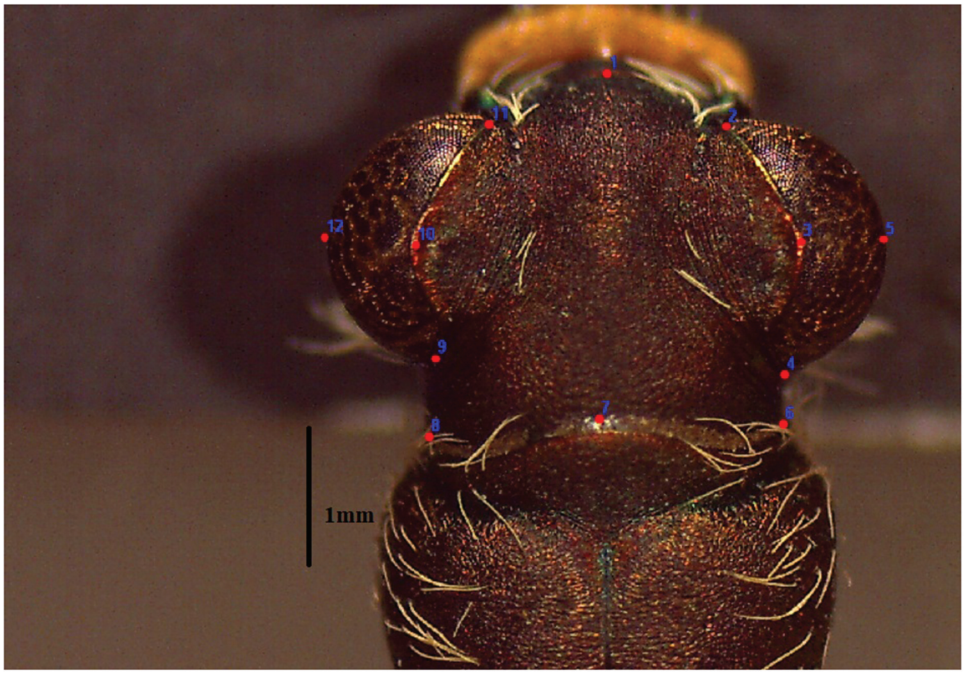

Figure 3. Dorsal views of the landmarks used to define the shape of head (see Table I).

A two-way analysis of variance (ANOVA) using CS as a dependent variable was performed to determine the size differences among taxa and between sexes. To reduce the data, a principal component analysis (PCA) using the covariance matrix of the Procrustes shape coordinates was conducted. Multivariate analysis of variance (MANOVA) was performed using the Procrustes coordinate (PrC)

Table I. Morphological landmarks.

Landmark	Description
1	The centre of the anterior margin of the clypeus
2	Anteriormost point of the right eye
3	Leftmost point at maximum width of the right eye
4	Posteriormost point of the right eye
5	Rightmost point at maximum width of the right eye
6	The intersection of the pronotum with the right posterior of the head
7	Centre of the posterior part of the head (left)
8	The intersection of the pronotum with the left posterior of the head
9	Posteriormost point of the left eye
10	Rightmost point at maximum width of the left eye
11	Anteriormost point of the left eye
12	Leftmost point at maximum width of the left eye

scores as shape variables to test sexual dimorphism and the significance of shape differences among taxa. In order to calculate and eliminate the effect of size on shape, multivariate regression was performed using the PrC as a dependent variable and CS as an independent variable. The residuals of this regression were used as size-corrected shape variables for further analyses (Fruciano 2016; Klingenberg 2016).

Canonical variate analysis (CVA) was employed to statistically test shape differences between sexes and among taxa and for graphical illustrations of results. A permutation test was applied for pairwise distances − 10,000 iterations to obtain Procrustes distance and their statistical significance. Finally, jackknife cross-validation procedures were carried out with PAST3.0 (Hammer et al. 2001) software to calculate an unbiased estimation of classification success. The ANOVA and MANOVA were performed using IBM SPSS 25, and all other analyses were performed using the MorphoJ software version 1.07a (Klingenberg 2011).

Results

A two-way ANOVA of mean centroid sizes indicated significant variations in head size among taxa ($F_{taxa} = 105.18$, $p = 0.000$) and a significant SSD ($F_{sex} = 67.99$, $p = 0.000$). The interaction between these two factors was found to be negligible ($F_{interaction} = 2.23$, $p = .114$). Additionally, females were generally larger than males, and the distribution of their sizes was more variable than that of males (Figure 4).

