

ALLOMETRIC SHAPE CHANGES INDICATE SIGNIFICANT DIVERGENCE IN THE WING SHAPE BETWEEN ASEXUAL AND SEXUAL LINEAGES OF *LYSIPHLEBUS FABARUM* (MARSHALL) (HYMENOPTERA: BRACONIDAE)

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Abstract

We used landmark-based geometric morphometrics to explore and quantify the forewing shape variation between asexual and sexual lineages of *Lysiphlebus fabarum* aphid parasitoids. We found a significant divergence in wing size and wing shape between the two reproductive lineages. Static allometry, which denotes size-related shape changes measured in different individuals at the same developmental stage within a population or species, accounts for the significant amount of variation in wing shape within each lineage (11.16 % in asexual, 7.5% in sexual). The allometric shape changes appear to be lineage specific, i.e., the allometric slopes of wing shape significantly diverge between lineages. Such a pattern indicates that asexual and sexual lineages differ in the covariation pattern of the wing shape. Further studies on larger datasets, including other *Lysiphlebus* taxa and closely related groups, would shed more light on the pattern of morphological variation and the significance of the reproductive mode on the morphological evolution of parasitoid wasps.

KEY WORDS: Allometry, Geometric morphometrics, parasitoids, reproductive strategies, wing shape

Introduction

Among 400 known species of aphid parasitoids in the world fauna (STARÝ, 1988; DOLPHINE & QUICKE, 2001), *Lysiphlebus fabarum* (Marshall, 1896) became famous and very well-studied parasitoid from many angles: morphology, reproduction, ecology, molecular phylogeny, etc. (e.g. STARÝ, 1986; SANDROCK *et al.*, 2007, 2011; SCHMID *et al.*, 2012; KALDEH *et al.*, 2012; RAKHSHANI *et al.* 2013). *Lysiphlebus fabarum* is a solitary

parasitoid of more than 155 aphid species, making over 750 tritrophic associations worldwide (YU *et al.*, 2012). Its target species are mostly small aphid hosts mainly from the genus of *Aphis* (e.g., black bean aphid, – *A. fabae* Scopoli, soybean aphid – *A. glycines* Matsumura, cowpea aphid – *A. craccivora* Koch and cotton aphid – *A. gossypii* Glover 1877) (WEI *et al.*, 2011). Also it parasitizes the aphid genus *Brachycaudus* (e.g. thistle aphid – *B. cardui* (Linnaeus) and the leaf-curling plum aphid – *B. helichrysi* (Kaltenbach)), which attack various plants from the family Asteraceae and Rosaceae (primarily the genus *Prunus*) (KAVALLIERATOS *et al.*, 2004; STARÝ, 2006).

Aside from its significance in biological control and in agriculture, the taxonomical status of *L. fabarum* is not resolved yet. *L. fabarum* and two other morphologically distinguished taxa, *L. cardui* (Marshall) and *L. confusus* (Tremblay & Eady), are traditionally assigned to the “*fabarum*” species group. Different genetic studies (BELSHAW *et al.*, 1999; SANDROCK *et al.* 2011; DEROCLES *et al.*, 2012) showed no or little support for the species status of these three morphologically clearly distinguishable groups. For the sake of simplicity, in this study we will keep the traditional approach and refer to the *L. fabarum* as separate taxa. Morphologically, *L. fabarum* is characterized by reduced forewing venation and long metacarpus, often reaching the apex of the wing (STARÝ *et al.*, 2010). Having lineages with two different modes of reproduction: asexual (thelytokous) and sexual (arrhenotokous) (STARÝ, 1999; BELSHAW *et al.*, 1999; SANDROCK *et al.*, 2011), the *L. fabarum* group is unique within the subfamily Aphidiinae.

The morphological variation within parasitoid species could be largely affected by their host. The size of the host is very important for parasitoids because bigger aphids provide more resources, although *L. fabarum* is not so fastidious a species. Several studies showed that the morphological variation of parasitoids is largely affected and induced by their hosts (e.g. ŽIKIĆ *et al.*, 2009, 2010; MITROVSKI-BOGDANOVIĆ *et al.*, 2009, 2013; TOMANOVIĆ *et al.*, 2013) including *L. fabarum* parasitoids (BARHOEI *et al.*, 2011). However, there is no data on possible morphological variation between reproductive lineages (asexual and sexual) of aphid parasitoids.

