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GEOMETRIC MORPHOMETRICS OF THREE SPECIES OF THE GENUS *DOCIOSTAURUS* (ORTHOPTERA: ACRIDIDAE) FROM THE MIDDLE ATLAS OF MOROCCO

Aziz Zahri[a], Nabil Errabhi[b], Wafae Squalli[a]*, Ismail Mansouri[c], Nabil Radouane[a, d], Said Ezrari[a, e], Houria Nekhla[a], Lazraq Abderrahim[a], Lahsen EL Ghadraoui[a]

[a]Department of Biology, Laboratory of Functional Ecology and Environmental Engineering, FST-Fez, Sidi Mohamed Ben Abdellah University, 2202, Route d'Imouzzer, Fez, Morocco; [b]Agricultural Zoology Unit, Ecole Nationale d'Agriculture de Meknès, BPS 40, Meknès, Morocco; [c]Research Team "Biology, Environment and Health", Department of Biology, Faculty of Sciences and Technologies Errachidia, Moulay Ismail University of Meknes, 52000 Errachidia, Morocco; [d]Phytopathology Unit, Department of Plant Protection, Ecole Nationale d'Agriculture de Meknès, BPS 40, Meknès, Morocco; [e]Laboratory of Bioresources, Biotechnology, Ethnopharmacology and Health, Faculty of Medicine and Pharmacy Oujda, University Mohammed First, Oujda, Morocco

*Corresponding author. Email: Wafaesqualli7@gmail.com

Aziz Zahri: https://orcid.org/0000-0003-3408-3468
Nabil Errabhi: https://orcid.org/0000-0003-1636-2420
Wafae Squalli: https://orcid.org/0000-0002-5480-8617
Ismail Mansouri: https://orcid.org/0000-0002-3679-6050
Nabil Radouane: https://orcid.org/0000-0002-1173-470X
Said Ezrari: https://orcid.org/0000-0003-3227-0948
Houria Nekhla: https://orcid.org/0000-0003-3507-8062
Abderrahim Lazraq: https://orcid.org/0000-0001-6394-9158
Lahsen El Ghadraoui: https://orcid.org/0000-0003-1766-5896

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Abstract. The genus *Dociostaurus* includes at least five species in the Mediterranean Basin. Some of them can damage agricultural fields and pastures. However, these species are almost not characterised by quantitative traits. To fill this gap, we used the geometric morphometrics method to characterise different morphological structures and flying organs of the most observed species of the genus *Dociostaurus*, namely *D. maroccanus* (Thunb, 1815), *D. dantini* (Bolivar, 1914), and *D. genei* (Ocskay, 1832), in Morocco. Results revealed that *D. maroccanus* has greater dispersal structures and other body organs, which are suggested to play a direct role in flying performance. On the contrary, *D. dantini* and *D. genei*, known as wandering species, have tiny structures, principally the tegmina and wings used for limited flights. In addition to their importance in the characterisation of studied species, these measurements could be used as a practical tool in their identification, particularly where the use of genetic approaches is not possible. Similarly, these results could serve as the first data for the implementation of potential comparative studies and population management of these pest species, especially *D. maroccanus*. Finally, further morphometric studies will be needed to create a database for taxonomic identification.

INTRODUCTION

The genus *Dociostaurus* includes up to 26 species (Savitsky 2007) distributed in south-east Europe and west, south-east, and central Asia, up to south-east Kazakhstan, Afghanistan, and north-west Pakistan (Uvarov 1932; Baldacchino et al. 2012; Şirn and Mol 2013). Five species are specific to the Mediterranean basin, namely, *D. maroccanus*, *D. dantini*, *D .genei*, *D. hammadae* (Ingrisch 1983), and *D. biskrensi* (Moussi et al. 2014; GonzÁlez-Serna et al. 2018). These species are found in different habitats and under variable climatic conditions. Recently, new species were described from Turkey, i.e. *D. icconium* (Şirn and Mol 2013). On the other hand, these species are known for their significant agricultural impacts (Çiplak 2021), causing serious damage to crops and forage, particularly in north Africa and the Middle East (Lockwood and Sardo 2021). In Morocco, the genus *Dociostaurus* is very common and diverse (Errabhi et al. 2017). These species are distributed across different regions from the coastal areas of both the Atlantic Ocean and the Mediterranean Sea to high altitude zones of the Atlas Mountains. The most relevant species are *D. maroccanus*, *D. genei*, and *D. dantini,* which are found principally in the Middle Atlas. *D. maroccanus* is known for its voracity against crops, with a wide diet spectrum and high mobility offered by its wings (El Ghadraoui et al. 2010). On the contrary, *D. genei* and *D. dantini* are very limited in terms of diet and mobility (Essakhi et al. 2015). Therefore, the analysis of dispersal capacity is required to identify the role of wings in this biological function.

