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Towards solving the taxonomic impasse of the biocontrol plant bug subgenus *Dicyphus* (*Dicyphus*) (Insecta: Heteroptera: Miridae) using molecular, morphometric and morphological partitions

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Species of *Dicyphus* (*Dicyphus*) (Insecta: Heteroptera: Miridae: Bryocorinae: Dicyphini) are routinely used as biocontrol agents of vegetable crop pests in the Northern Hemisphere. However, they are notoriously difficult to identify. In response, we employed an integrative approach, combining molecular, morphometrics and morphological data, for the delimitation of species. Sequences of three mitochondrial genes (*COI*, 16S and 12S) for 15 putative *Dicyphus* (*Dicyphus*) species were analysed using phylogenetic and genetic methods. Morphometric data were analysed using PCA and Ctree analyses to test their previous use in species differentiation. External and male genitalia morphology were re-examined as an additional partition for testing species boundaries. Twenty-one *Dicyphus* (*Dicyphus*) species, based on genetic distances >1%, external and male genitalic characters were determined. The subgenus and all of the included species are diagnosed, and previously recognized species that we determined as valid are redescribed. The following new synonyms are proposed: *D. marocannus* Wagner and *D. bolivari altanticus* Wagner are synonymized with *D. bolivari* Lindberg; *D. umbertae* Sanchez and Cassis is synonymized with *D. cerastii* Wagner; and, *D. baezi* Ribes is synonymized with *D. rubicundus* Blote. Two new species from Spain (***D. argensis* sp. nov.**) and Turkey (***D. caycumensis* sp. nov.**) are described.

ADDITIONAL KEYWORDS: Bryocorinae – Dicyphini – integrative taxonomy – male genitalia – mtDNA – morphometrics – Palaearctic region – biocontrol.

INTRODUCTION

Species diagnoses are based on morphological data, documented as either autapomorphies or a unique combination of characters. Morphology as a discriminating criterion is challenged where there is character homogeneity or variability is continuous. In such circumstances, taxonomists have commonly resorted to fine-scale morphometrics to differentiate between congeners. Although such fine-scale differences have proven to be reliable in groups such as aphids and mosquitoes (Mehrparvar *et al.*, 2012; Ruiz *et al.*, 2014; Wilke *et al.*, 2016), elsewhere they are of no value in discriminating cryptic species (Dayrat, 2005). For a time, mtDNA barcodes were proposed as a novel data source and cost-effective alternative (Hebert *et al.*, 2003a; Hebert, Ratnasingham & de Waard, 2003b), but this approach has not proven to be a panacea. More recently, arguments for integrative or iterative approaches, that combine or cross-reference multiple data partitions, have been promulgated (Dayrat, 2005; DeSalle, Egan & Siddall, 2005; Schlick-Steiner *et al.*, 2010; Yeates *et al.*, 2011).

Taxonomists face such a lack of diagnostic characters in the plant bug subgenus *Dicyphus* (*Dicyphus*) (Insecta: Heteroptera: Miridae: Bryocorinae: Dicyphini), where morphometric and genitalic characters have been used, but with limited success. Correct

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identification of these species is of economic importance because some are notable biocontrol agents of vegetable crop pests (Gabarra *et al.*, 1988; Ceglarska, 1999; Carvalho & Mexia, 2000; Castañé *et al.*, 2011; Ingegno *et al.*, 2013; Abbas *et al.*, 2014). Further, dicyphines are somewhat unusual as biocontrol agents because many species are zoophytophagous (Perdikis & Lykouressis, 2000; Sanchez, Gillespie & McGregor, 2004; Perdikis *et al.*, 2007; Ingegno, Pansa & Tavella, 2011a; Sanchez *et al.*, 2016); they can prey on target pests but also cause damage to crops during prey shortages (Sanchez, 2008, 2009; Calvo *et al.*, 2009; Arnó *et al.*, 2010). This zoophytophagous response and risk to crops varies among dicyphine species (Albajes *et al.*, 1999; Gillespie *et al.*, 2007; Sanchez & Lacasa, 2008; Castañé *et al.*, 2011), which places a premium on correct identification (Albajes *et al.*, 1999; Sanchez, 2009). Dicyphines have also become model organisms in recent chemical ecology (Pérez-Hedo *et al.*, 2015; Sanchez *et al.*, 2016), plant volatile perception (Ingegno *et al.*, 2016), host selection (Sanchez, Gillespie & McGregor, 2004; Ingegno *et al.*, 2011a) and metapopulation (Alomar, Goula & Albajes, 2002; Castañé *et al.*, 2004) studies.

Dicyphus (*Dicyphus*) species are primarily found in the Western Palaearctic, with 21 species described from this region (Kerzhner & Josifov, 1999; Linnavuori & Hosseini, 1999; Matocq & Ribes, 2004; Sanchez, Martínez-Cascales & Cassis, 2006); a handful of additional species are known from India and sub-Saharan Africa (Cassis, 1986; Schuh & Slater, 1995). Wagner (1951, 1964, 1970) and Wagner and Weber (1978) divided *Dicyphus* (*Dicyphus*) into three informal species-groups, with the included species diagnosed by a combination of colouration, morphometric and male genitalic characters. Misidentification of *Dicyphus* (*Dicyphus*) species is common, which hampers their use as biocontrol agents (Martínez-Cascales *et al.*, 2006a; Martínez-Cascales, Cenis & Sanchez, 2006b; Castañé *et al.*, 2011; Castañé *et al.*, 2012).

In this work we have applied an iterative approach in our study of *Dicyphus* (*Dicyphus*), incorporating mtDNA, morphometric and comparative morphological data; an approach we successfully employed in differentiating two species of the dicyphine genus *Macrolophus* (Martínez-Cascales *et al.*, 2006a). We obtained molecular data for three mitochondrial genes (*COI*, 16S and 12S) for 15 putative *Dicyphus* (*Dicyphus*) species, measured a suite of morphometric characters and re-examined external and male genitalia of all species currently assigned to the subgenus. These data sources were analysed to test the species concepts proposed by previous authors for *Dicyphus* (*Dicyphus*) species (e.g. Wagner, 1951, 1964, 1970; Wagner & Weber, 1978). Finally, we formally redescribe and diagnose all representatives of the subgenus for which we had sufficient material, establish new species-level synonyms, describe new species from Turkey and Spain and provide a key for the identification of all species of *Dicyphus* (*Dicyphus*).

METHODS AND MATERIALS

Materials

Morphological studies of *Dicyphus* (*Dicyphus*) species were based on examination of 1400+ specimens. Specimens were examined from the following collections:

AMNH – American Museum of Natural History, New York, USA.
BMNH – Natural History Museum, London, UK.
HNHM – Hungarian Natural History Museum, Budapest, Hungary.
IMIDA – Instituto Murciano de Investigación y Desarrollo Agrario y Alimentario, Murcia, Spain.
Jordi Ribes, personal collection.
MNHN – Muséum National d'Historie Naturelle, Paris, France.
MZH – Zoological Museum, University of Helsinki, Finland.
MZLU – Museum of Zoology, Lund University, Lund, Sweden.
RASHTIC – College of Agriculture, Rasht, Iran.
UNSW – University of New South Wales, Sydney, Australia.
ZISP – Zoological Institute, St. Petersburg, Russia.
ZMB – Zoologisches Museum, Berlin, Germany.

