



A Morphometric Approach to the Comparative Morphology of Aedeagus and Genital Plate Shapes in Two *Cercopis* Species (Hemiptera, Auchenorrhyncha, Cercopidae)

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Abstract: The species of the genus *Cercopis* Fabricius, 1775 are morphologically similar, and there are difficulties in identifying them due to the inadequacy of diagnostic keys and the colour and pattern variations. For this reason, it can be challenging to distinguish the species without carefully dissecting and examining the male genitalia. In the present study, we compared the morphology of the aedeagus and the genital plates of two *Cercopis* species using geometric morphometrics (GM). We investigated the size and shape of the aedeagus and genital plates of *C. intermedia* Kirschbaum, 1868 and *C. vulnerata* Rossi, 1807 to evaluate whether these structures could serve as useful tools for species differentiation. The centroid size of aedeagus was significantly different between species ($p=0.01$), but genital plate size was not ($p=0.8$). Both aedeagus and genital plate shape were significantly different between species, based on Procrustes ANOVA and Pillai trace (MANOVA) p value. The results of discriminant function analysis of aedeagus and genital plate indicate that species are clearly discriminated. The parametric p value of T^2 and permutation p value of T^2 and procrustes distances show that the differences were significant.

Key words: Shape variation, Türkiye, *Cercopis*, geometric morphometry

Introduction

Genital structures in insects are crucial for species identification and often represent the sole reliable method for distinguishing closely related species (Mutanen & Pretorius 2007). Cercopidae is the most diverse family within Cercopoidea (Hemiptera: Auchenorrhyncha) and consists of xylem-feeding

insects, comprising approximately 1,500 species across 173 genera worldwide (Soulier-Perkins 2019). However, only 20 genera and 93 species have been recorded in the Palearctic region (Bartlett et al. 2018). Cercopids distribution is heavily concentrated in tropical and subtropical zones, with nearly 70% of recorded species inhabiting tropical areas. Due to the foamy secretion produced by their

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nymphs, members of Cercopidae are commonly referred to as 'foamy cicadas' or 'spittlebugs'. Additionally, because the adults are capable of strong jumping, they are also known as 'frog jumpers' (Cryan & Svenson 2010). In the majority of species, adults exhibit distinctive and colourful tegmina patterns (Holzinger et al. 2003) and can display striking patterns that combine red, orange and yellow with black (Bartlett et al. 2018). Adults typically feed on the foliage and stems of a wide range of host plants, whereas nymphs are root feeders (Liang & Fletcher 2002; Liang & Webb 2002). Members of the family commonly range in size from 6 to 12 mm.

Cercopis, commonly called red-black froghoppers, has a forewing colour pattern as follows: red spots on the basal half of the clavus and in the middle of the corium, and a red horizontal band on its apical third. Species show a very high variation in patterning, including completely black forms and differences in the width of the dots or bands even among individuals of the same species (Holzinger et al. 2003, Tanyeri & Zeybekoğlu 2020, 2022, Demirel 2022). In *C. vulnerata*, all leg segments are uniformly black, whereas in related species the femora and tibiae are partially red. Male genitalia also differ: the anterior processes at the apex of the aedeagus are two-thirds the length of the posterior pair in *C. vulnerata*, while in *C. sanguinolenta* and *C. intermedia*, the anterior processes are approximately half as long (Holzinger et al. 2003, Demirel & Dinç 2021).

Cercopis fauna of Türkiye consists of 5 species: *C. vulnerata*, *C. sanguinolenta* (Scopoli, 1763), *C. intermedia*, *C. septemmaculata* (Melichar, 1903) and *C. distincta* Melichar, 1896 (Lodos and Kalkandelen, 1981, Önder et al. 2011). Demirel & Dinç (2021) gave the first local record of *C. distincta*, which is defined as an endemic species in Türkiye but whose terra typica is unknown. In the same study, rare species of *Cercopis* in Türkiye were redescribed. The limited studies conducted on the Cercopidae family in Türkiye in the following years can be grouped as faunistic records and taxonomic studies (Demirel & Dinç 2021, Demirel & Hasbenli 2021, Demirel 2022, Tanyeri & Zeybekoğlu 2022).

Due to this diversity, distinguishing species based solely on male genitalia can be challenging. Male genitalia in insects are among the most evolutionarily variable morphological structures, and their rapid rate of morphological change is widely believed to be driven by sexual selection (Arnqvist 1998). In particular, they have been considered one of the most important and useful specific diagnostic characteristics in insect systematics (Liu et al.

2023). In Auchenorrhyncha, the genital structures that serve as reliable taxonomic characters include the aedeagus, stylus, pygofer, genital plate and anal tube in males, and the seventh pregenital sternite in females (Ossiannilsson, 1978).

Geometric morphometric (GM) is a useful tool for shape analysis in biology (Rohlf & Bookstein 1990, Bookstein 1991, Zelditch et al. 2004) that not only offers precise and accurate descriptions, but also serves the equally important purposes of visualisation, interpretation and communication of results (Klingenberg 2013). With the help of GM, the sexual dimorphism, ecomorphology and minor morphological variation of characters can be statistically and scientifically defined and compared (Li et al. 2016, Harvey & Sherratt 2023, Ludoški et al. 2023). GM is a quantitative approach to insect species identification based on size and shape analyses. Body structures such as wing, head, pronotum, femur, elytra, aedeagus and mandible are used in geometric morphometry studies (Qubaiová et al. 2015, Zúniga-Reinoso & Benítez 2015, Li et al. 2016, Espinoza-Donoso et al. 2020, Kociński et al. 2021, Cheng et al. 2022, Zhao et al. 2022, Changbunjong et al. 2023, Oleksa et al. 2023). GM analysis is often used to determine the differences in shape and venation of insect wings (Bai et al. 2016, Suganya & Manimegalai 2021; Escobar-Suárez et al. 2023, Tarrís-Samaniego et al. 2023).