Here, we explored the variation in the wing size and wing shape between asexual/sexual lineages of the *L. fabarum*. More specifically, we addressed the following questions: i) whether asexual and sexual lineages of *L. fabarum* differ in wing size, and ii) whether two lineages differ in wing shape. The essential component of wing shape variation – the size dependent (allometric) shape changes were analysed. Allometry is the shape change associated with size variation (GOULD, 1966), while the non-allometric component accounts for the changes in shape which are not related to allometric scaling.

Material and Methods

Field sampling and determination of reproductive modes

In total 67 female specimens of *Lysiphlebus fabarum* were analysed; 36 asexual and 30 sexual. Parasitoids were sampled during 2009/10 in Serbia, Belgrade surroundings.

Asexual: 36 ♀, Vrbovski put, on *Cirsium arvense* ex *Aphis fabae cirsicanthoides*, 18.05.2009, Leg. M. Janković.

Sexual biotypes: 11 ♀, Zemun IPPE, on *Chenopodium album* ex *Aphis fabae fabae* 18.6.2010, Leg. A. Petrović; 17 ♀, Novi Beograd, on *Medicago sativa* ex *Aphis craccivora*, 13.7.2010, Leg. Ž. Tomanović; 1♀,

Batajnica, on *Cirsium arvense* ex *Aphis fabae cirsianthoides*, 6.7.2010, Leg. Ž. Tomanović; 1♀, Slankamen, on *Chenopodium album* ex *Aphis fabae fabae*, 20.7.2010, Leg. M. Janković.

Plant samples infested with live and mummified aphids, known to be hosts of *L. fabarum* parasitoids, were collected in the field and placed into plastic boxes covered with nylon mesh (KAVALLIERATOS *et al.*, 2001). The boxes with aphids were maintained in the laboratory and observed for the parasitoid emergence. Reproductive modes of those samples were determined according to the field evidence of their sex ratios. We presumed that the absence of males in samples is an indicator of asexual reproduction, while samples containing males and females were treated as samples with sexual mode of reproduction.

Geometric morphometrics analyses

Microscopic slides of the right wings were prepared in the Berlese medium and photographed using a Leica System Microscope DM2500 with a Leica DFC490 Digital Camera. Twelve landmarks were positioned by the *TPSDIG2* software package (ROHLF, 2005) (Fig. 1). The landmarks were positioned at the veins' junctions (1, 2, 4, 5, 6 and 7), radial abscissa 1 (R1) were defined by the landmarks 11 positioned at the end of R1 vein, landmark 12 is the very apex of the stigma, and landmarks 3, 8, 9 and 10 are projections of the three veins describing the wing edge. The nomenclature of wing venation is given after VAN ACHTERBERG (1993).

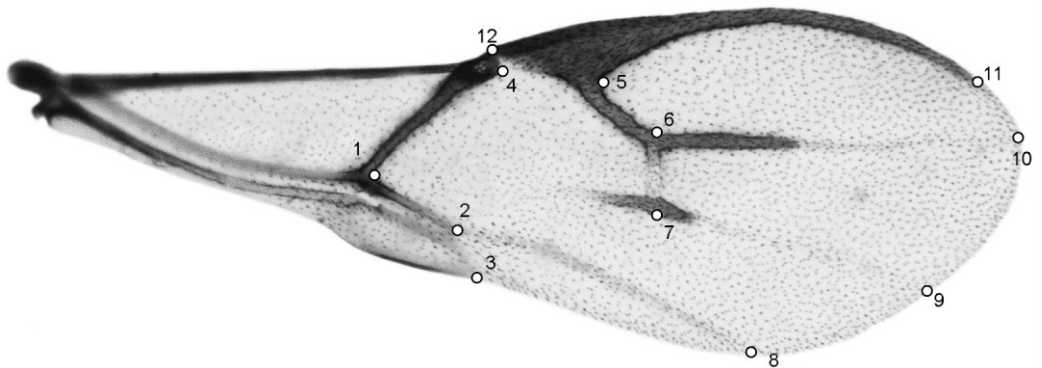


Figure 1. *Lysiphlebus* forewing with 12 selected landmarks. The landmarks (1-5, 12) define the proximal part of the forewing, and the distal part of the wing is defined by the landmarks 6-11. The landmarks 8, 9 and 10 are projections of the three veins on the wing edge. Stigma and radial abscissa 1 (R1) were defined by the landmarks 11 and 12 (12, marks the very apex of stigma, 11 marks the end of R1 vein), the landmarks 5 and 6 mark the first radial sector of the radial vein, and the vein between the landmarks 6 and 7 is defined as 2SR.

