



Revision of the Palearctic *Cicindela campestris* species complex—Part 1: On the taxonomy, identification and ecology of *Cicindela herbacea* Klug, 1832 and *Cicindela javetii* Chaudoir, 1861 (Coleoptera, Cicindelidae)

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Abstract

We revise the taxonomically problematic Palearctic *Cicindela campestris* species complex, a group of green tiger beetle species, using an integrative approach combining morphology, morphometry and biogeography. In this first part, an identification key to all subgroups of these green tiger beetles (*Cicindela herbacea*-subgroup, *Cicindela javetii*-subgroup, *Cicindela desertorum*-subgroup, *Cicindela campestris*-subgroup, *Cicindela turkestanica*-subgroup and *Cicindela asiatica*-subgroup) based on large series taken from private and museum collections as well as on literature sources is provided and diagnostic characters are illustrated by detailed photographs. The *Cicindela herbacea*- and *Cicindela javetii*-subgroups are revised and illustrated and identification keys as well as distribution maps for both are given. Four new synonyms are established: *Cicindela herbacea herbacea* Klug, 1832 = *Cicindela herbacea aleppensis* Deuve, 2012, **syn. n.**; *Cicindela herbacea turkestanicoides* W. Horn, 1938 = *Cicindela herbacea perreai* Deuve, 1987, **syn. n.** = *Cicindela herbacea colasi* Deuve, 2011, **syn. n.**; *Cicindela javetii javetii* Chaudoir, 1861 = *Cicindela thughurica* Franzen, 2007, **syn. n.**

Key words: chorology, distribution, identification key, phenology, taxonomy, tiger beetles

Introduction

Tiger beetles (Cicindelidae) are generally well studied due to their beauty and appeal to collectors (Cassola & Pearson 2000). However, some groups within the family are more cryptic than others due to large number of very similar, closely related taxa. The enigmatic Palearctic ‘*Cicindela campestris* species complex’ of several very similar green tiger beetle species is one of these groups. The taxa placed within this species complex are distributed from Morocco to Yakutia in Russia, from the North Cap in Norway to Israel, Iran and Afghanistan (Wiesner 2020).

The ‘*Cicindela campestris* species complex’ is considered one of the most problematic species groups in the Palearctic tiger beetle fauna for various reasons: (i) comparatively small numbers of specimens were available for many of the taxa and from large parts of the range of this group in previous revisions, (ii) historical difficulties in travel in many countries (especially in the Middle East where many of the taxa in question are endemic) made the acquisition of new material for a comparative assessment of this group difficult and (iii) this group overall shows rather low variability in many features, especially in the shape of the aedeagus, a character often used for differentiation between very similar taxa (Rivalier 1950), yet there is high intra-specific variability.

The *Cicindela campestris* species group has undergone multiple taxonomic revisions over the last decades,

mostly based on very limited amounts of specimens (Horn & Roeschke 1891; Horn 1938; Mandl 1944, 1988; Franzen 2007; Deuve 2011, 2012, 2019). The most conclusive and complete revision so far has been conducted by Deuve (2011, 2012) but unfortunately only included a very limited series of specimens which did not allow for an accurate assessment of the range of intra-specific variability or distribution ranges of separate taxa. Thus, this group remains in need of a thorough revision to clarify which of the currently accepted taxa are valid and which merely represent morphs within the range of natural variation of other species. In recent decades, however, with many entomologists collecting in countries from which material was scarce in the past, more material has become accessible. By accumulating a large portion of the available specimens in private and museum collections, a comprehensive revision has become possible.

In the first part of our revision, we focus on two species of the *Cicindela campestris* species complex inhabiting the mountainous regions of the Middle East, *Cicindela herbacea* and *Cicindela javetii* as well as their associated nominal taxa. Due to practical constraints, the gathering of fresh material for a comprehensive DNA barcoding-based phylogeny of the *Cicindela campestris* species complex remains difficult if not impossible for the near future. Therefore, we applied a traditional taxonomic approach including large-scale morphometric analyses and statistical methods combined with a parsimony assessment of the geographic distribution of the taxa in question to unravel the taxonomy of the *Cicindela herbacea* and *Cicindela javetii* subgroups. Our analyses are based on the largest series of specimens from this species group that has been analyzed so far gathered from various museum and private collections. With this contribution we hope to clarify the taxonomic structure of the *Cicindela campestris* species complex and therefore make a further step towards an upcoming monograph on the Cicindelidae of the Palearctic region.

Material and methods

Studied material

Based on the available material, the species of the *Cicindela campestris* species complex are distributed from northern Europe to the northern African Maghreb (Morocco, Algeria, Libya), the Levant, Iran and Afghanistan in the south, from Morocco and Portugal in the West to Yakutia in Russia in the East (Putchkov & Matalin 2017; Wiesner 2020) (Figure 1).

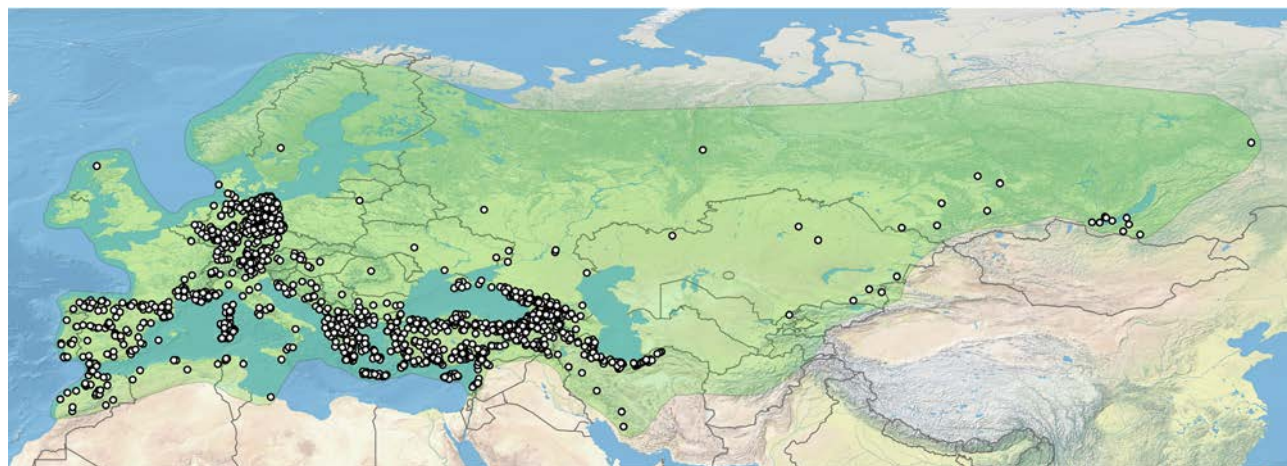


FIGURE 1. Distribution range of the *Cicindela campestris* species complex (see taxa stated in Table 1). The green opaque polygon represents the approximate maximum distribution range of the species belonging to this group derived from verified literature records and studied specimens. White circles represent large parts (but not all) of the material studied for this revision (map created using Natural Earth raster map data; naturalearthdata.com).

For our revision of the *Cicindela campestris* species complex, we borrowed specimens from 16 museum and 25 private collections (museum collections listed first), predominantly from regions where taxonomic diversity within the *Cicindela campestris* species complex is high and previous authors have described and revised many taxa (i.e. the Mediterranean, the Middle East and the Caucasus):

BMNH	British Museum of Natural History, London, United Kingdom
MNHNP	Muséum National d'Histoire Naturelle, Entomology Department, Paris, France
MNHUB	Museum für Naturkunde Humboldt-Universität zu Berlin, Germany
MSPU	Moscow State Pedagogical University, Russia
MTD	Senckenberg Museum für Tierkunde Dresden, Germany
NHM	Natural History Museum of University of Oslo, Norway
NHMW	Naturhistorisches Museum Wien, Wien, Austria
NMBE	Naturhistorisches Museum Bern, Switzerland
NMP	Národní muzeum Praha, Prague, Czech Republic
NMS	Naturkundemuseum Stuttgart, Germany
SDEI	Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany
SIZ	Schmalhausen Institute of Zoology National Academy of Sciences, Kyiv, Ukraine
SMNHTAU	Steinhard Museum of Natural History, National Collections, Tel Aviv University, Tel Aviv, Israel
ZIN	Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia
ZMUM	Zoological Museum of the Lomonosov-University Moscow, Russia
ZSM	Zoologische Staatssammlung München, Germany
CAL	Working collection Assmann, Lüneburg, Germany (part of ZSM)
CBD	Working collection, Brunk, Dresden, Germany
CCR	Collection Cassola (Part of Roman Museo Civico di Zoologia) Rome, Italy
CEI	Working collection Egger, Innsbruck, Austria
CFB	Working collection Bötzl, Würzburg, Germany
CFM	Working collection Feldmann, Münster, Germany.
CFN	Working collection Franzen, München, Germany
CGC	Working collection Grycz, České Budějovice, Czech Republic
CGD	Working collection Gebert, Dresden, Germany
CHJ	Working collection Hajdaj, Jezov, Czech Republik
CHP	Working collection Häckel, Prague, Czech Republic
CHS	Working collection Heinz, Schwanfeld, Germany (part of NMS)
CKE	Working collection Kerkering, Emsdetten, Germany
CKP	Working collection Kabátek, Prague, Czech Republik
CNR	Working collection Napolov, Riga (Riga-Zoo), Latvia
CPE	Working collection Pütz, Eisenhüttenstadt, Germany
CSC	Working collection Schnitter, Halle/S., Germany
CSH	Working collection Schüle, Herrenberg, Germany
CSM	Working collection Shankhiza, Moscow, Russia
CSK	Working collection Skoupý, Kamenné Žehrovice, Czech Republik
CSN	Working collection Schmidt, Neustadt am Rheinberge, Germany
CUM	Working collection Udovichenko, Moscow, Russia
CWB	Working collection Wrase, Gusow-Platkow, Germany (part of ZSM)
CWWe	Working collection Weigel, Wernburg, Germany
CWWo	Working collection Wiesner, Wolfsburg, Germany (part of ZSM)

In total, we examined at least 9.898 specimens of all the taxa belonging to the *Cicindela campestris* species complex including many type specimens (Fig. 1; this number represents specimens databased at the time of the submission of this first part of our revision; the final total will be higher). Location data provided with the specimens was translated to English and transferred into a common form. Historical location names were searched and transferred into currently accepted names (with both stated). Additionally, we gathered and georeferenced literature records published in Deuve (1987), Korell (1988), Cassola (1999), Franzen (2007), Assmann *et al.* (2018), Deuve (2011, 2012), Matalin and Chikatunov (2016) and Deuve (2019). All records solely obtained from previously published literature were subject to a critical plausibility check based on known distribution ranges (derived from the studied collection specimens) and on the origin of the referenced specimens (locations stated on old collection material are often very imprecise and sometimes incorrect). Many of the specimens mentioned in the literature, however,

were also found in the collection material investigated. For distribution maps and elevation histograms, only specimens with precise and plausible collecting location were used. In order to keep this work concise and clear, we do not list all single specimens with detailed collection information in the species accounts. Collection sites for each taxon can be seen in the distribution maps and are provided in the species accounts. Complete collection data for all specimens assessed in this revision is stored in a SQL-database (MultiBaseCS, 34u GmbH) by the authors. For this first part, we studied a total of 666 specimens from the *Cicindela herbacea*- and *Cicindela javetii*-subgroups (all studied material is listed in an online Supplementary Appendix).

Morphometry and statistical analyses

We measured representative subsets for each taxon (both sexes, spanning the whole distribution range). We used generally accepted distances also used in recent publications to allow for comparability (see e.g. Matalin (2019) or Boetzi and Franzen (2020)). Measurements include: Total body length (TL; from the anterior edge of the eyes to the ultimate posterior tip of the longer elytron—this section is least dependent on the method of preparation); pronotum length (PL; from the anterior to the posterior edge following the midline); head width (HW; maximum width on the broadest point across the eyes), maximal pronotum width (PWm; maximum width on the broadest point) and at the base (PWb; width near the base across the hind angles of the pronotum); elytral length (EL; from the tip of the scutellum to the ultimate posterior tip of the longer elytron); maximum elytral width (EWM; maximum width on the broadest point); basal elytral width (EWh; width of the elytra across the tip of the scutellum); labrum length (LL; measured vertically in the mid of the labrum from the tip of the median tooth to the base); labrum width (LW; maximum width on the broadest point measures vertically). Additionally, we noted the number of other setae on the first antennal segment apart from the always present apical sensory setae (OS; mean of both first antennal segments). Aedeagus length (AL) was measured laterally across the maximal length of the aedeagus.

As inter- and especially intra-specific differences between the taxa in this group in aedeagus shape are low and aedeagi are variable in size and shape between individuals of the same taxon and population (also depending on the state of preparation and conservation), we compared internal structures (endophallus) to differentiate between taxa. Genital internal sacs were inflated via entering the aedeagus tube with a fine hypodermic needle, inflating the internal sac with air using a syringe and subsequent drying with hot air (see Janovska, Anichtchenko, & Erwin (2013)). The nomenclature of inflated internal sac structures follows Matalin (1998) and Matalin (2019): with additions: bulges: VA—ventro-apical, VM—ventro-medial, VLL—ventro-lateral left, VLR—ventro-lateral right, DA—dorso-apical, DLL—dorso-lateral left, DLR—dorso-lateral right, BLL—basi-lateral left (formerly named ‘B—basal’ in (Matalin 1998, 1999a, 1999b, 2002a, 2002b)), BLR—basi-lateral right, M—median; sclerites: fl—flagellum, f—flag, mt—medial tooth, sh—shield, sp—spring, ul—upper limitator, ll—lower limitator.

All statistical analyses were performed in R (R Development Core Team 2019). Measurements as well as selected ratios were compared between taxa using ANOVA likelihood ratio tests (response ~ taxon + sex; type 2 SS) accounting for both taxon identity and sex (due to obvious sex specific differences in body size and shape; only results for taxon identity are displayed). For the *C. herbacea*-subgroup with three taxa, Tuckey post-hoc tests were performed to clarify which taxa were differing significantly from which others if the ANOVA indicated significant differences between taxa. We further compared overall morphometrical similarity between individuals of closely related taxa using non-metric multi-dimensional scaling (NMDS, 1000 iterations, Bray-Curtis distances, function ‘metaMDS’ from the package ‘vegan’ (Oksanen *et al.* 2019)). Used measurements included TL, EL, PL, PWb, PWm, EWh, EWM, HW and OS. Prior to NMDS, measurements were scaled using a square root transformation. NMDS fits were checked for significant differences between taxa using a permutational multivariate analysis of variance (PERMANOVA, 999 permutations, Bray-Curtis distances, function ‘adonis’) using taxon as well as sex as factors (response ~ taxon + sex). In all NMDS ordinations, we display original data points as well as centroids with 95% confidence intervals (CI) in x- and y-directions.

Results

The Palearctic *Cicindela campestris* species complex contains 13 currently accepted species (Table 1). Many of these species contain several more or less clearly geographically separated subspecies resulting in a total of 41 currently accepted taxa (Putchkov & Matalin 2017; Wiesner 2020). Based both on external and male genital morphologic similarities, we divided this complex into six subgroups in order to structure our revision (Table 1):

1. *Cicindela herbacea*-subgroup
2. *Cicindela javetii*-subgroup
3. *Cicindela desertorum*-subgroup
4. *Cicindela campestris*-subgroup
5. *Cicindela turkestanica*-subgroup (for a revision see Gebert (1993))
6. *Cicindela asiatica*-subgroup (currently not in need of revision)

This division does likely not resemble the real relationships between the species in these subgroups which only a barcoding based phylogeny could reveal.

In our revision, we chose a conservative approach based on biogeographical ranges taking intergradation between subspecies into account. Due to the resulting large variation within some of the taxa, we include distribution ranges in our key in order to facilitate identification.

TABLE 1. Taxonomic situation in the *Cicindela campestris* species complex before this revision (according to Wiesner (2020)).

subgroup	Currently accepted species	Currently accepted subspecies
<i>C. herbacea</i> -subgroup	<i>C. herbacea</i> Klug, 1832	<i>C. h. herbacea</i> Klug, 1832 <i>C. h. aleppensis</i> Deuve, 2012 <i>C. h. colasi</i> Deuve, 2011 <i>C. h. perreaui</i> Deuve, 1987
	<i>C. turkestanicoides</i> W. Horn, 1938	
<i>C. javetii</i> -subgroup	<i>C. javetii</i> Chaudoir, 1861	<i>C. j. javetii</i> Chaudoir, 1861 <i>C. j. azari</i> Deuve, 2011 <i>C. j. thughurica</i> Franzen, 2007
<i>C. desertorum</i> -subgroup	<i>C. desertorum</i> Dejean, 1825	<i>C. d. desertorum</i> Dejean, 1825 <i>C. d. dumetorum</i> Faldermann, 1835
	<i>C. colasiana</i> Deuve, 2019	
	<i>C. montreuili</i> Deuve, 2012	
<i>C. campestris</i> -subgroup	<i>C. campestris</i> Linnaeus, 1758	<i>C. t. talychensis</i> Chaudoir, 1846
		<i>C. t. mofidii</i> Deuve, 2011
		<i>C. c. campestris</i> Linnaeus, 1758
		<i>C. c. atlantis</i> Surcouf, 1933
		<i>C. c. balearica</i> Sydow, 1934
		<i>C. c. calabrica</i> Mandl, 1944
		<i>C. c. naxosica</i> Deuve, 2012
		<i>C. c. neopontica</i> Deuve, 2012
		<i>C. c. nigrita</i> Dejean, 1825
		<i>C. c. nymphiensis</i> Deuve, 2012
		<i>C. c. olivieria</i> Brullé, 1832
		<i>C. c. palustris</i> Motschulsky, 1840
		<i>C. c. perdita</i> Deuve, 2011
<i>C. c. pontica</i> Fischer von Waldheim, 1825		
<i>C. c. pseudojaveti</i> Deuve, 2012		
<i>C. c. saphyrina</i> Gené, 1836		
<i>C. c. sicularum</i> Schilder, 1953		
<i>C. c. suffriani</i> Loew, 1843		
	<i>C. cyprensis</i> Hlisnikowski, 1929	

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TABLE 1. (Continued)

subgroup	Currently accepted species	Currently accepted subspecies
	<i>C. georgiensis</i> Deuve, 2011	<i>C. g. georgiensis</i> Deuve, 2011 <i>C. g. prunieri</i> Deuve, 2012
	<i>C. maroccana</i> Fabricius, 1801	<i>C. m. maroccana</i> Fabricius, 1801 <i>C. m. schrammi</i> Antoine, 1950 <i>C. m. pseudomaroccana</i> Roeschke, 1891
<i>C. turkestanica</i> -subgroup	<i>C. turkestanica</i> Ballion, 1871	<i>C. t. turkestanica</i> Ballion, 1871 <i>C. t. badakschana</i> Mandl, 1955 <i>C. t. gissariensis</i> Dokhtoureff, 1885
<i>C. asiatica</i> -subgroup	<i>C. asiatica</i> Audouin & Brulle, 1839	<i>C. a. asiatica</i> Audouin & Brullé, 1839 <i>C. a. sumbarica</i> Putschkov, 1993

Key to the subgroups of the Palearctic *Cicindela campestris*-species group

- 1 Elytra with four large rounded spots each, located along a straight line from the shoulder to the apical edge, spots do not touch the side edges. Mountain ranges of the Middle East to Turkmenistan, in higher elevations *Cicindela asiatica*-subgroup
- Elytra with different maculation (some spots touch the lateral edges) 2
- 2 Elytra distinctly oval shaped, continuously rounded laterally (angle between width at shoulders and width at broadest point usually > 9°, Fig. 105–110, 154–159) 3
- Elytra more parallel sided and elongated, appearing less clearly rounded (angle between width at shoulders and width at broadest point usually < 9°, Figs. 6–16) 5
- 3 Pronotum with straight margins slightly convergent to the base; scape usually glabrous, rarely with one-two additional seta except apical ones; VLL undeveloped. Occurring in the mountain ranges of Central Asia (Tien Shan, Pamir and side chains) *Cicindela turkestanica*-subgroup
- Pronotum with rounded margins; scape usually with a different number of additional setae except apical ones (rarely glabrous); VLL small but clearly developed. Occurring elsewhere (an overlap of the ranges of *C. campestris* and *C. turkestanica* in south-eastern Kazakhstan seems plausible and demands caution) 4
- 4 Pale maculation on elytra usually containing a solid middle band originating from the lateral margin projecting towards the elytral disk (thickness can vary but the band is always clear), often ending in a forward protruding hook on the elytral disk. Levant (Israel, Lebanon, Syria, southern Turkey) *Cicindela javetii*-subgroup
- Pale maculation on elytra primarily in the form of clearly separated spots, middle lateral marginal spot sometimes connected to the spot on the elytral disk by a thin, often forward bent line (in these cases, connection is rather indistinct and spots still seem separate if the specimen is viewed from distance) *Cicindela campestris*-subgroup
- 5 Elytra noticeably flattened, strongly parallel sided (angle between width at shoulders and width at broadest point usually < 7.5°), aedeagus with a characteristic bend in the middle on the concave side and elongated tip (Fig. 62–67), VA large, with rounded or slightly extended apex, VLL undeveloped (Fig. 68–96). Lebanon, Syria, Turkey, Iran *Cicindela herbacea*-subgroup
- Elytra not noticeably flattened but elevated towards the suture, elytra laterally slightly more rounded, angle between width at shoulders and width at broadest point usually > 7.5°, aedeagus without bend in the middle on the concave side (similar to Figs. 138–140), VA small with distinctly extended apex, VLL in most cases well developed. Taurus-, Caucasus-, Alborz- and Zagros mountain ranges *Cicindela desertorum*-subgroup

Cicindela herbacea-subgroup

Cicindela herbacea was described by Klug (1832) from a single female collected near Beirut / Lebanon. A century later, Horn (1938) described the taxon *turkestanicoides* after two females collected in Northern Iran ('Taesh, N Persien, zwischen Astrabad und Schahrud, leg. Christoph 1871') as a subspecies of *C. campestris* (at that time *herbacea* Klug, 1832 was also placed as a subspecies of *C. campestris*). The description of *C. c. turkestanicoides* mentions eight additional specimens from the Taurus mountain range ('Moks' (= Çatak), 'Van' & 'Zeitün' (= Süleymanlı)) which differ from the type specimens from the Iranian Alborz mountain range in general shape and by a thinner maculation which Horn (1938) judged as intra-specific variability due to the otherwise high similarity among the specimens. Based on a specimen from Pülümür (Tunceli / Turkey) which is very similar to these eight specimens already mentioned by Horn (1938), Deuve (1987) described *Cicindela perreaui* but unfortunately did not

compare it to *C. turkestanicoidea* or *C. herbacea* at that time. Cassola (1999) placed *C. perreai* as subspecies under *C. turkestanicoidea* based on overall morphological similarity and mentions that future revisions need to examine whether *C. perreai* was not in fact a synonym of *C. turkestanicoidea*. A few decades later, Deuve (2011) for the first time noticed correctly that *C. perreai* is conspecific with *C. herbacea* based on aedeagus shape (characteristically elongated tip) and placed the former as a subspecies of the latter but unfortunately did not check for synonymy with *C. turkestanicoidea* as suspected by Cassola (1999). Deuve (2011, 2012), however, described two additional subspecies for *C. herbacea*: *C. herbacea colasi* Deuve 2011 based on one male and three females from one location near Pozanti, and *C. herbacea aleppensis* Deuve 2012 based on three males and 11 females from Aleppo, Syria.