Due to the high degree of morphological similarity observed among taxa, the shape of the median lobe of the aedeagus and its apex were analysed in two species of the subgenus *Cryobius* Chaudoir, 1838 (Coleoptera: Carabidae: Pterostichus Bonelli, 1810) to help in species delimitation (Zubrii et al. 2023). This finding underscores the value of geometric morphometric analysis in modern taxonomy and highlights the importance of integrating genital characters when dealing with morphologically cryptic taxa in Carabidae.

The utility of external female genitalia in taxonomic delimitation has been demonstrated through geometric morphometric (GM) analysis in Triatominae (Belintani et al. 2022). Building upon this approach, the male genital structures of *Pterostichus* (*Cryobius*) *brevicornis brevicornis* (Kirby, 1837) were examined across its broad Holarctic range, highlighting the value of genital traits in assessing intraspecific diversity within groups (Zubrii et al. 2022).

In this paper, two *Cercopis* species from Türkiye were examined. Two male genitalia structures (aedeagus and genital plate) were selected to investigate the morphological variation of *Cercopis* based

on a GM approach. The aedeagal shaft (aedeagus) and appendages were evaluated when making comparisons in the aedeagus. In addition to the difference in appendages in the aedeagus, we evaluated whether the aedeagal shaft would differ in species differentiation.

Material and Methods

Dry samples of *C. intermedia* and *C. vulnerata* were collected from different localities in Sinop province (Northern Anatolia, 42°01'40.71"N 35°09'06.21"E), placed in 5% acetic acid and softened a few hours before being photographed. The aedeagus and genital plate were softened using 5% KOH. A total of 49 male samples (*C. intermedia* Cİ n=24, *C. vulnerata* CV n=25) were used.

Data collection and geometric morphometric analysis

The aedeagus and genital plate were dissected and separated. Photos of these structures were taken with

a Nikon D-7000 camera connected to a Zeiss 7100 stereomicroscope. The aedeagus and genital plate samples were analysed through a Two-dimensional (2D) landmark based geometric morphometric procedure (Bookstein 1991, Rohlf & Marcus 1993). The landmarks were digitised using the tpsDig 2.64 software (Rohlf 2015). 12 landmarks were used for the aedeagus (Fig. 1A) and seven landmarks for the genital plate (Fig. 1B). The used landmarks were type II, which defines curved areas, and type III, which defines the end points (Bookstein 1991).

Statistical significance of the differences in centroid size (CS) (Zelditch et al. 2004), which is the total of the squares of each landmark to the centroid of the shape, was analysed with variance analysis. MorphoJ 1.06d (Klingenberg 2011) was used to perform the Procrustes ANOVA and the program PAST 4.10 (Hammer et al. 2001) was used to build the CS boxplot charts.

General Procrustes Analysis (GPA) was performed to scale, translate and rotate the landmark