The wing size was computed as centroid size (CS), which reflects the amount of dispersion around the centroid of the landmark configuration. We applied the Generalized Procrustes Analysis to obtain the matrix of the shape coordinates – Procrustes coordinates, from which the differences due to position, the scale and orientation had been removed (GPA; ROHLF & SLICE, 1990; DRYDEN & MARDIA, 1998; ROHLF, 2001). The CS was calculated and the shape variables (Procrustes coordinates) were obtained using MorphoJ software (KLINGENBERG, 2011).

Divergence in wing size and shape

The divergence in wing size between reproductive lineages was estimated through the Analysis of Variance (ANOVA) procedure in SAS (SAS Institute Inc., Cary, NC, version 9.1.3). Procrustes distance between the mean shape of asexual and sexual lineage was calculated. The statistical significance of differences in mean shape was obtained by a permutation test based on 10.000 iterations. To visualize the pattern of the variation in wing shape the PCA on covariance matrix of wing shape variables was calculated. The thin-plate spline deformation grids that illustrate forewing shape changes correlated with the first and the second axis were obtained from the regression of shape variables on the first two PC axes.

In geometric morphometrics, the most straightforward and most frequently used approach for analyzing allometry is multivariate regression of shape on size, i.e., the Procrustes coordinates on CS or log-transformed CS (KLINGENBERG, 2013). Therefore, to assess the effect of size on shape changes we explored the size-related shape changes within lineage by regressing shape variable on log CS, and calculated the amount of variation in shape attributable to the variation in size. For graphical presentation of allometric shape changes regression scores for all the observations in the sample were calculated (DRAKE & KLINGENBERG 2008). The resulting scatterplot of the regression scores can be interpreted as the shape variables that are most strongly associated with the *particular CS value*. All the above shape analyses were performed using MorphoJ software (KLINGENBERG, 2011).

To test if the allometric slopes differ between lineages, we performed multivariate analysis of covariance (MANCOVA), using lineage, size (log CS) and their interaction (lineage \times log CS) as factors. Statistical significance of interaction (lineage \times log CS) would indicate that lineages have different allometric shape changes. MANCOVA was performed using PROC GLM procedure in SAS (SAS Institute Inc., Cary, NC, version 9.1.3).

Results and Discussion

Size and shape differences

The asexual and sexual lineages significantly diverge in forewing size. The wing size of *Lisyphlebus fabarum* asexual lineage (mean CS \pm SE = 1353.9 \pm 91.3) appears to be significantly larger than *L. fabarum* sexual lineage (mean CS \pm SE 1266.9 \pm 92.5): ANOVA test, model df = 1, error df = 64, SS = 0.0729, F = 14.4, P < 0.001. Two lineages also significantly differ in wing shape (Procrustes distance = 0.032, P < 0.001).

The position of the specimens in the morphospace defined by the first two axes obtained by PCA analysis of wing shape variables and visualization of related wing shape changes are presented on Fig. 2. The first two PC axes accounted for 48.7% of the total shape variation. The PC1 described the gradient from asexual to sexual lineage showing that sexual lineages had longer and narrower wings and parallel margin of stigma and first radial vein. The second PC describes the variation in wing shape within each lineage and it is mostly related to change in the relative positions of veins in the proximal part of the wing.

Allometry

The size related shape changes appear to be statistically significant in both asexual and sexual lineages (P < 0.05) (Figs 3A and 3B). In the asexual lineage 11.16% of variation in the wing shape is attributable to the

allometric shape changes, while in the sexual lineage 7.5% of total variation in the wing shape could be explained by the size-related shape changes.

Static allometric shape changes in the asexual lineage are related to the change of the relative position of the veins in the proximal part of the wing, relative shortening of radial abscissa 1 (R1) and relative widening of the distal part of the wing in larger specimens (Fig. 3A). In sexual *L. fabarum* lineage, the static allometric shape changes are related to widening of the proximal part of the wing, elongation of the radial abscissa 1 (R1) and the relative narrowing of the distal part of the wing (Fig. 3B). MANCOVA test results showed that the allometric shape changes between sexual and asexual lineages significantly diverge (Tab. I), indicating that asexual and sexual lineages diverge in the covariance pattern of the wing shape.