For several years, investigators have investigated the factors influencing the voracity and agricultural impact of Acrididae (Pincebourde et al. 2017; Dakhel et al. 2020). Results showed that a wide diet spectrum and intense food consumption are considered the main factors (Basiouny and Ghoneim 2021; Egonyu et al. 2021). Acrididae are known for the intestinal diversity of microbial and enzymatic capacities, and these allow the consumption and digestion of food in large quantities (Zahri et al. 2021).

Other elements, such as sensory organs, principally chemoreceptors sensilla on the palps, antennae, and the epipharyngeal surface of the labrum are involved in the diet and voracity of Acrididae including the genus *Dociostaurus* (El Ghadraoui et al. 2002; Zaim et al. 2013; Guerrero et al. 2017). However, the mobility of locusts has the same importance as the digestive mechanisms. The species characterised by high mobility, such as *D. maroccanus*, *Locusta migratoria* (Linnaeus, 1758), and *Schistocerca gregaria* (Forskal, 1775), are known for their consumption of crops and plants along their migratory routes (Rajapakse et al. 2019; Maeno et al. 2020). In summary, the combination of a wide diet spectrum and high mobility capacity is of great interest for pest control. While the foraging and diet aspects are widely studied for management purposes, movement and flying traits are still unexplored, especially regarding their impact on crops. Investigations addressing the movement capacity of Acrididae species are fragmentary and rare. Most of these studies were focused only on two migratory species, while wandering species inhabiting specific habitats are not explored yet. Equally, the studied traits were limited to simple morphological measurements. However, to clarify which organs or structures are used in flight capacity, additional studies are needed. In this study, we used an original approach combining geometric morphometrics methods to characterise and measure the flying capacity of the most observed species of the genus *Dociostaurus* (*D. maroccanus, D. genei,* and *D. dantini*) in the Middle Atlas. We highlight the correlation between different morphological traits of wings directly related to flying capacity. We considered the insect's size and elytra deformation, which are directly related to flight. We defined the vein junction point's positions (landmark points). This allowed us to highlight the existing morphological differences between the three species.

MATERIALS AND METHODS

Specimen collection

The studied insects, *D. maroccanus*, *D. genei*, and *D. dantini*, were collected from Timahdite (33°13'48"N, 5°03'36"W), located in the Middle Atlas (Morocco) (Figure 1). This area is dominated by a humid climate with precipitation ranging from 500 to 800 mm and temperatures between 4 °C during winter and 48 °C during summer. We selected Timahdite due to the coexistence and abundance of the focal taxa.

Insects were collected in agricultural fields of cereals, herbaceous vegetation, and open areas far from forests and woodlands. During the morning (when insects were less active), we individually collected each insect by handling an insect net. Nets were swept over the foliage of study sites, and each captured insect was put in a 4 × 4 cm plastic bottle. On the same day, collected insects were transported to the laboratory for measurement.

Morphological measurements

In the laboratory, collected insects (10 males and 10 females per species) were separated and conserved at 4 °C in the fridge. The following traits were measured: body length (BL), wing length (WL), tegmen length (EL), hind femur length (FL), pronotum length (PL), and length of the abdomen (Abd). The measurements were taken using an electronic calliper with 0.01 mm accuracy. The values obtained were listed and classified by sex and species.

