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The variability of *Heteracris adspersa* (Redtenbacher, 1889) re-examined (Orthoptera: Acrididae, Eyprepocnemidinae)

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Abstract
A new subspecies of *Heteracris adspersa* was described in 1978 on the basis of morphometrics and structure configuration of the male subgenital plate from specimens collected in Sardinia. The present study examines specimens (n=175) from a broad suite of localities, ranging from the Middle East across to the western Mediterranean. Statistical analyses are subsequently carried out on a revised dataset comprising 94♂♂ and 55♀♀. Microscopic examination of the subgenital plate is also conducted on specimens from Sardinia, Sicily, Malta and Yemen and compared with those published in the original description. Findings demonstrate that the subspecies *massai* is practically an artefact of unintended consequence, essentially a case of taxonomic inflation, in view of evident intra and interpopulation variability across a wide geographic area; consequently, *H. a. massai* is synonymised.

Key words: Mediterranean Basin, biometric analysis, *H. adspersa massai* **syn. nov**., geographical variability, intra-population disparity.

Introduction

The genus *Heteracris* Walker, 1870, comprising 63 species (listed in Annex below), has a wide geographical distribution (Grunshaw, 1991; Cigliano et al. 2025). It is represented throughout much of the Afrotropical (formerly Aethiopian) realm as well as across southern parts of the Western Palaearctic, including the Saharo-Arabian and Irano-Turanian subregions, and extends into the Oriental (formerly Indomalayan) realm (zoogeographical realms and subregions adapted from Sclater, 1858; Wallace, 1876; Holt et al. 2013).

Within the Mediterranean Basin, the genus is represented by some seven species (some of which have a restricted distribution, while others extend beyond the region), including *Heteracris adspersa* (Redtenbacher, 1889), *H. littoralis* (Rambur, 1838), *Heteracris annulosa* Walker, 1870, *Heteracris harterti* (Bolívar, 1913), *Heteracris minuta* (Uvarov, 1921), *Heteracris syriaca* (Brunner von Wattenwyl, 1861), and *Heteracris lieutaghii* Defaut, 1986. Five other species of the genus, the distribution of which is indicated for countries bordering the Basin, actually occur within localities beyond the boundaries of the Mediterranean ecosystem, which in their majority are hyper-arid habitats. These comprise *Heteracris rantae* (Uvarov, 1936) from Arabia and beyond; *Heteracris pterosticha* (Fischer von Waldheim, 1833) from eastern Turkey, extending eastward of the Middle East; *Heteracris etbaica* (Ramme, 1928) from the Etbai or Eastern Egyptian desert; *Heteracris hoggarensis* (Chopard, 1929) from the hyper-arid Algerian south; and *Heteracris morbosa cincticollis* (Walker, 1870) from the Negev desert. Lastly, Otte (1995) proposed *Heteracris turbida* (Walker, 1870) and *Heteracris mutator* (Walker, 1870) **nomina dubia** (Cigliano et al. 2025).