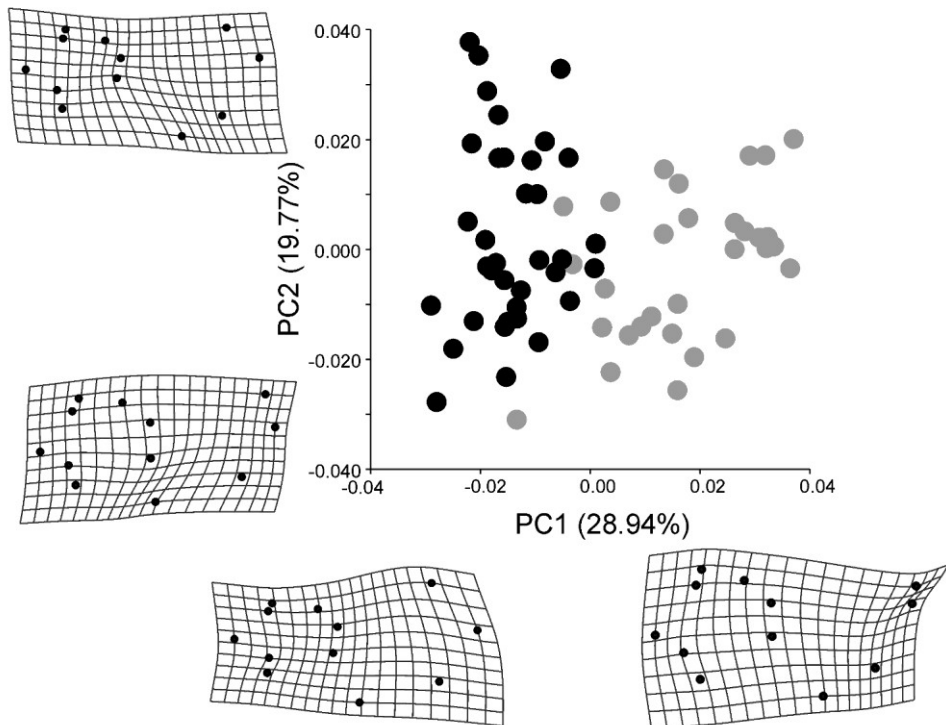


Figure 2. Positions of individuals from asexual (black dots) and sexual (gray dots) lineages of *L. fabarum* in the morphospace defined by the first and the second Principal Component (PC) axis obtained from covariance matrix of forewing shape variables. Observed morphological variation is summarized by the deformation grids.

Our study indicates that significant association between the wing shape and the reproductive mode could exist in parasitoid wasps. Such a result is surprising given that recent study on both asexual and sexual lineages in the genus *Lysiphlebus* (SANDROCK & VORBURGER, 2011) showed that asexual reproduction in *L. fabarum* group is inherited as a single-locus recessive trait, which indicates that the reproductive mode can be changed in just one generation.