All specimens were given a unique specimen identifier (e.g. IMIDA_ENT 00000001) and the collection event details are given in the materials examined section for each species. The data used in the morphometric analyses are provided in tabulated form in the Supporting Information (Tables S1 and S2).

The distribution maps we provide are based on the materials that we examined and type localities only. For species that have been recorded more broadly than we observed, we refer users to Kerzhner & Josifov (1999) who give coarse distribution descriptors for Palaearctic species of *Dicyphus* (*Dicyphus*), or to other authors in the description of species section.

Homology and terminology

Homologies and terminology follow mostly those given in Schuh & Slater (1995) and Cassis & Schuh (2012). In the case of the male genitalia, we follow Cassis (2008) in the use of endosoma for the inner tubule of the aedeagus, and large or small sclerotized processes attached apically to the endosoma are referred to as endosomal lobal sclerites, following Stonedahl (1988). Minute sclerotized endosomal processes are referred to as spinules.

The male genitalia were prepared by maceration in 5% KOH, rinsed in distilled water and examined in glycerol. The endosoma is mostly membraneous, with species exhibiting differences in the shape and number of the lobal sclerites. These structures were combined with differences in the shape of the left paramere in defining species. We did not illustrate the right paramere as it is greatly reduced and in the main does not vary significantly between species. We did not investigate the female genitalia in this group as the sclerotized rings and posterior wall show little variation between species (Sanchez *et al.*, 2006).

Habitus images of a representative specimens of each species were taken using a digital camera Canon 5D with 60 mm macro lens. When available, only males were photographed, as sexual dimorphism is trivial in species of the subgenus. Multiple images were captured for each specimen and combined into a single image using Helicon focus software (HeliconSoft, Kharkiv, Ukraine).

For fine details of external morphology, *Dicyphus* (*Dicyphus*) specimens were examined using a Hitachi TM3000 desktop scanning electron microscope, at low voltage with specimens uncoated. Our SEMs document the morphology of the head, pronotum, external efferent system of the metathoracic glands (MTG), pretarsus, abdominal sternal processes and pygophore. We provide images of these characters for representatives of the major clades found in our phylogenetic analysis.

Morphometric methods

Measurements were taken using a Leica MZ16 stereomicroscope and the Leica application suite V3 software (Leica Microsystems, Wetzlar, Germany). Measurements are all maximal lengths, unless stated otherwise, and recorded in millimetres. The following measurements were recorded (Fig. 1): TL = total body length (TL from the tip of the clypeus to the end of hemelytra in macropters and from the tip of the clypeus to the end of the abdomen in brachypters); CHL = clypeus–hemelytral length (CHL differs from TL in brachypters but not in macropters); HL = head length; HW = head width across the eyes; IO = interocular distance; EW = eye width; A1, A2, A3 and A4 = length of the four antennomeres; PL = pronotal length; PW = pronotal width across humeral angles; CW = pronotal collar width across middle line; PCL = pronotal collar length across middle line; DRL = pronotal disk region length across middle line; CRL = pronotal callosite region length across middle line; SL = scutellum length; SW = scutellum width; HemL = hemelytral length; CL = cuneal length; TIBL = tibial length. A minimum of five males and five females (including brachypters and macropters when present) were measured; in some cases, measurements were restricted to fewer individuals because of limited material (Table 4; Supporting Information, Table S1).

The following ratios were calculated: A1:IO, A1:HW, A2:PW, A2:HW, IO:EW, HL:PL, DRL:CRL and CRL:PCL. Absolute values and ratios were used in the statistical

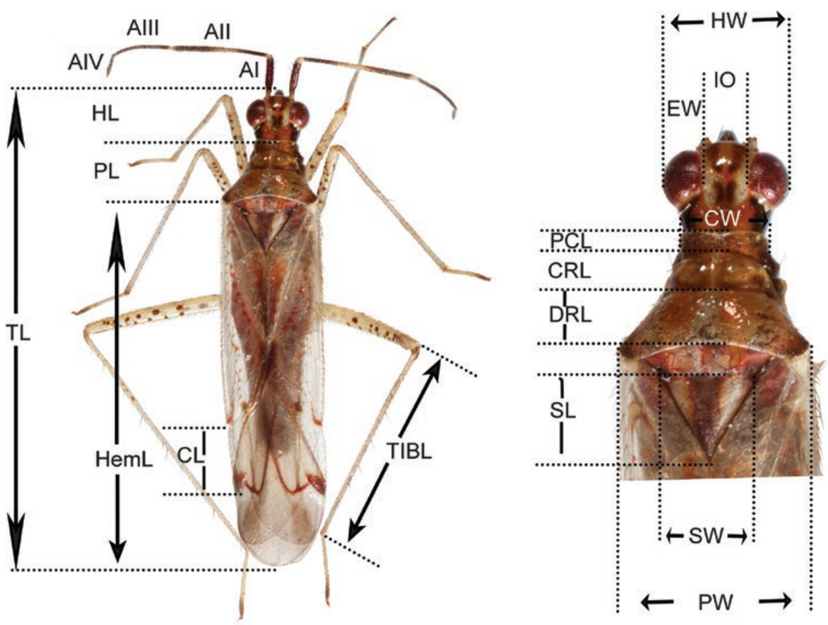

Figure. 1. Morphometric characters for *Dicyphus* (*Dicyphus*) spp. See Methods and Materials for abbreviations.

analyses. Principal component analyses (PCA) were used to reduce dimensions to a few orthogonal variables, and performed separately for males and females. Conditional inference trees (Ctree) (Hothorn, Hornik & Zeileis, 2006) were used to define variables and thresholds for the separation of species. Ctree is based on the Cquad-type statistical test that uses the identity influence function for numeric responses and the asymptotic χ^2 distribution. For the stopping criterion, a simple Bonferroni correction was used with $\alpha = 0.05$.
Two Ctree analyses were performed:

(1) Quantitative characters of brachypterous and macropterous morphs (males and females separately) (Supporting Information, Table S1).

(2) Quantitative characters in combination with qualitative external and genitalic characters for males only (brachypterous and macropterous morphs together) (Supporting Information, Table S2).