The distribution of *H. adspersa* lies along an east-west axis, comprising the Irano-Turanian subregion and much of the Mediterranean Basin (eastern sub-basin, central Mediterranean area and western sub-basin, including the Maghrebian segment of the Saharo-Arabian subregion). A new subspecies of *H. adspersa* from Sardinia, named '*massai*', was described by Galvagni (1978). The name of the present work's last author was the eponym (source of the subspecies' name), used as an expression of appreciation. Galvagni based his assumptions on morphological characters of the terminalia and on the biometrics of 34 male specimens and 13 females [Galvagni, 1978, Tabella delle dimensioni di *Heteracris adspersa massai* n. subsp., p. 167], which he compared with morphometric measurements in Bey-Bienko & Mistshenko (1951, p. 265; 1963 English translation, pp. 280-281, figs. 551-552) – see Discussion below. In a revision of the genus *Heteracris*, Grunshaw (1991) regarded subspecies *massai* a synonym of *H. adspersa*, a consideration based on the significant variability demonstrated following an extensive morphometric examination of a large suite of specimens from a broad geographical range. Likewise, on the basis of morphological assessment, Massa & Rizzo (1998) maintained that specimens from the western Mediterranean, notably Sardinia, Sicily, Tunisia and Spain, were demonstrably smaller in size than individuals of *H. a. adspersa* from other geographical locations. In their conclusions, Massa & Rizzo (1998), tended to concur with Galvagni (1978) that the subgenital plate in the males of the two taxa (ssp. *massai* and ssp. *adspersa*) was distinctively different. However, the authors added that the examination of more material was required in order to establish whether the two subspecific taxa retained well-defined respective distributions. Meanwhile, various subsequent works acknowledged the presence of *Heteracris adspersa massai* Galvagni, 1978 within the western Mediterranean Basin (Cassar et al. 2018; Iorio et al. 2019; Buzzetti et al. 2021; Cigliano et al. 2025).

The aim of the current contribution is to examine and compare the morphometrics of specimens of *H. adspersa* from various locations across the Mediterranean and the Middle East with a view to assess the dependability of the taxonomic description by Galvagni (1978).

Methodology

A total of 174 specimens were examined biometrically, of which 105 were male and 69 were female (Table 1). Geographical provenance of the specimens comprised the western Mediterranean sub-basin, the central Mediterranean area and the Irano-Turanian subregion. In addition, a male from Yemen was among the suite of specimens whose terminalia were examined for comparative purposes, rendering the total 175.

Apart from the significantly larger sample from a considerably broader geographical provenance, the current approach also varies from the methodology employed by Galvagni (1978) in the following manner: while Galvagni (1978) included the total length of the body (which includes soft tensile tissue that binds the abdominal tergites

Fig. 1 – A pair of *Heteracris adspersa* (♀ in the foreground) on *Arthrocnemum macrostachyum* at Salina, Malta. (Photo: G. Bonett).

Table 1. Entire dataset of measurements (sample size, mean ±s.d. for each parameter and each locality).

Provenance	*Length hind femora*	*Height hind femora*	*Length pronotum*	*Height pronotum*	*Length tegmina*
Males					
Spain (n=5)	11.9±0.5	2.3±0.1	3.4±0.2	3.0±0.1	15.0±0.8
Tunisia & Algeria (n=14)	12.1±0.4	2.3±0.2	3.4±0.2	2.9±0.2	15.4**±1.5**
Sicily (n=34)	11.8±0.5	2.2**±0.2**	3.3±0.2	3.0±0.1	14.2±0.8
Sardinia (n=34)	11.3±0.4	2.2±0.1	3.1±0.1	2.5±0.2	13.0±0.7
Malta (n=12)	12.5±0.5	2.5±0.2	3.5±0.3	3.2±0.2	15.5±0.8
Iran (n=6)	13.0±1.2	2.5±0.2	3.5±0.5	2.9±0.4	15.8±3.2
Females					
Spain (n=8)	17.8±1.8	3.6±0.4	5.1±0.8	4.5±0.5	22.8±3.6
Tunisia & Algeria (n=19)	18.2±1.1	3.3±0.2	5.3±0.4	4.6±0.4	22.9**±2.3**
Sicily (n=16)	16.4±1.0	3.1**±0.2**	4.8±0.4	4.0±0.3	19.4±1.4
Sardinia (n=17)	16.5±1.3	3.2±0.2	4.8±0.4	3.8±0.3	20.3±1.7
Malta (n=8)	16.7±6.8	3.1±1.3	5.7±0.6	4.6±0.4	24.6±1.9
Iran (n=1)	21.2	3.7	5.9	4.7	25.9

and sternites) in his calculations, the morphometrics used in the present study comprised only sclerotized parts of the body structure (Figure 2), notably the pronotum (dorsal length and lateral height), hind femur (length and maximum height) and tegmen (length). These were measured with an electronic digital calliper (resolution: 0.01mm/ accuracy: ±0.02). Measurement of the total length of the body structure, contrary to Galvagni's methodology, was thus not included in the present study in view of the presence of less strongly sclerotized membranes that may in-