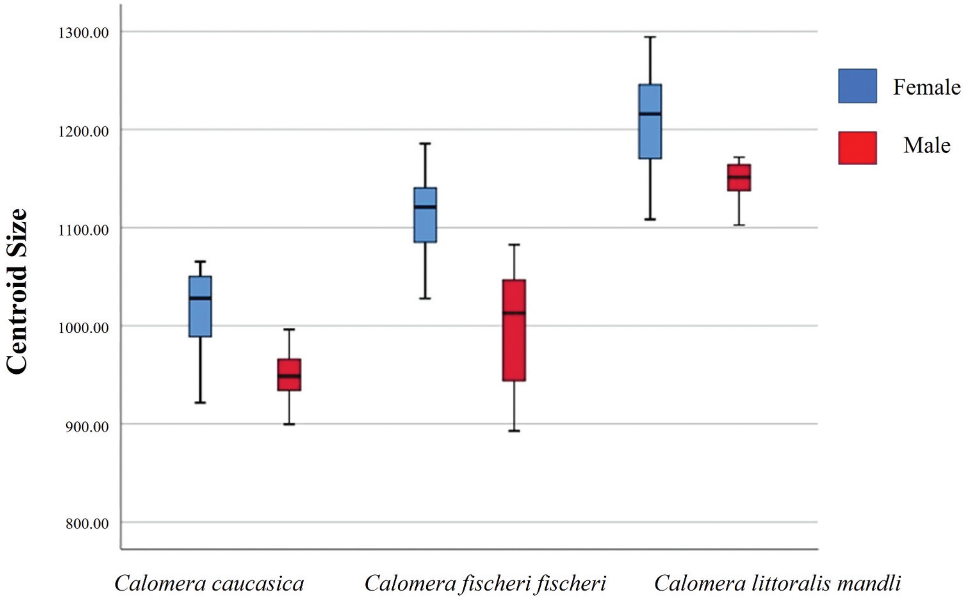

Figure 4. Box plot of centroid size of the head for three species.

According to the PCA, the first two principal components account for 55.76% of the total variance, with PC1 and PC2 explaining 40.21% and 15.55%, respectively. A minimum of 10 components was necessary to explain more than 90% of the shape variation; therefore, 10 principal components were utilized as shape variables for the MANOVA. The MANOVA procedure revealed significant differences regarding head shape among taxa and between sexes (for taxa: Pillai's trace = 0.815, F = 5.23, $p < 0.001$; for sex: Pillai's trace = 0.507, F = 7.71, $p < 0.001$). The interaction between these two effects was negligible (Pillai's trace = 0.337, F = 1.54, $p = 0.076$).

A multivariate regression analysis examining the relationship between shape and size, in which size correction was based on pooled within-group regression, showed a significant correlation between head size and shape. Specifically, size accounted for 5.24% of the variation in shape ($p < 0.0001$). The residuals from this multivariate regression were used as size-corrected shape variables for subsequent analyses (see Figure 5).

The CVA plot demonstrated a clear separation among different taxa; however, there was no evidence of sexual dimorphism with regard to head shape (Figure 6). The first two canonical variates (CVs) accounted for 89.58% of the total shape variation, with CV1 explaining 80.95% and CV2 explaining 8.63%. Additionally, the jackknifed cross-validated correct classification percentage among taxa for head shape was 87.78% (87% for *C. caucasica*, 84% for *C. fischeri fischeri* and 93% for *C. littoralis mandli*). Three major clusters were obtained: *C. caucasica*, *C. fischeri fischeri*, and *C. littoralis mandli* were clearly separated from each other by the first canonical axis. CV1 shows that *C. caucasica* was on the negative side, while *C. littoralis mandli* was on the positive side, and *C. fischeri fischeri* was in the middle of the CVA plot. In contrast to the clear discrimination among species, there was some overlap between females and males within the same taxon.

Moreover, wire-frame graphs (Figure 6) indicated that the head shape of *C. littoralis mandli*, characterized by a more pointed anterior part and a concave posterior part, is narrower than that of the other species. However, the head shape of *C. caucasica*, with a more flattened anterior part and convex posterior part, is wider than that of the others. Additionally, *C. littoralis mandli* has the largest eyes, while *C. caucasica* has the smallest. Nevertheless, once the Procrustes distances were compared with the permutation test, statistically significant differences were found between pairwise comparisons of shape variation among species, but the difference between sexes of the same species was not statistically significant (Table II).

