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# When size and shape matter: morphometric characterization of two sympatric dragonflies of the genus *Perithemis* Hagen 1861 (Odonata: Libellulidae)

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**Abstract:** *Perithemis mooma*, Kirby, 1889 and *Perithemis icteroptera* (Selys in Sagra, 1857) live in sympatry from southern Brazil to central Argentina. The taxonomy of the genus *Perithemis* Hagen, 1861 has been hampered by the use of characters that are highly variable or show slight differences among species. Our objective was to assess the efficiency of traditional morphometrics (TM) and geometric morphometrics (GM) to discriminate between these species using wing size and shape and vulvar lamina contour, and to analyze the presence of sexual dimorphism in wing size and shape in both species. The TM and landmark-GM methods were applied on the fore and hind wings, while the outline-based GM method was applied on the vulvar lamina. GM allowed species delimitation using shape variables of either wing. The wing and vulvar lamina shapes were confirmed to be good diagnostic characters to separate these species and appear to be promising tools for distinguishing among other species of this genus. Centroid size failed to achieve species separation. Both species exhibited sexual size dimorphism (SSD). In contrast to what would be expected for *Perithemis* whose males are strongly territorial, *P. icteroptera* and *P. mooma* showed female-biased SSD suggesting a common pattern in *Perithemis*.

**Key words:** Anisoptera, dragonflies, sexual dimorphism, specific delimitation, vulvar lamina, wing morphometry.

## INTRODUCTION

The order Odonata, comprising about 6400 described species (Paulson et al. 2022), is divided into the suborders Anisoptera (i.e. dragonflies), Zygoptera (i.e. damselflies) and Anisozigoptera (genus *Epiophlebia* from Asia). The adults are associated with aquatic environments and females lay eggs in the water, where larvae develop (von-Ellenrieder & Garrison 2008). The genus *Perithemis* Hagen, 1861 (Anisoptera: Libellulidae) is composed of 14 species widely distributed in the Neotropical Region (Costa et al. 2006). Traditionally, the systematic study of *Perithemis* has been based on the use of characters (*e.g.* color pattern of wings and thorax, number of wing veins) that are highly variable and do not allow species discrimination (Ris 1910, 1930). In the earlier taxonomic studies of the genus, some authors (*e.g.* Hagen 1861, Calvert 1907, Ris 1910) erroneously considered variations in color or color patterns as specific characters. In the revision of *Perithemis*, Ris (1930) mainly used wing venation (*e.g.* presence/absence of cross-veins in the triangles and of both pairs of wings) and wing color pattern. von-Ellenrieder & Muzón (1999) considered that these characters were uninformative and proposed to use traits from the male secondary genitalia (e.

g. anterior hamuli and vesica spermalis) and female vulvar lamina as diagnostic characters, but these structures show slight differences between species.

Traditional morphometric (TM) studies generally involve the analysis of linear and areal (*e.g.* wing area) measurements, providing information on the size rather than on the shape of objects. TM is also used to assess the relationship between linear variables (*e.g.* body length/width ratio) considered as shape indicators despite being poorly informative (Tatsuta et al. 2018). The basic concepts of morphometry, size and shape, were differentiated by Kendall (1977), who defined the latter as "all geometric information that remains when location, scale, and rotational effects are filtered out from an object". Some decades later, this definition gave rise to geometric morphometrics (GM), which was used to overcome the mentioned weakness of TM (Adams et al. 2004). GM allows visualization of shape changes while disregarding size and quantifies the shape in numeric variables (Bookstein 1996) that are used for statistical analysis. The wings of insects are particularly suited for geometric morphometric analysis (*e.g.* Lorenz et al. 2017) because they are flat structures that can be treated with biological realism in only two dimensions (Mamat et al. 2021). Moreover, wing venation provides many well-defined landmarks (*e.g.* vein junctions) allowing easy reproducibility. In Odonata, wings have been used in studies dealing with phylogeny (Kiyoshi & Hikida 2012, Huang et al. 2020), taxonomy (Stewart & Vodopich 2018, Mamat et al. 2021) and sexual dimorphism (Gallesi et al. 2015). The vulvar lamina can also be subjected to geometric morphometrics owing to its flat plate-like shape. This structure lacks identifiable landmarks and therefore the contour analysis (Kuhl & Giardina 1982) using the Elliptical Fourier analysis (EFA) is the most appropriate analytic method (Tatsuta et al. 2018).