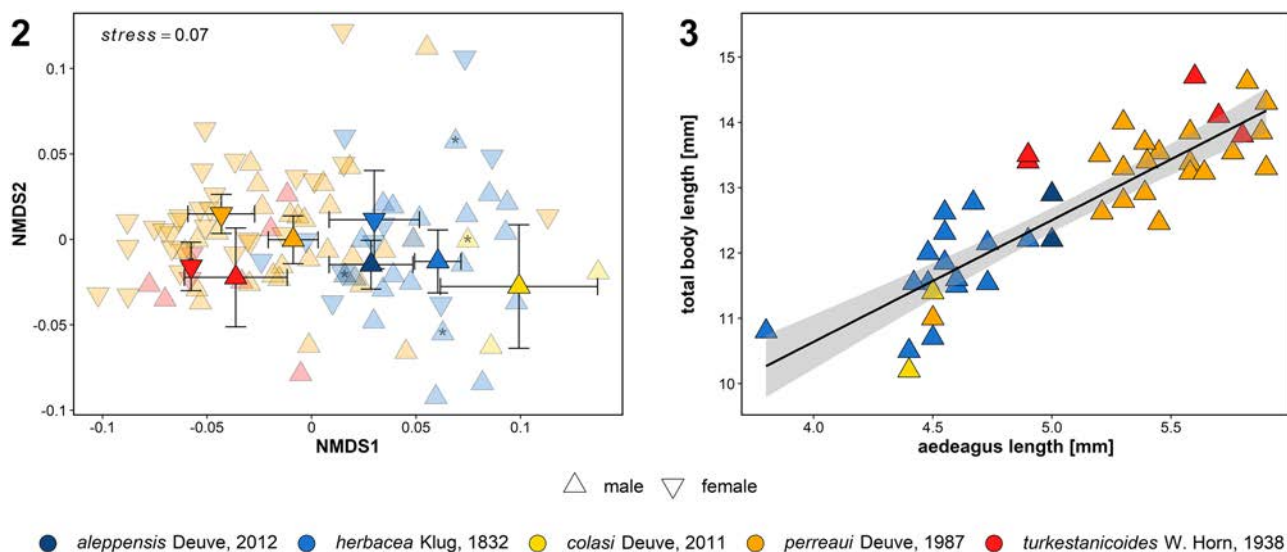
This brief recapitulation of the taxonomic history of this subgroup shows the limitations that have complicated previous revisions: Descriptions were often based on single specimens or very limited series. The type material often consisted of female specimens or old material with doubtful and imprecise collection information. Older collection material often originates from large commercial insect trading companies that only provided very limited, coarse and imprecise, sometimes even completely wrong, collection data for specimens as this was not regarded important for collectors at that time (Draeseke 1962). Generally, revisions lacked the ability to assess natural variability or parsimonious plausibility based on geographic distributions. Intraspecific variability in coloration and elytral maculation is a well-known phenomenon in tiger beetles that has so far been underestimated in this subgroup. The use of colouration or elytral maculation for the description of a taxon without clear knowledge about the range of variability and in absence of clear morphological differences should therefore be avoided. Gathering large series covering the entire range of this subgroup, we are for the first time able to judge the natural variability within series.

Based on our analyses, we find no sufficient difference between the taxa, neither in morphology (Fig. 2; Table 2) nor in aedeagus shape (Figs. 62–67), to reject conspecific status of the taxa of the *Cicindela herbacea*-subgroup. All taxa in this subgroup share characteristically flattened and elongated elytra and a characteristic elongated aedeagus which is clearly bent near the middle on the concave side and has an elongated tip unique in the whole *C. campestris* species complex (Fig. 62–67). The taxon *turkestanicoidea* is therefore for the first time placed as subspecies to *C. herbacea*. The taxa were previously often differentiated based on the outer shape and the size of the aedeagus (Deuve 2011, 2012). However, aedeagus shape varies within a certain range between individuals and populations and its perception is often influenced by the method of preparation and conservation of the specimen (e.g. the size and shape of the soft bulge near the tip depends on how far the endophallus is inflated). Aedeagus size correlates with the total body-size and is therefore merely a measure for the size of the specimen and not useful for differentiation (Fig. 3).

The only two taxa differing clearly from all other previously described taxa in this subgroup are *herbacea* Klug, 1832 and *aleppensis* Deuve, 2012 which are generally smaller (Table 2) and have a differently shaped endophallus (Fig. 68–96). *C. herbacea aleppensis* was described after individuals originating from Aleppo in northern Syria, within the natural range of *C. h. herbacea*. As differentiation criterion, Deuve (2012) states a smaller aedeagus as in *C. h. perreai*, the differentiation from *C. h. herbacea* is not addressed in the original description (as mentioned above, aedeagus size depends on overall body-size and is not a valid differentiation criterion; Fig. 3). *C. h. aleppensis* is therefore a junior synonym to *C. h. herbacea* (also based on our morphometric analyses (Fig. 2)). The specimens placed to *C. h. aleppensis* by Deuve (2012) from eastern Turkey (Kastamonu, Amasya, Çorum, Bingöl, Erzurum, Muş and Van provinces) and Iran (Fars province) are sympatric with populations of *C. h. perreai* (which is not possible for different subspecies of the same species) and thus likely resemble smaller specimens of this taxon. An examination of large series of specimens from the locations stated in the original descriptions confirmed this assumption.

As indicated by Horn (1938) and suspected by Cassola (1999), our analyses show that *perreai* Deuve, 1987 is a junior synonym of *turkestanicoidea* W. Horn, 1938. Both taxa do not differ significantly in morphology, genital shape or endophallus (Figs. 2, 11–16, 65–67, 69–73, 75–79, 81–85, 93–96). The populations from the Taurus- and Zagros mountain ranges previously considered as *perreai* Deuve, 1987 have a narrower maculation (especially humeral and apical maculations) than the typical populations from the Northern Iranian Alborz mountain range which resemble Horn's type specimens perfectly. However, maculation is highly variable in all populations and enlarged maculations do also occur commonly in Eastern Turkey and Western Iran. In larger series, specimens captured on the same location and on the same day exhibit a considerable variation in size and maculation which indicates that these characteristics are weak for differentiation between the taxa, especially when only single specimens are available. The populations of *C. h. turkestanicoidea* inhabit a more or less continuous span of mountain ranges from

Southern and Eastern Turkey to Northern and Central Iran without uncrossable natural barriers that would plausibly cause and explain speciation processes. However, as gene flow likely only takes place between adjacent populations, the populations on the most extreme edges of the distributional range differ from each other in some features (e.g. maculation width), a phenomenon called cline (or genetic gradient; see e.g. Endler (1977) or Thorpe (1987)).



FIGURES 2 & 3. (2) NMDS ordination for the previously recognized taxa of the *Cicindela herbacea*-subgroup based on different morphological measurements (see Materials & Methods). Based on the ordination, the taxon *aleppensis* Deuve, 2011 (origin Aleppo) is a junior synonym of *herbacea* Klug, 1832. The taxa *perreai* Deuve, 1987 and *turkestanicoides* Horn, 1938 cannot be differentiated morphologically. The taxon *colasi* Deuve, 2011 clusters closer to *herbacea* Klug, 1832 but is a junior synonym of *perreai* Deuve, 1987 based on endophallus shape (see Figs. 68–96). Semi-transparent datapoints represent measured specimens, bold points represent the centroid for each taxon with 95% confidence interval. * indicates specimens from the type series. Upwards pointing triangles represent males, downwards pointing triangles represent females. (3) Correlation between aedeagus length and total body length in male specimens of the previously recognized taxa of the *Cicindela herbacea*-subgroup (sensu Deuve 2011 & 2012; prediction with 95% confidence interval). Aedeagus length is positively correlated with total body length, indicating that aedeagus length is not a good differentiation character but only indicates the size of the specimen. In both figures, different colours represent different previously described taxa: dark blue: *aleppensis* Deuve, 2012; blue: *herbacea* Klug, 1832; yellow: *colasi* Deuve, 2011; orange: *perreai* Deuve, 1987; red: *turkestanicoides* W. Horn, 1938.

In southern Turkey, in the provinces Adana, Niğde and Hatay, populations intergrade between *C. h. herbacea* and *C. h. turkestanicoides* and individuals can sometimes not easily be assigned to one of the two subspecies. The individuals are overall a bit larger than regular *C. h. herbacea* (from Lebanon) and appear more elongated. From one of these populations in the Bolkar Dağları (Bolkar mountains), Deuve (2011) described the subspecies *C. h. colasi*. We assigned the populations of Adana and Niğde provinces to *C. h. turkestanicoides* based on endophallus shape which clearly resembles *C. h. turkestanicoides* although morphometry would indicate a closer relation with *C. h. herbacea* (Figs. 68–96). There is no clear sharp division line between both subspecies but rather a gradual transition and the subspecies do intergrade along the line of contact in southern Turkey. A comprehensive phylogeny is needed to confirm our results and to clarify, how distant from each other the populations from the western and eastern edges of the range of *C. herbacea* really are.

These subspecies of *C. herbacea* inhabit a continuous range from Lebanon to the Zagros mountain range in Northern Iran (Fig. 4). *C. herbacea* occurs sympatrically with *Cicindela javetii* and *Cicindela campestris* in many regions but can be easily distinguished from these by the elongated and more parallel sided elytra and a more parallel sided pronotum. Within their respective ranges, *C. h. herbacea* is found in colline and montane elevations from 300 m to 1550 m, *C. h. turkestanicoides* in montane to alpine elevations from 1150 m to 3600 m (Fig. 5).

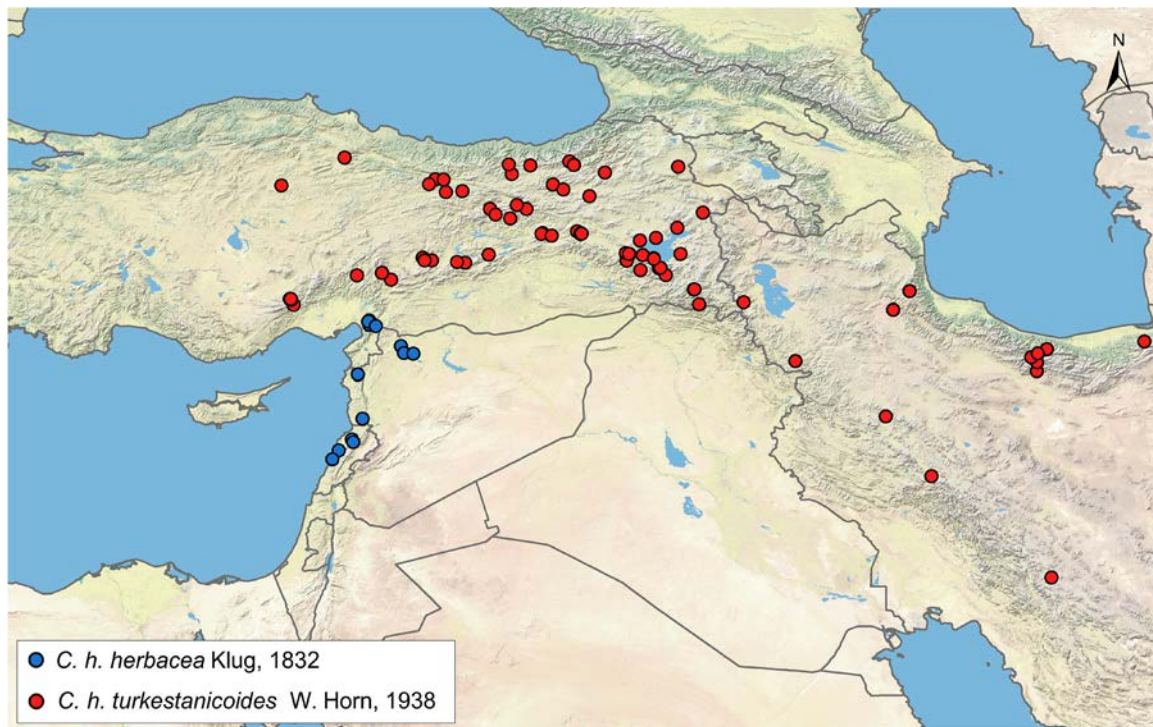


FIGURE 4. Distribution map of *C. herbacea*. Blue circles: *C. herbacea herbacea* Klug, 1832; red circles: *C. herbacea turkestanicoidea* W. Horn 1938 (map created using Natural Earth raster map data; naturalearthdata.com).

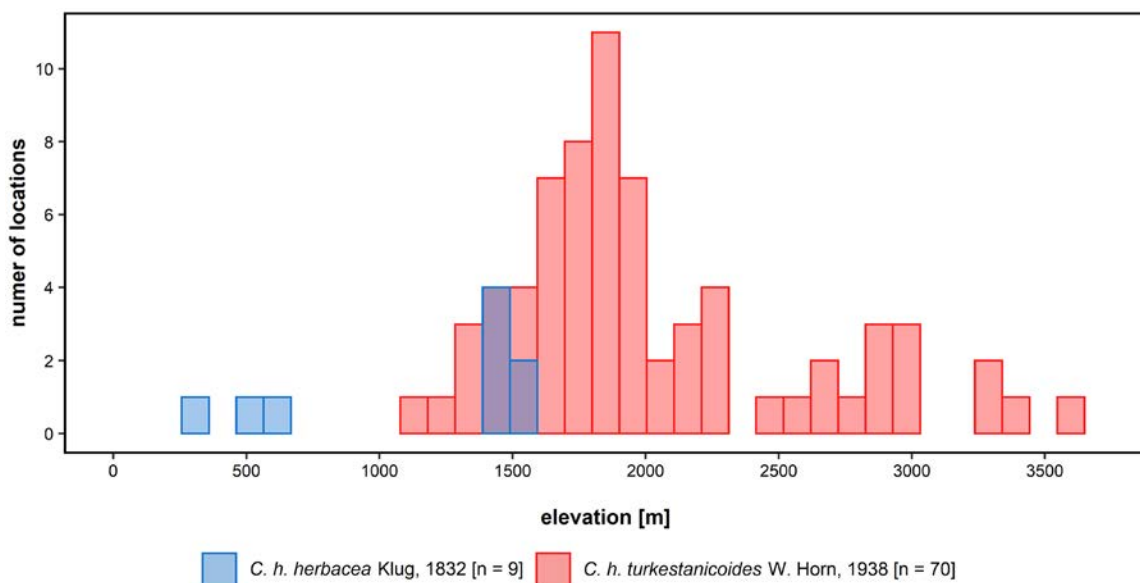


FIGURE 5. Elevation range of the two subspecies of *C. herbacea*. Blue: *C. herbacea herbacea* Klug, 1832; red: *C. herbacea turkestanicoidea* W. Horn 1938. Numbers in the legend represent the number of unique collecting locations (only including records that included collection information with sufficient precision).

Key to the subspecies of *C. herbacea*

- 1 Generally smaller, TL 11.8 (10.5–12.9) mm in males and 12.5 (11.4–13.4) mm in females. Internal sack overall shorter, BLL shorter, VA larger and VLR larger and clearly visible in the left lateral view (Figs. 68). Colline to montane habitats, Lebanon, Syria and the southernmost provinces of Turkey (south of the Taurus main ridge) *C. herbacea herbacea* Klug, 1832
- Generally larger, TL 13.6 (11.0–14.7) mm in males and 14.4 (11.3–15.4) mm in females. Internal sack overall longer, BLL longer, VA smaller and VLR smaller and nearly invisible in the left lateral view (Figs. 69–73). Montane to alpine habitats, Taurus-, Caucasus-, Alborz- and Zagros mountain ranges *C. herbacea turkestanicoidea* W. Horn, 1938

TABLE 2. Differences in measurements and selected ratios between the three of the previously recognized taxa (sensu Deuve 2011, 2012) within the *Cicindela herbagea*-subgroup (the taxa *colasi* and *aleppensis* were not included; based on a variety of features, the former is a synonym of *perreai* and the latter is a synonym of *herbagea*). The absence of significant differences supports the synonymy of *perreai* and *turkestanicoidea*. The large overall similarity (especially in ratios) supports the conspecific status of *herbagea* and *turkestanicoidea*. All measurements in mm (rounded to one decimal (measurements) or two decimals (ratios)) showing mean \pm standard error and range below in brackets. Statistics are taken from models accounting for sex differences—only the results for differences between the taxa are shown (see Materials & Methods section). * indicates $p < 0.05$; ** indicates $p < 0.01$; *** indicates $p < 0.001$, different letters in posthoc test indicate which taxa differ from each other (from left to right as displayed in this table).

Measure / Ratio	<i>herbagea</i> Klug, 1832		<i>perreai</i> Deuve, 1987		<i>turkestanicoidea</i> W.Horn, 1938		Difference between taxa (ANOVA)	Posthoc tests for differences between taxa
	21 ♂	10 ♀	26 ♂	28 ♀	6 ♂	2 ♀		
Total length (TL)	11.8 \pm 0.2 [10.5–12.9]	12.5 \pm 0.2 [11.4–13.4]	13.4 \pm 0.2 [11.0–14.6]	14.4 \pm 0.1 [11.3–15.4]	13.7 \pm 0.3 [12.5–14.7]	14.3 \pm 0.2 [14.2–14.5]	$F_{2,89} = 70.9$; $p < .001$ ***	a, b, b
Elytra length (EL)	7.4 \pm 0.1 [6.5–8.0]	7.9 \pm 0.1 [7.1–8.5]	8.4 \pm 0.1 [7.0–9.2]	9.1 \pm 0.1 [7.4–9.8]	8.8 \pm 0.2 [8.0–9.6]	9.3 \pm 0.1 [9.2–9.4]	$F_{2,89} = 76.4$; $p < .001$ ***	a, b, b
Pronotum length (PL)	2.0 \pm 0.0 [1.8–2.2]	2.0 \pm 0.0 [1.7–2.2]	2.3 \pm 0.0 [2.0–2.6]	2.4 \pm 0.0 [1.9–2.6]	2.3 \pm 0.1 [2.1–2.5]	2.3 \pm 0.1 [2.2–2.3]	$F_{2,92} = 68.6$; $p < .001$ ***	a, b, b
Maximal pronotum width (PWm)	2.7 \pm 0.1 [1.4–2.9]	2.9 \pm 0.0 [2.6–3.2]	3.0 \pm 0.0 [2.7–3.3]	3.3 \pm 0.1 [2.5–3.9]	3.1 \pm 0.1 [2.8–3.2]	3.3 \pm 0.0 [3.3–3.3]	$F_{2,89} = 36.0$; $p < .001$ ***	a, b, b
Basal pronotum width (PWb)	2.2 \pm 0.0 [2.0–2.4]	2.3 \pm 0.0 [2.0–2.5]	2.6 \pm 0.0 [2.2–2.9]	2.7 \pm 0.0 [2.1–3.0]	2.6 \pm 0.1 [2.4–2.8]	2.7 \pm 0.1 [2.6–2.7]	$F_{2,89} = 46.6$; $p < .001$ ***	a, b, b
Elytra basal width (EWh)	3.9 \pm 0.0 [3.5–4.2]	4.2 \pm 0.1 [3.8–4.6]	4.3 \pm 0.1 [3.7–4.8]	4.7 \pm 0.1 [3.4–5.2]	4.6 \pm 0.1 [4.1–4.9]	4.9 \pm 0.0 [4.9–4.9]	$F_{2,89} = 29.9$; $p < .001$ ***	a, b, (b)
Elytra maximum width (EWM)	4.9 \pm 0.0 [4.4–5.2]	5.4 \pm 0.1 [4.9–5.7]	5.4 \pm 0.1 [4.6–6.0]	5.9 \pm 0.1 [4.5–6.4]	5.5 \pm 0.1 [4.8–5.8]	5.8 \pm 0.1 [5.7–5.8]	$F_{2,89} = 32.7$; $p < .001$ ***	a, b, b
Head width (HW)	3.1 \pm 0.0 [2.8–3.3]	3.3 \pm 0.0 [3.0–3.5]	3.3 \pm 0.0 [2.9–3.6]	3.5 \pm 0.0 [2.9–3.8]	3.4 \pm 0.1 [3.2–3.6]	3.6 \pm 0.0 [3.6–3.6]	$F_{2,89} = 32.1$; $p < .001$ ***	a, b, b
Labrum width (LW)	1.8 \pm 0.0 [1.5–2.0]	1.9 \pm 0.1 [1.8–2.0]	1.9 \pm 0.1 [1.6–2.2]	2.1 \pm 0.0 [1.6–2.4]	2.0 \pm 0.0 [1.8–2.1]	2.0 \pm 0.0 [2.0–2.1]	$F_{2,89} = 10.8$; $p < .001$ ***	a, b, b
Labrum length (LL)	0.8 \pm 0.0 [0.6–1.0]	1.0 \pm 0.0 [1.0–1.1]	1.0 \pm 0.1 [0.8–1.3]	1.2 \pm 0.0 [0.8–1.3]	1.1 \pm 0.0 [1.0–1.1]	1.2 \pm 0.1 [1.1–1.2]	$F_{2,92} = 22.4$; $p < .001$ ***	a, b, b
Other setae (OS)	2.8 \pm 0.3 [0.5–5.5]	2.8 \pm 0.5 [0–5.0]	3.8 \pm 0.3 [0–7.0]	3.8 \pm 0.4 [0–9.0]	5.8 \pm 0.9 [2.5–8.5]	5.5 \pm 0.5 [5.0–6.0]	$F_{2,89} = 9.5$; $p < .001$ ***	a, b, c
Aedeagus length (AL)	4.6 \pm 0.1 [3.8–5.0]	-	5.5 \pm 0.1 [4.5–5.9]	-	5.4 \pm 0.2 [4.9–5.8]	-	$F_{2,40} = 39.3$; $p < .001$ ***	a, b, b