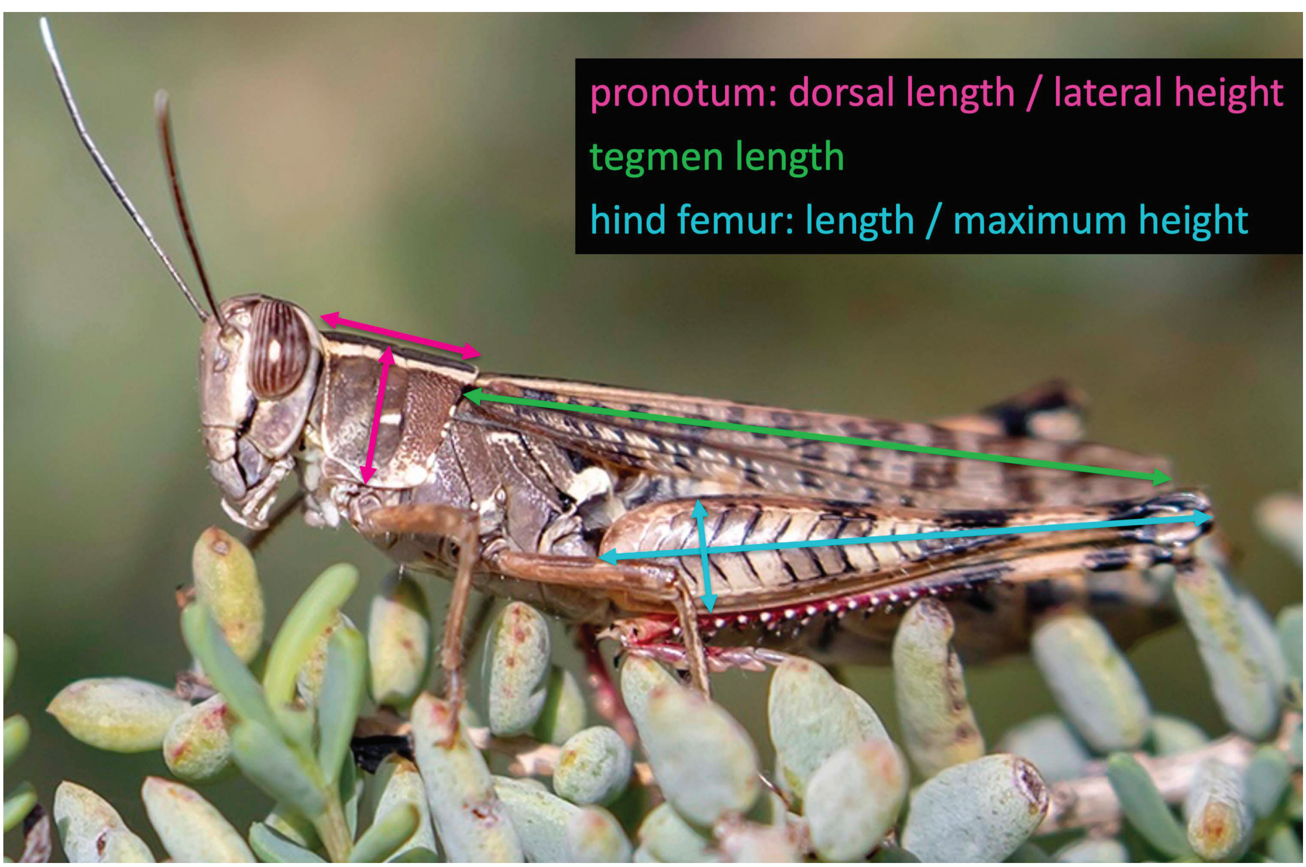

Fig. 2 – Selected sclerotized sections of the body structure used for morphometric analysis.

troduce a degree of variance – see paragraph below for details.