Several studies in the genus *Perithemis* have addressed behaviors linked to sexual dimorphism, such as male-male competition (Switzer & Eason 2000, Switzer 2004, Silva-Pinto et al. 2013), habitat selection (De-Marco & Resende 2004), courtship and selection of oviposition sites (Wildermuth 1991, 1992). According to Outomuro et al. (2021), wing size is generally highly correlated with body size.

*Perithemis mooma* Kirby, 1889 and *P. icteroptera* (Selys in Sagra, 1857) which live in sympatry from southern Brazil to central Argentina are morphologically similar. The presence of sexual dimorphism in the shape and size of their fore and hind wings has not been investigated yet. The objective of the present study was to assess the efficiency of TM and GM to discriminate between *P. mooma* and *P. icteroptera* using wing size and shape and vulvar lamina contour, and to analyze the presence of sexual dimorphism in wing size and shape in both species using TM and GM.

## MATERIALS AND METHODS

In this study we did not consider the synonymy between *Perithemis tenera* (Say, 1840) and *Perithemis mooma*, Kirby, 1889 proposed by Paulson (2020).

**Traditional morphometrics of wings.** Three linear distances were measured from the fore and hind wings: maximum length (ML), maximum width (MW) and pterostigma length (PL); in addition, the pterostigma area (PA) was calculated (Table I). All measurements were standardized and Permutational Multivariate Analysis of Variance (PERMANOVA) with 10,000 permutations was performed to test for differences among the four groups (species and sexes) followed by *a posteriori* Bonferroni

**Table I. Analysis of fore and hind wing measurements between sexes for each wing and studied species.**

| | **Fore wing** | | | | | | |
|---|---|---|---|---|---|---|---|
| | ***Perithemis mooma*** | | | | ***Perithemis icteroptera*** | | |
| | **Mean (SD)** | | **p-value** | | **Mean (SD)** | | **p-value** |
| Measurements | Males | Females | (**) | | Males | Females | (**) |
| ML | 17.92 (0.81) | 19.14 (1.15) | ** | | 18.08 (0.56) | 19.30 (0.77) | ** |
| MW | 4.76 (0.22) | 5.18 (0.29) | ** | | 4.97 (0.20) | 5.29 (0.26) | ** |
| PL | 2.24 (0.16) | 2.50 (0.18) | ** | | 2.00 (0.13) | 2.39 (0.13) | ** |
| PA | 1.10 (0.1) | 1.30 (0.20) | ** | | 1.10 (0.1) | 1.20 (0.10) | ** |
| | Hind wing | | | | | | |
| | Males | Females | (**) | | Males | Females | (**) |
| ML | 17.56 (0.72) | 18.32 (1.37) | ** | | 17.03 (0.51) | 18.51 (0.69) | ** |
| MW | 5.73 (0.27) | 6.41 (0.44) | ** | | 6.58 (0.24) | 7.07 (0.29) | ** |
| PL | 2.42 (0.17) | 2.68 (0.23) | ** | | 2.27 (0.14) | 2.64 (0.18) | ** |
| PA | 1.20 (0.10) | 1.50 (0.20) | ** | | 1.30 (0.1) | 1.50 (0.10) | ** |

**Standard deviation (SD); maximum length (ML); maximum width (MW); pterostigma length (PL), pterostigma area (PA). Linear measurements in mm and pterostigma area in mm$^2$. (**) p < 0.01, Bonferroni test for multivariate analysis. ** p < 0.01, Mann-Whitney U test.**

tests. A discriminant analysis was conducted to determine the discriminating power of the measurements used here, and the percentage of correct classification was calculated using the jackknife procedure. For each species, non-parametric Mann–Whitney U tests were used to test for differences in each variable between sexes, for fore and hind wings separately. Statistical analyses were performed for each wing using PAST 3.22.