.....continued on the next page

TABLE 2. (Continued)

Measure / Ratio	<i>herbacea</i> Klug, 1832		<i>perreai</i> Deuve, 1987		<i>turkestanicoidea</i> W.Horn, 1938		Difference between taxa (ANOVA)	Posthoc for differences between taxa
	21 ♂	10 ♀	26 ♂	28 ♀	6 ♂	2 ♀		
EL / TL	0.63 ± 0.00 [0.60–0.65]	0.63 ± 0.00 [0.62–0.64]	0.63 ± 0.00 [0.61–0.65]	0.63 ± 0.00 [0.59–0.66]	0.65 ± 0.00 [0.63–0.66]	0.65 ± 0.00 [0.65–0.65]	F_{2,89} = 8.9; p < .001***	a, a, b
PL / EL	0.27 ± 0.00 [0.25–0.29]	0.25 ± 0.00 [0.24–0.27]	0.28 ± 0.00 [0.25–0.30]	0.26 ± 0.00 [0.22–0.29]	0.27 ± 0.00 [0.26–0.28]	0.24 ± 0.00 [0.24–0.25]	F_{2,89} = 2.7; p = .074(*)	a, a, a
PL / PWm	0.76 ± 0.03 [0.68–1.3]	0.68 ± 0.01 [0.65–0.72]	0.77 ± 0.01 [0.69–0.81]	0.71 ± 0.01 [0.57–0.77]	0.76 ± 0.01 [0.70–0.78]	0.69 ± 0.01 [0.68–0.70]	F_{2,89} < 0.1; p = .938	a, a, a
PWb / PWm	0.85 ± 0.03 [0.77–1.47]	0.78 ± 0.01 [0.74–0.82]	0.84 ± 0.01 [0.79–1.0]	0.81 ± 0.01 [0.70–0.87]	0.84 ± 0.01 [0.81–0.88]	0.81 ± 0.01 [0.80–0.82]	F_{2,89} = 0.2; p = .860	a, a, a
PWb / EWh	0.56 ± 0.00 [0.52–0.60]	0.54 ± 0.00 [0.52–0.56]	0.59 ± 0.01 [0.55–0.71]	0.57 ± 0.01 [0.48–0.64]	0.57 ± 0.01 [0.55–0.59]	0.54 ± 0.01 [0.54–0.55]	F_{2,89} = 11.0; p < .001***	a, b, a
EWh / EWm	0.81 ± 0.00 [0.78–0.84]	0.79 ± 0.00 [0.77–0.81]	0.80 ± 0.00 [0.76–0.85]	0.80 ± 0.01 [0.73–0.87]	0.83 ± 0.01 [0.81–0.85]	0.85 ± 0.01 [0.84–0.86]	F_{2,89} = 11.9; p < .001***	a, a, b
PWm / EWm	0.54 ± 0.01 [0.33–0.57]	0.55 ± 0.00 [0.53–0.58]	0.56 ± 0.00 [0.53–0.60]	0.57 ± 0.00 [0.54–0.63]	0.56 ± 0.01 [0.54–0.58]	0.57 ± 0.01 [0.56–0.58]	F_{2,89} = 6.3; p = .003**	a, b, ab
LL / LW	0.47 ± 0.01 [0.40–0.53]	0.54 ± 0.01 [0.51–0.56]	0.53 ± 0.01 [0.47–0.59]	0.56 ± 0.01 [0.47–0.63]	0.54 ± 0.02 [0.48–0.61]	0.57 ± 0.03 [0.54–0.60]	F_{2,48} = 12.5; p < .001***	a, b, b

Cicindela herbacea herbacea Klug, 1832

Figs 6–10, 17–20, 26–29, 38–45, 62–64, 68,74, 80, 92, 97–98

Cicindela campestris herbacea Klug, 1832: pl. XXI (Type locality: ora Syriae prope Berytum).

Cicindela campestris herbacea Klug, 1832: Roeschke in Horn & Roeschke 1891: 64, 66–67, 75; Fleutiaux 1892: 111; Horn 1915: 342; 1926: 230; 1938: 46, Taf. 66 f. 4, 5; Rivalier 1950: 227; Cassola & van Nidek 1984: 11; Korell 1988: 98, 100; 1994: 43, 49; Avgin & Özdikmen 2007: 91.

Cicindela herbacea Klug, 1832: Mandl, 1944: 2; Werner 1991: 21, 43, 65, Tab. 20 f. 157; Wiesner 1992: 127; 2020: 195; Lorenz 1998: 43; 2005: 133; Cassola 1999: 237; Putschkov, Matalin 2003: 105; 2017: 229; Franzen, 2007: 13; Avgin & Wiesner 2009: 356; Deuve 2011: 129; Matalin & Chikatunov 2016: 127; Assman *et al* 2018: 53, 68.

= *Cicindela herbacea aleppensis* Deuve, 2012: 13, **syn. n.** (ex parte) (Type locality: Aleppo).

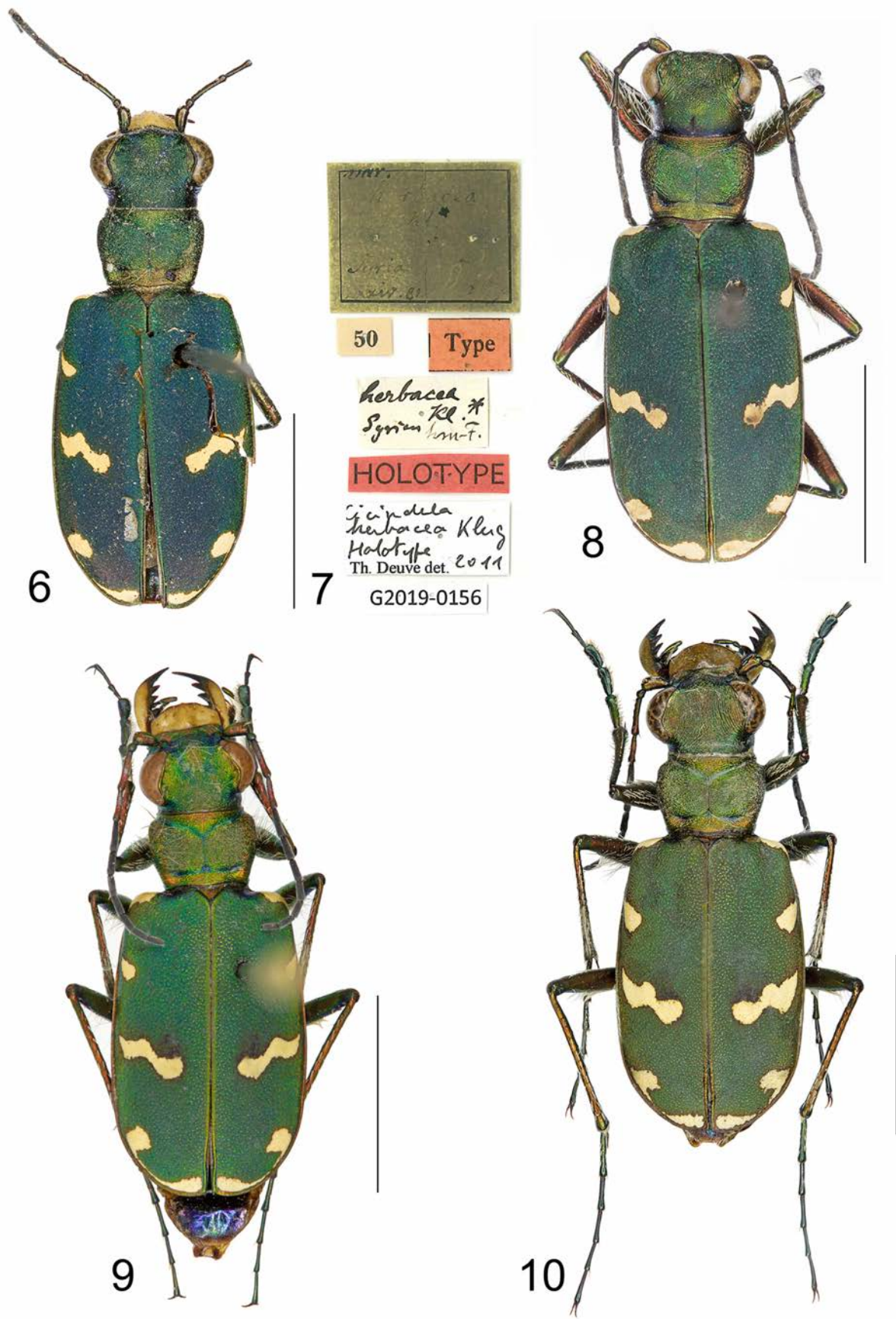
Type material examined: HOLOTYPE of *Cicindela campestris herbacea* Klug, 1832 (by monotypy): ♀: ‘Holotype’, ‘Type’, ‘50’, ‘var. *herbacea*/Kl.’, ‘Syria, Lxxiv. 81 Ehrbg.’, ‘*herbacea* Kl. * Syria hm-F.’ (the label of the historical collection on yellowish cardboard handwritten and thin black framed), ‘*Cicindela herbacea* Klug Holotype, Th. Deuve det. 2011’ (handwritten on white paper), ‘G2019-156’ [MNHUB]; HOLOTYPE of *Cicindela herbacea aleppensis* Deuve 2012: ♂: ‘Holotype’, ‘Aleppo’, ‘EC 7797’, ‘*Cicindela herbacea aleppensis*, Th. Deuve det. 2011’ (species name handwritten on white cardboard, authors note printed on laser printer), ‘G2019-0309’ [MNHNP].

Distribution: We examined 103 specimens (57 males and 45 females) from the following locations (Fig. 4): **LEBANON:** Bcharré (Bischarri), Beirut, Ouâdi Tlaa (Horsh Ehden), Taran (Sfireh forest), Zeytoun; **SYRIA:** **Aleppo:** Aleppo, Ain-Abad, Rasm al-Abed; **Homs:** Tannourine; **TURKEY:** **Hatay:** Akbez, Hassa; **Kahramanmaraş:** Kahramanmaraş; **Osmaniye:** Zorkun.

Redescription: Base colouration green to blueish-green, often with coppery, red-golden sheen, head, labial- and maxillar plapi coloured similarly, base colour of mandibles white with dark metallic colouration towards the inside, four visible teeth with a fifth hidden beneath the labrum (Figs. 6–10). Head with not very protruding eyes, cheeks glabrous, vertex loosely setose with long white setae, clypeus glabrous metallic green to red-coppery, scapus apart from the group of distal sensory setae with 0 to 6 (2.8 ± 0.3) additional setae, labrum more elongated in females than in males (Tab. 2), with 6 to 8 long, lightly coloured sub-marginal setae, median tooth and anterior edge of labrum darkened (Figs. 17–20). Pronotum shorter than wide (Tab. 2), slightly narrower near the anterior and near the posterior edges then in the middle, near the base narrowed slightly rounded to straight, basal edge slightly curved, anterior edge almost straight (Figs. 26–29). Elytra rather parallel sided, only weakly broadened from the shoulders to the broadest point (not stronger in females than in males; Tab. 2), elytra dorsally noticeably flattened, elytral punctures vary in coloration between green and deep blue, humeral (shoulder) lunula separated into two isolated spots, apical lunula often separated into two spots but in some specimens connected with a narrow central portion, middle band protruding slightly diagonally towards the apex in two short bows, its width varying from rather narrow to noticeably broadened (Figs. 38–45), apical edge serrated, sutural spine retracted behind apical edge. Aedeagus with characteristic bend near the middle on the concave side and characteristically elongated tip (Figs. 62–64). Internal sack shorter, less protruding beyond the penis tube; BLL virtually shorter with apical field of decumbent longitudinal spinules; BLR small with small basi-medial area of short spinules; VA larger; VLR larger and clearly visible in the left lateral view; VLL undeveloped; *mt* typically with sharply curved apex (Figs 68, 74, 80, 92). For mean body-size measurements, see Table 1.

Nomenclature notes: In the “Monographie der paläarktischen Cicindelen” (Horn & Roeschke 1891) the name *Cicindela campestris herbacea armeniaca* Roeschke, 1891 is mentioned. In the latest editions of the Catalog of Palaearctic tiger beetles (Putschkov & Matalin 2017) and the Checklist of Cicindelidae of the world (Wiesner 2020) the name ‘*armeniaca* Roeschke, 1891’ is considered as a synonym of *C. herbacea*. However, according to the Articles 12.1 and 45.5 of ICZN (2000) this name is infrasubspecific because it was published as a fourth name added to a trinomen. Moreover, the name ‘*armeniaca* Roeschke, 1891’ is the *nomen nudum*, because it is not accompanied by a description or by an indication (e.g., association with an illustration, etc.). Thus, this name did not meet the requirements of the Articles 11 and 12 of the ICZN (2000) and it is therefore unavailable and should be excluded from the species group.

Remarks: The type locality ‘Berytum’ (= Zeytoun) likely refers to Zeytoun approximately 30 km north of Beirut / Lebanon as mentioned by Franzen (2007) and not to Zeytoun (=Süleymanlı) / Turkey where *C. h. turkes-tanicoides* occurs. Records of *C. h. herbacea* from Karamanmaraş province (Avgin 2006) should be checked for a possible confusion with *Cicindela javetii* as indicated by Deuve (2011). As previously mentioned by Matalin and



FIGURES 6–10. *Cicindela herbacea herbacea*, habitus: 6, 7—lectotype of *Cicindela herbacea* Klug, 1832, Syria [MNHUB]; 7—labels; 8—holotype of *Cicindela herbacea aleppensis* Deuve, 2012, Syria (Aleppo) [MNHNP]; 9, 10—Lebanon (Bcharré); 6, 7—female; 8–10—males. Scales—5 mm.

Chikatunov (2016), *C. h. herbacea* has so far not been collected in Israel and older records were likely confused with *C. j. azari* Deuve, 2011. Older, doubtful records from the western Taurus have been assigned to *C. campestris* by Franzen (2007) based on his own collected material from these locations.

Ecology: Information on the habitat of *C. herbacea herbacea* are sparse. The little information available originates mostly from specimens collected in Turkey. Populations occur on wet, loamy spots in forested areas, on forest roads, often close to waterbodies (brooks, rivers, lake shores). In Lebanon, *C. herbacea herbacea* was observed and collected in cedar forests (*Cedrus libani* A. Rich.) in the northern half of the country (Figs. 97–98). Based on the examined material, *C. h. herbacea* is found in colline and montane elevations between 300 m and 1550 m (Fig. 5; 1128 ± 171 m; only including records that included collection information with sufficient precision). The investigated specimens were collected between 13 April and 18 June. Based on collection specimens, *C. h. herbacea* occurs sympatrically with *Cicindela javetii* around Zorkun (Hatay province / Turkey) and *C. campestris neopontica* Deuve 2012 around Darboğaz (Niğde province / Turkey).

Cicindela herbacea turkestanicoidea W. Horn, 1938

Figs 11–16, 21–25, 30–37, 46–61, 65–67, 69–73, 75–79, 81–85, 93–96, 99–102

Cicindela campestris turkestanicoidea W. Horn, 1938: 13, Taf. 66, figs. 10, 11 (Type locality: Taesh, N Persien, zwischen Astrabad und Schahrud).

Cicindela desertorum turkestanicoidea W. Horn, 1938: Mandl, 1944: 2; Cassola & van Nidek 1984: 11; Korell 1988: 101; 1994: 49; Werner 1991: 22, 44, 66, Taf. 20 f. 165, 166; Wiesner 1992: 127; Lorenz, 1998: 43; 2005: 142.

Cicindela turkestanicoidea W. Horn, 1938: Franzen 2007: 13; Puchkov & Matalin 2003: 108; Puchkov & Matalin 2017: 233; Avgin & Özdikmen 2007: 91; Deuve 2011: 132; 2012: 15; Wiesner 2020: 196.

= *Cicindela perreai* Deuve, 1986: 74, **syn. n.** (Type locality: Pülümür / Tunceli / Turkey).

Cicindela perreai Deuve, 1986: Korell 1988: 99.

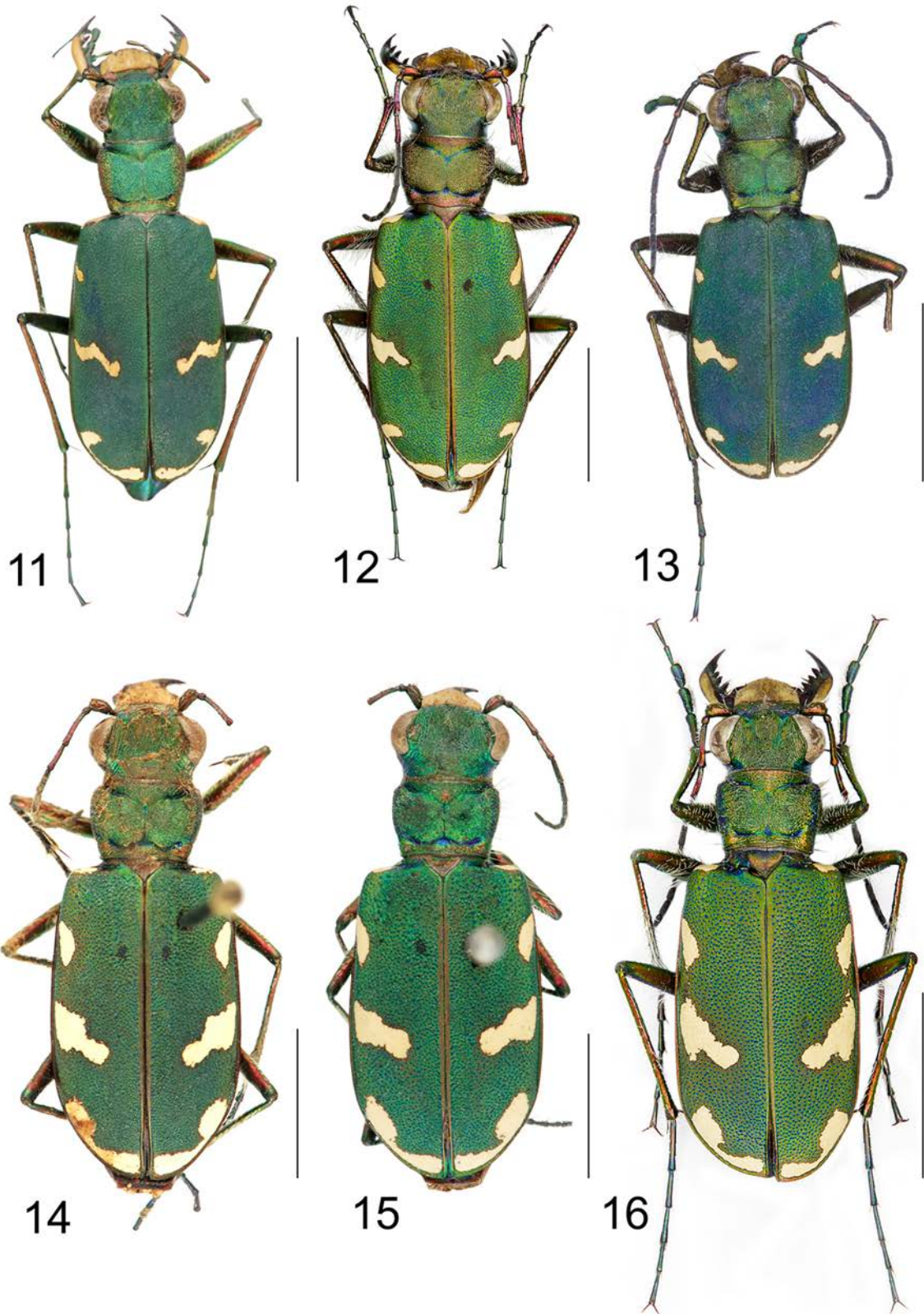
Cicindela desertorum perreai Deuve, 1986: Werner 1991: 22, 44, 66, Taf. 21 f. 167, 168; Wiesner, 1992: 127; Korell 1994: 44, 49; Lorenz, 1998: 43.

Cicindela turkestanicoidea perreai Deuve, 1986: Cassola 1999: 241; Puchkov & Matalin 2003: 108; Lorenz, 2005: 142; Franzen 2007: 13; Avgin & Özdikmen 2007: 91.