Data management and analysis – The dataset comprised morphometric information for the specimens listed above, collected from the six different geographical locations also listed above. Each specimen was characterised on the basis of sex and five continuous morphological variables: Hind Femur Length, Hind Femur Maximum Height, Pronotum Dorsal Length, Pronotum Lateral Height, and Tegmina Length.

Prior to statistical testing, the data were cleaned, and any specimens with missing values for site or morphometric traits were excluded from the analysis. Given that preliminary assessments indicated that morphometric differences between sexes, due to sexual dimorphism, outweighed differences arising from geographic provenance, male and female specimens were analysed separately. Consequently, 94 males and 55 females were used for the statistical analysis, grouped in the following manner: Spain: 3♂♂, 6♀♀; Tunisia/Algeria: 6♂♂, 9♀♀; Sardinia: 33♂♂, 16♀♀; Sicily: 34♂♂, 16♀♀; Malta: 12♂♂, 7♀♀; Iran: 6♂♂, 1♀.

To investigate multivariate morphometric differentiation, three techniques were utilised: Principal Component Analysis (PCA) to visualise geometric clustering; Permutational Multivariate Analysis of Variance (PERMANOVA) to test the statistical significance of among-site differences (using Euclidean distances and 999 permutations); and Linear Discriminant Analysis (LDA) with stratified cross-validation (3 folds) to quantify the diagnosability of populations. To ensure the robustness of the morphometric comparisons, a collinearity assessment was performed on the five selected structural variables prior to multivariate modelling. Pairwise Pearson correlation coefficients were calculated, and Variance Inflation Factors (VIF) were derived for both the male and female datasets. Variables exhibiting a VIF > 10 are generally considered to display problematic multicollinearity that could destabilise classification algorithms like LDA.

A preliminary multivariate analysis suggested that 'Total Body Length' was a major contributor to the variability between female specimens. The first Principal Component (PC1) alone explained 88.4% of the variability in Total Body Length itself, with very little residual variation contributing to shape differences (PC2). Given that the Total Body Length of an individual can vary seasonally in view of the laxer tissue that binds the tergites and sternites of the abdomen, especially but not exclusively in the case of females, then the variability of this factor makes it unsuitable for precise morphometric differentiation.

Examination of terminalia – Male terminalia of specimens from different geographical locations, including a male specimen from Yemen, were also examined. Those that appear in Figure 4 were photographed with a Nikon Coolpix 995 mounted on a Wild Heerbrugg M3 stereomicroscope and with a Leica DVM6 digital microscope with a field of view (FOV) of 43.73 mm and Z-stacking capability.

Results and Discussion

Multivariate analysis of structural traits – Collinearity assessment confirmed the suitability of the five-variable structural set for both sexes. In males, pairwise correlations were moderate (r max = 0.80 between tegmina length and hind femur length), and all Variance Inflation Factors (VIF) were well below the critical threshold (maximum VIF = 4.07). In females, stronger isometric scaling resulted in higher inter-variable correlations (r max = 0.88 between pronotum length and tegmina length); however, the maximum VIF was 6.38, indicating that multicollinearity was not severe enough to compromise the integrity of the linear discriminant models. Furthermore, the inherent dimensionality reduction of the subsequent PCA effectively transformed these correlated traits into orthogonal axes. As indicated in the Methodology above, males (n=94) and females (n=55) were analysed separately with a view to isolate geographic patterns in morphology, using the dataset of the five selected structural variables, notably the dorsal length of pronotum, lateral height of pronotum, length of tegmina, length of hind femur, and maximum height of hind femur.