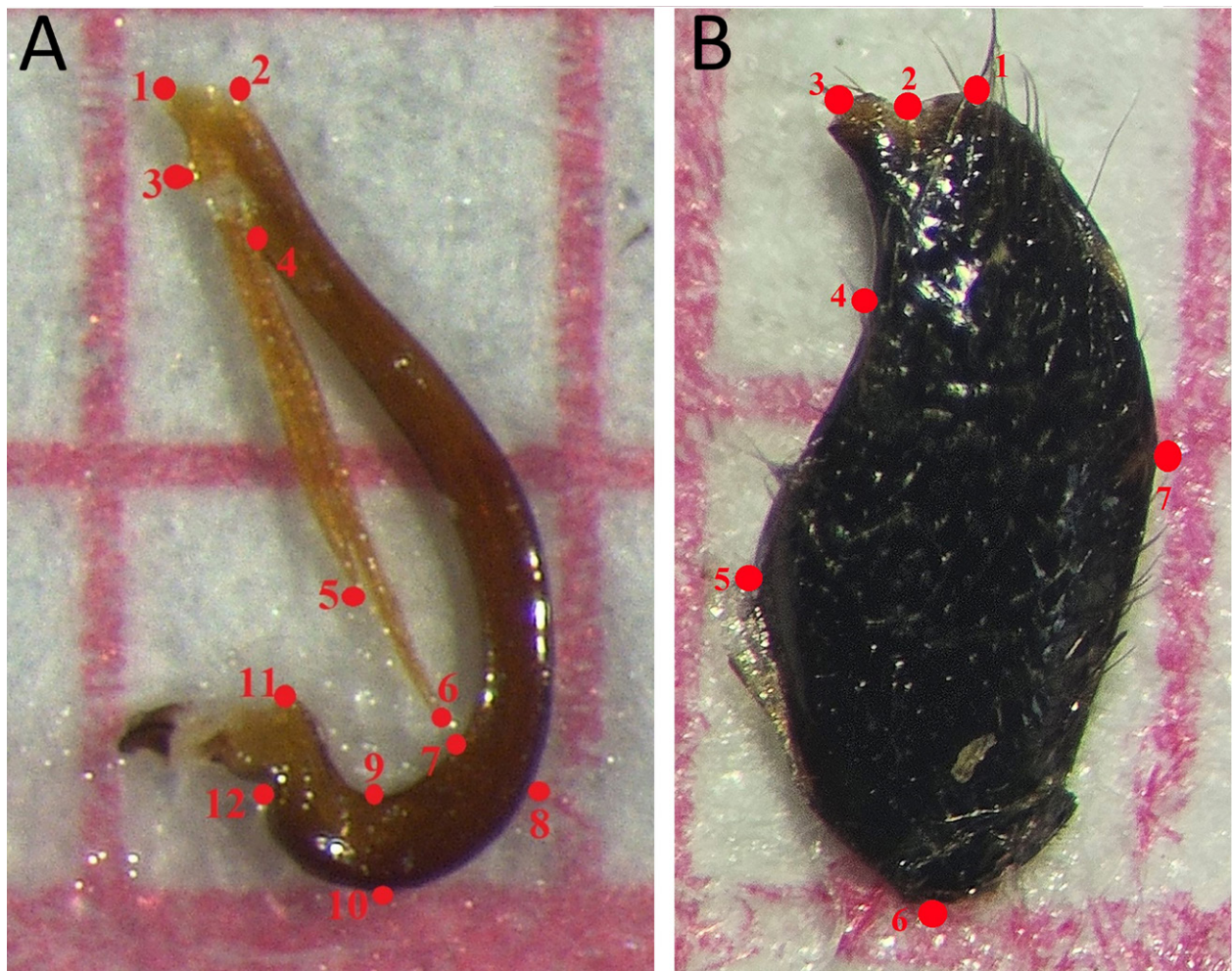


Fig. 1. Collected landmarks on the aedeagus (A) and genital plate (B) of *Cercopis vulnerata*.

coordinates and Procrustes coordinates which contain information on shape only (Rohlf & Slice 1990). After a covariance matrix of shape coordinates was obtained, Principal Component Analyses (PCA) was performed by MorphoJ (Klingenberg 2011) to see the shape variations. In order to compare the groups, Canonical Variance Analysis (CVA) and Discriminant Function Analysis (DFA) were performed with MorphoJ (Klingenberg 2011). CVA and DFA are different from each other: while the relative separation of groups is analysed by CVA by a pooled variance-covariance matrix, the separation of every pair of the groups is analysed by DFA by the covariance matrices of two groups for every comparison. In addition, the focusing process on the degree of different groups is made by CVA as DFA deals with the degree among the different groups and the possibility of the right group's members for every kind. To determine the statistical difference pairwise in mean shapes, a permutation test which has Procrustes and Mahalanobis distance (10000 replication) was used.

Results

The CS of aedeagus was significantly different between species ($p=0.01$), but genital plate size was not ($p=0.8$). Both aedeagus and genital plate shape were significantly different between species, based on Procrustes ANOVA and Pillai trace (MANOVA) p values (Table 1, Fig. 2).

The PC analysis for genital plate (PC1 35.2% and PC2 27%) explain the total variation and factors affecting PC1 min are the 7th and 5th LMs being lower, the 2nd LM being higher, and shortening and widening of the genital plate. Factors affecting PC1 max are the 7th and 5th LMs being higher, the 2nd LM being lower, and elongation and expansion of the plate. Factors affecting PC2 min are narrowing in the 5th and 6th LM part of the plate, and elongation between the 4th and 5th LM. Factors affecting PC2 max are widening of the 5th, 6th and 7th LMs, and shortening of the 4th and 5th LMs (Fig. 3A).

The PC1 39.2% and PC2 22% (Fig. 3B) explain the total variation of the aedeagus shaft between species. Shorter apex (1st and 2nd LMs), end of the 1st pair of appendages in the aedeagus (5th LM), basal part (11th and 12th LMs) and narrowing at the width (7-10 LMs) are the factors affecting PC1 min. Narrowing in the apex, elongation at the end of the first pair of appendages of the aedeagus, widening of the width, and elongation in the basal are the factors affecting PC1 max. Factors affecting PC2 min are the contraction at the end of the 2nd pair of the appendages in the aedeagus (6th LM), narrowing and contraction in the width, and a wider angle at the basal. Factors affecting PC2 max are elongation at the end of the 2nd pair of appendages in the aedeagus, widened and elongated width, and a narrower angle at the basal part (Fig. 3B).

Table 1. Procrustes ANOVA results (F: Goodall's F, CS: Centroid size, Bolded: Significant difference), genital plate and aedeagus sample number respectively; *Cercopis intermedia* N: 8 / 15, *Cercopis vulnerata* N: 15 / 20.