## Geometric morphometric approach

**Wing shape analysis.** We used a landmark-based GM technique on the left fore and hind wings of 30 males and 30 females of *P. mooma* and 30 males and 27 females of *P. icteroptera*. The wings were removed, mounted on a slide and then photographed with a Canon PowerShot SX500 IS digital camera. Cartesian coordinates of 15 landmarks from each wing (Fig. 1) were digitized from the images using tps-UTILS v. 1.38 and tps-DIG v. 2.05 (Rohlf 2015). We selected as landmarks (Fig. 1a, b) points that were found in all specimens (homologous points). Landmark configurations were scaled, translated, and rotated using the generalized least-squares (GLS) Procrustes superimposition method (Bookstein 1996). Subsequently, a thin-plate spline analysis was performed to visualize shape differences as deformation grids from consensus configurations. Permutation tests (10,000 permutation rounds) were performed for Mahalanobis and Procrustes distances among species and sexes. Shape variables were subjected to canonical variate analysis (CVA). The percentage of correct classification was calculated by linear discriminant analysis (LDA) and jackknife procedure. All these analyses were carried out using the statistical softwares MorphoJ (Klingenberg 2011) and PAST 3.22 (Hammer et al. 2001).

**Wing size analysis.** Centroid size (CS) was used as an isometric size estimator. It was computed as the square root of the sum of squared distances from all landmarks to the centroid of the landmarks configuration

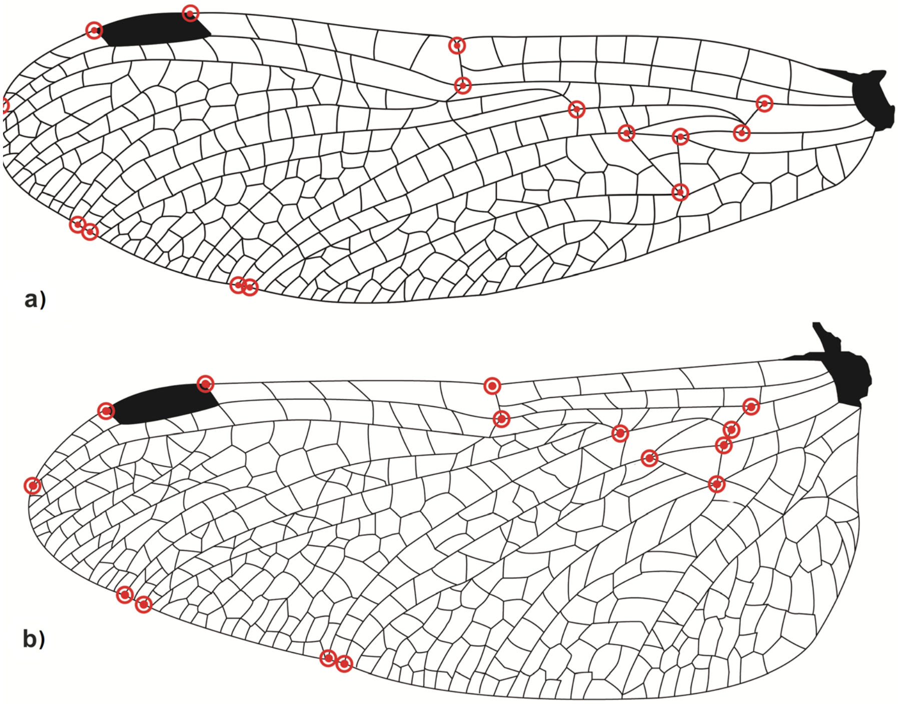

**Figure 1.** Location of the landmarks in the wings. **a)** in fore and **b)** in hind wings.

(Bookstein 1996). Differences in CS among species and sexes were assessed through a Kruskal-Wallis test followed by *a posteriori* Bonferroni tests. Statistical analyses were performed for each wing separately, using PAST 3.22.