For females (Figure 3a), the Principal Component Analysis (PCA) revealed a variation pattern dominated by a single size-related axis. The first principal component (PC1) explained 83.6% of the total variance, with all five variables showing strong positive correlations (r > 0.85). The second component (PC2) explained 7.1% of the variance, driven primarily by the maximum height of the hind femur (r = 0.54). Despite the overlap observed in the ordination plot, Permutational Multivariate Analysis of Variance (PERMANOVA) detected a significant, albeit moderate, geographic signal (F = 7.19, p = 0.001). Linear Discriminant Analysis (LDA) reached a classification accuracy of 51.9%, indicating that while populations differ statistically, individual specimens remain difficult to diagnose based on structural traits alone.

For males (Figure 3b), the analysis yielded a substantially stronger geographic resolution. The first two principal components explained 83.7% of the variance (PC1 = 72.1%, PC2 = 11.6%). Unlike in females, the male PC2 defined a distinct shape contrast, representing a trade-off between the overall dimensions of the hind femur (r = 0.56) and the overall dimensions of the pronotum (r = -0.50). This structural divergence was supported by a highly significant PERMANOVA result (F = 14.20, p = 0.001), with an F-statistic nearly double that of the females. LDA classification accuracy reached 74.5%, the highest value observed in this study, confirming that male populations