Dataset		F	p-value	Pillai tr.	p-value
Aedeagus	CS	6.74	0.01		
	Shape	56.97	<.0001	0.98	<.0001
Genital Plate	CS	0.07	0.8		
	Shape	7.25	<.0001	0.92	<.0001

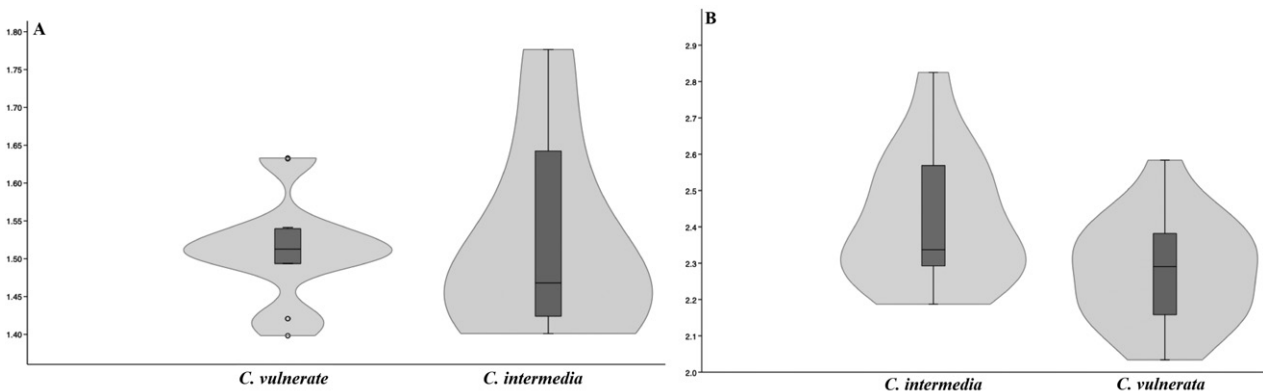


Fig. 2. Genital plate (A) and aedeagus (B) boxplots of CS (*Cercopis intermedia* and *Cercopis vulnerata*).

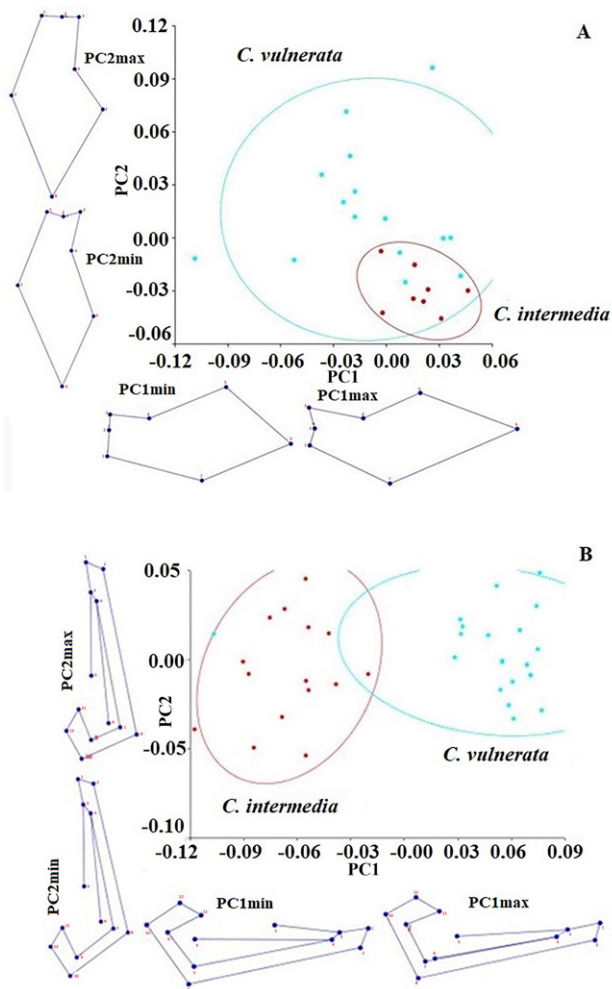


Fig. 3. Genital plate (A) and aedeagus (B) PCA and minimum-maximum effect of PC1-2 (*Cercopis intermedia* and *Cercopis vulnerata*).

Table 2. CVA results for aedeagus and genital plate (Mah. Dist.: Mahalanobis distance, Proc. Dist.: Procrustes distance, Perm. p: Permutation *p* value, Bolded: Significant difference.).

Groups	<i>Cercopis vulnerata</i> / <i>Cercopis intermedia</i>	
	Mah. Dist./Perm. p	Proc. Dist./Perm. p
Aedeagus	12.5771/ <.0001	0.1400/ <.0001
Plate	6.8700/ <.0001	0.0665/ <.0001

Table 3. DFA results for aedeagus and genital plate (T²: T-square, Param. p: Parametric *p* values, Perm. p: Permutation *p* value.).

Groups	<i>Cercopis vulnerata</i> / <i>Cercopis intermedia</i>		
	T ²	Param. p	Perm. p (T ² /Proc.)
Aedeagus	1355.8641	<.0001	<.0001/<.0001
Plate	246.2427	<.0001	<.0001/<.0001

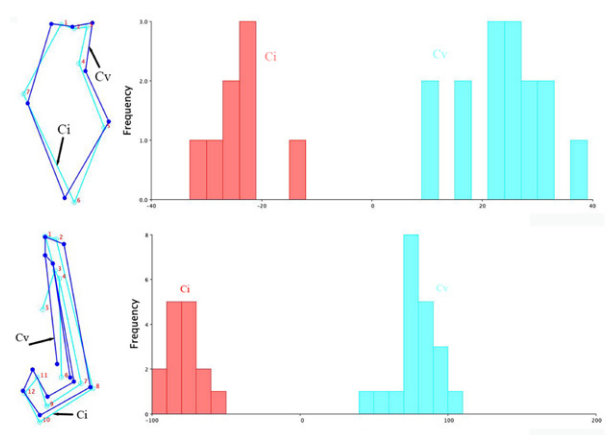


Fig. 4. DFA plot and shape differences of the genital plate (A) and aedeagus (B) of the species (*Ci*: *Cercopis intermedia* and *Cv*: *Cercopis vulnerata*).