Discussion

Geometric morphometrics is a well-recognized analytical method widely employed to address issues

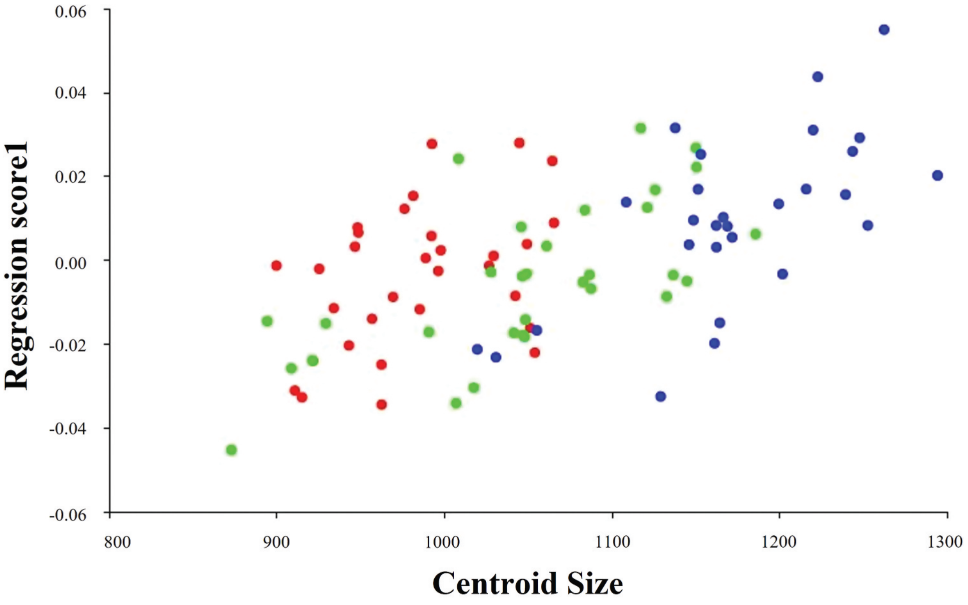

Figure 5. Multivariate regression analysis of shape as a dependent variable (y-axis regression scores 1) and size (x-axis centroid size) as an independent variable. The red points represent *C. caucasica* specimens, green points represent *C. fischeri fischeri* specimens and blue points represent *C. littoralis mandli* specimens.

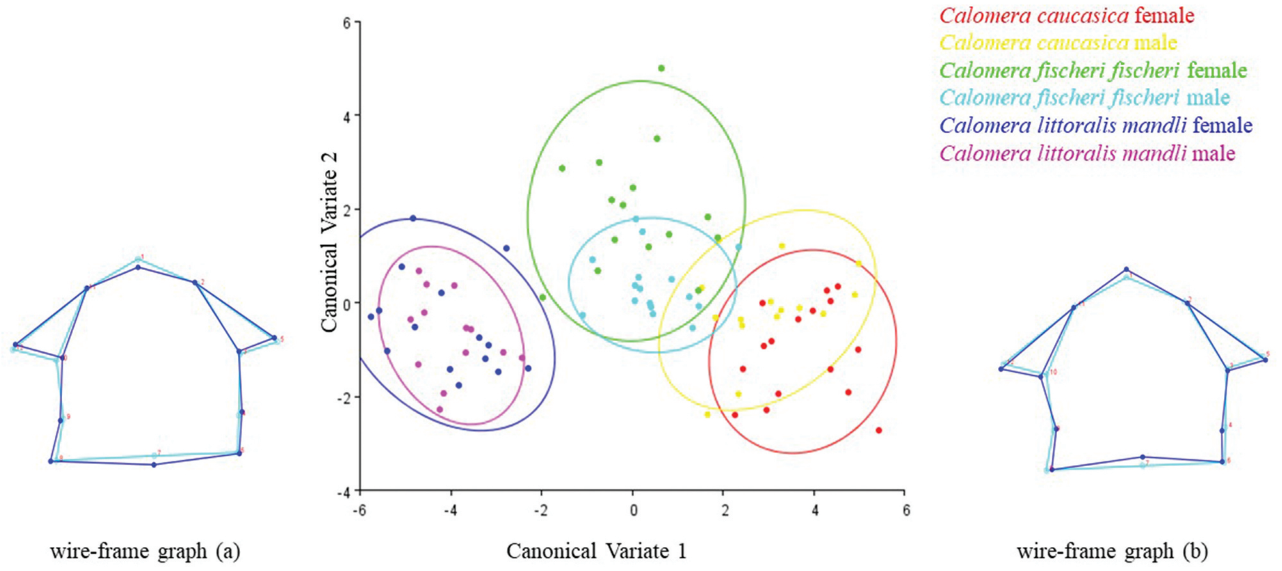

Figure 6. Canonical variate analysis and wire-frame graphs.

Table II. Procrustes distances and *p* values (upper and lower diagonal, respectively) from permutation tests (10,000 permutation rounds) for sex and species (*<0.05).