**Outline analysis of the vulvar lamina.** The shape of the vulvar lamina was analyzed in 25 and 21 females of *P. mooma* and *P. icteroptera*, respectively. Only specimens with intact vulvar laminae were used. The sterna of segments 8-10 were dissected and the sclerites were treated with a 10% NaOH solution to remove soft tissue remains. Then, they were rinsed with water and placed on a slide with glycerine to avoid structural deformation. The vulvar lamina was stained with aceto-carmine for enhancing image contrast. Two images were taken *per* vulvar lamina to minimize position error. Images were converted to black and white (binary) images for contour detection. The parameters that best defined the shape of the vulvar lamina were calculated using Elliptical Fourier Analysis (EFA) (Tatsuta et al. 2018) and analyzed using SHAPE software (Iwata & Ukai 2002). The protocol included the extraction of the contour, the calculation and derivation of the normalized elliptical Fourier coefficient, and the determination of the principal component, which summarizes the information contained by the coefficients. Finally, the graphs of the mean shapes of the vulvar lamina were obtained by applying the inverse Fourier transform. The contours were processed and converted into a chain code containing geometric information on shape. The shape was then reconstructed by 7 harmonics. Fourier coefficients were standardized based on the ellipse of the first harmonics. They were considered as a set of transformed variables and used in Principal Component Analysis (PCA).

## RESULTS

**Traditional morphometrics of wings.** The results of the measurements are listed in Table I. PERMANOVA showed significant differences in hind wing shape among the four groups with 97% of correct classification. However, the difference in the fore wing between females of the two species was not significant. In a univariate framework, significant differences were found only in maximum width ($p < 0.05$) and pterostigma length ($p < 0.05$) of hind wings between species but with overlapping distributions, thus hindering species differentiation. Table I shows the presence of SSD in both species and wings. Female-biased SSD was observed in all measurements.

## Geometric morphometric approach

**Wing shape analysis.** The plots of the Canonical Variate Analysis (CVA) clearly show that the shapes of the wings of *P. mooma* and *P. icteroptera* occupy different morphospaces, both for the fore (Fig. 2a) and hind (Fig. 3a) wings. In addition, both species showed sexual dimorphism in the shape of fore and hind wings (Figs. 2a, 3a, respectively). The first axis (CV1) discriminates between species and the second axis between sexes (CV2). Partial deformations of the fore (Fig. 2b, c) and hind (Fig. 3b, c) wings represent changes in wing shape between species (CV1) and sexes (CV2). There were significant differences ($p < 0.05$) in the shape of fore and hind wings among