The qualitative characters used in the Ctree analyses were: (1) vertex marking X-(Fig. 1) or V-shaped (Fig. 2, i.e. *D. epilobii*) (HMXs); (2) A1 uniformly coloured (Fig. 1) or banded (Fig. 3) (DarkA1); (3) corium with three (Fig. 1) or less pairs of spots (Fig. 4) (CorS); (4) hind femora with or without large overlapping spots (Fig. 5) (FemSO); (5) presence or absence of tumose external process on the left sternal margin of abdominal segment VIII (Fig. 6F) (ExtProcT1); (6) presence or absence of denticulate external process on the left

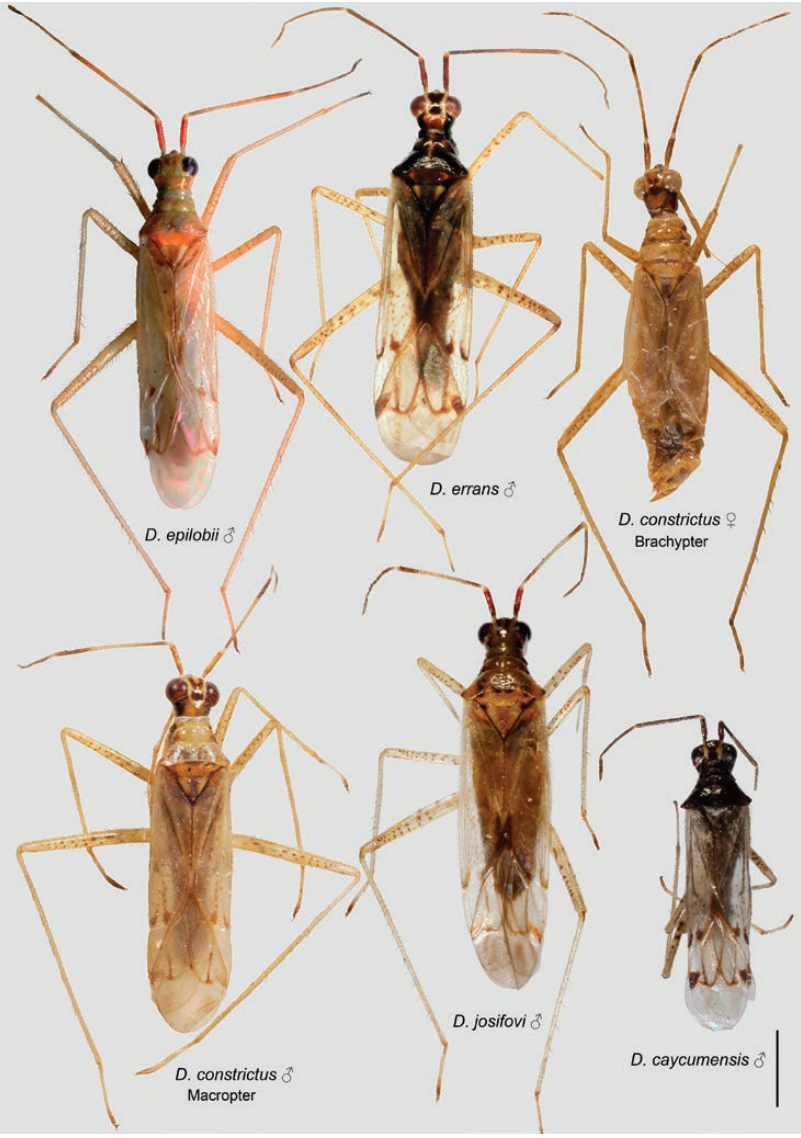

Figure 2. Habitus of males of *D. epilobii*, *D. errans*, *D. constrictus* (macropter and brachypter), *D. josifovi* and ***D. caycumensis* sp. nov.** Scale bar = 1 mm.

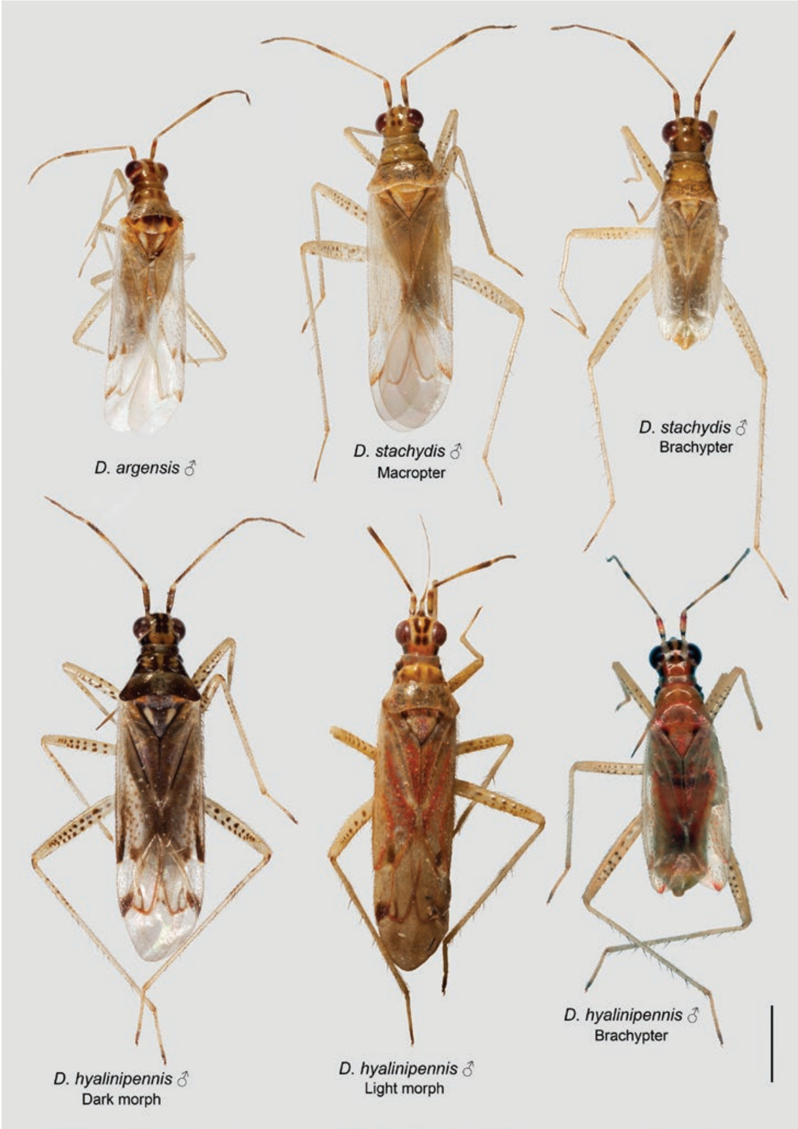

Figure 3. Habitus of males of ***D. argensis* sp. nov.**, *D. stachydis* (macropter and brachypter), *D. hyalinipennis* (macropters, dark and light morph, and brachypter). Scale bar = 1 mm.

sternal margin of abdominal segment VIII (Figs 7D, 8F) (ExtProcT2); (7) left paramere long (Fig. 9C–F) or short (Fig. 9A, B) (LP_L); (8) left paramere rounded (Fig. 9A, B) or angulate (Fig. 9C–F) (LP_R); (9) left paramere short with spatulate apical tooth (acutely joining apophysis) (Fig. 10B) or with other shape (LP_ST); (10) apex of left paramere expanded (Fig. 11C) or flat (Fig. 11A) (LP_CExp); (11) aedeagus with (Fig. 12C) or without (Fig. 12A–B, D–G) field of spinules (AedFS); and, (12) endosomal lobal sclerites absent (Fig. 13C), small (Fig. 14C, D) or large (Fig. 14A, B) (LobSc).