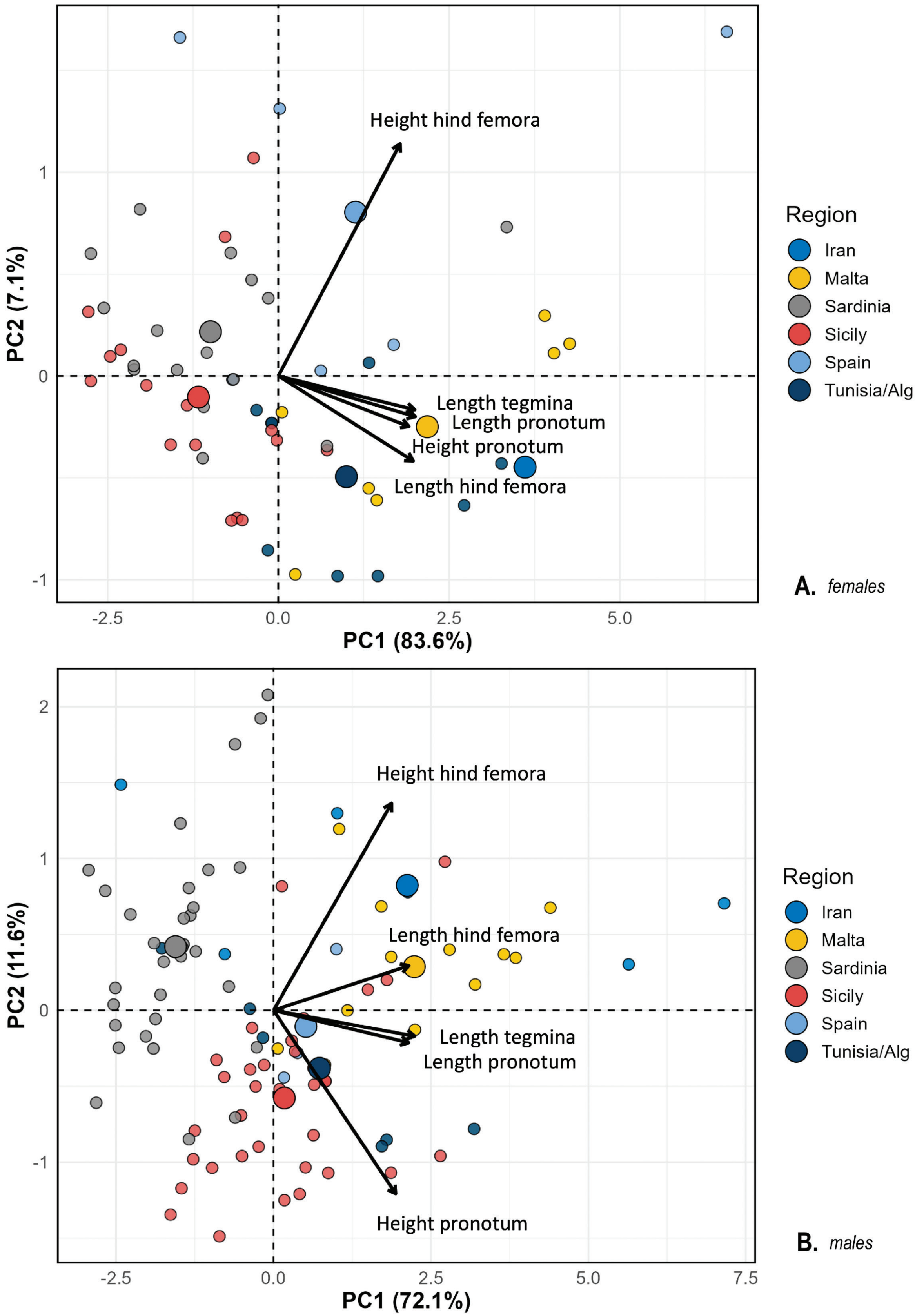

Fig. 3 – PCA Biplots for *Heteracris* populations **A**, females; **B**, males. Points represent individual specimens; arrows indicate the direction and weight of the morphometric variables. The larger dots represent group mean points (centroids).