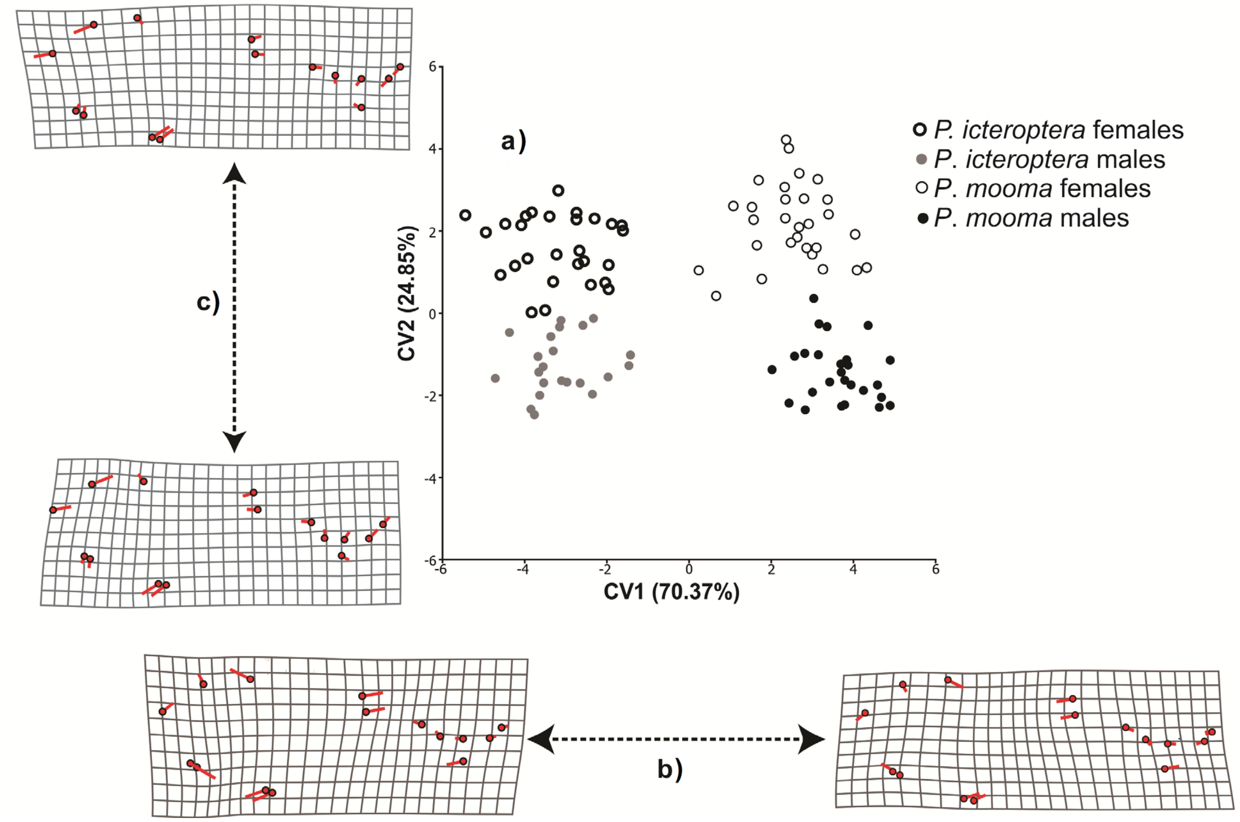

**Figure 2.** Canonical variates analysis (CVA) of fore wing shape. **a)** Scatterplot of individual scores from CVA comparing the fore wing shape of *Perithemis icteroptera* and *P. mooma* males and females; **b)** and **c)** Thin-plate spline deformation grids associated with **b)** CV1 and **c)** CV2 axes showing wing shape at the positive and negative ends. Circles correspond to landmarks, and lines attached to them indicate the magnitude and direction of the difference between the average wing shape and the wing shapes at the positive and negative ends. The amount of variation explained by each axis is in parentheses.

species and sexes. The percentages of correct classification were 92% and 79%, for fore and hind wing shapes, respectively. At the species level, the percentage of correct classification for the fore wing data set was 100 and 98% by linear discriminant analysis (LDA) and jackknife procedure, respectively, while for the hind wing data set it was 100 and 95% by LDA and jackknife procedure, respectively.

**Wing size analysis.** For fore and hind wings, no significant differences in the centroid size (CS) were found between males of each species and a similar result was obtained for females (Fig. 4). In addition, the analysis revealed female-biased sexual size dimorphism (SSD; $p < 0.05$) in both species.

**Outline analysis of the vulvar lamina.** The PCA scatterplot shows that the vulvar laminae of the two species occupy different morphospaces (Fig. 5a). The first PC discriminates between species ($p < 0.05$), with 100% of correct classification. The extreme shapes of the vulvar laminae corresponding to the PC1 axis are shown in Fig. 5 (b, c). These highlight the differences between species, with *P. mooma* having a smaller plate and shorter posterior expansions (Fig. 5b) than *P. icteroptera* (Fig. 5c).