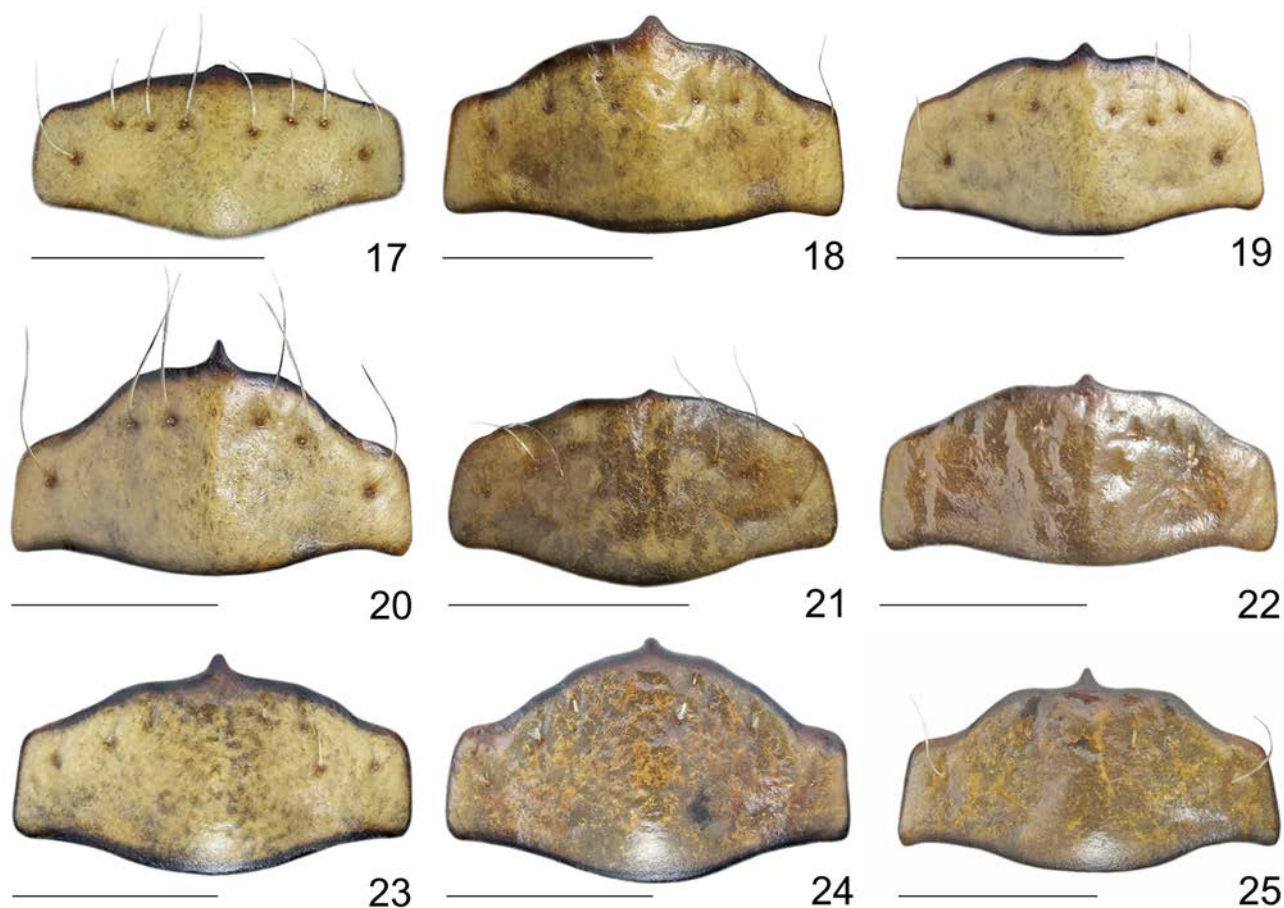
= *Cicindela herbacea colasi* Deuve, 2011: 132, **syn. n.** (Type locality: Pozantı / Adana / Turkey).

Type material examined: LECTOTYPE of *Cicindela campestris turkestanicoidea* W. Horn, 1938: ♀: “Taesh, N Persien, zwischen Astrabad und Schahrud, leg. Christoph 1871” [SDEI]; PARALECTOTYPE of *Cicindela campestris turkestanicoidea* W. Horn, 1938: ♀: ‘Shaku, N Persien, zwischen Astrabad und Schahrud, leg. Christoph 1871’ [SDEI] (digital images provided by Thierry Deuve). HOLOTYPE of *Cicindela perreai* Deuve, 1987: ♂: ‘Holotype’ (red cardboard label dyed through), ‘*Cicindela perreai* n.sp. Th. Deuve det. 1987’ (species name and year handwritten on white cardboard, authors note printed on laser printer), ‘Turquie, environs de Tunceli, Pülümür, 1 600 m, Th. Deuve, juillet 1986’ [MNHNP] (digital image provided by Thierry Deuve). HOLOTYPE of *Cicindela herbacea colasi* Deuve, 2011: ♂: ‘Holotype’ (red cardboard label dyed through), ‘*Cicindela herbacea colasi* n.sp. Th. Deuve det. 2011’ (species name and year handwritten on white cardboard, authors note printed on laser printer), ‘EC 7798’, ‘Turkey, Adana, environs of Pozantı, Taurus mts., Bolkar Dağları, 1.000–1.600 m, Colas, Guy leg.’, ‘G2019-0310’ [MNHNP].

Distribution: We examined 305 specimens (143 males and 132 females; sex of the remaining specimens was not identified) from the following locations (Fig. 4): **IRAN:** **Alborz:** Dizin; **Ardabil:** Ardabil, Khalkhal (Hero Abad), Kuh-e Andarak (50 km S Galugah), Heyrat; **Golestan:** Tāsh-e-olyā; **Hamadan:** Tarik Darreh Ski Resort; **Isfahan:** Hanna (85 km W Abadeh); **Kordestan:** Baneh-Saqez pass; **Lorestan:** Dorud; **Māzandarān:** Karvan-sara-ye Shah Abbasi, Kamarbon; **Teheran:** Teheran, Shemshak, Kuh-e Si Chal (Sichal); **West Azerbaijan:** Qimmat Jaynuk Mahinuk (Rajan vill.); **Zanjan:** Takht-i Suleiman; **TURKEY:** **Adana:** Pozantı, Saimbeyli (Hadjin); **Ağrı:** Doğubeyazıt; **Amasya:** Amasya; **Bayburt:** Salmankas Geçidi; **Bingöl:** Bingöl, Kuruca Geçidi, Solhan; **Bitlis:** Bölüküyazi, Kuskunkiran Geçidi, Örenlik, Resadiye, Tatvan, Yolbilen; **Çorum:** Kurbaglı; **Elazığ:** Sakabaşı; **Erzincan:** Caglayan, Kızıldağ Geçidi, Sarıyazı; **Erzurum:** Kirçeli Geçidi, Kop Geçidi, Kopköy, Ovit Dağı Geçidi, Palandöken Dağı; **Gümüşhane:** Gümüşhane, Köseadağ Geçidi; **Hakkâri:** Hakkâri, Karadağ; **Kahramanmaraş:** Gücüksu, Zeytoun (= Süleymanlı); **Kars:** Digor İlçesi; **Malatya:** Karahan Geçidi, Kubbe Geçidi, Malatya, Yukarıulupınar; **Muş:** Buğlan Geçidi; **Niğde:** Bolkar dağları, Darboğaz; **Sivas:** İmranlı Geçidi, Karabayır Geçidi, Kurbağalıbeli Geçidi; **Tunceli:** Gözen, Pülümür; **Van:** Aygır Gölü, Çatak (= Moks), Erciş, Karabet Geçidi, Kuskunkiran Geçidi, Van.



FIGURES 11–16. *Cicindela herbacea turkestanicoides*, habitus: 11—holotype of *Cicindela perreaui* Deuve, 1987, Turkey (Tunceli, Pülümür) [MNHNP]; 12—Turkey (Tunceli, Pülümür); 13—holotype of *Cicindela herbacea colasi* Deuve, 2011, Turkey (Adana, Pozanti, Bolkar Dagh Mountain) [MNHNP]; 14—lectotype of *Cicindela campestris turkestanicoides* W. Horn, 1938, Iran (Gilan, Taesch [= Tash]) [SDEI]; 15—paralectotype of *Cicindela campestris turkestanicoides* W. Horn, 1938, Iran (Isfahan, Schaku [= Shah Kuh]) [SDEI]; 16—Iran (Māzandarān, Heyrat); 11, 13, 16—males; 12, 14, 15—females; 11, 14, 15—photos provided by Thierry Deuve. Scales—5 mm.



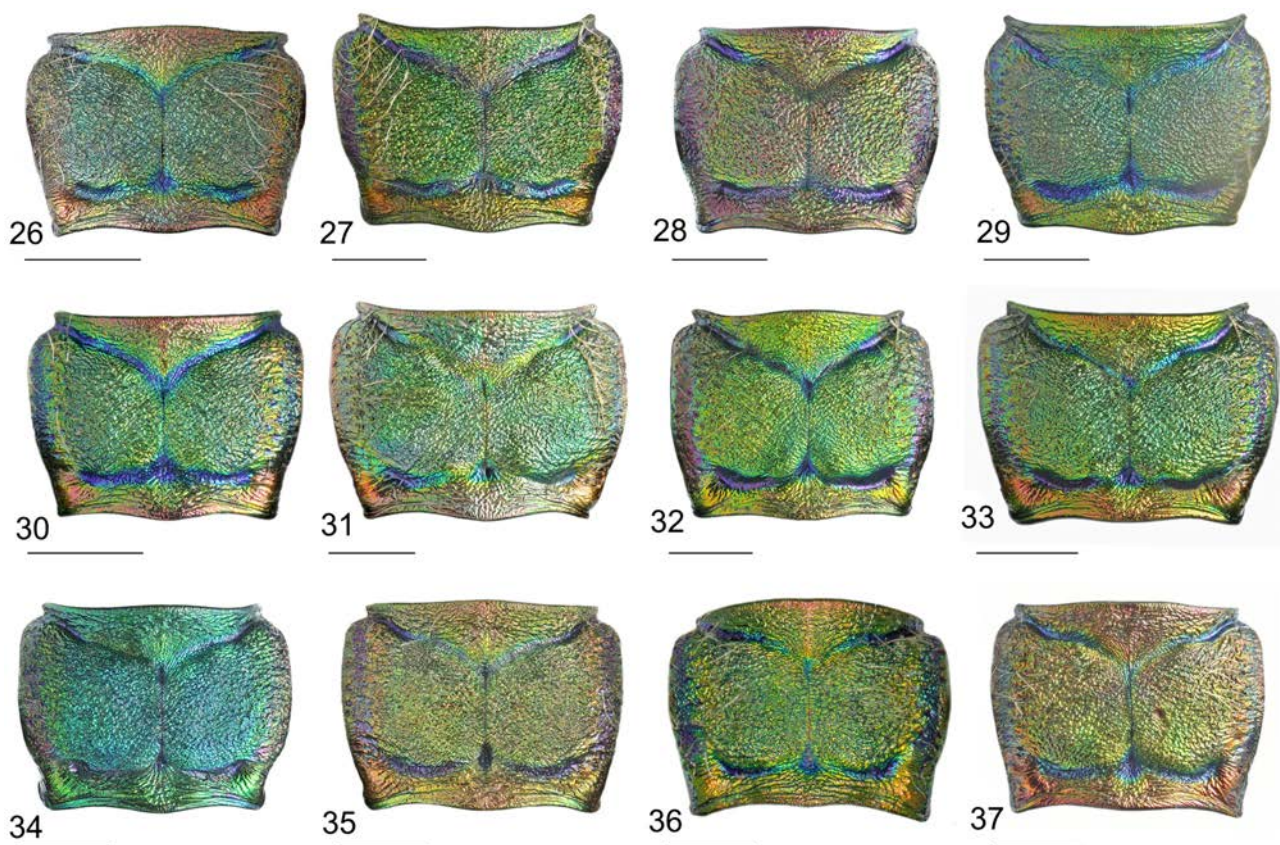
FIGURES 17–25. *Cicindela herbacea*, labrum: 17–20—*C. h. herbacea*; 21–25—*C. h. turkestanicoidea*; 17, 18—Lebanon, Bcharré; 19, 20—Syria, Aleppo; 21, 22—Turkey (21—Adana, Karanfil Mt.; 22—Solhan); 23–25—Iran (23, 24—West-Azerbaijan, Rajan; 25—Māzandarān, Ilka); 17, 19, 21–23, 25—males; 18, 20, 24—females. Scales—1 mm.

Redescription: Base colouration green to red-, coppery-green, often with coppery, red-golden sheen, head, labial- and maxillar plapi coloured similarly, base colour of mandibles white with dark metallic colouration towards the inside, four visible teeth with a fifth hidden beneath the labrum (Figs. 11–16). Head with not very protruding eyes, cheeks glabrous, vertex coarsely wrinkled, loosely setose with long white setae, frons setose, clypeus usually glabrous, rarely with single setae, metallic green to red-golden, scapus apart from the group of distal sensory setae with 0 to 10 (6.1 ± 0.6) additional setae. Labrum more elongated in females than in males (Tab. 2), with 6 to 8 long, lightly coloured sub-marginal setae, median tooth and anterior edge of labrum darkened (Figs. 21–25). Pronotum shorter than wide (Tab. 2), slightly narrower near the anterior and near the posterior edges than in the middle, narrowed almost straight towards base, basal edge slightly curved, anterior edge almost straight, slightly curved, deep grooves on the pronotum green to deep blue metallic (Figs. 30–37). Elytra noticeably elongated and parallel sided, only weakly broadened from the shoulders to the broadest point (not stronger in females than in males; Tab. 2), dorsally noticeably flattened, elytral punctures vary in coloration between pure / dark green to deep blue, humeral lunula separated into two isolated spots, apical lunula usually complete (spots sometimes only narrowly connected), in some specimens from the western part of the range separated into two isolated spots, broad middle band protruding slightly diagonally almost straightly towards the apex (Figs. 46–61), middle band (as well as humeral and apical lunules) characteristically enlarged in specimens from the Northern Iranian Alborz mountain range (as depicted in Horn (1938): plate 66, figs 10, 11; Figs. 14–16 & 59–61), maculations (in most specimens) noticeably narrower and middle band in two recognizable short bows in the rest of the range (enlarged maculation do, however, occur in some specimens; described as *perreai* Deuve, 1987; as depicted in Horn (1938): plate 66, figs 12–14 and in Deuve (1987); Fig. 56), apical edge weakly serrated, sutural spine retracted behind apical edge. Aedeagus near the base more elongated than in *C. h. herbacea* and with characteristic bend near the middle on the concave side and

characteristically elongated tip (Figs. 65–67). Internal sack longer, protruding farther beyond the penis tube; BLL virtually longer with apical field of decumbent longitudinal spinules; BLR small with little basi-medial area of short spinules, in some specimens from southwestern localities relatively large and covered by short spinules; VA smaller; VLR smaller and practically invisible in the left lateral view; VLL undeveloped; *mt* typically with less curved apex (Figs. 69–73, 75–79, 81–85, 93–96). For mean body-size measurements, see Table 1.

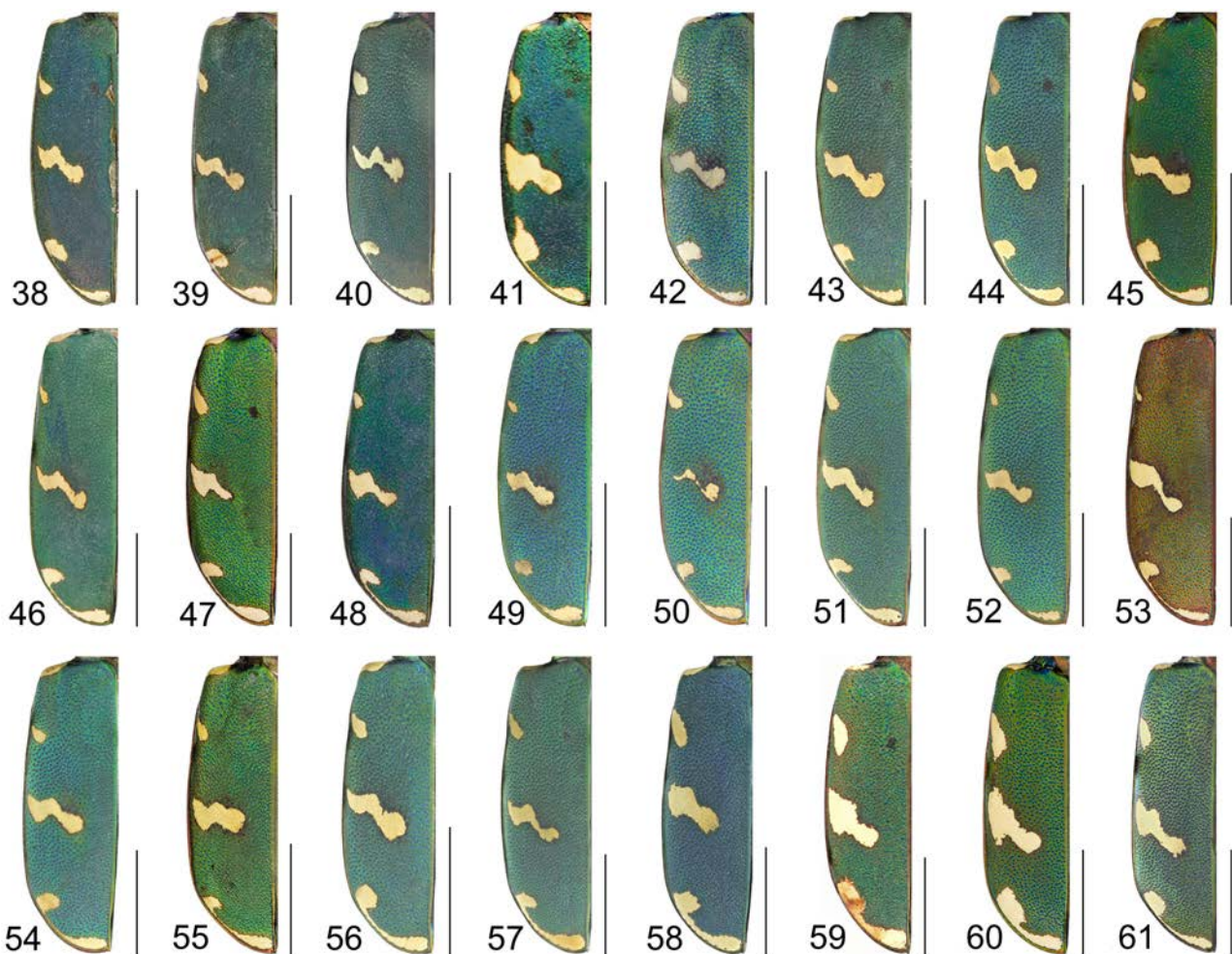
Remarks: Cassola (1999) states that *C. h. turkestanicoidea* (as *C. turkestanicoidea perreai*) can be differentiated from *C. desertorum* with which it may occur sympatrically in Eastern Turkey by a larger elytra-length to pronotum-length ratio ($EL / PL > 3.6$ or $PL / EL < 0.28$ in *C. h. turkestanicoidea* and $EL / PL < 3.4$ or $PL / EL > 0.295$ in *C. desertorum*). While this is generally supported by our results (Tab. 2), individual specimens may vary, and a clear differentiation may require analyses of additional features (elytra shape, aedeagus, endophallus).

Specimens from Iran are still rare in collections and more collection is needed to assess the distribution of *C. h. turkestanicoidea* in Iran. Avgin and Özdikmen (2007) reported *C. h. turkestanicoidea* from Hatay province/ Turkey which likely refers to *C. h. herbacea*.



FIGURES 26–37. *Cicindela herbacea*, pronotum, dorsal view: 26–29—*C. h. herbacea*; 30–37—*C. h. turkestanicoidea*; 26, 27—Lebanon, Bcharré; 28, 29—Syria, Aleppo; 30–33—Turkey (30—Adana, Karanfil Mt.; 31—Buğlan; 32—Solhan; 33—Tatvan); 34–37—Iran (34, 35—West-Azerbaijan, Rajan; 36—Māzandarān, Heyrat; 37—Māzandarān, Ilka); 26, 28, 30, 32–34, 36, 37—males; 27, 29, 31, 35—females. Scales—1 mm.

Specimens from the Alborz mountain range in Northern Iran (Alborz, Ardabil, Golestan, Māzandarān, Teheran provinces) resemble Horn's type specimens depicted in Deuve (2011). They have a characteristically enlarged maculation compared to specimens from the rest of the range. They, however, do not differ in any morphological features or in aedeagus shape or endophallus structure from specimens from Turkey (previously considered as *perreai* Deuve, 1987). We therefore follow Horn's assessment of the original description: Additional to the two typical females from Iran, Horn describes 6 additional specimens from Zeytoun (= Süleymanlı), Moks (= Çatak) and Van (elytra of three of these specimens depicted on plate 66, figures 12–14) which he regarded as the same species and mentioned the variability in elytral maculation (Horn 1938). Specimens from these locations have previously been assigned to *C. h. perreai* Deuve, 1987.



FIGURES 38–61. *Cicindela herbacea*, left elytron: 38–45—*C. h. herbacea*; 46–61—*C. h. turkestanicoides*; 38—lectotype of *Cicindela herbacea* Klug, 1832, Syria [MNHUB]; 39—holotype of *Cicindela herbacea aleppensis* Deuve, 2012, Syria (Aleppo) [MNHNP]; 40, 41—Syria (40—Aleppo); 42–45—Lebanon (42, 43, 45—Bcharré; 44—Horsh Ehden); 46–56—Turkey (46, 47—Tunceli, Pülümür; 48–50—Adana; 51—Buğlan; 52, 53—Tatvan; 54—Solhan; 55—Salmankas; 56—Van, İncesu); 46—holotype of *Cicindela perreaui* Deuve, 1987 [MNHNP]; 48—holotype of *Cicindela herbacea colasi* Deuve, 2011 [MNHNP]; 57–61—Iran (57, 58—West-Azerbaijan, Rajan; 59—Gilan, Taesch [= Tash]; 60—Māzandarān, Heyrat; 61—Māzandarān, Ilka); 59—lectotype of *Cicindela campestris turkestanicoides* W. Horn, 1938 [SDEI]; 39, 40, 42, 45, 46, 48–50, 52–56, 58, 60, 61—males; 38, 41, 43, 44, 47, 51, 57, 59—females; 41, 46, 59—photos provided by Thierry Deuve. Scales—3 mm.

Additionally, there are two further females with collection label ‘Wernyi, Staudinger’ (= Almaty / Kazakhstan) in the collection of Walter Horn (now SDEI) also mentioned in Horn (1938). As the region around Almaty is rather well studied and no further specimens are known to us from anywhere near this location, we expect that these specimens were confused by the collectors or mislabeled later on.

Ecology: Based on the examined material, *C. h. turkestanicoides* is found in montane to alpine elevations between 1150 m and 3600 m (Fig. 5; 2022 ± 67 m; only including records that included collection information with sufficient precision; see also Cassola (1999)). Many specimens were collected near mountain passes on alpine grasslands, some even close to remaining snow fields (Figs. 99–102), others in mixed forests and close to waterbodies (brooks, rivers, lake shores; see also original description in Deuve (1987)). The examined specimens were collected between 05 April and 26 July.