The results of the canonical variance analysis of the aedeagal shaft (aedeagus) and plate reveal that species are clearly separated. The *p* values of the Mahalanobis and Procrustes distances show that the differences are significant (Table 2).

The results of the discriminant function analyses of the aedeagus and genital plate indicate that species are clearly discriminated. The parametric *p* value of T² and permutation *p* value of T² and Procrustes distances show that the differences were significant (Table 3, Fig. 4).

In *C. vulnerata*, the genital plate is wider and shorter. Between the 1st and 3rd LMs is longer, between the 4th and 5th LMs is shorter and between 1-3 LM and 4-5 LM there is less concavity (Fig. 4). In *C. vulnerata*, the aedeagus shaft is wider, the end of the 1st pair of the aedeagus (5th LM) is longer, and the bases of the 1st and 2nd pairs of the aedeagus (3rd and 4th LMs) are closer to the apex. The basal tip is longer and more broadly angled (Fig. 4).

Discussion

Morphological variation has long served as a cornerstone in insect taxonomy and systematics. However, traditional morphometric approaches often fall short in capturing subtle shape differences, particularly among closely related species or populations with cryptic morphological traits. In recent decades, geometric morphometrics (GM) has emerged as a powerful tool for quantifying and visualising shape variation in biological structures with high precision and statistical rigor (Pretorius & Scholtz 2001). GM has been increasingly adopted in systematic studies to assess morphological differentiation among taxa (Adams et al. 2004, Börtstler et al. 2014, Saiwichai et

al. 2023, Laojun et al. 2024). Unlike linear morphometrics, GM retains geometric relationships among landmarks, allowing for a more accurate representation of shape changes. This method is particularly valuable in visualising morphological variation and testing hypotheses of taxonomic distinction (Mutanen & Pretorius 2007, Bai et al. 2014, Nugroho et al. 2020). Various anatomical structures have been investigated using GM in insects, including the head, pronotum, thorax, mandibles, and reproductive organs (Pretorius & Scholtz 2001, Polihronakis 2006, Romiti et al. 2017, Sarkaya et al. 2019, Tanyeri et al. 2025). In beetle systematics, GM has played a significant role in clarifying species boundaries where external morphology provides limited resolution (Smith-Pardo et al. 2025). Notably, the analysis of male and female genitalia, often considered taxonomically informative structures, has become increasingly common. Beyond Coleoptera, GM applications in Hemiptera have demonstrated its versatility. Studies have utilised this method to differentiate wing shape and venation patterns, as well as to assess variation in sexual organs (Gumiel et al. 2003, Campos et al. 2011, Li et al. 2017). Wing geometry has proven effective in addressing taxonomic challenges, such as distinguishing 11 mosquito species within the genus *Anopheles* (Jaramillo-O et al. 2015). When combined with DNA barcoding, wing geometry has also been proposed as a novel approach for differentiating morphologically similar mosquito species in the genus *Armigeres* (Diptera: Culicidae) (Laojun et al. 2024). These findings collectively underscore the method's utility in both interspecific and intraspecific analyses.

Despite its widespread application in other insect orders, the use of GM analyses in Hemiptera remains relatively limited. Existing studies primarily focus on wing patterns and male genital structures within certain families (Gumiel et al. 2003, Campos et al. 2011, Li et al. 2017).

To overcome the limitations of morphology-based taxonomy, recent research has emphasized integrative approaches that combine multiple lines of evidence. For instance, Bluemel et al. (2014) employed a combination of vibration signals, mitochondrial DNA, and aedeagus morphology to delimit species within the taxonomically complex genus *Aphrodes* (Hemiptera: Cicadellidae). Their work highlights the value of incorporating behavioural, genetic and morphological data in taxonomic decision-making, particularly in groups with subtle interspecific differences. These developments underscore the need for further application of GM and integrative methods in Hemiptera to improve the

resolution of species boundaries and better understand evolutionary relationships within the group.

In this study, shape analyses of the aedeagus and genital plate revealed clear interspecific differences. Aedeagus size differed significantly between species ($p = 0.01$), whereas genital plate size did not ($p = 0.8$). Principal Component Analysis explained 62.2% of the total variation for the genital plate and 61.2% for the aedeagus, with shape changes associated with landmark elongation, shortening, and widening. Canonical variance and discriminant function analyses confirmed clear species separation. In *Cercopis vulnerata*, the genital plate was shorter and wider, with reduced concavity between landmarks 1–3 and 4–5, while the aedeagus shaft was wider, with a longer apex, extended first pair appendages, and a broader, longer basal tip. These results indicate that both aedeagus and genital plate morphometrics are highly informative for species discrimination.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