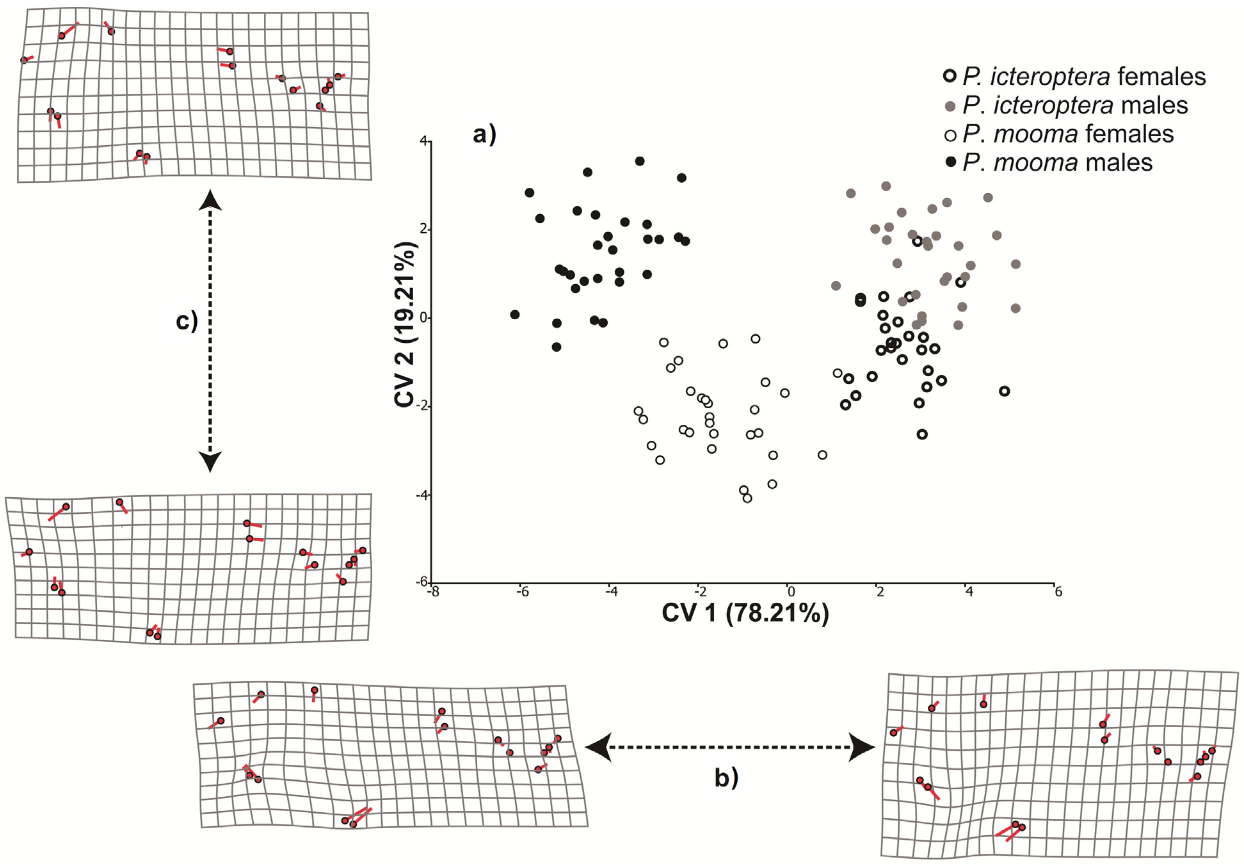

**Figure 3.** Canonical variates analysis (CVA) of hind wing shape. **a)** Scatterplot of individual scores from Canonical variate analysis (CVA) comparing the hind wing shape of *Perithemis icteroptera* and *P. mooma* males and females; **b)** and **c)** Thin-plate spline deformation grids associated with **b)** CV1 and **c)** CV2 axes showing wing shape at the positive and negative ends. Circles correspond to landmarks, and lines attached to them indicate the magnitude and direction of the difference between the average wing shape and the wing shapes at the positive and negative ends. The amount of variation explained by each axis is in parentheses.