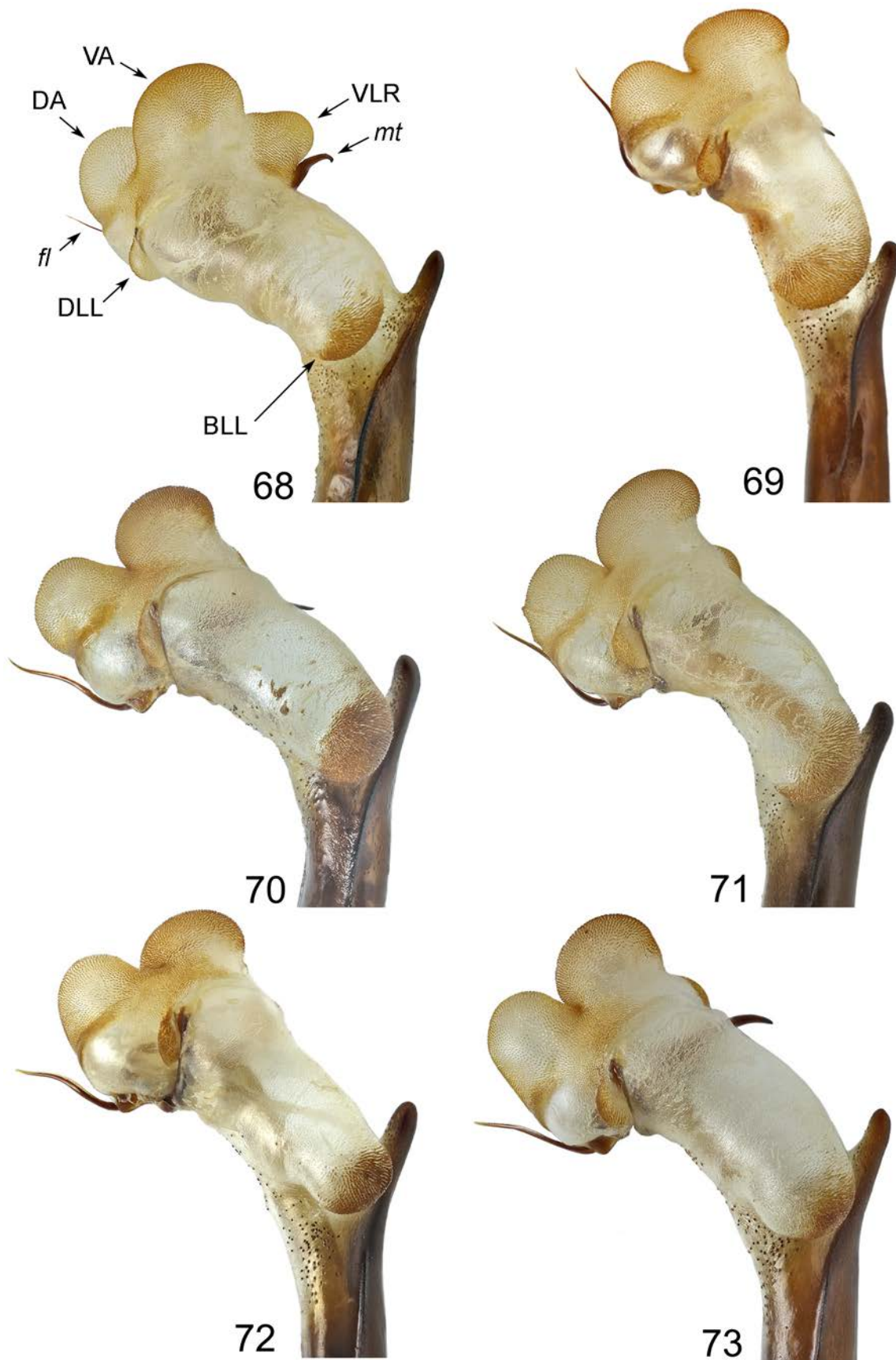


FIGURES 62–67. *Cicindela herbacea*, aedeagus, left lateral view: 62–64—*C. h. herbacea*; 65–67—*C. h. turkestanicoides*; 62—holotype of *Cicindela herbacea aleppensis* Deuve, 2012, Syria (Aleppo) [MNHNP]; 63, 64—Lebanon (Bcharré); 65—holotype of *Cicindela herbacea colasi* Deuve, 2011, Turkey (Adana, Bolkar Dag Mountain) [MNHNP]; 66—Turkey (Tatvan); 67—Iran (West-Azerbaijan, Rajan). Scales—1 mm.

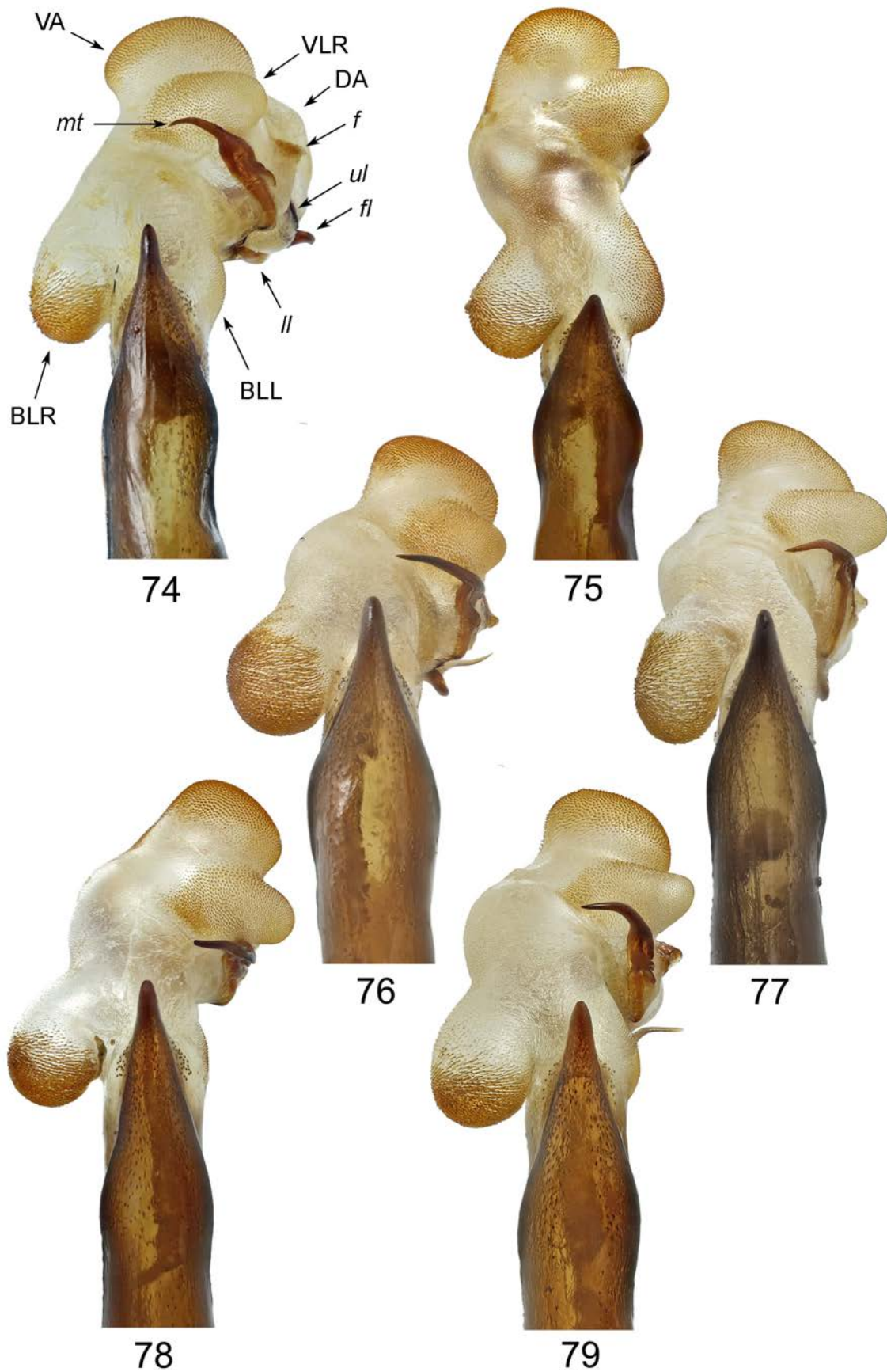
Cicindela javetii-subgroup

The taxa *azari* Deuve 2012, *javetii* Chaudoir, 1861 and *thughurica* Franzen 2007 were regarded as subspecies of *Cicindela javetii* after the latest revision by Deuve (2011). *Cicindela javetii* was first described by Chaudoir (1861) after a single male specimen (in coll. Oberthür, MNHNP, see Horn (1930)) and it remained largely enigmatic with almost no other specimens found (or better: recognized) until the recent past. Unfortunately, the holotype seems to be in poor condition—it was obviously glued imperfectly after being damaged in the past. Thus, we studied the holotype of *C. javetii* only from a photo provided to us by Ms Azadeh Taghavian (MNHNP). However, we found several specimens of similar colouration and maculation from older collections deposited in museum collections (one deposited in Horn's collection) that originate from the same area in Turkey as the holotype (deposited in CFM, MTD & SDEI).

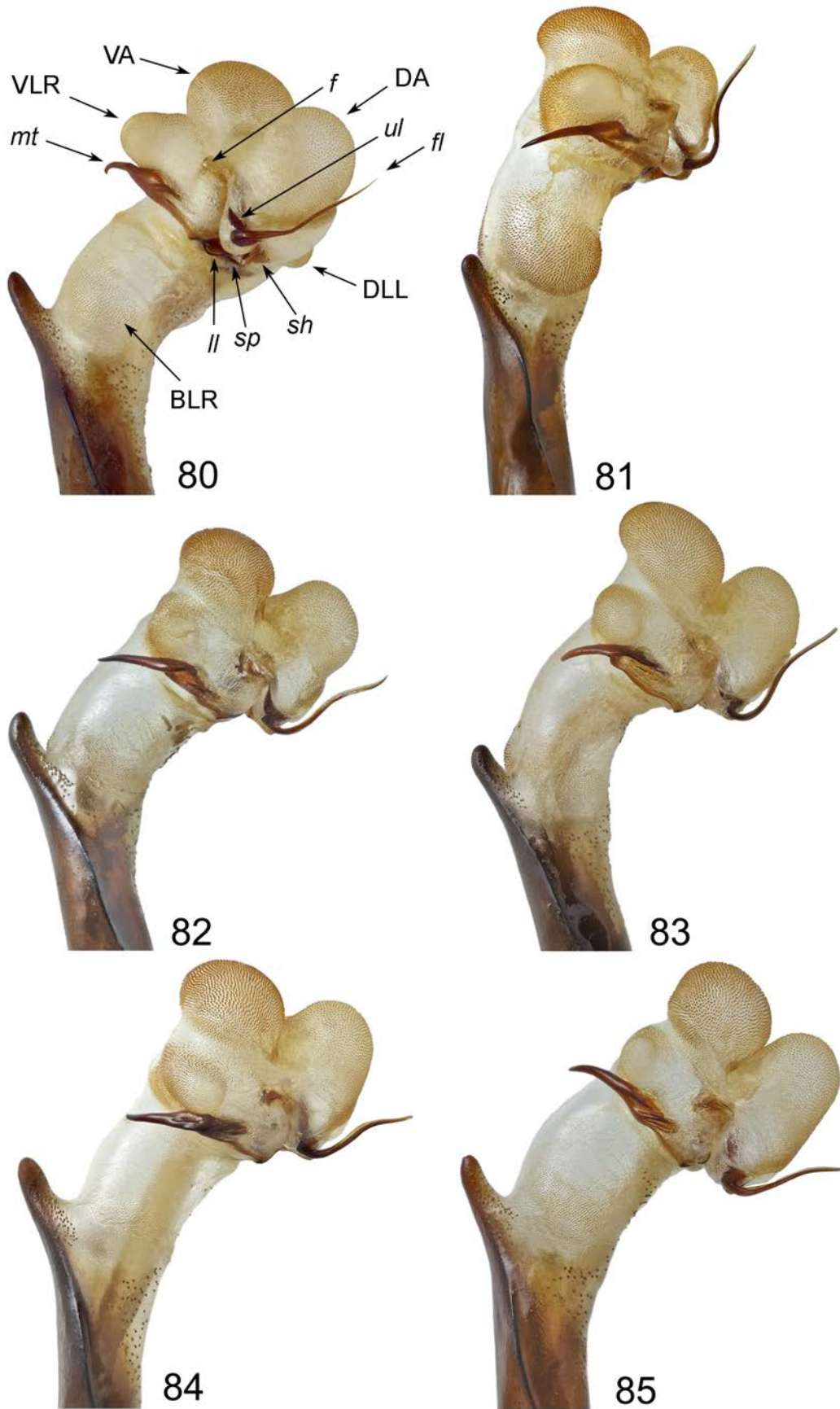
When Franzen (2007) described *Cicindela thughurica*, he assumed that it was not conspecific with *C. javetii* to which the new taxon was unfortunately not compared likely due to the lack of specimens identified as *C. javetii* in collections. Deuve (2011) correctly recognized the high similarity between both taxa and placed *thughurica* Franzen, 2007 as subspecies to *C. javetii*. Our morphometric and morphological analyses, however, show that *C. thughurica* is in fact a junior synonym of *C. javetii* (Fig. 103) which is supported by the fact that both taxa do occur within the same range (Figs. 104). Thus, the holotype specimen of *C. javetii* does not resemble the normal appearance of the species but rather a unique aberrant morph with much enlarged elytral maculation (it resembles *Cicindela normanni* Chaudoir, 1848 in maculation which already Chaudoir (1861) noticed). This has likely caused specimens in collections to remain unrecognized: While the aberrant holotype was recognized as distinct species, the normal



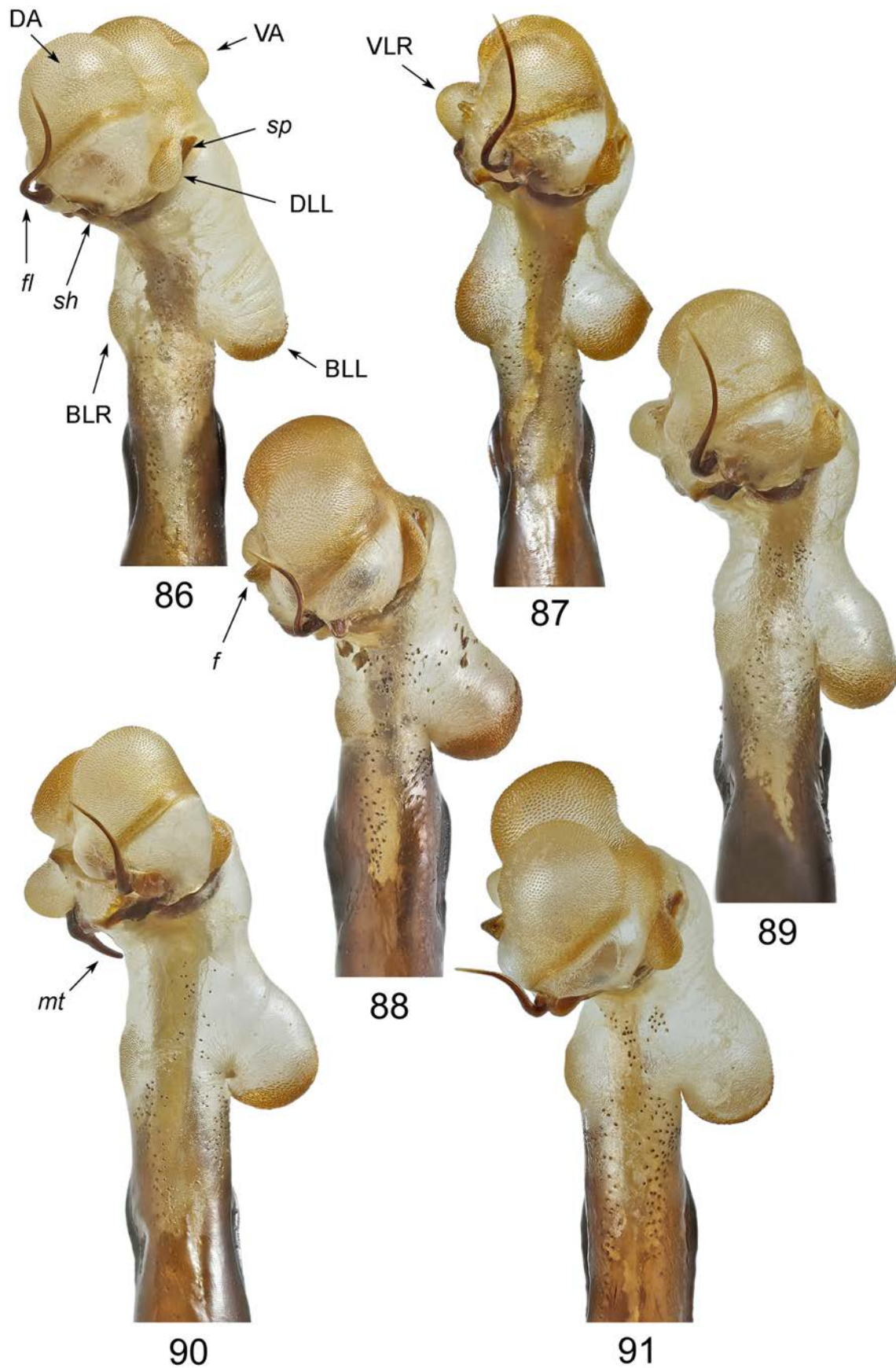
FIGURES 68–73. *Cicindela herbacea*, internal sack, left lateral view: 68—*C. h. herbacea* (Lebanon, Bcharré); 69–73—*C. h. turkestanicoidea*; 69–71—Turkey (69—Adana, Karanfil Mt.; 70—Solhan; 71—Tatvan); 72, 73—Iran (72—West-Azerbaijan, Rajan; 73—Māzandarān, Ilka). Not to scale. Abbreviations see text.



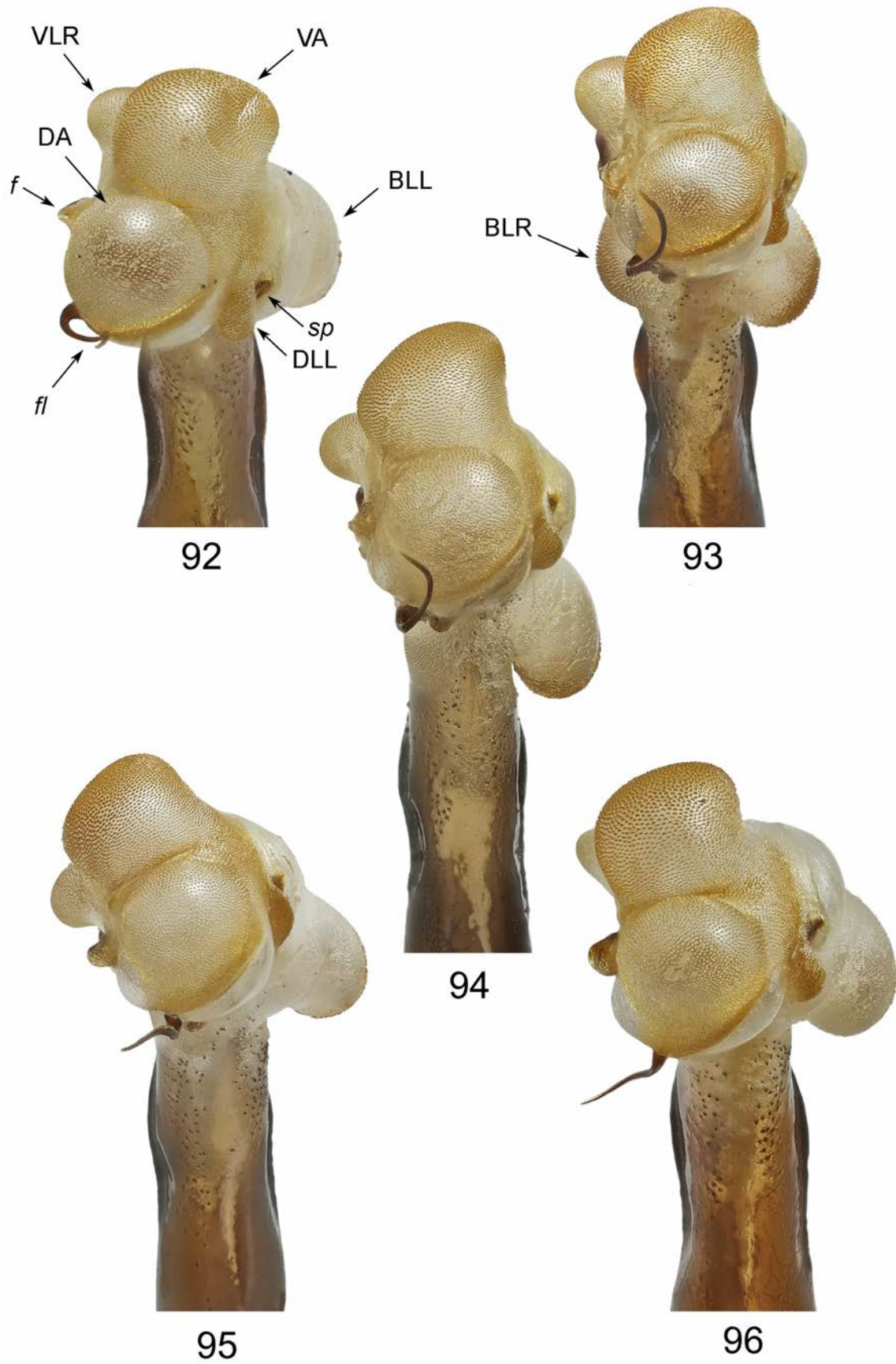
FIGURES 74–79. *Cicindela herbacea*, internal sack, dorsal view: 74—*C. h. herbacea* (Lebanon, Bcharré); 75–79—*C. h. turkestanicoides*; 75–77—Turkey (75—Adana, Karanfil Mt.; 76—Solhan; 77—Tatvan); 78, 79—Iran (78—West-Azerbaijan, Rajan; 79—Māzandarān, Ilka). Not to scale. Abbreviations see text.



FIGURES 80–85. *Cicindela herbacea*, internal sack, right lateral view: 80—*C. h. herbacea* (Lebanon, Bcharré); 81–85—*C. h. turkestanicoidea*; 81–83—Turkey (81—Adana, Karanfil Mt.; 82—Solhan; 83—Tatvan); 84, 85—Iran (84—West-Azerbaijan, Rajan; 85—Māzandarān, Ilka). Not to scale. Abbreviations see text.