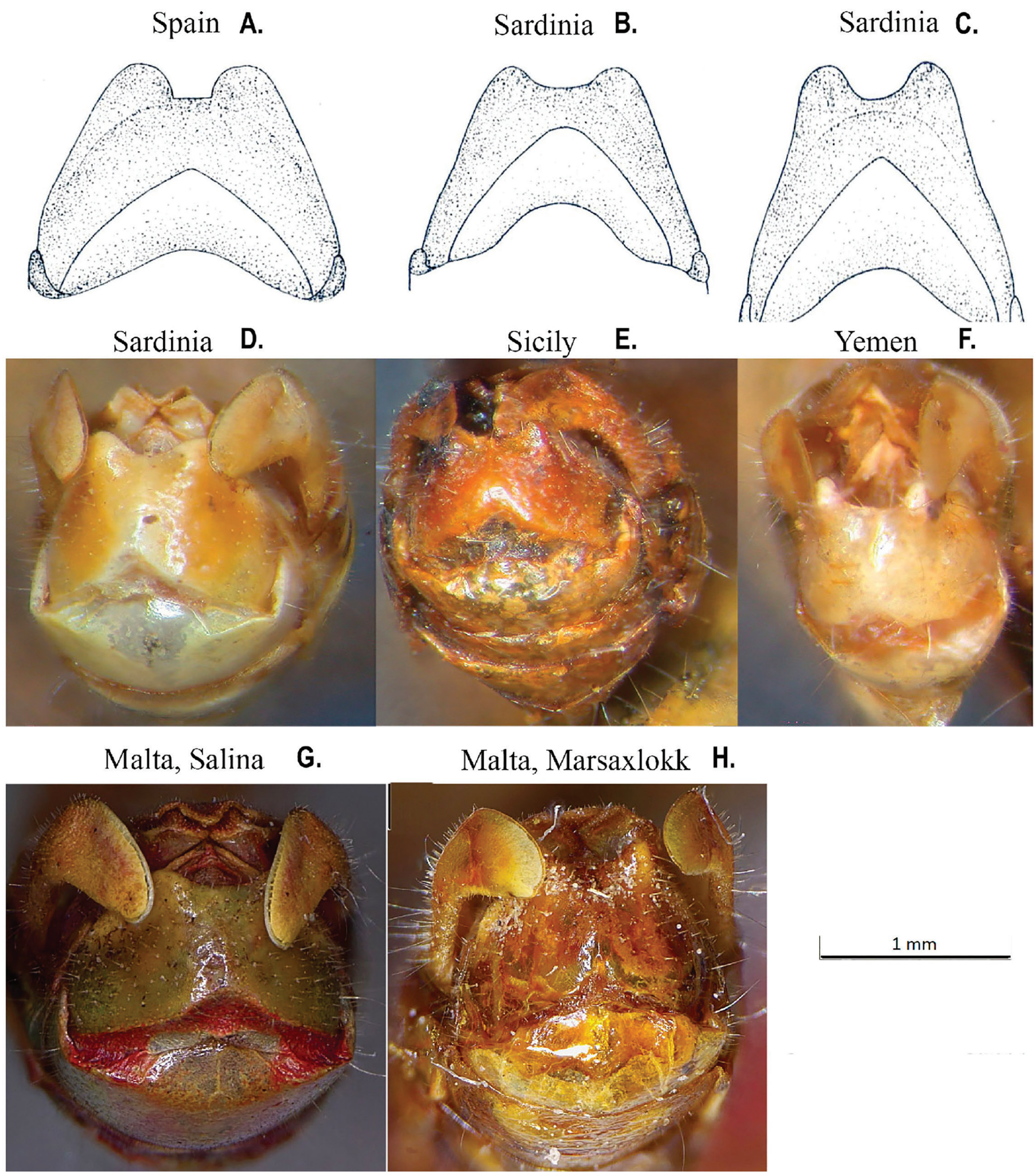

Fig. 4 – The male subgenital plate is demonstrably variable within and across populations to a notable extent. The line drawings of specimens (*top row*, **A**-**C**) from Spain and Sardinia, adapted from Galvagni (1978), and the digital microscopy images from Sardinia, Sicily, Yemen (*middle row*, **D**-**F**), and from two localities in Malta (*bottom row*, **G**-**H**) indicate this quite clearly.

are morphometrically distinct and diagnosable based on specific allometric proportions.

Variable contributions – Analysis of variable contributions (communality) indicated that the five-variable set captured the majority of morphometric variation in both sexes. In females, all variables were well-represented by the first two axes (>84% variance explained). In males, the maximum height of the hind femur and lateral height of the pronotum were important for defining the secondary axis of variation.

Male terminalia – Based on examination, via microscopy, of a number of male specimens representative of the geographical areas under study, it is apparent that the male subgenital plate varies geographically, while also exhibiting a level of intra-population disparity (Figure 4). The apex of Spanish specimens has two slightly rounded tips, while in the Sicilian and Sardinian specimens the tips of the apex are slightly more pointed; similarly in specimens from Algeria, while those from Iran have exceptionally pointed apical tips. However, while a degree of variability appears to occur (possibly a west-east cline due to geographical isolation), the present authors find no justifiable reason to maintain nor warrant separate taxonomic ranking based on such minor biometric unevenness.

Conclusion

Given the results attained, both statistically and biometrically, demonstrating a marked variability and consequent unevenness within populations and across geographic regions, findings tend to support a more 'unified taxonomy'. Therefore, rather than relying on fragmentary or 'split' taxonomic ranking based on potentially clinal, hypothetically ambiguous and, to a degree, inconsistent biometric separation, the present authors support the notion of a singular taxon. Accordingly, it is proposed to synonymise *Heteracris adspersa massai* (**syn. nov.**), currently of subspecific rank within the *H. adspersa* complex, under the senior synonym *Heteracris adspersa* (Redtenbacher, 1889).

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Annex – List of known taxa of the genus *Heteracris*

nomen dubium *grossus* (Schulthess, 1894)
nomen dubium *mutator* (Walker, 1870)
nomen dubium *turbidus* (Walker, 1870)

species group *adspersa* (Redtenbacher, 1889)
1) species *adspersa* (Redtenbacher, 1889)
2) species *rantae* (Uvarov, 1936)

species group *brevipennis* (Bolívar, 1914)
3) species *brevipennis* (Bolívar, 1914)

species group *caloptenoides* (Bolívar, 1914)
4) species *caloptenoides* (Bolívar, 1914)
5) species *festae* (Giglio-Tos, 1893)
6) species *glabra* (Uvarov, 1938)
7) species *sabaea* Popov, 1981

species group *coerulescens* (Stål, 1876)
8) species *coerulescens* (Stål, 1876)
9) species *nefasitensis* Grunshaw, 1991

species group *cyanescens* (Uvarov, 1939)
10) species *cyanescens* (Uvarov, 1939)
11) species *juliea* Grunshaw, 1991

species group *herbacea* (Serville, 1838)