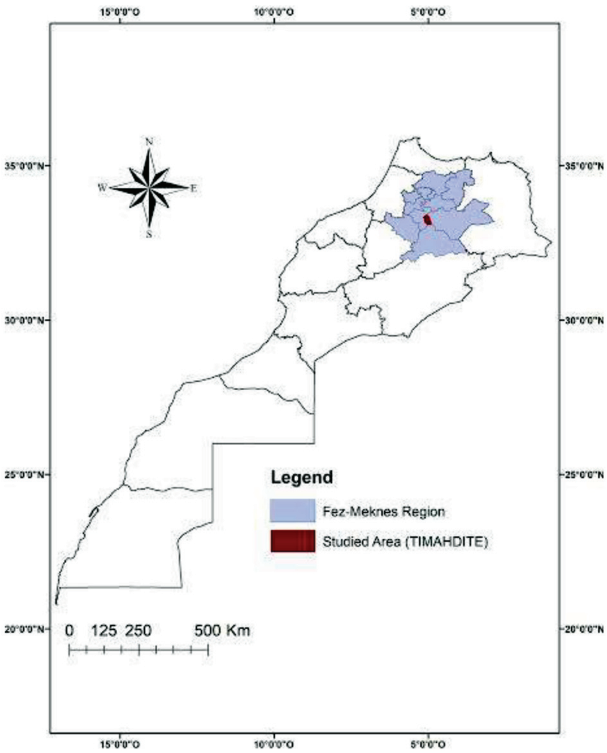

Figure 1. Location of the study area, Timahdite (Morocco).

Geometric morphometrics measures

For geometric traits, 20 insects (10 males and 10 females per species previously manipulated for morphological measurements) were used. The elytra were detached from the insect body with fine forceps and fine scissors, then placed between two microscope slides and photographed under a binocular microscope. The obtained pictures were considered the basis for calculating wing dimensions and surfaces with the software ImageJ. On each picture (elytra), we pinned the point mark 'PR' with a unique number and automatically identified it by its coordinates (x, y) in a plane with the GST package. Further, we positioned and rotated all obtained pictures (for elytra of all individuals) using a technique known as generalised Procrustes analysis (GPA) to clearly show the marked points. Then, digitalised data were transmitted and analysed with MorphoJ.

During digitalisation, sometimes the median cell bounded by the veins MA_1 and MA_2 was absent in some individuals and was ignored (only 3 to 4 individuals had degraded elytra) (Figure 2). Furthermore, subadult or damaged individuals were not considered. Finally, the geometric morphometry technique considered the point marks (PR) homologous across species, ensuring the characterisation of elytra shape.

The software MorphoJ calculates the partial deformation recorded on the elytra to generally compare the shape of the wing. The distance between RA 2, 3, 4, and 6 and PR 1 describes the proximal portion, and the distance between PR 4, 5, and 8 defines the central area, while the distance between PR 4 and PR 9 shows the distal portion. Finally, large elytral surfaces are assumed to be more suited for long distance flights.

Statistical analysis

Before running the statistical analysis, we tested for normality and homogeneity of variance for all measured parameters via the Kolmogorov–Smirnov test. Morphological structures, including the wings (WL), femur (FL), elytra (EL), body (BL), pronotum (PL), and abdomen (Abd), as well as elytra geometric measurements counting length, width, area, and angle (α), were compared among *D. genei*, *D. dantini*, and *D. maroccanus* via one-way ANOVA. To evaluate the morphological differences of the species studied, we considered the morphometric measurements of the organs as variables, while the morphological structures, including the wings (WL), femur (FL), elytra (EL), body (BL), pronotum (PL), and abdomen (Abd), were considered as unobserved (main factors). These data were processed with PCA, which is a powerful tool for the analysis of multivariate data, by recording only those factors with a value >1.0. We interpreted the meaning of the principal components, which explains the highest amount of combined variation within the morphological data, by analysing the component loadings of every variable. Finally, statistic tests were realised in Statgraphics Centurion software, version XVII. Results were considered significant at $p < 0.05$.