The morphometric analyses were performed using R (R-Development-Core-Team, 2015). We used 'prcomp' from the MASS package for Principal Component Analysis and 'Ctree' from the 'party' package for Conditional inference trees.

Molecular materials

We surveyed dicyphines in Europe and the Canary Islands between 2006 and 2009 to obtain fresh material for mtDNA sequencing (Table 1). Seventy-five samples were sequenced, including five putative outgroup taxa: *Monalocoris filicis* (L.) (root of tree), *Cyrtopeltis canariensis* (Lindberg), *N. tenuis*, *Dicyphus albonasutus* Wagner and *Dicyphus globulifer* (Fallén). Outgroup selection was based on previous molecular-based mirid studies (Martínez-Cascales *et al.*, 2006a; Sanchez,

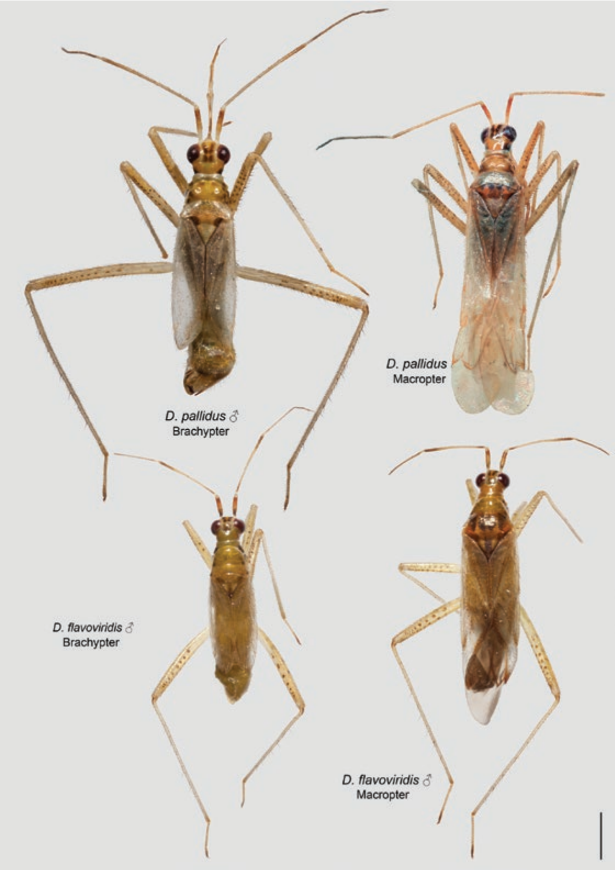

Figure 4. Habitus of *D. pallidus* (macropter and brachypter) and *D. flavoviridis* (macropter and brachypter). Scale bar = 1 mm.

Martínez-Cascales & Cassis, 2006; Schuh, Weirauch & Wheeler, 2009).

DNA extraction, primers, PCR amplification and sequencing

Prior to DNA extraction, specimens were photographed, dissected and identified, based on comparison with type material and/or original descriptions and revisionary works of Wagner (Wagner, 1951, 1964, 1970; Wagner & Weber, 1978). Total genomic DNA was extracted from the whole specimens using the OMEGA bio-tek Insect DNA isolation Kit (Norcross, GA). A fragment of the 16S rDNA, 12S rDNA and *COI* mitochondrial genes, comprising approximately 525, 380 and 850 bp, respectively, were amplified using the illustraTM puReTaq Ready-To-Go PCR Beads (GE Healthcare, Chicago, Illinois). Amplification reactions were prepared using 2 µl of approximately 0.5 ng/µl of genomic DNA, 1 µM of each primer, in a total volume of 25 µl. The following primers were used for the amplification of mitochondrial genes: LCO (5’ GGG CAA CAA ATC ATA AAG ATA TTG G 3’) and HCOoutout (5’ GTA AAT ATA TGR TGD GCT C 3’) for the *COI* region (Folmer *et al.*, 1994); 16Sar-L (5’ CGC CTG TTT ATC AAA AAC AT 3’) (Folmer *et al.*, 1994; Palumbi, 1996) and 16SB (5’ CTC CGG TTT GAA CTC AGA TCA 3’) (Tan, Gillespie & Oxford, 1999) for the 16S rDNA loci; and 12SAI (5’ AAA CTA GGA TTA GAT ACC CTA TTA T 3’) and 12SBI (AAG AGC GAC GGG CGA TGT GT 3’) for the 12S rDNA loci (Kocher *et al.*, 1989). PCRs were carried out in an Eppendorf Mastercycler EPgradient (Eppendorf AG, Hamburg, Germany). The *COI* and 16S fragments were amplified under the following conditions: 2 min at 94ºC, followed by 38 cycles of 30 s at 93ºC, 45 s at 50ºC (annealing) and 1 min at 72ºC (elongation), and then 10 min incubation at 72ºC. For the 12S fragment, the annealing temperature was 46ºC, and the duration of the annealing and elongation cycles were 30 s each. The amplifications were checked by agarose gel electrophoresis and purified using the Geneclean turbo for PCR (QBiogene Inc, Montreal, Quebec). DNA was sequenced by Secugen (Madrid, Spain) using 3730 and 3730 XL DNA analysers (Applied Biosystems, Foster City, California). The sequences were read and incorporated using MEGA7 (Kumar, Stecher & Tamura, 2016). The alignment was performed independently for *COI*, 16S and 12S DNA fragments using MAFFT (Katoh *et al.*, 2005) on the online server (http://mafft cbrc.jp/alignment/server/), using the E-INS-i strategy (Katoh *et al.*, 2005; Katoh & Toh, 2008) with the default settings: gap opening penalty = 1.53 and offset value = 0.00. The matrices of post-aligned and trimmed sequences comprised the following number of columns, including gaps: 794 for *COI*, 503 for 16S and 353 for 12S.

Phylogenetic analyses and species discrimination

The rationale for the molecular phylogenetic analysis was twofold:

(1) To determine species boundaries on the basis of mtDNA data.
(2) To determine the relationship of the included species.

The general time-reversible + invariant + gamma (GTR+I+G) was selected by PartitionFinder v1.1.0 (Lanfear *et al.*, 2012) as the most suitable model for explaining the evolution of the *COI*, 16S and 12S nucleotide sequences, based on Bayesian information criteria and likelihood values. The phylogenetic analyses were performed using Maximum Likelihood (ML) and Bayesian inference (BI) methods. BI was performed using Mr. Bayes 3.2.6 (Ronquist *et al.*, 2012)

Table 1. Accession numbers for mtDNA fragments (*COI*, 16S and 12S) and sample information of Dicyphini used in the molecular phylogeny. * indicates the outgroups, code is the ID sample, year is date of collection. (†) Identified as *D. umbertae* (Syn. *D. cerastii*). (ϕ) Identified as *D. baezi* (Syn. *D. rubicundus*).