12) species *acuticercus* Grunshaw, 1991
13) species *calliptamoides* Uvarov, 1921
14) species *drakensbergensis* Grunshaw, 1991
15) species *herbacea* (Serville, 1838)
16) species *speciosa* (Sjöstedt, 1913)
17) species *zulu* Grunshaw, 1991

species group *littoralis* (Rambur, 1838)

18) species *annulosa* Walker, 1870
19) species *harterti* (Bolívar, 1913)
20) species *littoralis* (Rambur, 1838)
21) species *minuta* (Uvarov, 1921)
22) species *persa* (Uvarov, 1933)
23) species *theodori* (Uvarov, 1929)

species group *morbosa* (Serville, 1838)

24) species *etbaica* (Ramme, 1928)
25) species *hemiptera* (Uvarov, 1935)
26) species *hoggarensis* (Chopard, 1929)
27) species *iranica* (Bey-Bienko, 1960)
28) species *morbosa* (Serville, 1838)
29) species *puntica* (Popov, 1981)

species group *nigricornis* (Saussure, 1899)

30) species *antennata* (Bolívar, 1914)
31) species *concinnicrus* Descamps & Wintrebert, 1966
32) species *nigricornis* (Saussure, 1899)

species group *pulchripes* (Schaum, 1853)

33) species *aethiopica* (Ramme, 1929)
34) species *coeruleipennis* (Uvarov, 1921)
35) species *coerulipes* (Sjöstedt, 1910)
36) species *guineensis* (Krauss, 1890)
37) species *jeanneli* (Bolívar, 1914)
38) species *prasinata* (Stål, 1876)
39) species *pulchripes* (Schaum, 1853)
40) species *trimaculata* Grunshaw, 1991

species group *syriaca* (Brunner von Wattenwyl, 1861)

41) species *popovi* (Uvarov, 1952)
42) species *punctata* (Uvarov, 1936)
43) species *somalica* (Popov, 1981)
44) species *syriaca* (Brunner von Wattenwyl, 1861)
45) species *attenuata* (Uvarov, 1921) [= *caudatus* (Ramme, 1929), *oxyurus* (Uvarov, 1939), *similis* Ramme, 1931]
46) species *buxtoni* (Uvarov, 1921)
47) species *coniceps* Walker, 1870
48) species *finoti* (Bolívar, 1914) [= *praestans* (Carl, 1916)]
49) species *hannai* Wandji & Kekeunou, 2021
50) species *jucundus* (Carl, 1916)
51) species *leani* (Uvarov, 1941)
52) species *lecoqi* Yetchom-Fondjo & Kekeunou, 2021
53) species *lieutaghii* Defaut, 1986
54) species *muscatensis* Popov, 1981
55) species *nobilis* (Brancsik, 1893)
56) species *notabilis* (Uvarov, 1942) [= *nobilis* (Uvarov, 1942)]
57) species *pterosticha* (Fischer von Waldheim, 1833) [= *dorsatum* (Fischer von Waldheim, 1839), *fischeri* (Fieber, 1853)]
58) species *pulchra* (Bolívar, 1902)
59) species *reducta* Dirsh, 1962
60) species *rufitibia* Walker, 1871
61) species *sikorai* (Bolívar, 1914) [= *brevicornis* (Carl, 1916)]
62) species *vinacea* (Sjöstedt, 1923)
63) species *zolotarevskyi* Dirsh, 1962 [= *uvarovi* Wintrebert, 1972]