RESULTS

Morphological comparison

Morphometric measurements of studied species are presented in Table 1. Dispersal organs, including the wings (WL), femur (FL), and elytra (EL), as well as the body (BL), pronotum (PL), and abdomen (Abd), are shorter

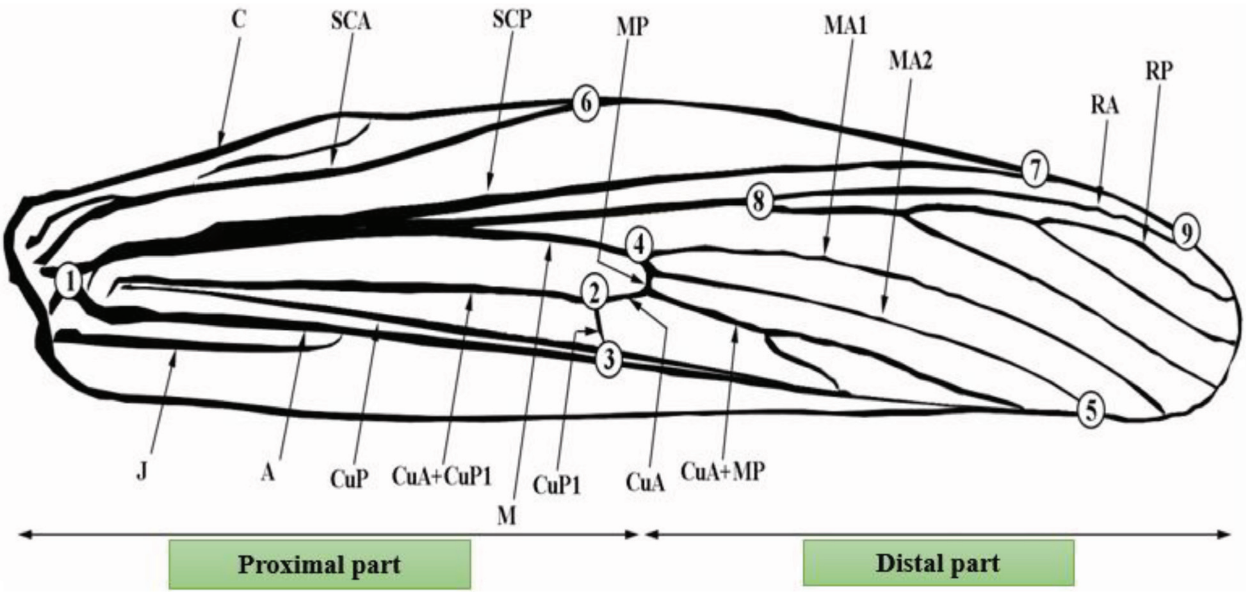

Figure 2. Location of landmarks on a locust male elytrum. **C**: costal; **SC**: subcostal; **R**: radius; **M**: media; **Cu**: cubitus; **A**: anal; **J**: jugal; **A**: anterior; **P**: posterior.

Table 1. Comparison of female morphological structures between study species via one-way ANOVA test.

Parameters	*D. maroccanus*	*D. dantini*	*D. genei*	DF	F	*p*
Body (BL)	24.08 ± 1.24	22.77 ± 0.78	14.55 ± 0.37	2	346.80	< 0.001
Wings (WL)	20.53 ± 0.56	16.95 ± 0.45	9.99 ± 0.53	2	1069.01	< 0.001
Elytra (EL)	20.65 ± 0.46	17.9 ± 0.39	11.64 ± 0.41	2	1167.95	< 0.001
Femur (FL)	13.32 ± 0.35	13.16 ± 0.39	8.39 ± 0.26	2	660.25	< 0.001
Thorax (Tho)	5.31 ± 0.23	5.4 ± 0.19	2.48 ± 0.42	2	306.99	< 0.001
Abdomen (Abd)	12.31 ± 0.41	11.37 ± 0.22	8.4 ± 0.29	2	406.01	< 0.001