- Adams D. C., Slice D. E. & Rohlf F. J. 2004. Geometric morphometrics: ten years of progress following the 'revolution.' *Italian Journal of Zoology* 71: 5-16. <https://doi.org/10.1080/11250000409356545>.
- Arnqvist G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. *Nature*, 393 (6687): 784-786.
- Bai M., Beutel R. G., Liu W.G., Li S., Zhang M. N., Lu Y. Y., Song K. Q., Ren D. & Yang X. K. 2014. Description of a new species of Glaresidae (Coleoptera: Scarabaeoidea) from the Jehol Biota of China with a geometric morphometric evaluation. *Arthropod Systematics & Phylogeny* 72: 223-236.
- Bai Y., Dong J. J., Guan D. L., Xie J. Y. & Xu S.O. 2016. Geographic variation in wing size and shape of the grasshopper *Trilophidia annulata* (Orthoptera: Oedipodidae): morphological trait variations follow an ecogeographical rule. *Scientific Reports* 6 (32680): 1-15.
- Bartlett C. R., Dietz L. L., Dmitriev D. A., Sanborn A. F., Soulier-Perkins A. & Wallace M. S. 2018. "The Diversity of the True Hoppers (Hemiptera: Auchenorrhyncha), 501-590". In: *Insect Biodiversity: Science and Society Volume II*. (Eds.): Footitt R. G. & Adler P. H.). Wiley Blackwell, Chichester/England, 1024 pp.
- Belintani T., de Paiva V. F., de Oliveira J. & da Rosa J. A. 2022. New in morphometry: Geometric morphometry of the external female genitalia of Triatominae (Hemiptera: Reduviidae). *Acta Tropica* 229 (106383): 1-8.
- Bluemel J. K., Derlink M., Pavlovčič P., Russo I. R. M., Andrew King R., Corbett E., Blejec A., Wilson M. R., Symondson W. O. C. & Virant-Doberlet M. 2014. Integrating vibrational signals, mitochondrial DNA and morphology for species determination in the genus *Aphrodes* (Hemiptera: Cicadellidae). *Systematic Entomology* 39 (2): 304-324.
- Bookstein F. L. 1991. *Morphometric Tools for Landmark Data*. Cambridge University Press, New York Cambridge, 455 p.