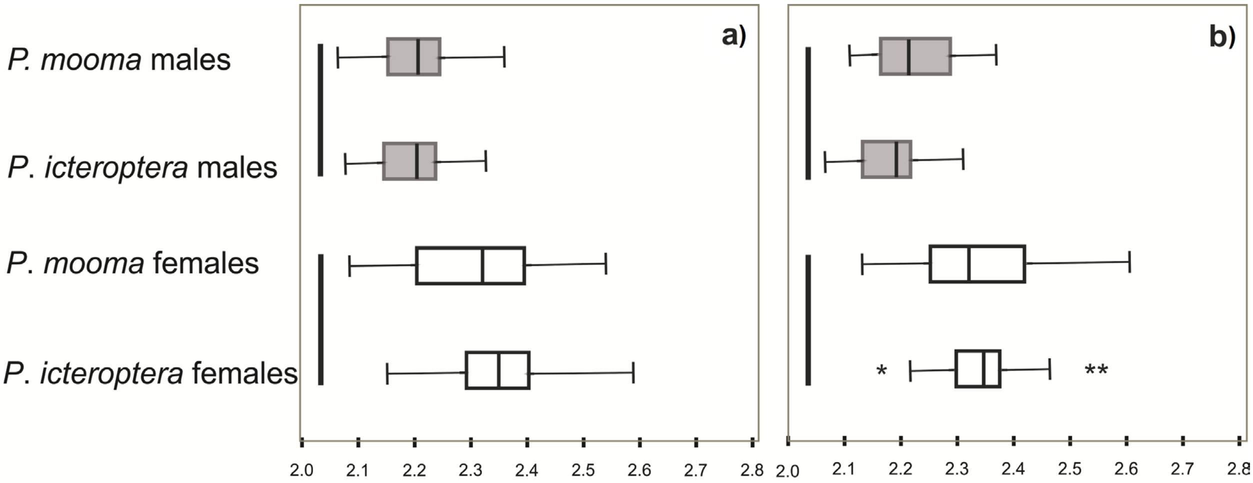

**Figure 4.** Box plot of the wings centroid sizes (CSs). **a)** and **b)** CSs of the female (white) and male (grey) of fore wings **a)** and hind wings **b)** of *Perithemis mooma* and *P. icteroptera*. In both wings, CSs were significantly different ($p < 0.05$) between sexes of the same species but not between females or males of different species. Bar: no significant differences between CSs ($p > 0.05$). *outlier.

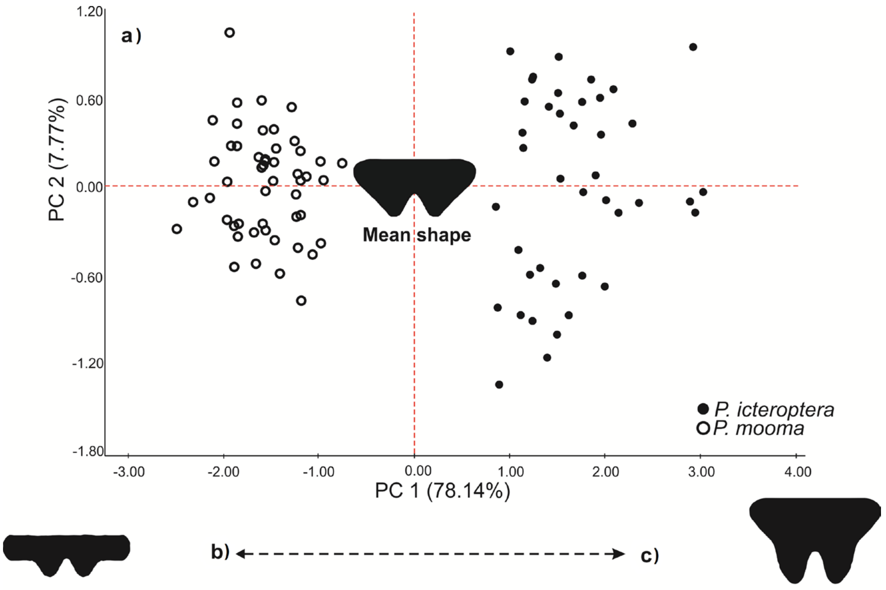

**Figure 5.** Principal component analysis (PCA) of vulvar laminae shape. **a)** PCA of vulvar laminae from females of *Perithemis mooma* and *P. icteroptera*; **b)** and **c)** Extreme shapes of the vulvar laminae corresponding to the PC1 axis. The amount of variation explained by each axis is in parentheses.