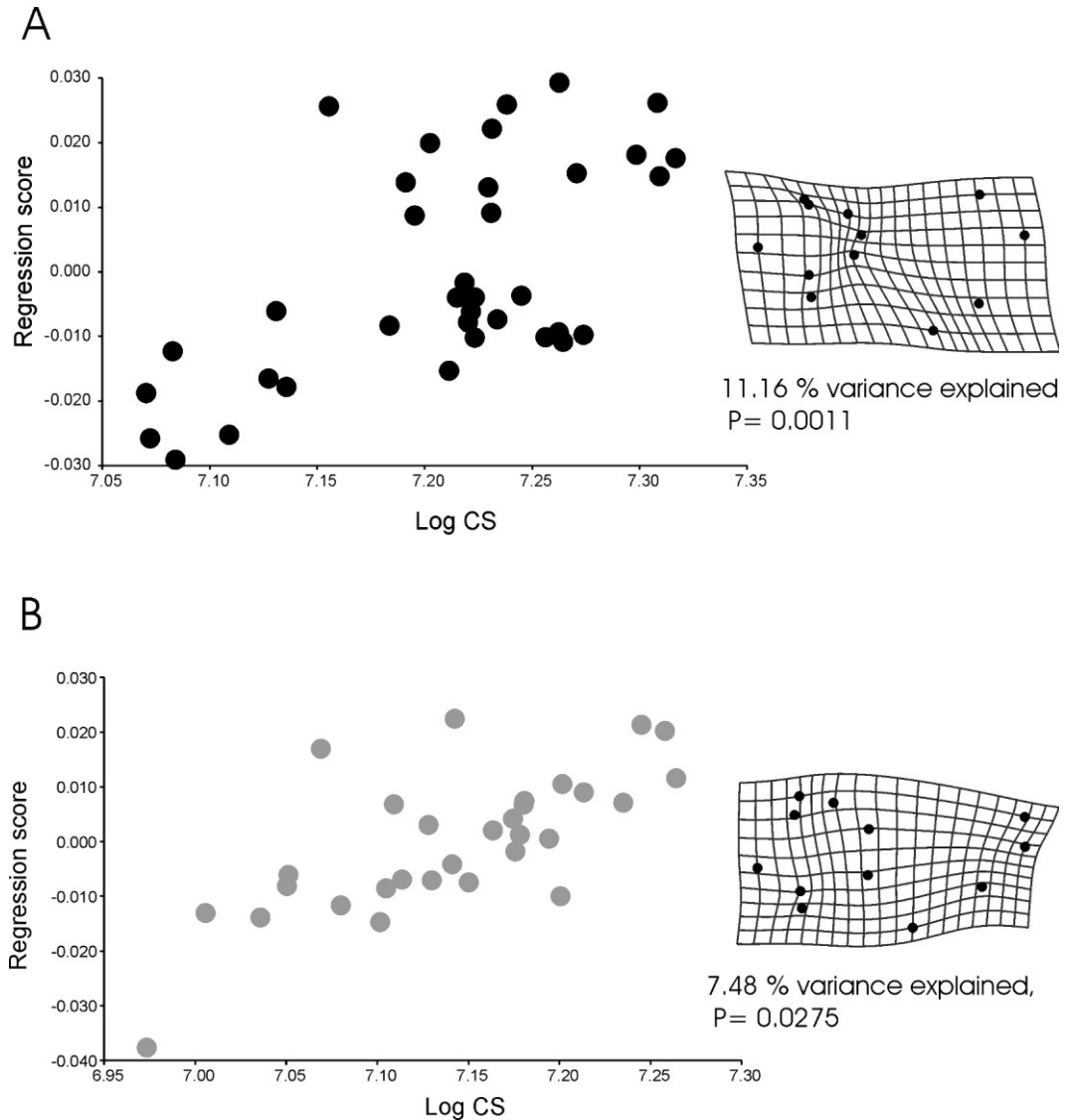


Figure 3. The allometric changes in wing shape. A) asexual lineage, B) sexual lineage. The shape changes from the individuals with the smallest CS to the shape of the individuals with the largest CS are presented by the deformation grids.

Table I. The allometric relations between two reproductive lineages tested by a multivariate analysis of covariance (MANCOVA). df: degrees of freedom; log CS: centroid size. The significant lineages \times log CS interaction indicates that the allometric slopes of reproductive lineages diverge.

Effect	Wilks' lambda	Effect df	Error df	F	P
Lineage	0.43691702	20	43	2.77	0.0025
log CS	0.47138925	20	43	2.41	0.0078
Lineage \times log CS	0.43505684	20	43	2.79	0.0024

The study on the allometric variation in the wing shape within another group of parasitoid wasps, *Ephedrus persicae* (ŽIKIĆ *et al.*, 2010), showed that the pattern and the direction of allometric changes differed between the individuals that emerged from different hosts. Therefore, the observed divergences in the directions of allometric slopes of reproductive lineages observed in this study could not be clearly separated from possible host-induced shape changes. Further studies that include a possible host-induced morphological variation and variation between asexual and sexual lineages of other closely related taxa of *Lysiphlebus parasitoides* could provide more data on the structure and pattern of morphological variation within this group.

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АЛОМЕТРИЈА И ВАРИЈАБИЛНОСТ У ОБЛИКУ КРИЛА ИЗМЕЂУ ЛИНИЈА СА АСЕКСУАЛНОМ И СЕКСУАЛНОМ РЕПРОДУКЦИЈОМ КОД *LYSIPHLEBUS FABARUM* (MARSHALL) (HYMENOPTERA: BRACONIDAE)

ВЛАДИМИР ЖИКИЋ, АНЂЕЉКО ПЕТРОВИЋ И АНА ИВАНОВИЋ

Извод

Варијабилност у облику крила између линија са асексуалном и сексуалном репродукцијом код врсте *Lysiphlebus fabarum* је анализирана и квантификована применом геометријске морфометрије и анализом конфигурације специфичних тачака које дефинишу облик предњих крила. Утвђене су значајне разлике у величини и облику крила између различитих репродуктивних линија. Статичка алометрија, која означава промене облика условље променом величине међу јединкама на истом развојном стадијуму у оквиру популације или врсте, чини значајан извор варијабилности у облику крила код обе репродуктивне линије (11,16 % код асексуалне; 7,5 % код сексуалне). Алометријске промене облика су специфичне за сваку линију. Нагиби алометријских права се статистички значајно разликују. Разлике у алометријама указују на значајне разлике у обрасцима коварирања облика крила код асексуалне и сексуалне линије. Даља истраживања на већем узорку, који би укључио и друге, филогенетски блиске таксоне, у оквиру рода *Lysiphlebus* омогућила би боље сагледавање морфолошке варијабилности и значаја различитих репродуктивних стратегија на морфолошку еволуцију паразитоидних оса.

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