Species	code	Acc. *COI*	Acc. 16S	Acc. 12S	Year	Province	Country	Lat	Long	Host plant
Dicyphus argensis	D27-2	KY274582	KY274659	KY274734	2006	Huelva	Spain	37º13'12"N	7º22'58"W	*Solanum lycopersicum*
	D27-3	KY274583	KY274660	KY274735	2006	Huelva	Spain	37º13'12"N	7º22'58"W	*Solanum lycopersicum*
Dicyphus bolivari	D26-1	KY274623	KY274664	KY274739	2006	Málaga	Spain	36º45'29"N	3º50'53"W	*Cucurbita maxima*
	D40-1	KY274624	KY274665	KY274740	2006	Zaragoza	Spain	41º06'31"N	1º24'51"W	*Epilobium hirsutum*
	D46-1	KY274625	KY274666	KY274741	2006	León	Spain	42º44'39"N	5º08'21"W	*Epilobium hirsutum*
	D49-1	KY274626	KY274667	KY274742	2006	Teruel	Spain	40º19'20"N	0º34'29"E	*Epilobium hirsutum*
	D97-1	KY274627	KY274668	KY274743	2008	Tenerife, CI	Spain	28º34'17"N	16º18'58"W	*Hyoscyamus albus*
	D97-2	KY274628	KY274669	KY274744	2008	Tenerife, CI	Spain	28º34'17"N	16º18'58"W	*Hyoscyamus albus*
	D133-1	KY274620	KY274661	KY274736	2009	La Palma, CI	Spain	28º44'34"N	17º44'37"W	*Solanum lycopersicum*
	D134-1	KY274621	KY274662	KY274737	2009	La Gomera, CI	Spain	28º11'07"N	17º13'16"W	*Nicotiana tabacum*
	D137-1	KY274622	KY274663	KY274738	2009	Gr. Canaria, CI	Spain	28º03'25"N	15º32'19"W	*Datura stramonium*
Dicyphus caycumensis	D78-1	KY274584	KY274670	KY274745	2007	Zonguldak	Turkey	41º20'38"N	32º05'20"E	*Solanum lycopersicum*
	D80-1	KY274585	KY274671	KY274746	2007	Zonguldak	Turkey	41º20'38"N	32º05'20"E	*Cucurbita maxima*
Dicyphus cerastii	D43-1†	KY274589	KY274675	KY274750	2006	Algarve	Portugal	37º22'05"N	7º58'11"W	*Solanum lycopersicum*
	D50-1†	KY274590	KY274676	KY274751	2006	Huesca	Spain	42º42'26"N	0º07'12"W	*Ononis natrix*
	D75-1	KY274591	KY274677	KY274752	2007	Crevena	Greece	40º17'53"N	21º39'16"E	Lamiaceae
	D88-1	KY274592	KY274678	KY274753	2008	Torino	Italy	45º01'53"N	7º17'05"E	Compositae
	D91-1	KY274593	KY274679	KY274754	2009	Savona	Italy	44º14'48"N	8º15'47"E	Lamiaceae
	D158-1	KY274586	KY274672	KY274747	2009	Torino	Italy	45º01'53"N	7º17'05"E	Compositae
	D159-1	KY274587	KY274673	KY274748	2009	Torino	Italy	45º01'45"N	7º18'13"E	Lamiaceae
	D160-1	KY274588	KY274674	KY274749	2009	Torino	Italy	45º01'45"N	7º18'13"E	*Salvia glutinosa*
Dicyphus epilobii	D104-1	KY274595	KY274680	KY274755	2008	Modena	Italy	44º15'44"N	10º33'07"E	*Epilobium hirsutum*
	D105-1	KY274596	KY274681	KY274756	2008	Torino	Italy	45º02'48"N	7º18'26"'E	*Epilobium hirsutum*
Dicyphus errans	D73-1	KY274600	KY274682	KY274757	2007	Olympia	Greece	37º38'18"N	21º46'17"E	*Epilobium hirsutum*
	D76-1	KY274601	KY274683	KY274758	2007	Magnesia	Greece	39º25'10"N	23º08'23"E	*Solanum lycopersicum*
	D81-1	KY274602	KY274684	KY274759	2009	Torino	Italy	45º24'58"N	7º37'00"E	*Lagenaria* sp.
	D86-1	KY274603	KY274685	KY274760	2008	Torino	Italy	45º01'53"N	7º17'05"E	*Salvia glutinosa*
Dicyphus escalerae	D32-2	KY274605	KY274686	KY274762	2006	Granada	Spain	36º57'19"N	3º.21"21"W	Antirrhinum sp.
	D47-1	KY274606	KY274687	KY274763	2006	Cádiz	Spain	36º45'35"N	5º21'56"W	Antirrhinum sp.
	D53-1	KY274607	KY274688	KY274764	2006	Huesca	Spain	42º42'26"N	0º07'12"W	Antirrhinum sp.