	C. caucasica female	*C. caucasica* male	*C. fischeri fischeri* female	*C. fischeri fischeri* male	*C. littoralis mandli* female	*C. littoralis mandli* male
C. caucasica female		0.0202	0.0369	0.0317	0.0709	0.0762
C. caucasica male	0.1695		0.0390	0.0295	0.0654	0.0682
C. fischeri fischeri female	0.001*	0.0004*		0.0205	0.0627	0.0723
C. fischeri fischeri male	<.0001*	0.0023*	0.1329		0.0540	0.0623
C. littoralis mandli female	<.0001*	<.0001*	<.0001*	<.0001*		0.0189
C. littoralis mandli male	<.0001*	<.0001*	<.0001*	<.0001*	0.3836	

where morphology plays a crucial role (Toro et al. 2010; Adams et al. 2013). Additionally, the metric features of the head have been effectively analysed in various beetle groups, including tiger beetles (Tatsuta et al. 2018). Our study presents the first geometric morphometric analysis of the heads in adult tiger beetles from three congener species to capture subtle differences that traditional morphometric comparisons often overlook.

Interspecific differences

Tiger beetle species, despite their varying sizes, often exhibit remarkable similarities in body shape and proportions worldwide (Pearson & Cassola 1992; Hudgins et al. 2011). Unsurprisingly, the three species investigated in this research did not exhibit any apparent differences in their body configurations or, more specifically, in the shape of their heads. In contrast, we revealed significant interspecific differences in head size and shape among congener taxa through landmark-based geometric morphometrics analysis. *Calomera littoralis mandli* is the species with the largest head, while *C. caucasica* has the smallest head. The observed divergences in shape between the taxa cannot be explained by allometrics since a very low correlation between size and shape was found in the regression analysis.

The morphological divergence between sympatric closely related tiger beetle species may be linked to different resource use due to ecological niche differentiation (Pearson & Stemberger 1980; Chou & Yeh 2019). While rare for insects, the divergence of characters has been regularly observed in tiger beetles and has been well investigated, with particular emphasis on microhabitats and the partitioning of foraging habitats (Pearson & Stemberger 1980; Brosius & Higley 2013). Interestingly, broad niche overlap has been evidenced within the complex of co-occurring species, especially those restricted to saline habitats (Hoback et al. 2000; Brosius & Higley 2013). The head morphology of tiger beetles is associated with several ecologically relevant characteristics, including predatory behaviour (Vesović et al. 2019; Budečević et al. 2021; da Silva et al. 2023). In our research, we analysed three species inhabiting the same area that can easily occur in the same saline habitat simultaneously (Price 1972), allowing us to suppose that observed morphological divergence would be related to an asymmetry of resource use. Besides, these results are in agreement with our previous observations on differentiated eye morphology in the same species (Talarico et al. 2024).

Sexual dimorphism

Body size is often the most obvious morphological trait that differentiates males from females in animals, even if both the direction and magnitude of SSD vary considerably among taxa (Gannon & Rácz 2006; Stillwell et al. 2010). In insects, however, the vast majority of species show a female-biased SSD (Shine 1988; Talarico et al. 2007; Rudoy & Ribera 2017; Espinoza-Donoso et al. 2020). This also applies to tiger beetles, including the species analysed in this study (*C. fischeri fischeri*, *C. littoralis mandli*, and *C. caucasica*), where females are larger than males (Kritsky & Simon 1995; Pearson & Vogler 2001; Jaskuła 2005; Talarico et al. 2024).

Our findings clearly indicated that head size significantly differed between males and females across all three studied species, with females having larger heads; in contrast, no differences were observed in head shape. According to previous studies on tiger beetles, sexual dimorphism in head size may reflect differences in body size between males and females, which in turn represent important morphological traits due to their potential role in predation. It should be noted that the size of the prey is a crucial parameter for a predator, regardless of sex, since it determines the energy available for future activities (Teder & Tammaru 2005; Rewicz & Jaskuła 2018). This consideration becomes especially important for female predators as the energy demand is greater in females, since they allocate a large amount to oviposition site choice, egg production and development (Brosius & Higley 2013; Rewicz & Jaskuła 2018; Talarico et al. 2024).

Furthermore, a larger head is required to accommodate the large eyes. As suggested for other insect groups, in females of tiger beetles, finding an optimal oviposition site seems primarily a visually guided task (Bentley & Day 1989; Sumba et al. 2004; Navarro-Silva et al. 2009; Purse & Thompson 2009; Bawin et al. 2014; Raitanen et al. 2014; Cury et al. 2019; Elsensohn et al. 2021). Accordingly, we recently showed, in the same three species considered here, that females display a significantly greater eye distance, thus suggesting that head size dimorphism would be related to one or more tasks (Talarico et al. 2024).

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Compliance with ethical standards

All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

Data availability statement

Data analysed in this study are available from the corresponding author upon reasonable request.

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