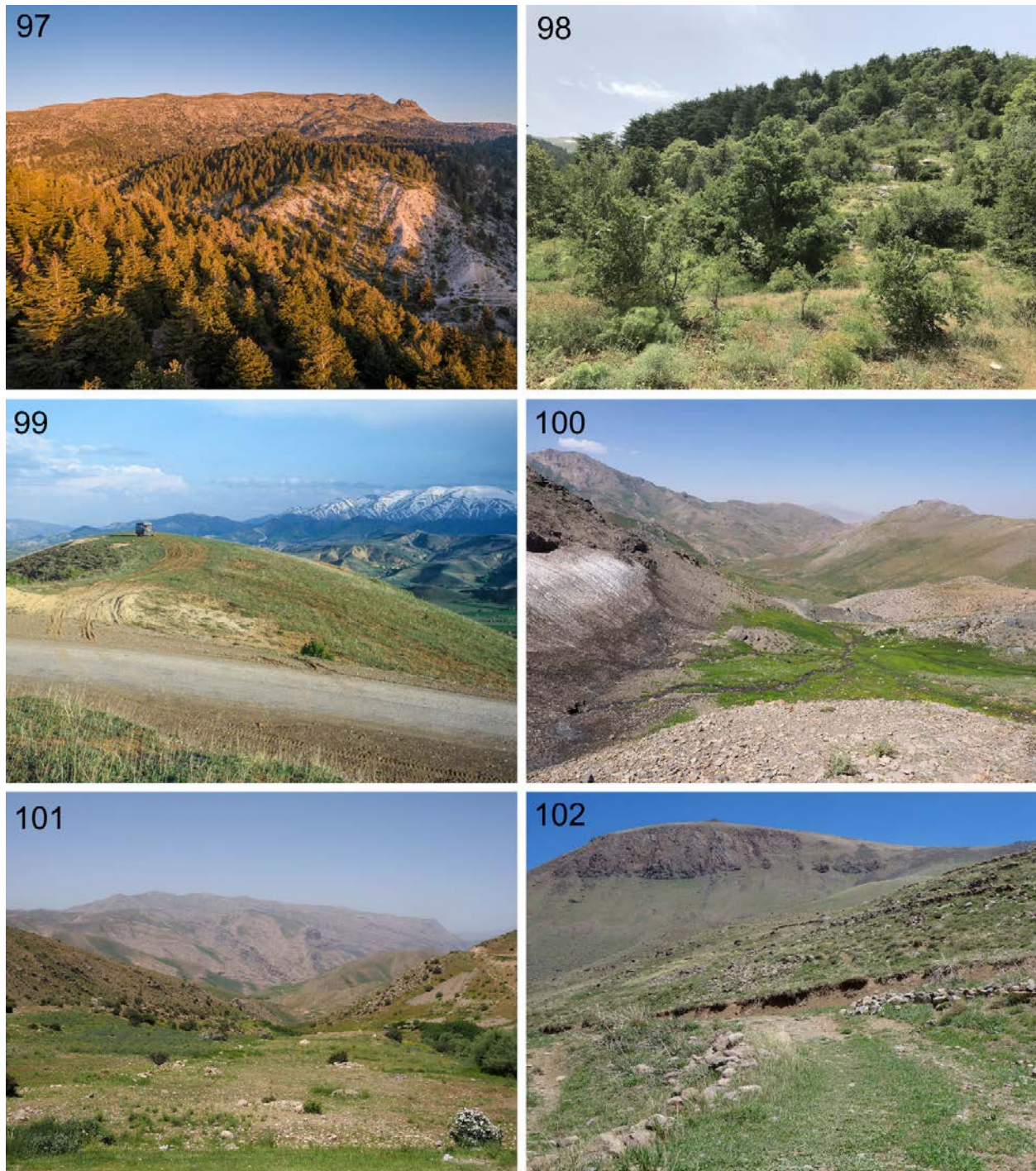
FIGURES 86–91. *Cicindela herbacea*, internal sack, ventral view: 86—*C. h. herbacea* (Lebanon, Bcharré); 87–91—*C. h. turkestanicoides*; 87–89—Turkey (87—Adana, Karanfil Mt.; 88—Solhan; 89—Tatvan); 90, 91—Iran (90—West-Azerbaijan, Rajan; 91—Māzandarān, Ilka). Not to scale. Abbreviations see text.



FIGURES 92–96. *Cicindela herbacea*, internal sack, ventro-apical view: 92—*C. h. herbacea* (Lebanon, Bcharré); 93–96—*C. h. turkestanicoidea*; 93, 94—Turkey (93—Adana, Karanfil Mt.; 94—Tatvan); 95, 96—Iran (95—West-Azerbaijan, Rajan; 96—Māzandarān, Ilka). Not to scale. Abbreviations see text.

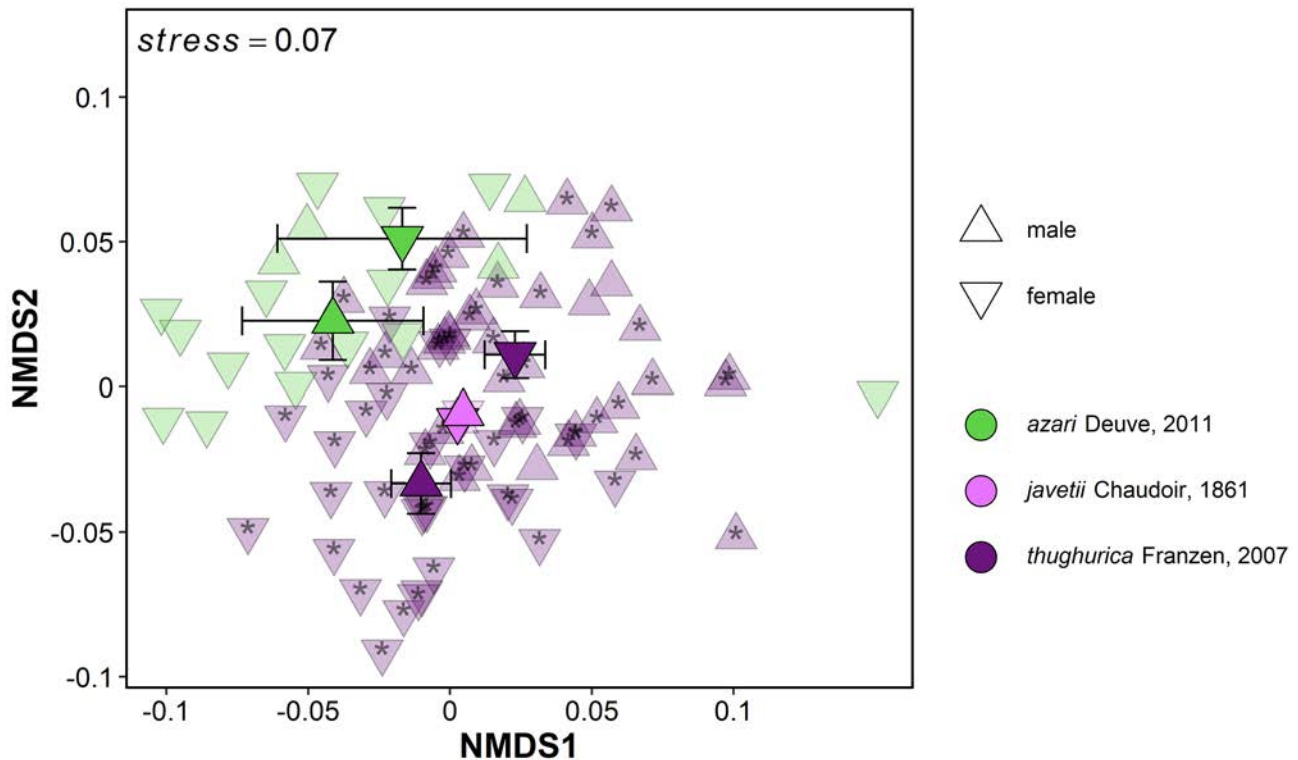
maculated specimens were mistaken for *C. campestris* until Franzen (2007) recognized them as distinct taxon and described them as *C. thughurica*.

C. javetii azari was first recognized as distinct taxon by Deuve (2011) and differentiated by its pure green colour without any coppery-brown reflections (in comparison to *C. javetii javetii*) and placed in subspecific rank. This judgement is confirmed by our analyses (Fig. 103).



FIGURES 97–102. Habitats of *Cicindela herbacea*: 97, 98—*C. h. herbacea*; 97—colline cedar forest near Qamouaa / Lebanon (Akkar forest; photo: K. Taleb); 98—colline mixed cedar forest near Ehden / Lebanon (Horsh Ehden; photo: C. Reuter); 99–102—*C. h. turkestanicoides*; 99—alpine environments at a road pass near İmranlı (Sivas province, Turkey; photo: H. Peks); 100—alpine environments with remaining snow fields at mount Dalamper (West Azerbaijan province, Iran; photo: T. Keil); 101—alpine environments near Dorud (Oshtoran Kuh mountains, Lorestan province, Iran; photo: T. Keil); 102—alpine environments near Dorud (Lorestan province, Iran; photo: S. Dementyev).

Based on the examined material, *C. j. javetii* occurs in the Western Taurus mountain range, the plains around Adana and the Nur mountains (Hatay province / Turkey; Fig. 104). Some collection labels of older specimens refer to Aleppo in Syria, but specimens might stem from the mountainous areas in the surroundings of Aleppo. A single doubtful record from northern Lebanon that lies far off the currently known range could unfortunately not be verified. *C. j. azari* occurs in the Lebanon and Anti-Lebanon mountain ranges from northern Israel to central Lebanon and the adjacent regions in Syria (Fig. 104). From the studied material, there seems to be a gap between both taxa in Western Syria (Dschebel Ansariye mountain range, Latakia & Tartus governates) which is likely due to undersampling in this region and further records in this region can be expected as *C. javetii* is found very close to the Syrian border in Turkey.



FIGURES 103. NMDS ordination for the taxa of the *Cicindela javetii*-subgroup based on different morphological measurements (see Materials & Methods). Based on the ordination, the taxon *thughurica* Franzen 2007 (dark purple) is a junior synonym of *javetii* Chaudoir, 1867 (pink). The separation between *C. j. javetii* and *C. j. azari* Deuve, 2011 (green) is supported by the clustering in the ordination. Semi-transparent datapoints represent measured specimens, bold points represent the centroid for each taxon with 95% confidence interval. * indicates specimens from the type series. Upwards pointing triangles represent males, downwards pointing triangles represent females.

Key to the subspecies of *C. javetii*

- 1 Elytra more parallel sided, with a row of larger punctures from scutellum along the suture. Pronotum narrowed rather straightly towards base. Aedeagus apically less protruding not bent near the middle (Figs. 136, 137), BLL medium sized with apical field of decumbent longitudinal spinules, BLR broad and smooth without any spinules, VLL well developed, VLR small and invisible in the left lateral view (Figs 141). Levant: Turkey, Lebanon (?), Syria *C. javetii javetii* Chaudoir, 1861
- Elytra clearly rounded, without larger punctures along the suture, markedly narrower near the base than near the broadest point. Pronotum clearly rounded towards base. Aedeagus apically more protruding and bent near the middle (Figs. 138–140), BLL larger with apical field of semi-erect longitudinal spinules, BLR smaller with a small basal area of short spinules, VLL undeveloped, VLR large and clearly visible in the left lateral view (Figs. 142). Levant: Israel, Lebanon, Syria (south)
 *C. javetii azari* Deuve 2012

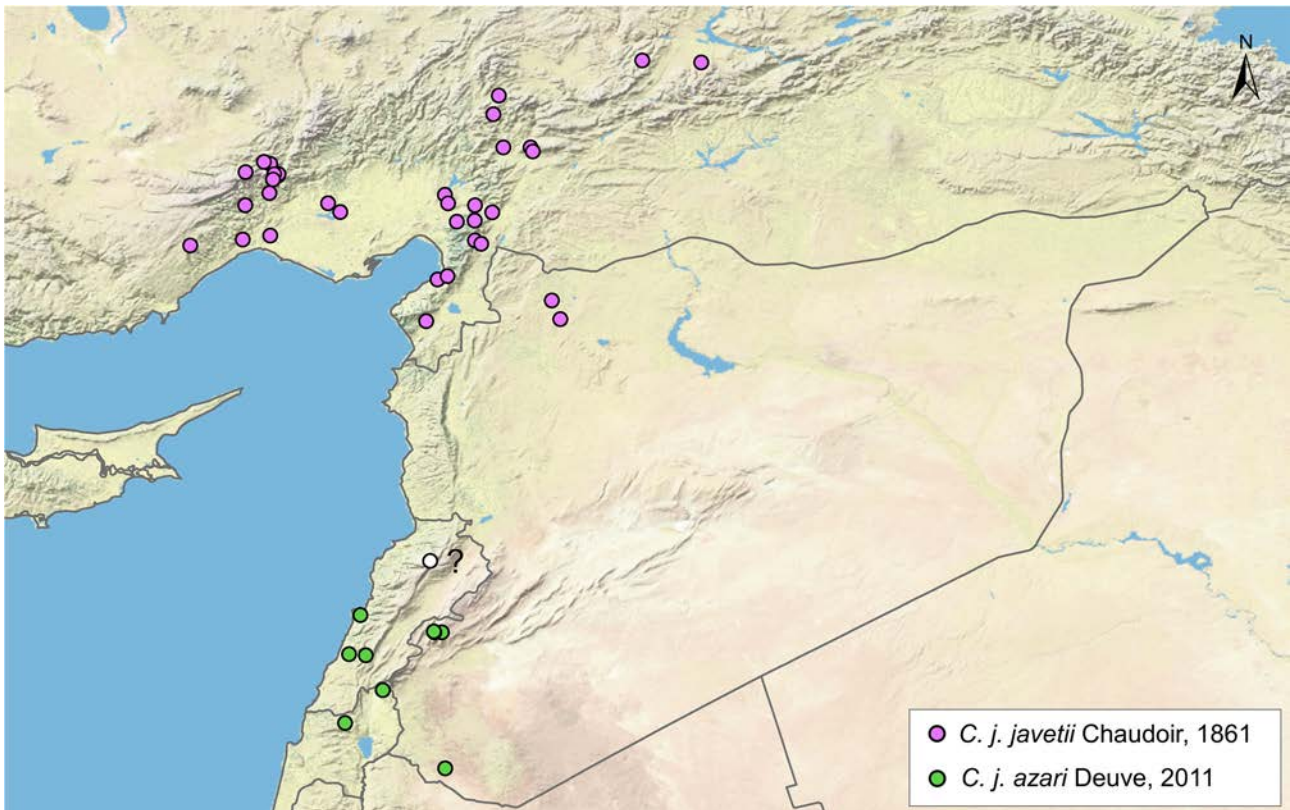


FIGURE 104. Distribution map of *C. javetii*. Pink: *C. javetii javetii* Chaudoir, 1861; green: *C. javetii azari* Deuve, 2011. The open circle in north Lebanon refers to a literature record of *C. javetii* which could not be verified and is therefore marked with ‘?’ (map created using Natural Earth raster map data; naturalearthdata.com).

TABLE 3. Differences in measurements and selected ratios between the two subspecies of *Cicindela javetii*: *C. j. azari* Deuve 2012 and *Cicindela j. javetii* Chaudoir, 1861. All measurements in mm showing mean \pm standard error and range below in brackets. Statistics are taken from models accounting for sex differences—only the results for differences between the taxa are shown (see Materials & Methods section). * indicates $p < 0.05$; ** indicates $p < 0.01$, *** indicates $p < 0.01$.

Factor / Ratio	<i>Cicindela azari</i> Deuve 2012		<i>Cicindela javetii</i> Chaudoir, 1861		Difference between taxa (ANOVA)
	4 ♂	15 ♀	44 ♂	31 ♀	
Total length (TL)	11.0 \pm 0.4 [10.2–11.9]	11.6 \pm 0.2 [10.0–12.8]	10.8 \pm 0.1 [9.9–11.8]	11.9 \pm 0.1 [10.8–13.2]	$F_{1,91} = 1.44$; $p = .233$
Elytra length (EL)	6.8 \pm 0.2 [6.2–7.1]	7.4 \pm 0.2 [6.3–8.3]	6.6 \pm 0.1 [5.7–7.2]	7.2 \pm 0.1 [6.5–8.0]	$F_{1,91} = 14.27$; $p < .001$ ***
Pronotum length (PL)	1.8 \pm 0.0 [1.8–1.9]	1.8 \pm 0.1 [1.2–2.0]	1.9 \pm 0.0 [1.7–2.2]	2.1 \pm 0.0 [1.9–2.4]	$F_{1,91} = 20.70$; $p < .001$ ***
Maximal pronotum width (PWm)	2.6 \pm 0.1 [2.4–2.7]	2.8 \pm 0.1 [2.4–3.2]	2.6 \pm 0.0 [2.3–2.8]	2.9 \pm 0.0 [2.6–3.3]	$F_{1,91} = 0.07$; $p = .794$
Basal pronotum width (PWb)	2.0 \pm 0.1 [1.8–2.2]	2.2 \pm 0.0 [1.8–2.5]	2.1 \pm 0.0 [1.8–2.2]	2.2 \pm 0.0 [2.0–2.6]	$F_{1,91} = 0.02$; $p = .883$
Elytra basal width (EWh)	3.5 \pm 0.2 [3.1–4.0]	3.9 \pm 0.1 [3.0–4.4]	3.7 \pm 0.0 [3.3–4.1]	4.1 \pm 0.0 [3.7–4.7]	$F_{1,91} = 2.01$; $p = .159$
Elytra maximum width (EWm)	4.7 \pm 0.2 [4.2–5.0]	5.1 \pm 0.1 [4.3–5.6]	4.6 \pm 0.0 [4.1–5.0]	5.2 \pm 0.1 [4.7–5.7]	$F_{1,91} = 4.67$; $p = .033$ *

.....continued on the next page

TABLE 3. (Continued)

Factor / Ratio	<i>Cicindela azari</i>		<i>Cicindela javetii</i>		Difference between taxa (ANOVA)
	Deuve 2012		Chaudoir, 1861		
	4 ♂	15 ♀	44 ♂	31 ♀	
Head width (HW)	2.9 ± 0.0 [2.8–3.0]	3.1 ± 0.1 [2.8–3.5]	3.0 ± 0.0 [2.6–3.4]	3.3 ± 0.0 [3.0–3.6]	F _{1,91} = 0.12; p = .733
Labrum width (LW)	1.6 ± 0.0 [1.6–1.7]	1.8 ± 0.0 [1.5–2.0]	1.7 ± 0.0 [1.6–1.8]	1.6 ± 0.0 [1.6–1.6]	F _{1,22} = 0.61; p = .444
Labrum length (LL)	0.7 ± 0.0 [0.7–0.8]	1.0 ± 0.0 [0.8–1.1]	0.8 ± 0.0 [0.7–0.9]	1.2 ± 0.0 [1.2–1.2]	F _{1,22} = 1.04; p = .319
Other setae (OS)	5.0 ± 1.0 [3–7]	5.1 ± 0.5 [0–9]	2.3 ± 0.2 [0–5]	1.9 ± 0.2 [0.5–4]	F_{1,91} = 68.78; p < .001 ***
Aedeagus length (AL)	3.8 ± 0.2 [3.5–4.2]	-	3.7 ± 0.0 [3.3–4.5]	-	F _{1,42} = 1.66; p = .204
EL / TL	0.62 ± 0.01 [0.60–0.65]	0.64 ± 0.01 [0.60–0.66]	0.61 ± 0.0 [0.58–0.63]	0.61 ± 0.0 [0.59–0.63]	F _{1,91} = 71.83; p < .001 ***
PL / EL	0.27 ± 0.01 [0.25–0.29]	0.25 ± 0.01 [0.17–0.26]	0.30 ± 0.0 [0.28–0.32]	0.28 ± 0.0 [0.27–0.31]	F_{1,91} = 126.53; p < .001 ***
PL / PWm	0.71 ± 0.01 [0.69–0.73]	0.66 ± 0.02 [0.47–0.74]	0.76 ± 0.0 [0.70–0.81]	0.71 ± 0.0 [0.66–0.77]	F_{1,91} = 55.50; p < .001 ***
PWb / PWm	0.78 ± 0.02 [0.73–0.82]	0.79 ± 0.01 [0.75–0.82]	0.80 ± 0.0 [0.75–0.86]	0.77 ± 0.0 [0.72–0.81]	F _{1,91} = 0.11; p = .742
PWb / EWh	0.57 ± 0.02 [0.55–0.61]	0.56 ± 0.01 [0.52–0.61]	0.56 ± 0.0 [0.52–0.61]	0.54 ± 0.0 [0.52–0.56]	F_{1,91} = 10.30; p = .002 **
EWh / EWm	0.75 ± 0.03 [0.67–0.80]	0.75 ± 0.01 [0.69–0.80]	0.80 ± 0.0 [0.74–0.83]	0.80 ± 0.0 [0.77–0.83]	F_{1,91} = 69.65; p < .001 ***
PWm / EWm	0.56 ± 0.01 [0.54–0.57]	0.54 ± 0.01 [0.49–0.59]	0.56 ± 0.0 [0.51–0.59]	0.56 ± 0.0 [0.53–0.61]	F_{1,91} = 10.42; p = .001 **
LL / LW	0.46 ± 0.02 [0.41–0.50]	0.55 ± 0.01 [0.51–0.61]	0.47 ± 0.02 [0.44–0.51]	0.75 ± 0.0 [0.75–0.75]	F _{1,22} = 0.27; p = .610

***Cicindela javetii javetii* Chaudoir, 1861**

Figs 105–127, 136, 137, 141, 143, 145, 147, 149, 151

Cicindela javetii Chaudoir, 1861: 3 (Type locality: ‘Syrien’ (= Syria)).

Cicindela javeti Chaudoir, 1861[sic!]: Horn 1891: 15; 1915: 342; 1926: 231; 1930: 32; Fleutiaux 1892: 100; Werner 1991: 22, 44, 66, Taf. 20 f. 161.

Cicindela javetii javetii Chaudoir, 1861: Wiesner 1992: 126; 2020: 195; Lorenz 1998: 44; 2005: 135; Puchkov & Matalin 2003: 106; Putschkov & Matalin 2017: 230.