Table1. *Continued*

Species	code	Acc. *COI*	Acc. 16S	Acc. 12S	Year	Province	Country	Lat	Long	Host plant
Dicyphus flavoviridis	D92-1	KY274610	KY274691	KY274767	2008	Torino	Italy	44º47'47"N	7º03'11"E	Compositae
	D156-2	KY274608	KY274689	KY274765	2009	Torino	Italy	45º01'45"N	7º18'13"E	*Stachys sylvatica*
	D157-2	KY274609	KY274690	KY274766	2009	Torino	Italy	45º01'45"N	7º18'13"E	*Rubus* sp.
Dicyphus hyalinipennis	D146-1	KY274616	KY274697	KY274773	2009	Jihomoravsky	Czech Rep.	48º50'29"N	17º21'16"E	*Hyoscyamus niger*
	D146-2	KY274617	KY274698	KY274774	2009	Jihomoravsky	Czech Rep.	48º50'29"N	17º21'16"E	*Hyoscyamus niger*
	D163-1	KY274618	KY274699	KY274775	2009	Jihomoravsky	Czech Rep.	48º50'29"N	17º21'16"E	*Atropa* bella-donna
	D163-2	KY274619	KY274700	KY274776	2009	Jihomoravsky	Czech Rep.	48º50'29"N	17º21'16"E	*Atropa* bella-donna
Dicyphus josifovi	D145-1	KY274597	KY274701	KY274777	2009	Jihomoravsky	Czech Rep.	48º52'50"N	17º31'05"E	*Epilobium hirsutum*
	D145-2	KY274598	KY274702	KY274778	2009	Jihomoravsky	Czech Rep.	48º52'50"N	17º31'05"E	*Epilobium hirsutum*
	D148-1	KY274599	KY274703	KY274779	2009	Zlinsky	Czech Rep.	49º06'30"N	18º04'43"E	*Epilobium hirsutum*
Dicyphus pallidus	D150-1	KY274629	KY274704	KY274780	2009	Zlinsky	Czech Rep.	48º56'41"N	17º48'23"E	*Stachys sylvatica*
	D152-2	KY274630	KY274705	KY274781	2009	Zlinsky	Czech Rep.	49º06'46"N	18º06'27"E	*Stachys alpina*
	D155-1	KY274631	KY274706	KY274782	2009	Zlinsky	Czech Rep.	49º08'22"N	18º03'36"E	*Salvia glutinosa*
	D155-2	KY274632	KY274707	KY274783	2009	Zlinsky	Czech Rep.	49º08'22"N	18º03'36"E	*Salvia glutinosa*
Dicyphus rubicundus	D98-1	KY274639	KY274714	KY274790	2008	Tenerife, CI	Spain	28º22'49"N	16º35'55"W	*Aeonium canariensis*
Dicyphus stachydis	D100-1	KY274633	KY274708	KY274784	2008	Tenerife, CI	Spain	28º32'02"N	16º19'35"W	*Aeonium canariensis*
	D132-1ϕ	KY274634	KY274709	KY274785	2009	La Gomera, CI	Spain	28º06'57"N	17º11'58"W	*Aeonium subplanum*
	D132-2ϕ	KY274635	KY274710	KY274786	2009	La Gomera, CI	Spain	28º06'57"N	17º11'58"W	*Aeonium subplanum*
	D138-1ϕ	KY274636	KY274711	KY274787	2009	La Palma, CI	Spain	28º39'57"N	17º48'32"W	*Aeonium palmense*
	D138-2ϕ	KY274637	KY274712	KY274788	2009	La Palma, CI	Spain	28º39'57"N	17º48'32"W	*Aeonium palmense*
	D139-2ϕ	KY274638	KY274713	KY274789	2009	La Palma, CI	Spain	28º43'19"N	17º45'03"W	*Aeonium palmense*
	D140-1	KY274640	KY274715	KY274791	2009	Zlinsky	Czech Rep.	49º08'16"N	18º01'17"E	*Rubus* sp.
	D141-2	KY274641	KY274716	KY274792	2009	Zlinsky	Czech Rep.	49º08'16"N	18º01'17"E	*Stachys sylvatica*
	D142-2	KY274642	KY274717	KY274793	2009	Zlinsky	Czech Rep.	49º07'57"N	18º01'60"E	*Atropa* bella-donna
	D143-1	KY274643	KY274718	KY274794	2009	Zlinsky	Czech Rep.	49º07'57"N	18º01'60"E	*Salvia glutinosa*
	D144-1	KY274644	KY274719	KY274795	2009	Jihomoravsky	Czech Rep.	48º50'29"N	17º21'16"E	*Urtica dioica*
	D147-1	KY274645	KY274720	KY274796	2009	Zlinsky	Czech Rep.	49º07'57"N	18º01'60"E	*Lycopus aeropaeus*
	D149-1	KY274646	KY274721	KY274797	2009	Zlinsky	Czech Rep.	49º07'57"N	18º01'60"E	*Stachys alpina*
*Nesidiocoris tenuis**	N25-1	KY274649	KY274724	KY274800	2007	Sardegna	Italy	39º00'31"N	9º00'32"E	*Solanum lycopersicum*
	N26-1	KY274650	KY274725	KY274801	2007	Sardegna	Italy	39º17'05"N	9º13'26"E	*Solanum lycopersicum*
	N30-1	KY274651	KY274726	KY274802	2008	Lanzarote, CI	Spain	29º11'55"N	13º29'30"W	*Solanum lycopersicum*
	N31-1	KY274652	KY274727	KY274803	2008	Tenerife, CI	Spain	28º34'17"N	16º18'58"W	*Hyoscyamus albus*

Table1. *Continued*

Species	code	Acc. *COI*	Acc. 16S	Acc. 12S	Year	Province	Country	Lat	Long	Host plant
*Cyrtopeltis canariensis**	C13-1	KY274576	KY274653	KY274728	2009	Tenerife, CI	Spain	28º20'12"N	16º52'08"W	*Cistus monspeliensis*
	C15-1	KY274577	KY274654	KY274729	2009	La Palma, CI	Spain	28º47'32"N	17º55'05"W	*Cistus monspeliensis*
	C16-1	KY274578	KY274655	KY274730	2009	La Palma, CI	Spain	28º47'32"N	17º55'05"W	*Cistus symphytifolius*
	C17-1	KY274579	KY274656	KY274731	2009	La Gomera, CI	Spain	28º07'36"N	17º17'06"W	*Cistus monspeliensis*
*Dicyphus albonasutus**	D69-1	KY274580	KY274657	KY274732	2007	Sicilia	Italy	37º56'19"N	13º23'58"E	Fabaceae
	D69-2	KY274581	KY274658	KY274733	2007	Sicilia	Italy	37º56'19"N	13º23'58"E	Fabaceae
*Dicyphus globulifer**	D82-1	KY274614	KY274695	KY274771	2009	Torino	Italy	45º02'03"N	7º27'18"E	*Silene* sp.
	D83-1	KY274615	KY274696	KY274772	2008	Cuneo	Italy	44º20'18"N	7º03'54"E	*Silene* sp.
	D102-1	KY274611	KY274692	KY274768	2008	Gr. Canaria, CI	Spain	28º08'31"N	15º34'30"W	*Solanum lycopersicum*
	D151-1	KY274612	KY274693	KY274769	2009	Stredocesky	Czech Rep.	49º54'49"N	14º00'16"E	*Silene* sp.
	D151-2	KY274613	KY274694	KY274770	2009	Stredocesky	Czech Rep.	49º54'49"N	14º00'16"E	*Silene* sp.
*Monalocoris filicis**	B1-1	KY274647	KY274722	KY274798	2009	Torino	Italy	45º01'53"N	7º17'05"E	*Pteridium aquilinum*
	B1-2	KY274648	KY274723	KY274799	2009	Torino	Italy	45º01'53"N	7º17'05"E	*Pteridium aquilinum*

on the concatenated sequences partitioned by single genes, set at 20 million generations with sampling and diagnosis frequency every 1000 generations. The burn-in was set at 30% of sampled trees. Convergence was confirmed by standard deviation of split frequencies approaching zero (<0.0001) and stabilization of likelihood values. ML analysis was performed on the same partitioned dataset using RAxML with 1000 bootstraps (Stamatakis, 2014). Trees were visualized using FIGTREE v.1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/).

Discrimination of species within *Dicyphus* (*Dicyphus*) was assessed in part on genetic distances (Hebert *et al.*, 2003a). The divergences in nucleotide sequence between individuals were calculated using the Kimura-two-parameter (K2P), which assumes distinct rates for both kinds of transition and transversions. This model is considered the best option for low distances (Nei & Kumar, 2000; Hebert *et al.*, 2003a). The distances were calculated using MEGA7 (Kumar *et al.*, 2016). Standard errors of the pairwise distances were calculated by 1000 bootstraps.