- Börstler J., Lühken R., Rudolf M., Steinke S., Melaun C., Becker S., Garms R. & Kruger A. 2014. The use of morphometric wing characters to discriminate female *Culex pipiens* and *Culex torrentium*. *Journal of Vector Ecology* 39: 204-212.
- Campos R., Botto-Mahan C., Coronado X., Jaramillo N., Panzera F. & Solari A. 2011. Wing shape differentiation of *Mepraia* species (Hemiptera: Reduviidae). *Infection, Genetics and Evolution* 11: 329-333.
- Changbunjong T., Chaiphongpachara T. & Weluwanarak T. 2023. Species discrimination of *Stomoxys* flies *S. bengalensis*, *S. calcitrans*, and *S. sitiens* (Diptera: Muscidae) using wing geometric morphometrics. *Animals* 13 (4): 647-655.
- Cheng L., Tong Y., Zhao Y., Sun Z., Wang X, Ma F. & Bai, M. 2022. Study on the relationship between richness and morphological diversity of higher taxa in the darkling beetles (Coleoptera: Tenebrionidae). *Diversity* 14 (1): 60-72.
- Cryan J. R. & Svenson G. J. 2010. Family-level relationships of the spittlebugs and froghoppers (Hemiptera: Cicadomorpha: Cercopoidea). *Systematic Entomology* 35: 393-415.
- Demirel E. & Dinç H. 2021. *Cercopis sanguinolenta* (Scopoli, 1763) (Hemiptera: Auchenorrhyncha: Cercopidae) dilemma and redescription of rare *Cercopis* Fabricius, 1775 species from Turkey. *Turkish Journal of Entomology* 45 (1): 99-114.
- Demirel E. 2022. Some color variations of *Cercopis distincta* (Melichar, 1896) and a recent contribution to the asset of Hatay Cercopids: *Triecphorella geniculata* (Horváth, 1881) *Biological Diversity and Conservation* 15 (3): 332-338. <https://doi.org/10.46309/biodicon.2022.1194694>
- Demirel E. & Hasbenli A. 2021. Contributions to the Cercopidae Leach, 1815 (Hemiptera: Auchenorrhyncha) fauna of the Bolkar Mountains. *Biological Diversity and Conservation* 14 (3): 456-463.
- Escobar-Suárez S., Villalobos-Leiva A., Fabres A., Ordenes-Calavería R., Cruz-Jofré F., Laroze D. & Benítez H. A. 2023. A geometric morphometrics and genetics characterization of *Vanessa carye* in an extreme elevational gradient in the Chilean Altiplano. *Zoologischer Anzeiger* 304: 105-112.
- Espinoza-Donoso S., Angulo-Bedoya M., Lemic D. & Benítez H. A. 2020. Assessing the influence of allometry on sexual and non-sexual traits: An example in *Cicindelidia trifasciata* (Coleoptera: Cicindelinae) using geometric morphometrics. *Zoologischer Anzeiger* 287: 61-66.
- Gumiel M., Catalá S., Noireau F., Rojas de Arias A., García A. & Dujardin J.P. 2003. Wing geometry in *Triatoma infestans* (Klug) and *T. melanosoma* Martínez, Olmedo & Carcavallo (Hemiptera: Reduviidae). *Systematic Entomology* 28: 173-179.
- Hammer Ø., Harper D. A. T., Ryan P. D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologica Electronica* 4: 1-9.
- Harvey A. & Sherratt E. 2023. A comparison of ecomorphology between introduced and native Australian dung beetles. *Australian Journal of Zoology* 70 (4): 115-125.
- Holzinger W. E., Kammerlander I. & Nickel H. 2003. The Auchenorrhyncha of Central Europe. Fulgoromorpha, Cicadomorpha excl. Cicadellidae. (Volume:1) Koninklijke Brill NV, 673 p.
- Jaramillo-O. N., Dujardin J. P., Calle-Londoño D. & Fonseca-González I. 2015. Geometric morphometrics for the taxonomy of 11 species of *Anopheles mosquitoes*. *Medical and Veterinary Entomology* 29: 26-36. <https://doi.org/10.1111/mve.12091>.
- Klingenberg C.P. 2011. MorphoJ: An integrated software package for geometric morphometrics. *Molecular Ecology Resources* 11 (2): 353-357. <https://doi.org/10.1111/j.1755-0998.2010.02924.x>
- Klingenberg C.P. 2013. Visualizations in geometric morphometrics: how to read and how to make graphs showing shape changes. *Hystrix* 24, 15.
- Kociński M., Grzywacz B., Hristov G. & Chobanov D. 2021. A taxonomic outline of the *Poecilimon affinis* complex (Orthoptera) using the geometric morphometric approach. *PeerJ* 9: 1-20. <https://doi.org/10.1016/j.vetpar.2023.110092>.
- Laojun S., Changbunjong T., Sumruayphol S., Pimsuka S. & Chaiphongpachara T. 2024. Wing geometric morphometrics and DNA barcoding to distinguish three closely related species of *Armigeres* mosquitoes (Diptera: Culicidae) in Thailand. *Veterinary Parasitology* 325:110092. <https://doi.org/10.1016/j.vetpar.2023.110092>.
- Li S., Ricchiardi E., Bai M. & Yang X. 2016. A taxonomy review of *Oreoderus* Burmeister, 1842 from China with a geometric morphometric evaluation (Coleoptera, Scarabaeidae, Valgini). *ZooKeys* 552: 67-89.
- Li R., Zhang H., Li S. & Bai M. 2017. Geometric morphometric analysis of *Eysarcoris guttiger*, *E. annamita* and *E. ventralis* (Hemiptera: Pentatomidae). *Systematic Zoology* 42: 90-101. <https://doi.org/10.11865/zs.201708>.
- Liang A. P. & Fletcher M. J. 2002. Morphology of the antennal sensilla in four Australian spittlebug species (Hemiptera: Cercopidae) with implications for phylogeny. *Australian Journal of Entomology* 41: 39-44.
- Liang A. P. & Webb M. D. 2002. New taxa and revisionary notes in Rhinaulacini spittlebugs from southern Asia (Homoptera: Cercopidae). *Journal of Natural History* 36: 729-756.
- Liu H. Y., Du, R. L., Zhao, W., Yang, X. K., & Yang, Y. X. 2023. A morphometric approach to the comparative morphology of aedeagi shapes in net-winged beetles: A case study on the *Macrolycus dotatus* species group (Coleoptera: Lycidae). *Arthropod Systematics & Phylogeny* 81: 897-916.
- Lodos N. & Kalkandelen A. 1981. Preliminary list of Auchenorrhyncha with notes on distribution and importance of species in Turkey VI. families Cercopidae and Membracidae. *Türkiye Bitki Koruma Dergisi* 5 (3): 133-149.
- Ludoški J., Francuski L., Gojković N., Matić B. & Milankov V. 2023. Sexual size and shape dimorphism, and allometric scaling in the pupal and adult traits of *Eristalis tenax*. *Ecology and Evolution* 13 (3): 1-17.
- Mutanen M. & Pretorius E. 2007. Subjective visual evaluation vs. traditional and geometric morphometrics in species delimitation: a comparison of moth genitalia. *Systematics Entomology* 32: 371-386. <https://doi.org/10.1111/j.1365-3113.2006.00372.x>.
- Nugroho S. S., Mujiyono S. P. S., Prasetyo A. S. & Garjito T. A. 2020. Wing geometry analysis as a potential tool for species identification for *Anopheles mosquitoes* (Diptera: Culicidae) in Indonesia. *Serangga* 25 (1): 93-104.
- Oleksa A., Căuia E., Siceanu A., Puškadija Z., Kovačić M., Pinto M. A. & Tofilski A. 2023. Honey bee (*Apis mellifera*) wing images: a tool for identification and conservation. *GigaScience* 12: 1-13.
- Ossiannilsson, F. 1978. The Auchenorrhyncha (Homoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 7 (1): 1-122.