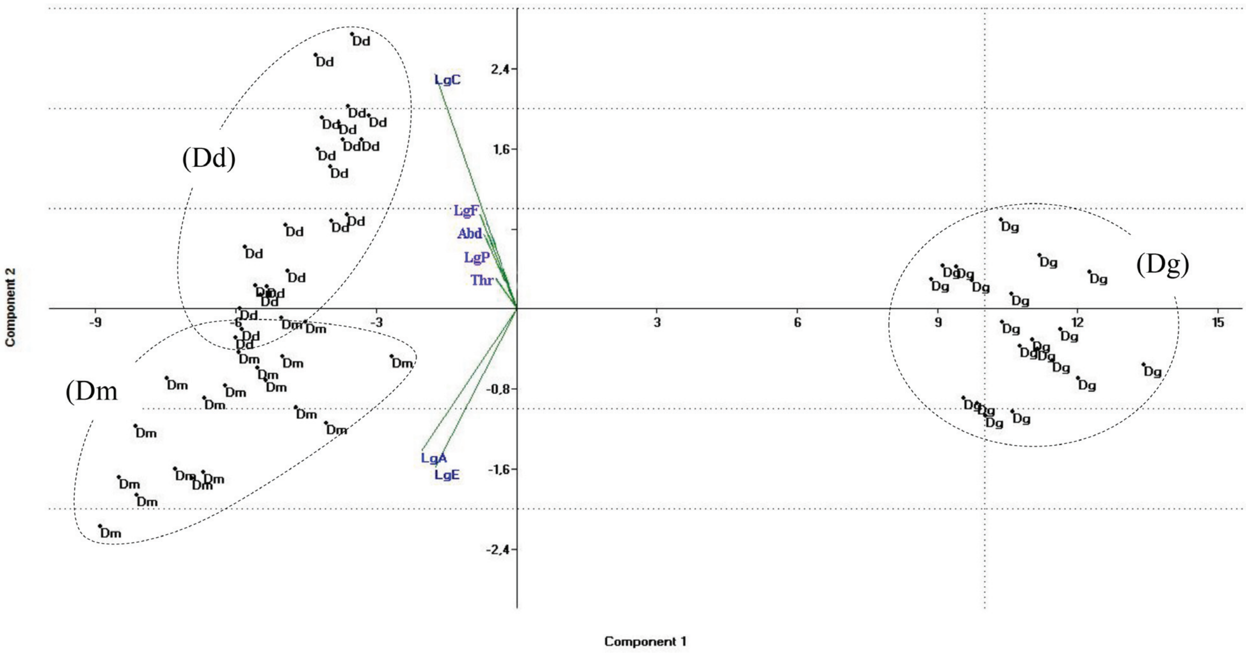

Figure 3. Principal component analysis (PCA) of the main biometric measurements (**LGC**: body length; **LGA**: hind wing length; **LGE**: length of the elytra; **LGF**: hind femur length; **Abd**: abdomen; **Thr**: thorax; **LGP**: length of the pronotum) characterising each species (**Dm**: D. maroccanus, **Dd**: D. dantini, and **Dg**: D. genei).

in *D. genei*. On the other hand, morphological structures differ between *D. maroccanus* and *D. dantini*. The wings (WL) and elytra (EL) are superior in *D. maroccanus*. In contrast, the femur (FL), body (BL), thorax (Tho), and abdomen (Abd) are similar between *D. maroccanus* and *D. dantini*.

The principal component analysis (PCA) explains the principal morphological structures characterising each species (Figure 3). *D. maroccanus* is characterised by long wings (WL) and elytra (EL). *D. dantini* has a robust body, including the thorax (Tho), abdomen (Abd), and femur (FL). On the other hand, *D. genei* is characterised by inferior structures and dispersal organs.

Flying organs and dispersal capacities

Measurements of flying organs in the studied species are presented in Figure 4. The length, width, and surface area of the elytra are superior in *D. maroccanus*, while *D. dantini* has a superior angle (α). On the contrary, all measured structures are inferior for *D. genei*.