## DISCUSSION

Geometric morphometrics (GM) has emerged as a powerful tool to discriminate between species as it detects minimal shape variations which often are undetectable by traditional morphological studies and emphasizes differences between groups (Villemant et al. 2007). In comparison to other methods (e. g. molecular), GM has the advantage of not requiring expensive equipment or specific infrastructure.

In odonates, the venation pattern has provided a valuable source of diagnostic traits at all taxonomic levels (Rehn 2003, Garrison et al. 2006, 2010). According to Ris (1930), *P. mooma* differs from *P. icteroptera* in lacking cross-veins in wing triangles and sub-triangles. However, about 20% of the examined specimens of *P. mooma* showed at least one triangle or sub-triangle crossed, indicating that it is a highly variable feature (von-Ellenrieder & Muzón 1999).

Moreover, Ris (1930) used the length/width ratio of the hind wings to classify *Perithemis* species as belonging to the broad-winged series (*e.g. P. icteroptera*) and the narrow-winged series (*e.g. P. mooma*). However, these species showed overlapping variation ranges, hindering their identification. In the present study, TM separated *P icteroptera* from *P. mooma* only when multivariate analysis was performed using measurements (see Table I) from the hind wing. GM revealed that the fore and hind wings are wider in *P. icteroptera* than in *P. mooma*, and most important, it was useful to discriminate between these species. On the other hand, the centroid size failed to achieve species separation. Moreover, we found significant differences in size between the sexes of the same species but not between species.

The SSD reflects the interplay between selection pressures that act simultaneously in various directions and magnitudes, leading to a different equilibrium for each sex (Blanckenhorn 2005, Iglesias et al. 2012). In insects, the major evolutionary forces selecting for larger body size are fecundity selection in females (Reeve & Fairbairn 1999, Davidowitz 2008) and sexual selection in males (Blanckenhorn 2005). In the present study, *P. icteroptera* and *P. mooma* showed female-biased SSD, in contrast to what would be expected for species of this genus whose males are strongly territorial (Wildermuth 1991, 1992, De-Marco & Resende 2004). Such a result is probably related to increased fecundity and the fact that it was found in both species suggests a common pattern in the genus *Perithemis*.

The underlying mechanisms leading to SSD have been studied in *Libellula luctuosa* Burmeister, 1839, a territorial species with male-biased SSD (Moore 1990).

Ris (1930) stated that sex-specific characters in males or females which are useful in many Libellulinae species, are almost absent in *Perithemis*. In this sense, we found that the CS of the wings of both females and males failed to distinguish between *P. icteroptera* and *P. mooma*. In contrast, the shape variables of both fore and hind wings showed a high discriminant power, regardless of the sex of the specimen.

The shape of the vulvar lamina (with longer posterior expansions in *P. icteroptera*) was confirmed to be a valuable diagnostic trait, with a correct classification of 100%. To our knowledge, this is the first study applying GM to the genital plate as a tool for the taxonomic identification of dragonflies.

In summary, the present study demonstrated the great potential of morphometric analysis of wing and female external genitalia shapes for delimitating among species of the genus *Perithemis*. We propose that fecundity selection may have acted as an important evolutionary driver of female-biased SSD in this genus.

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## Author contributions

S.T.S.: preparation of specimens, data acquisition, contribution to the manuscript. M.S.I and S.T.S.: preparation of figures and data curation. J.M: specimen collection, taxonomic supervision, and contribution to the manuscript. M.S.I: formal analysis, supervision, and writing of the manuscript. M.S.I and J.M: conceptualization. All authors reviewed the manuscript.