RESULTS AND DISCUSSION

Morphometric and morphological character analysis

PCA analysis of body measurements

In the PCA analyses for males, the first three components explain 82.6% (CP1 48.2%, CP2 22.4%, CP3 12.0%) of the variance of the experimental data. Brachypterous and macropterous males are discretely split into two clusters, although individuals within both wing types strongly overlap amongst species (Fig. 15). Male brachypters of *Dicyphus alkannae* Seidenstucker, *Dicyphus pallidus* Herrich-Schaeffer and *Dicyphus flavoviridis* Tamanini segregate into discrete groups. *Dicyphus pallidus* macropterous males segregate from the group that includes *Dicyphus constrictus* Boheman, *Dicyphus errans* Wolf, *Dicyphus epilobii* Reuter, *D. flavoviridis* and *Dicyphus josifovi* Rieger. In turn, this group is separated from other species, with the exception of *Dicyphus cerastii* Wagner and *Dicyphus umbertae* Sanchez & Cassis, which overlaps with the two main clusters; and *Dicyphus tumidifrons* Ribes is further segregated (Fig. 15). Females exhibit a pattern similar to that of males (Fig. 16); the first three components explain 82.0% (CP1 42.3%, CP2 29.2%, 10.5% CP3) of the variance. CP1 explains most of the distribution of individuals at the species level, whereas CP2 splits the dataset into two groups, with most of brachypters on the positive and macropters on the negative side of the axis, respectively. The interocular distance–eye width (IO:EW) and AII–head width

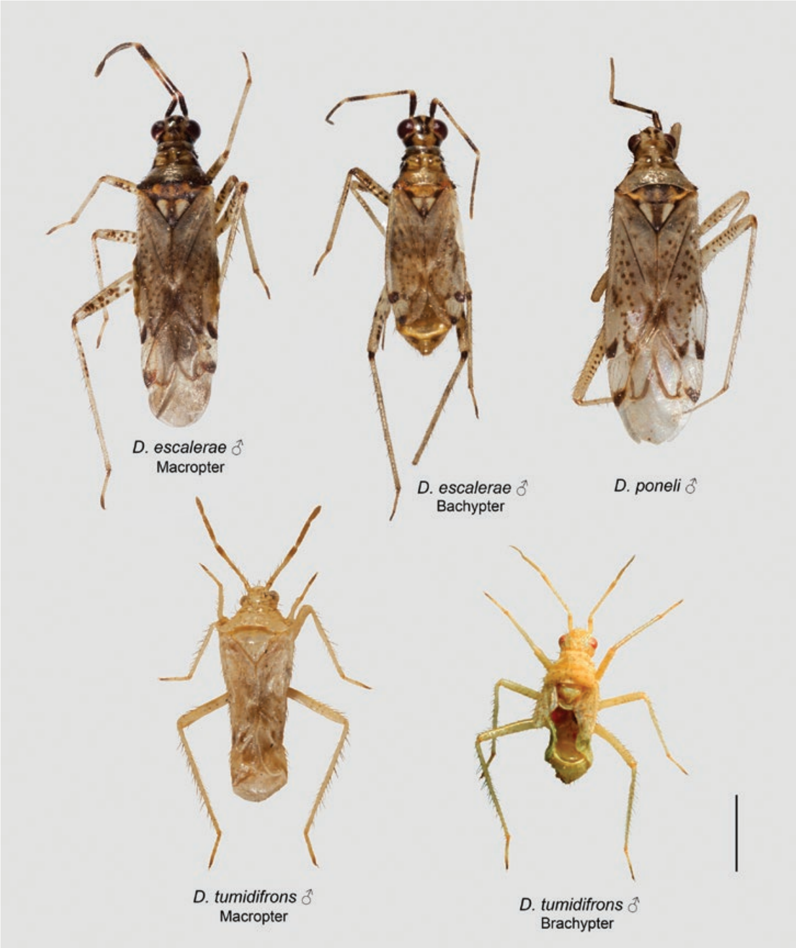

Figure 5. Habitus of *D. escalerae* (macropter and brachypter), *D. poneli* and *D. tumidifrons* (macropter and brachypter). Scale bar = 1 mm.

(A2:HW) ratios contribute mainly to CP1, whereas the head–pronotum length (HL:PL) and disk–calli ratio (DRL:CRL) contribute mainly to CP2. The remaining variables contribute both to CP1 and CP2. Brachypterous females of *D. alkannae*, *D. constrictus*, *D. pallidus* and *D. flavoviridis* segregate into distinct groups. The macropterous females of *D. constrictus*, *D. errans* and *D. epilobii* are grouped apart from the remaining species, with the exception of *D. josifovi*, which is distributed amongst the two main clusters.

Conditional inference tree (Ctree) analyses

In the Ctree analyses for macropterous males using body measurements alone, A2 versus pronotum width (A2:PW), interocular distance versus eye width (IO:EW), total length (TL), AI versus head width (A1:HW), hemelytral length versus pronotum length (HL:PL), the disk versus callosite region length (DRL:CRL) and hemelytral length (HemL) were the covariates that contributed significantly ($P < 0.05$) to the split of the individuals (Fig. 17). The ratio A2:PW in the first and third nodes splits *Dicyphus* species into two large clusters: the first cluster includes all species with A2:PW <1.411 (incl. *Dicyphus argensis* **sp. nov.**, *Dicyphus baezi* Ribes, *Dicyphus bolivari* Lindberg, *Dicyphus caycumensis* **sp. nov.**, *D. cerastii*, *Dicyphus eckerleini* Wagner, *Dicyphus escalerae* Lindberg, *Dicyphus hyalinipennis* Burmeister, *Dicyphus lindbergi* Wagner, *Dicyphus maroccanus* Wagner, *Dicyphus poneli* Matocq & Ribes, *Dicyphus rubicundus* Blöte, *Dicyphus stachydis* Sahlberg, *Dicyphus tamaninii* Wagner, *D. tumidifrons* and *D. umbertae*); and the second cluster includes species with A2:PW>1.411 (incl. *D. constrictus*, *D. epilobii*, *D. errans*, *D. flavoviridis*, *D. josifovi* and *D. pallidus*). To the left of node 3 (A2:PW ≤ 1.411), IO:EW, A2:PW, A1:HW and HL:PL ratios and TL are used in splits, but in all cases individuals from the same species are assigned to several terminal nodes. Nodes 17 and 19 of the second largest cluster branches on the basis of the disk–callosite region ratio (DRL:CRL). All *D. pallidus* macropterous males, and eight out of the nine *D. constrictus* and one out of 25 *D. epilobii*