Cicindela campestris javeti Chaudoir, 1861 [sic!]: Schilder 1911: 202; Horn 1938: 46, Taf. 66 f. 15; Rivalier 1950: 227; Cassola & van Nidek 1984: 11.

= *Cicindela thughurica* Franzen, 2007: 19 **syn. n.** (Type locality: Turkey, Osmaniye, Kaypak, NW Fevzipasa).

Cicindela thughurica Franzen, 2007: Avgin & Wiesner 2009: 354.

Cicindela javeti javeti Chaudoir, 1861 [sic!]: Deuve 2011: 136.

Cicindela javeti thughurica Franzen, 2007 [sic!]: Deuve 2011: 136.

Cicindela javetii thughurica Franzen, 2007: Putschkov & Matalin 2017: 230; Assmann et. al. 2018: 66–68.

Type material examined: HOLOTYPE (by monotypy) of *Cicindela javetii* Chaudoir, 1861, ♂: ‘HOLOTYPE’, ‘TYPE’, ‘Museum Paris, Orient, coll. De Chaudoir 1874’. ‘Sac interne 533 Rivalier’, ‘Cicindela Javeti (type de Chaudoir)’, ‘Javetii Chaud., Orient, 59, Javet’ [MNHN] (digital image provided by Azadeh Taghavian). HOLOTYPE of *Cicindela thughurica* Franzen, 2007: ♂: ‘TR, Prov. Osmaniye: Strassenkr. Ri. Kaypak (nw. Fevzipasa), 680 m. Feuchte, lehmige Böschung. 08.04.1998, Franzen & Gruber leg.’ [ZSM]; PARATYPES of *Cicindela thu-*

ghurica Franzen, 2007: 15♂ + 9♀: ‘TR, Prov. Osmaniye: Strassenkr. Ri. Kaypak (nw. Fevsipasa), 680 m. Feuchte, lehmige Böschung, 08.04.1998, Franzen & Gruber leg.’ [CFM & ZSM]; 1♀: ‘TR, Prov. Osmaniye: Hasanbeyli NW, Straßenkreuzung Richtung Kaypak, 08.04.1998, Franzen & Gruber leg.’ [CFM]; 3♂ + 4♀: ‘5 km N Hieropolis-Castabala (Osmaniye prov.), 150 m, 9.4.1997, Franzen leg.’ [CFM]; 2♂ + 1♀: ‘above (E of) Yarpuz (Osmaniye prov.), 1550 m, 19.6.1997, Franzen leg.’ [CFM]; 1♀: ‘environments of Akbez (“Akbez, Syr.”, Gaziantep prov.), Winkler’ [CFM]; 4♂ + 2♀: ‘environments of Çiftehan (Nigde prov.), 850 m, 3.4.1988, de Freina leg.’ [CHS, CFM]; 1♂ + 2♀: ‘eastern slope of Karahan pass (Malatya prov.), 1300 m, 30.4.1999, Franzen leg.’ [CFM]; 5♂ + 2♀: ‘N of Tekir (Kahramanmaraş prov.), 1100 m, 7.4.1998, Franzen & Gruber leg.’ [CFM]; 9♂ + 7♀: ‘30 km NW Kahramanmaraş (Kahramanmaraş prov.), 580 m, 7.4.1998, Franzen & Gruber leg.’ [CFM]; 1♀: ‘environments of Kahramanmaraş (“Marasch, Syrien”, Kahramanmaraş prov.), Reitter’ [CFM]; 1♂: ‘between Çiftehan and Pozantı (Adana prov.), 900–1000 m, 17.4.1973, Heinz leg.’ [CFM]; 1♂ + 1♀: ‘E of Pozantı (Adana prov.), 800 m, 11.4.1998, Franzen leg.’ [CFM]; 1♀: ‘Pozantı (Adana prov.), 25.5. 1961, Cadamuro leg.’ [CHS]; 1♀: ‘Çatalan (“Anatolia, Prov. Adana, Catalan”, Adana prov.), 50–100 m, 18.4.1985, Barries leg.’ [CFM]; 1m + 2♀: ‘E of Çamliyayla (Içel prov.), 1100 m, 11.4.1998, Franzen leg.’ [CFM].

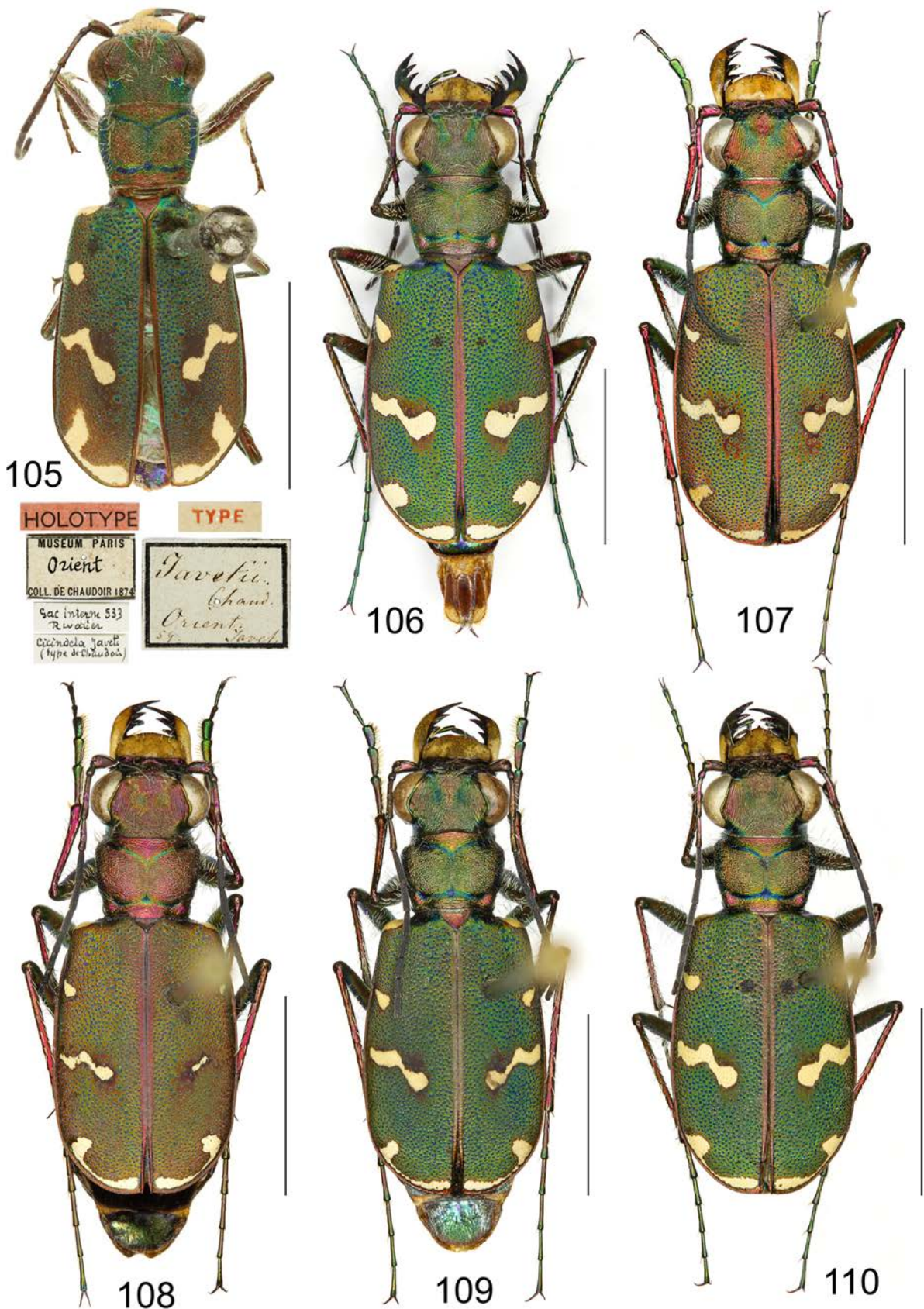
Distribution: We examined 207 specimens (51 males and 34 females; sex of the remaining specimens was not identified) from the following locations (Fig. 104): **LEBANON:** Mount Leban (Gebail) (literature record that could not be verified and is therefore marked with ‘?’ in the distribution map); **SYRIA:** **Aleppo:** Aleppo; **TURKEY:** **Adana:** Adana, Çatalan, Pozantı, Tarsus; **Amasya:** Amasya; **Gaziantep:** Fevzipaşa; **Hatay:** Akbez, Antakya (Antiochia), Iskenderun; **Kahramanmaraş:** Göksun, Kahramanmaraş, Tekir; **Malatya:** Gürkaynak, Malatya; **Mersin:** Çamliyayla, Gülek, Hacıalanı, Mersin; **Niğde:** Çiftehan; **Osmaniye:** Hasanbeyli, Karatepe, Osmaniye, Yarpuz.

Redescription: Base colouration green to coppery-red and brown, head, labial- and maxillar plapi coloured similarly, base colour of mandibles white with dark metallic colouration towards the inside, four visible teeth with a fifth hidden beneath the labrum (Figs. 105–110). Head clearly wider than pronotum, cheeks glabrous, frons and vertex loosely setose with long white setae, clypeus glabrous metallic green to red-coppery, scapus apart group of distal sensory setae with 0 to 5 (2.2 ± 0.1) additional setae, otherwise antennal segments 1–4 glabrous and coppery-red, segments 5–11 black and covered with fine hairs. Labrum more elongated in females than in males (Tab. 3), with 6 long, lightly coloured sub-marginal setae, median tooth and anterior edge of labrum darkened (Fig. 111). Pronotum clearly shorter than wide (Tab. 3), with deep grooves, towards the base straightly narrowed, basal edge curved, anterior edge slightly curved (Figs. 112–118). Elytra clearly rounded near the shoulders, noticeably broadened from the shoulders to the broadest point (not stronger in females than in males; Tab. 3) but rather parallel sided along after the first quarter; elytral with rows of larger blue-green punctures from the sides of the scutellum along the suture and near the shoulders additional to smaller blueish punctures, epipleura and suture red-golden, humeral lunula always separated into two dots, apical lunula rarely separated, middle band usually complete, rarely separated into two unconnected dots (such specimens can be confused with *C. campestris*), protruding diagonally towards the suture in a very small angle in two short bows, its width varying from rather narrow to noticeably broadened (Figs. 119–127), apical edge serrated, sutural spine retracted behind apical edge. Aedeagus without bend near the middle (Figs. 136–137). Internal sack moderately protruding beyond the penis tube, BLL medium sized with an apical field of decumbent longitudinal spinules, BLR broad and smooth without any spinules, VLL well developed, placed before *sp*, VLR smaller and invisible in the left lateral view, *mt* long with gradually curved apex (Figs. 141, 143, 145, 147, 149, 151). For mean body-size measurements, see Table 2.

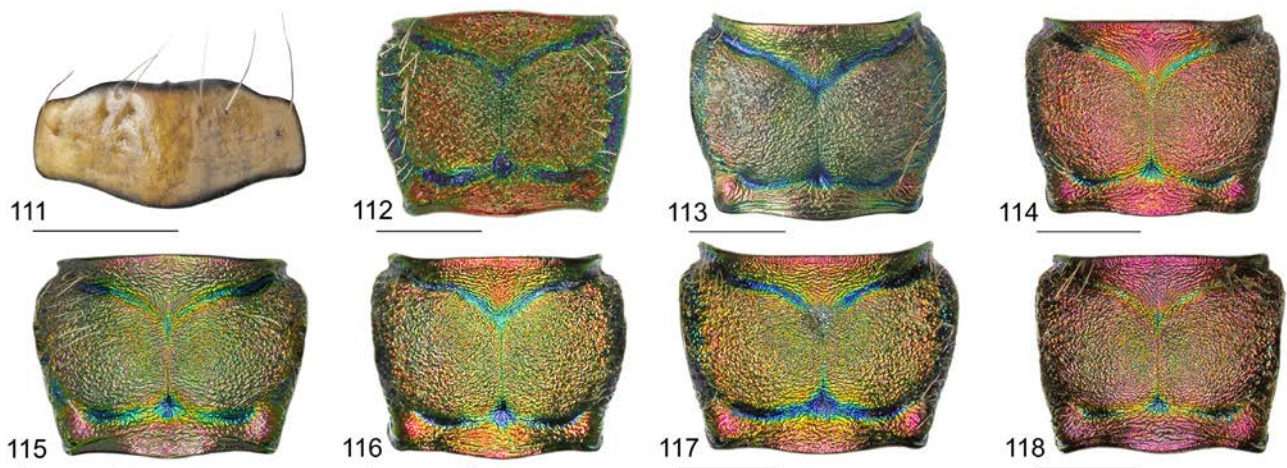
Remarks: The type locality ‘Syria’ most likely does not refer to present day Syria. During the 19th century, many specimens collected in the southern provinces of today’s Turkey (among others Adana, Gaziantep, Hatay, Kahramanmaraş, Kilis, Osmaniye) were commonly referred to as ‘Syria’ on collection labels. It can thus be assumed that the holotype was collected within the current distribution range of the species in Turkey from where we have also seen other specimens with similarly enlarged maculation.

The label “Syrie, Kindermann” referred to by Deuve (2011) as the label of the holotype of *C. javetii* does not correspond with any label pinned under the holotype (Fig. 105).

Ecology: According to collection information given with the examined specimens, *C. j. javetii* was collected in elevations from 60 to 1600 m (Fig. 153; 791 ± 89 m; only including records that included collection information with sufficient precision) predominantly on grasslands (from pioneer vegetation over dry grasslands to alpine grasslands) and *Pinus*-forests (Figs. 168–171). Specimens were also collected close to waterbodies (brooks, rivers, lake shores). Specimens were collected between 29 March to 19 June (with one specimen collected on 02 October probably indicating a second phase of activity in fall).



FIGURES 105–110. *Cicindela javetii javetii*, habitus: 105—holotype of *Cicindela javetii* Chaudoir, 1861 with labels (photos provided by Azadeh Taghavian) [MNHN]; 106–110—Turkey (106—Mersin, Hacıalanı; 107, 108—Osmaniye, Kaypak; 109, 110—Adana, Hieropolis); 108—paratype of *Cicindela thughurica* Franzen, 2007 [ZSM]; 105, 107–109—males; 106, 110—females. Scales—5 mm.



FIGURES 111–118. *Cicindela javetii javetii*, labrum (111) and pronotum (112–118): 111, 113–118—Turkey (111, 113, 114—Osmaniye, Kaypak; 115, 116—Mersin, Hacıalanı; 117, 118—Adana, Hieropolis); 112—holotype of *Cicindela javetii* Chaudoir, 1861 (photo provided by Azadeh Taghavian) [MNHNP]; 111, 113—paratype of *Cicindela thughurica* Franzen, 2007 [ZSM]; 111–114, 116, 118—males; 115, 117—females. Scales—1 mm.

***Cicindela javetii azari* Deuve, 2011 stat. n.**

Figs 128–135, 138–140, 142, 144, 146, 148, 150, 152, 154–167

Cicindela javetii azari Deuve, 2011: 134 fig. 17, 136 [sic!] (Type locality: ‘Lebanon: Jezzine’).

Cicindela campestris herbacea Klug, 1835: Valdenberg 1983: 42, 48; 1985: 37; Nussbaum 1987: 7, 8.

Cicindela herbacea Klug, 1835: Wiesner 1992: 127; Matalin & Chikatunov 2016: 126; Puchkov & Matalin 2003: 105; Chikatunov *et al.* 2006: 293; Franzen 2007: 13.

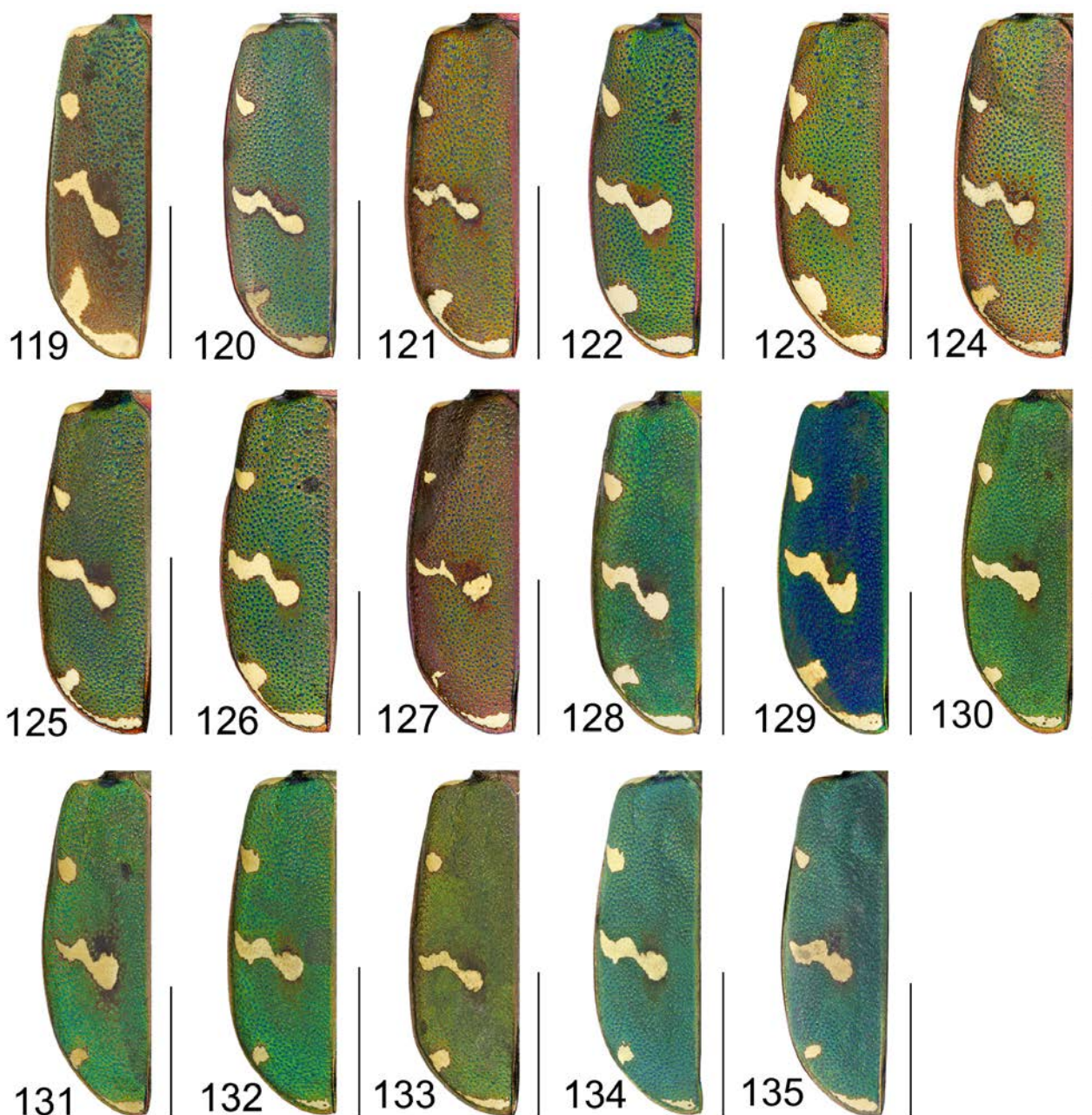
Lophyra herbacea Klug, 1835: Ptashkovsky 2009: 8, 9.

Cicindela javetii azari Deuve, 2011: Puchkov & Matalin 2017: 230; Assmann *et al.* 2018: 66–68; Wiesner 2020: 195.

Type material examined: **HOLOTYPE** of *Cicindela javetii azari* Deuve, 2011: ♂: ‘Lebanon, Jezzine (Djezzine, Jazzin), P. Pharès’, ‘EC 7799’, (ex. coll. Fleutiaux) [MNHNP].

Distribution: We examined 51 specimens (18 males and 28 females; sex of the remaining specimens was not identified) from the following locations (Fig. 104): **ISRAEL:** Nakhla Habiz (Mount Meron), Majdal Shams, Neve Ativ & Nimrod (Mt. Hermon); **LEBANON:** Beirut, Jezzine, Lebaa (Lebaâ, Libaah); **SYRIA:** Bloudan (Rif Dimashq governorate), Sayda (= Saida; Daraa governorate).

Redescription: Base colouration brightly green to blueish, sometimes dull olive-green with coppery sheen, head, labial- and maxillary palpi coloured similarly, base colour of mandibles white with dark metallic colouration towards the inside, four visible teeth with a fifth hidden beneath the labrum (Figs. 154–159). Head with eyes not very protruding, cheeks glabrous, vertex and frons loosely setose with long white setae, clypeus glabrous metallic green to red-coppery, scapus apart from the group of distal sensory setae with 0 to 9 (5.1 ± 0.5) additional setae, labrum more elongated in females than in males (Tab. 3), with 6 to 8 long, lightly coloured sub-marginal setae, median tooth and anterior edge of labrum darkened (Figs. 160). Pronotum shorter than wide (Tab. 3), towards the base clearly rounded (cordiform), basal edge curved, anterior edge slightly curved, pronotal grooves colored green to deep blue (Figs. 161–167). Elytra clearly rounded (Tab. 3), elytral margin colored golden to red-coppery, punctures vary in coloration between golden-green and deep blue, suture golden to red-coppery; humeral lunula always complete, apical lunula often separated into two spots, middle band complete, variable in shape, sometimes rather horizontal, often protruding slightly diagonally towards the apex (Figs. 128–135); apical edge serrated, sutural spine retracted behind apical edge. Aedeagus short, without bend near the middle (Figs. 138–140). Internal sack moderately protruding beyond the penis tube, BLL larger with an apical field of semi-erect longitudinal spinules, BLR smaller with a small basal area of short spinules, VLL undeveloped, VLR larger and visible in the left lateral view, *mt* long with more sharply curved apex (Figs. 142, 144, 146, 148, 150, 152). For mean body-size measurements, see Table 3.