To clarify the biometric differences (elytra) and, consequently, the dispersal capacity of each species, we highlighted the different deformations of elytra surfaces via geometric morphometric measurements (Figure 5). The three species showed sexual dimorphism. A very pronounced difference of six landmarks was documented between the sexes of all species. The junction of the SCA rib meeting the posterior margin of the wing shaft tends to be more distal in females than in males. On the other hand, the different positions of the markers with items 2, 3, 4, 6, 7, and 8 vary among the Acrididae species studied. These items are more oriented towards the translation of the discoid field.

In *D. maroccanus,* the projection of the elytra on strain grids shows a reduction of the length of the discoidal field (in the vicinity of PR 2 and 4), while the distal portion is larger. Further, at the distal part, the cells of the central area are extended, and cells of the radius field increase. Equally, cells are increased between PR 8 and the rear edge of the elytra, as well as between PR 8 and 7 in the end portion of the radius sector.

In *D. dantini,* the deformation of the distal portion leads

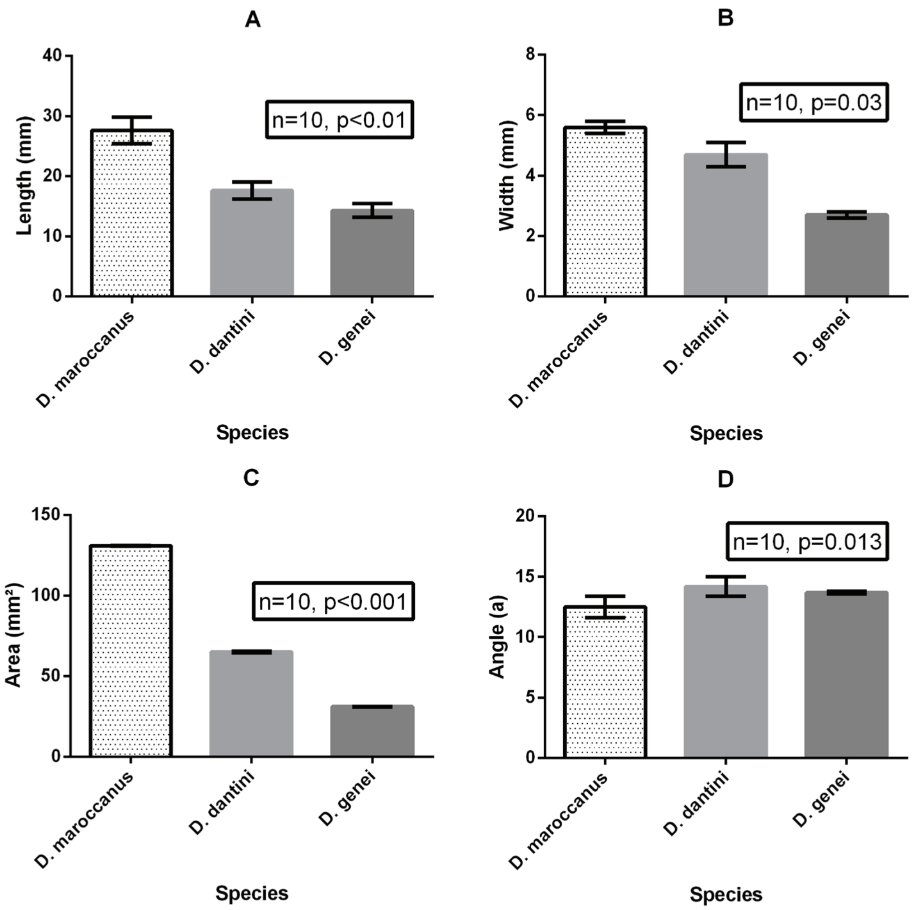

Figure 4. Graphic representation of the (**A**) length (in mm), (**B**) width (in mm), (**C**) area (in mm²), and (**D**) angle (α) of the elytra.

to the transposition of points 7 and 8. The deformation of the elytra is in the opposite direction with the end of the distal portion, and the expansion of the anterior and posterior cells of the subcostal and the proximal portions accompanies this. On the other hand, the dispersal of PR 2, 3, and 4 is more proximal via the increasing length of the proximal area inversely to *D. maroccanus* where this field is more elongated. The elytra of *D. dantini* show a reduction of cells in the radius field, which seems to be a direct handicap for the long-range flights.