- Qubaiová J., Růžička J. & Šípková H. 2015. Taxonomic revision of genus *Ablattaria* Reitter (Coleoptera, Silphidae) using geometric morphometrics. *ZooKeys* 477: 79-87.
- Önder F., Tezcan S., Karsavuran Y. & Zeybekoğlu Ü. 2011. Türkiye Cicadomorpha, Fulgoromorpha ve Sternorrhyncha Kataloğu, Meta Basım, İzmir, 157 p.
- Polihronakis M. 2006. Morphometric analysis of intraspecific shape variation in male and female genitalia of *Phyllophaga hirticula* (Coleoptera: Scarabaeidae: Melolonthinae). *Annals of the Entomological Society of America* 99 (1): 144-150.
- Pretorius E. & Scholtz C. H. 2001. Geometric morphometrics and the analysis of higher taxa: a case study based on the metendosternite of the Scarabaeoidea (Coleoptera). *Biological Journal of the Linnean Society* 74 (1): 35-50.
- Rohlf F. J. 2015. The tps series of software. *Hystrix* 26: 9-12.
- Rohlf F. J. & Bookstein F. L. 1990. Proceedings of the Michigan morphometrics workshop. University of Michigan Museum of Zoology.
- Rohlf F. J. & Marcus L. F. 1993. A revolution in morphometrics. *Trends in Ecology & Evolution* 8 (4): 129-132.
- Rohlf F. J. & Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Zoology* 39 (1): 40-59.
- Romiti F., Redolfi De Zan L., Piras P. & Carpaneto G. M. 2017. Shape variation of mandible and head in *Lucanus cervus* (Coleoptera: Lucanidae): a comparison of morphometric approaches. *Biological Journal of the Linnean Society* 120 (4): 836-851.
- Saiwichai T., Laojun S., Chaiphongpachara T. & Sumruayphol S. 2023. Species identification of the major Japanese encephalitis vectors within the *Culex vishnui* subgroup (Diptera: Culicidae) in Thailand using geometric morphometrics and DNA barcoding. *Insects* 131: 1-14.
- Sarıkaya A. D., Okutaner A. Y. & Sarıkaya Ö. 2019. Geometric morphometric analysis of pronotum shape in two isolated populations of *Dorcadion anatolicum* Pic, 1900 (Coleoptera: Cerambycidae) in Turkey. *Turkish Journal of Entomology* 43 (3): 263-270.
- Smith-Pardo, A. H., Lingafelter, S. W., Laroze, D., Piñeiro-Gonzalez, A., & Benítez, H. A. 2025. Shape as a Key to Taxonomy: Morphometric Analysis of *Tetropium* Species (Coleoptera: Cerambycidae). *Insects* 16 (4): 386. <https://doi.org/10.3390/insects16040386>
- Soulier-Perkins A. Cercopoidea Organised On Line. The Catalogue of Life Partnership. 2019. doi: 10.15468/2jxczc.
- Suganya M. & Manimegalai K. 2021. Landmark-based Geometric Morphometric Analysis of Wing Shape of *Trilophidia annulata* (Orthoptera: Acrididae). *Journal of Huazhong University of Science and Technology* 50 (6):1-13.
- Tanyeri R. & Zeybekoğlu Ü. 2020. Color/Pattern Variation of *Cercopis vulnerata* Rossi, 1807 (Auchenorrhyncha: Cercopidae) Populations of Northwestern Turkey. *The Black Sea Journal of Sciences* 10 (2): 266-273.
- Tanyeri R. & Zeybekoğlu Ü. 2022. Evaluation of Cercopidae (Hemiptera: Auchenorrhyncha: Cicadomorpha) Species Distributed in Sinop and Kastamonu (Turkey) in Taxonomic Terms. *Kahramanmaraş Sütçü İmam University Journal of Agriculture* 25 (1): 133-139.
- Tanyeri R., Kaya A., Selçuk A. Y., Kefelioğlu H. & Zeybekoğlu H. 2025. Discrimination of the three *Aphrophora* species: Linear morphometric and 2D-geometric morphometric approach. *Biologia* 80: 1997-2006.
- Tarrís-Samaniego S., Muzón J. & Iglesias M. S. 2023. When size and shape matter: morphometric characterization of two sympatric dragonflies of the genus *Perithemis* (Odonata: Libellulidae). *Anais da Academia Brasileira de Ciências* 95 (Supply 1): 1-10.
- Zúniga-Reinoso Á. & Benítez H. A. 2015. The overrated use of the morphological cryptic species concept: An example with *Nyctelia* darkbeetles (Coleoptera: Tenebrionidae) using geometric morphometrics. *Zoologischer Anzeiger* 255: 47-53.
- Zelditch M. L., Swiderski D. L. & Sheets H. D. 2004. Geometric morphometrics for biologists: a primer. Academic press. New York and London, 437p.
- Zhao W., Liu H., Geiser M. & Yang Y. 2022. Morphology and geometric morphometrics unveil a new genus of Cantharidae (Coleoptera, Elateroidea) from mid-Cretaceous Burmese amber, with a preliminary investigation on the phylogenetic position. *Invertebrate Systematics* 36 (7): 608-621.
- Zubrii N. A., Filippov B. Y., Kondakov A. V., Khruleva O. A., Rybalov L. B. & Vikhreva D. V. 2022. DNA Barcoding versus morphological variability of *Pterostichus brevicornis brevicornis* (Kirby, 1837) (Coleoptera, Carabidae) in the Arctic and Subarctic. *Insects* 13 (2): 204-221.
- Zubrii N. A., Filippov B. Y., Kondakov A. V., Khruleva O. A. & Rybalov L. B. 2023. Integrative taxonomy of two morphologically similar species of the subgenus *Cryobius* Chaudoir, 1838 (Coleoptera: Carabidae: *Pterostichus* Bonelli, 1810) from northern Eurasia and North America. *Ecologica Montenegrina* 61: 8-15.

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