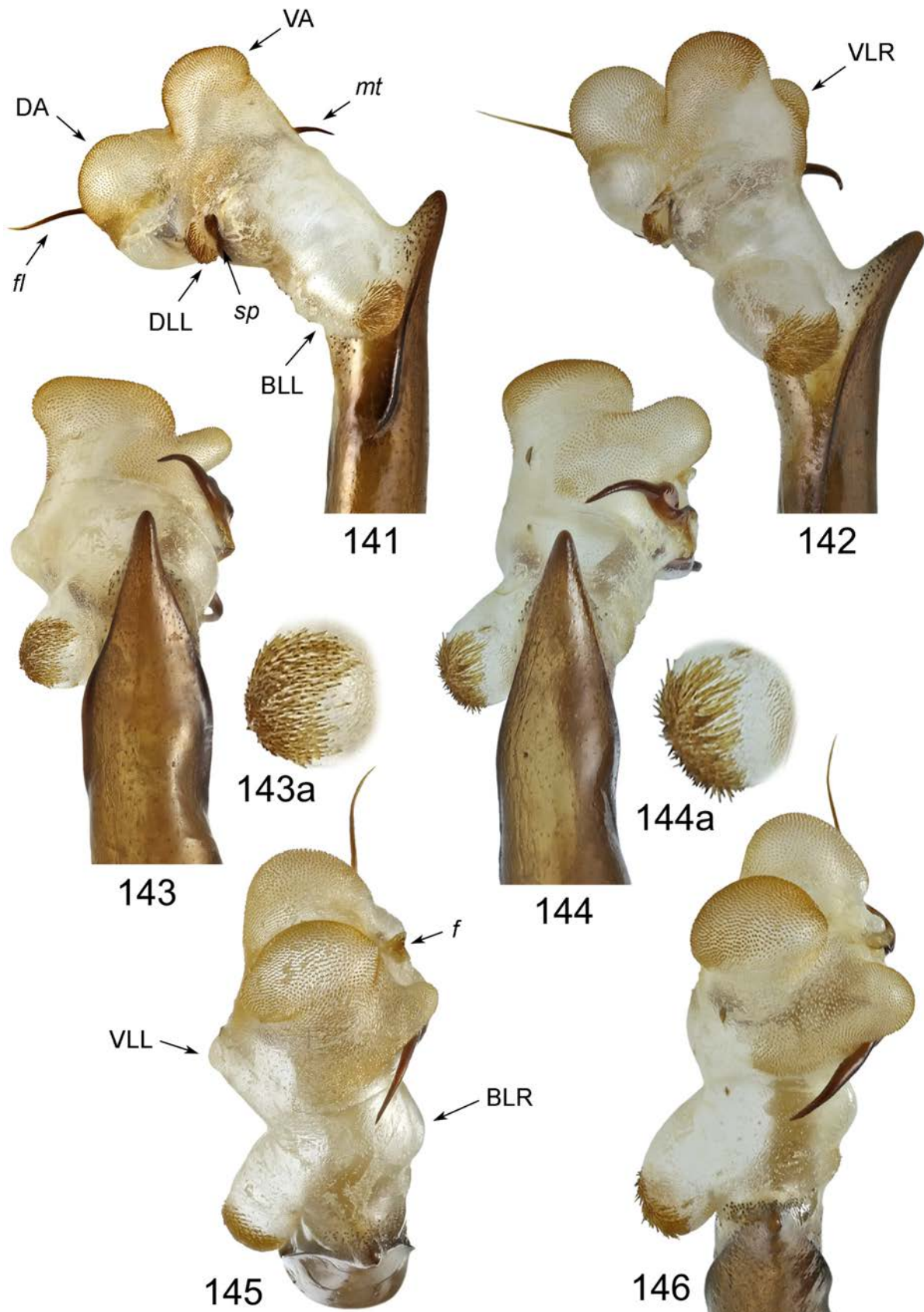
FIGURES 119–135. *Cicindela javetii*, left elytron: 119–127—*C. j. javetii*; 128–135—*C. j. azari*; 119—holotype of *Cicindela javetii* Chaudoir, 1861 (photo provided by Azadeh Taghavian) [MNHNP]; 120—paratype of *Cicindela thughurica* Franzen, 2007, Turkey (Osmaniye, Kaypak) [ZSM]; 121–127—Turkey (121—Osmaniye, Kaypak; 122–124—Mersin, Hacıalanı; 125–127—Adana, Hieropolis); 128—holotype of *Cicindela javeti azari* Deuve, 2011, Lebanon (Jezzine) [MNHNP]; 129—Lebanon (Beirut); 130–134—Syria (Bloudan); 135—Israel (Mount Hermon); 119–121, 124, 125, 127, 128, 132–135—males; 122, 123, 126, 129–131—females. Scales—3 mm.

Remarks: Older records for *C. herbacea* or *C. campestris* from Israel and southern Syria refer to *C. javetii azari* (Matalin & Chikatunov 2016; Assmann *et al.* 2018). Occurrence of *C. javetii azari* in northern Jordan (Irbid governate) seems plausible given the known populations in adjacent regions in Israel and Syria.

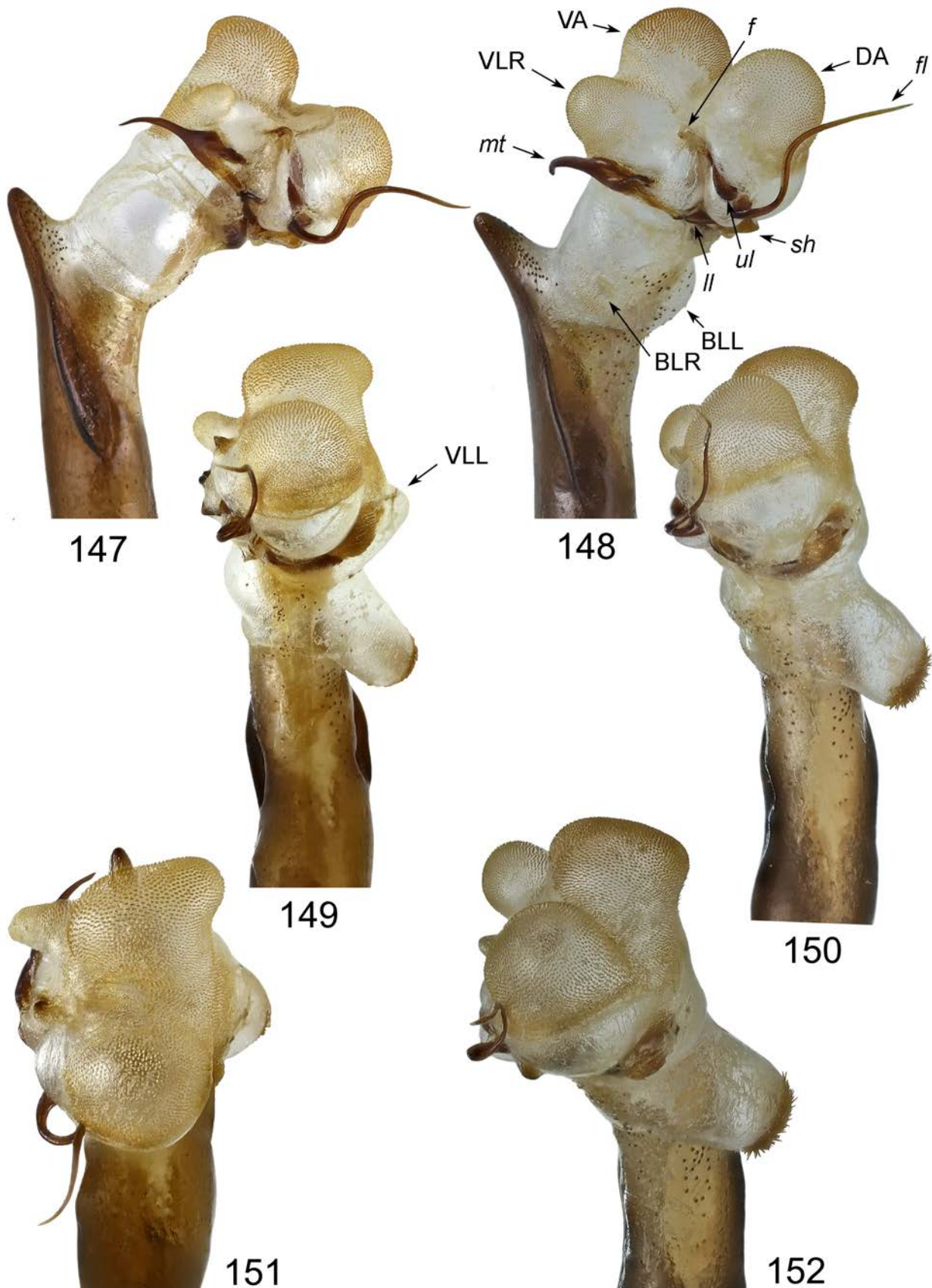
Ecology: According to collection information given with the examined specimens, *C. j. azari* was collected in elevations from 40 to 1700 m (Fig. 153; 786 ± 208 m; only including records that included collection information with sufficient precision) in dry oak forests, on chalky and loamy soils (Figs. 172, 173). Assmann *et al.* (2018) additionally state open habitats with dwarf shrubs and quarries as habitats. Specimens in the examined collections were collected from 08 April to 09 June (see also Matalin & Chikatunov 2016). According to Assmann *et al.* (2018), peak activity is reached in May.



FIGURES 136–140. *Cicindela javetii*, aedeagus, left lateral view: 136–137—*C. j. javetii*; 138–140—*C. j. azari*; 136—paratype of *Cicindela thughurica* Franzen, 2007, Turkey (Kahramanmaraş) [ZSM]; 137—Turkey (Kahramanmaraş, Göksun); 138—holotype of *Cicindela javetii azari* Deuve, 2011, Lebanon (Jezzine) [MNHNP]; 139—Syria (Bloudan); 140—Israel (Mount Hermon). Scales—1 mm.



FIGURES 141–146. *Cicindela javetii*, internal sack: 141, 143, 145—*C. j. javetii* (paratype of *Cicindela thughurica* Franzen, 2007, Turkey (Osmaniye, Kaypak) [ZSM]); 142, 144, 146—*C. j. azari*, Syria (Bloudan); 141, 142—left lateral view; 143, 144—dorsal view (143a, 144a—apex of BLL); 145, 146—dorso-apical view. Not to scale. Abbreviations see text.



FIGURES 147–152. *Cicindela javetii*, internal sack: 147, 149, 151—*C. j. javetii* (paratype of *Cicindela thughurica* Franzen, 2007, Turkey (Osmaniye, Kaypak) [ZSM]); 148, 150, 152—*C. j. azari*, Syria (Bloudan); 147, 148—right lateral view; 149, 150—ventral view; 151, 152—ventro-apical view. Not to scale. Abbreviations see text.

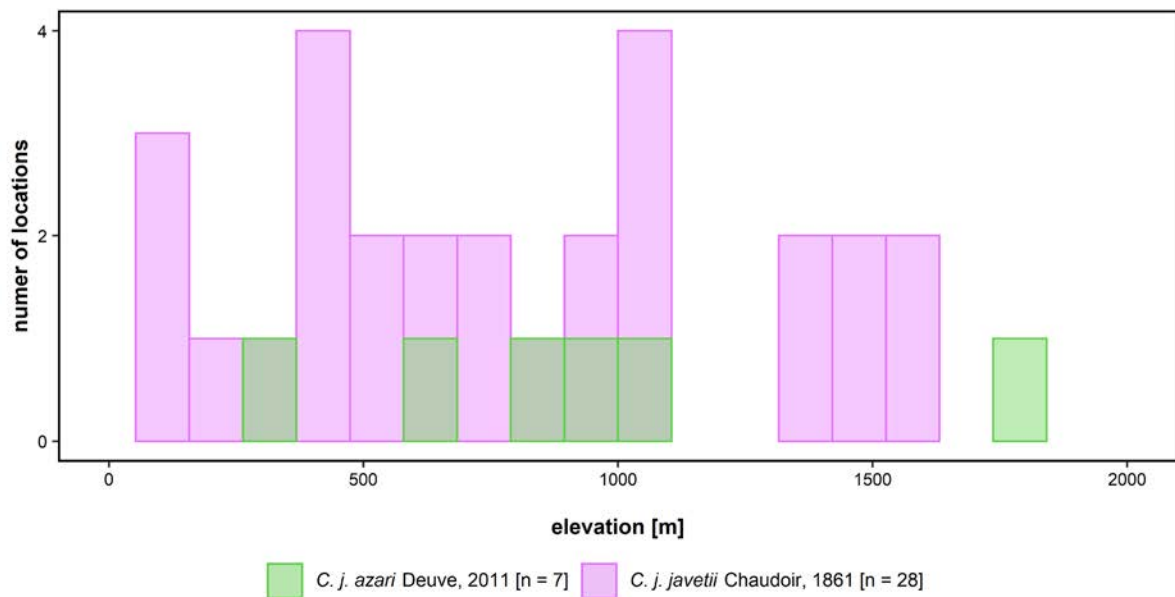
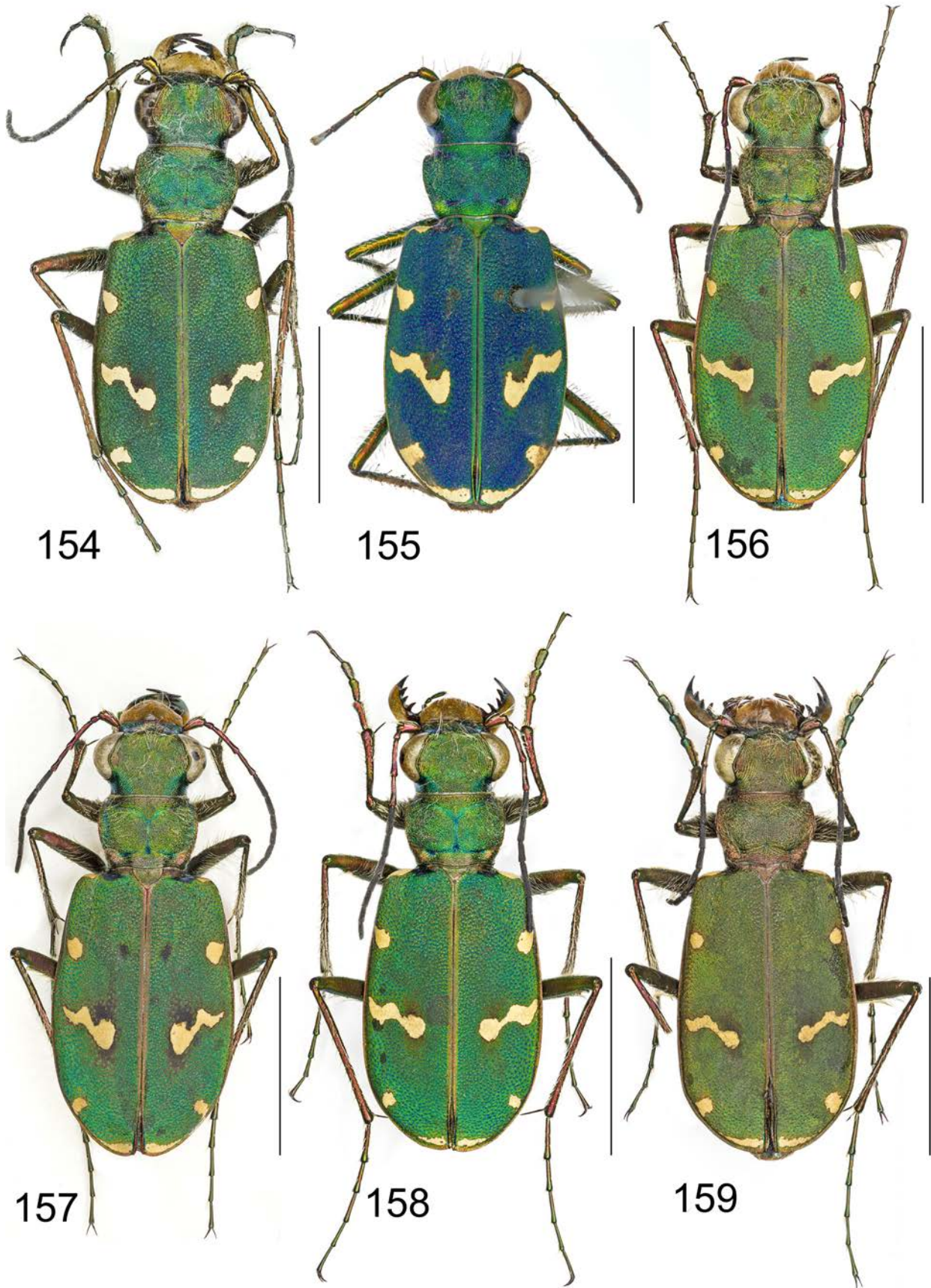


FIGURE 153. Elevation range of the two subspecies of *C. javetii* Chaudoir, 1861. Pink: *C. javetii javetii* Chaudoir, 1861; green: *C. javetii azari* Deuve, 2011. Numbers in the legend represent the number of unique collecting locations (only including records that included collection information with sufficient precision).

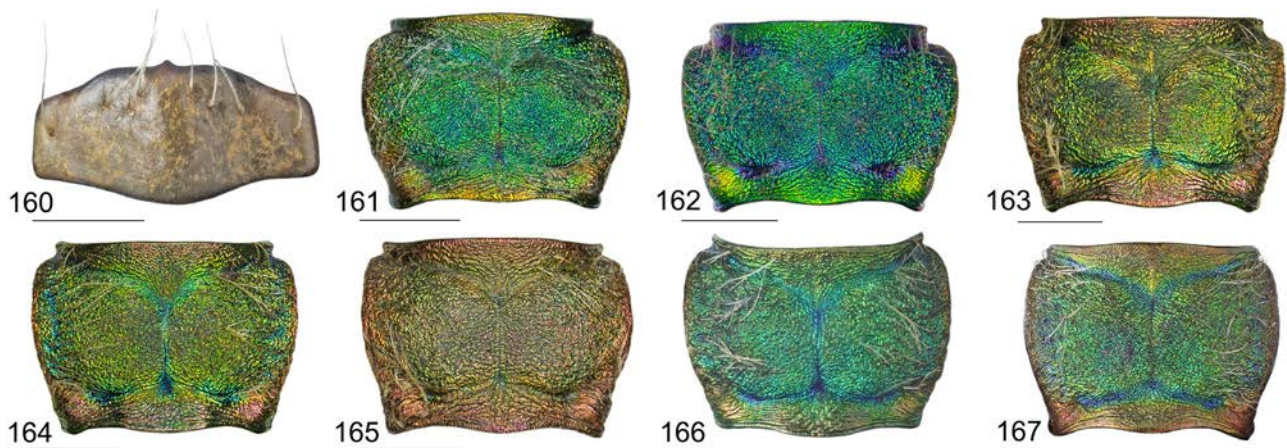
Discussion

In the first part of our revision of the Palaearctic *Cicindela campestris* species complex, we show that intra-specific variation is large in some of the taxa and has previously been underestimated. Rather than distinct species, some taxa represent a gradual transition between extremes in their distribution range with intermediate populations showing different mixtures of features. This has led to many unnecessary synonyms being described when only single specimens or small series were examined. Our analyses show that single features cannot easily be used to differentiate between taxa if the range of variability is not known. Previous revisions often relied heavily on the aedeagus shape which may be useful to differentiate between different larger groups but can vary considerably within populations of the same species or subspecies and is affected by factors such as the body-size of the individual or the type of preparation. Taxonomic description as well as revisions should be performed based on an integrative approach and solid morphological features rather than differentiations based on one single factor or variable features such as coloration or maculation (when the range of variation is not known).

Our revision could only assess taxonomic diversity based on mostly relatively old collection material. We can thus not answer questions about how closely related the investigated taxa are and whether individuals showing different combinations of features due to a genetic cline along a geographical gradient could actually be considered different taxa (e.g. in the case of *C. h. turkestanicoidea* as discussed above). Based on the observed intra-specific variation, we decided to follow the principle of parsimony and conservatively lump rather than split taxa. Ultimately, we call for a phylogenetic assessment of this group that could potentially answer these questions in the future. However, the collection of fresh material will be needed for this approach which is difficult to impossible to do at the present as the geographic range is extensive and many of the taxa treated here occur in regions where collection is currently impossible. We are convinced that large genetic datasets will be required to fully understand the phylogenetic relationships and the definite taxonomy within the *C. campestris* species complex, including the taxa and populations covered in this first part of our revision.



FIGURES 154–159. *Cicindela javetii azari*, habitus: 154—holotype of *Cicindela javetii azari* Deuve, 2011, Lebanon (Jezzine) [MNHNP]; 155—Lebanon (Beirut); 156–159—Syria (Bloudan); 154, 158, 159—males; 155–157—females. Scales—5 mm.



FIGURES 160–167. *Cicindela javetii azari*, labrum (160) and pronotum (161–167): 160, 163–166—Syria (Bloudan); 161—holotype of *Cicindela javetii azari* Deuve, 2011, Lebanon (Jezzine) [MNHN]; 162—Lebanon (Beirut); 167—Israel (Mount Hermon); 160, 161, 165–167—males; 162–164—females. Scales—1 mm.

Acknowledgements

We dedicate this work to the remembrance of our late friend and colleague, Dr. Aleksandr Putschkov (Kiev) who tragically died from the consequences of a COVID-19 infection on 30 April 2021. Aleksandr was an expert for Palearctic tiger beetles and especially focussed on tiger beetle larval taxonomy. He has described the larval stages of many species in his numerous publications. The gap he leaves behind cannot be filled. For the monography of the Palearctic Cicindelidae (which is currently in preparation), he already provided keys for and detailed information on the larval stages which will be included and published in memory of his achievements.

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FIGURES 168–173. Habitats of *Cicindela javetii*: 168–171—*C. j. javetii*; 168—colline meadow east of Yarpuz (Osmaniye province, Turkey) at ~ 1550 m (photo: M. Franzen); 169—open forest north of Hieropolis–Casta-bala (Osmaniye province, Turkey) at ~ 150 m (photo: M. Franzen); 170—forest road north of Kahramanmaraş (Kahramanmaraş province, Turkey) at ~ 580 m (photo: M. Franzen); 171—litoral of a small mountain stream north of Tekir (Kahramanmaraş province, Turkey) at ~ 1100 m (photo: M. Franzen); 172, 173—*C. j. azari*; 172—colline meadow at mount Hermon / Israel (photo: F. Popa); 173—colline habitat near Bloudan / Syria (photo: A. Wrze-cionko).

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