In *D. genei*, all studied structures and cells are characterised by smaller measurements than those of *D. dantini* and *D. maroccanus.* In addition, the small cells near the wing shank reduce the ability to move over long-distance flights; however, items 3, 4, and 6 are oriented in the same way as in *D. maroccanus,* and this indicates a similar aerodynamics of flight between the two species but with a limited range in *D. genei*.

DISCUSSION

To our knowledge, this is the first exhaustive investigation concerning the morphology of flying structures of Moroccan acridids. Our major goals were to provide geometric morphometric data capable of distinguishing morphological structures and flying capacities of the most observed species of the genus *Dociostaurus* (*D. maroccanus, D. genei,* and *D. dantini*) in the Middle Atlas. We gained novel geometric morphometrics data characterising each species. These data are of crucial importance for the identification of Acrididae species, for piloting a possible comparative research and for management actions of these pests in Morocco and worldwide.

As expected, this study showed clear evidence of differences in morphological structures of the studied species despite their close evolutionary relationships and geographical distribution (Essakhi et al. 2014; GonzÁlez-Serna et al. 2018; Zahri et al. 2021). The obtained results unveil that *D. genei* is characterised by tiny body organs and structures for dispersion. These results are similar to those cited by other authors (Uvarov 1966; Inigo et al. 1993; Defaut 2017) in their descriptions of morphological structures of *D. genei.* They also revealed that the cross-shaped pattern characterising the pronotum of the genus *Dociostaurus*, as well as the pronotum itself, in this species are short and narrowed compared to *D. maroccanus* and *D. dantini* (Chopard

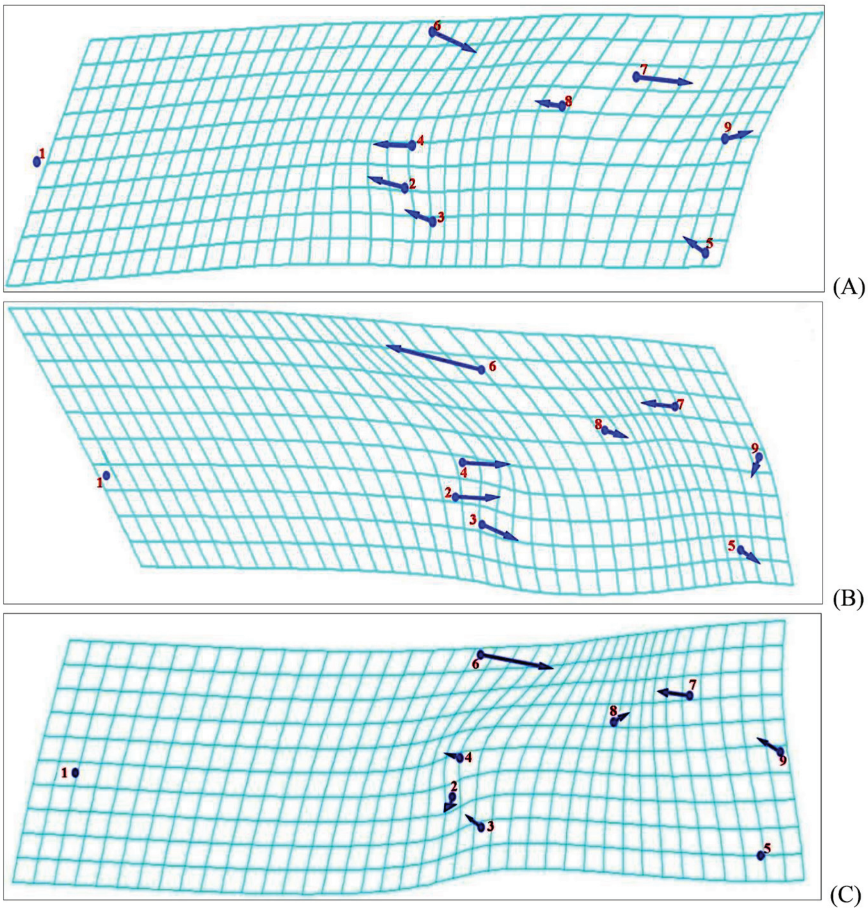

Figure 5. Projection of the elytra translocation point benchmarks of three Acrididae species (**A**: *D. maroccanus,* **B**: *D. dantini,* and **C**: *D. genei*) on deformation grids.

1943; Uvarov 1966). Also, this species is very close to *D. jagoi* (Soltani 1974) and seems to be distinguished only by the shape of the penis (Defaut 2004).

On the other hand, *D. dantini* and *D. maroccanus* are very close. They differ only in elytra and wings, which are greater in *D. maroccanus.* Since the difference is only recorded in dispersal organs (flying organs), we suggest that the greater length recorded in the wings and elytra of *D. maroccanus* is crucial for long-range dispersals. In reality, *D. maroccanus* is known for its migration behaviour between Morocco and Algeria (Benfekich et al. 2002), and therefore it needs developed wings and elytra to complete these flights, as demonstrated by El Ghadraoui et al. (2002). On the other hand, *D. dantini*, known as a wandering species in north Africa and Europe (Moussi et al. 2014; Massa and Fontana 2020), is characterised by the shorter wings and elytra. Moreover, for systematists, the difference in morphological measurements could be of great importance in the taxonomic identification of species, particularly in cases where genetic tools are not accessible. These morphometric approaches are widely used in the identification and characterisation of a wide range of animal species, including mosquitoes (Wilke et al. 2016), honey bees (Francoy et al. 2008), and lizards (Gabelaia et al. 2018). Moreover, these approaches permit identifying the closely related species of the same genus as in the case of *Lutjanus* spp. (Sadighzadeh et al. 2012) and morphologically close *Tabanus* spp. (Changbunjong et al. 2021).

The geometric morphometric approach revealed great differences among the studied species. *D. maroccanus* demonstrated more developed elytra compared to *D. dantini* and *D. genei*, while it also had a more elongated distal portion and radius sector, as well as extended cells of both the central area and the radius field. These robust elements are of crucial importance in insect flight, as demonstrated in the elytra of beetles (Dai et al. 2008; Dai and Yang 2010). In the case of *D. maroccanus,* the more developed wings and elytra with extended surfaces might be more efficient for long-range aerial dispersal. Similar results were recorded for the elytra of *Goliathus orientalis* (Pener and Simpson 2009), which were characterised by extended surfaces to ensure the best flying performances (Godeau et al. 2018), since the larger elytra permit an increase in the volume of air displaced during flights (Salcedo and Socha 2020). On the other hand, *D. dantini* and *D. genei* have small wings and elytra in correlation with their local movements. Both are wandering species with a limited dispersal ability. Wing flexibility is at the origin of the aerodynamic force which influences the flight performance in these insects, as demonstrated in other Acrididae of north Africa (Errabhi et al. 2017; Pass 2018; Salcedo and Socha 2020). Furthermore, wing venation patterns could be decisive for the taxonomic distinction between species of the genus *Dociostaurus* (Jago 1971).

CONCLUSION

This study provides the first data on morphological structures and flying capabilities of three species of the genus *Dociostaurus* (*D. maroccanus, D. genei,* and *D. dantini*) in Morocco and north Africa. *Dociostaurus maroccanus* displayed larger dispersal structures and other locomotory organs, which are suggested to play a direct role in their migratory performance. On the other hand, *D. genei* and *D. dantini*, known for their wandering status, are characterised by tiny structures, principally flying organs. In addition to their importance in the characterisation of studied species, these measurements could be used as a practical identification tool, particularly in cases where the use of genetic approaches is not possible. These results will be useful for future comparative studies and management actions for these pest species, especially *D. maroccanus*.

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