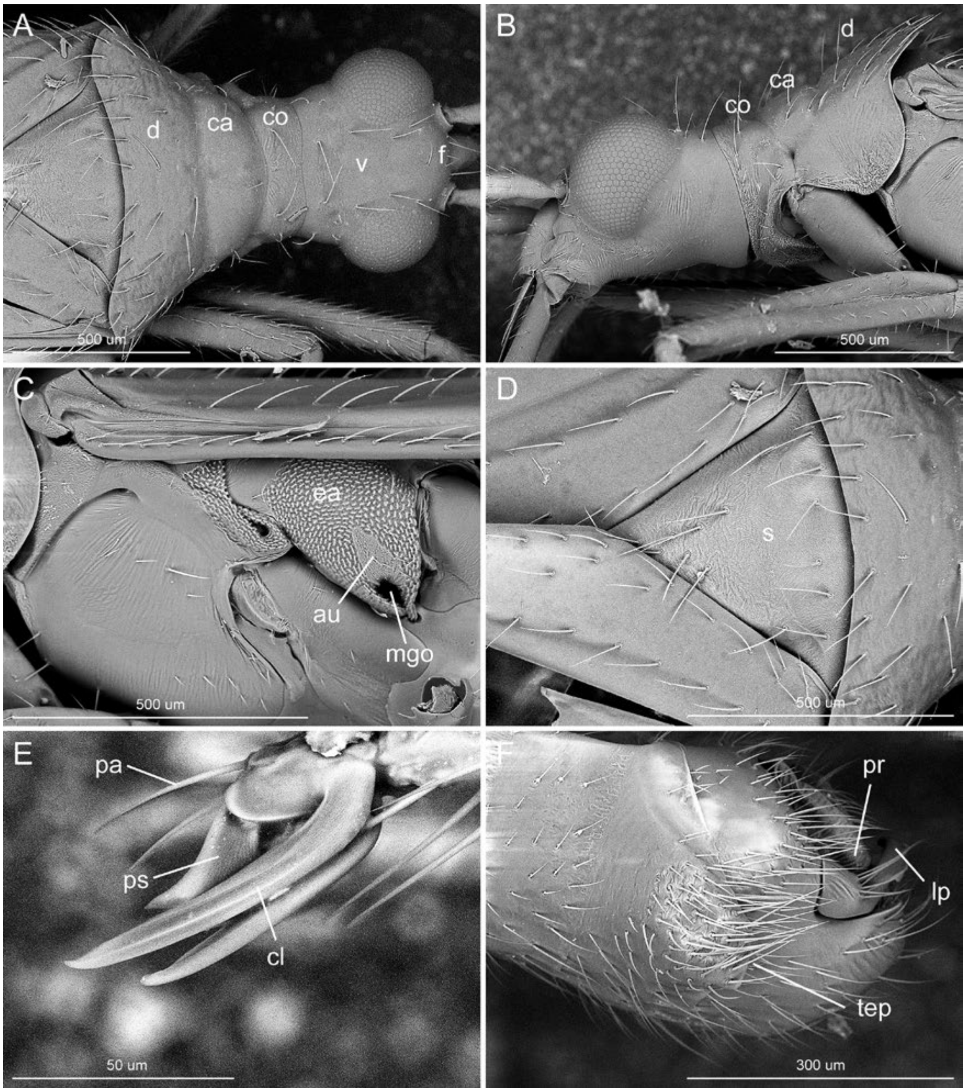

Figure 6. Scanning electron micrographs of *D. cerastii*. A, head and pronotum, dorsal view. B, head and pronotum, lateral view. C, external efferent system, metathoracic glands. D, scutellum(s). E, pretarsus, lateral view. F, genital segment, lateral view external. Abbreviations: au, auricle; ca, calli; cl, claw; co, collar; d, disk; ea, evaporatory area; f, frons; lp, left paramere; mgo, metathoracic gland ostiole; pa, paraempodium; pr, proctiger; ps, pseudopulvillus; tep, tergalprocess; v, vertex.

individuals, were segregated at terminal nodes 18 and 20 (DRL:CRL ratios ≤1.199). *Dicyphus errans*, *D. josifovi*, most of *D. epilobii* (24 out of 25) and one out of nine *D. constrictus* individuals are distributed at nodes 22, 24 and 25, which includes all the specimens with A2:PW>1.411 and DRL:CRL>1.199. In brachypterous males using measurements alone, A2:HW, A1:HW and DRL:CRL were the only variables that contributed significantly ($P < 0.05$) to the differentiation of individuals (Fig. 18). In the first node, A2:HW splits the dataset in two groups. *D. pallidus* and most of *D. flavoviridis* (11 out of 12) segregate at node 1 (A2:HW >1.844). Nodes 2 and 3 split *D. rubicundus* (A2:HW >1.693) and *D. stachydis* (A1:HW >0.592), respectively. The left split of node 3 includes specimens from six of nine species with brachypterous morphs. In macropterous females, A2:PW, IO:EW, HL:PL, TL, A1:HW, DRL:CRL and the clypeus hemelytra length (CHL), were the covariates that contributed significantly ($P < 0.05$) to branching. However, no clearcut clusters were found and, as a result, many species are clustered at the same terminal nodes (Fig. 19). In brachypterous females, A2:HW, IO:EW and A2:PW contributed significantly to the sorting of specimens. However, only *D. pallidus* (all specimens, $N = 6$), and most of *D. flavoviridis* (nine of ten) and most of *D. stachydis* (49 of 56) were assigned to a single terminal node (Fig. 20). For the remaining species, individuals were distributed in several classes.

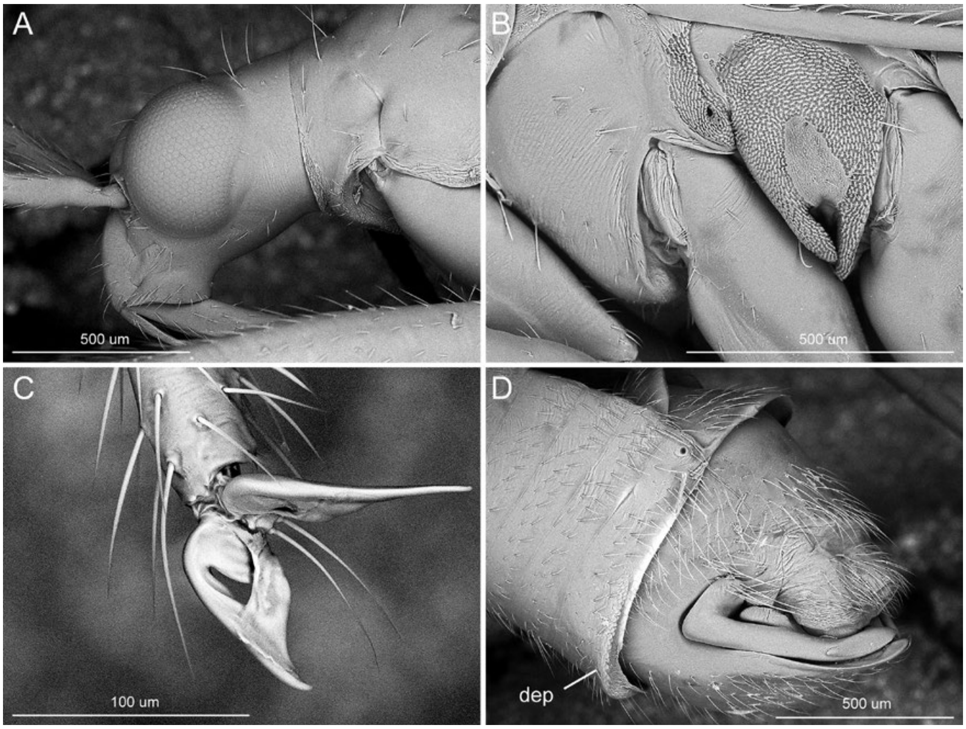

Figure 7. Scanning electron micrographs of *D. flavoviridis*. A, head and pronotum in lateral view. B, external efferent system, metathoracic glands. C, pretarsus in frontal view with paraempodia in between the pseudopulvilli and claws. D, pygophore and pregenital abdominal segments, incl. denticulate external process (dep) of abdominal sternite VIII, left paramere and proctiger in lateral view.

A higher level of resolution was achieved in the separation of species when body measurements were combined together with external and genitalic characters in males. A total of 14 classes were established, to which most *Dicyphus* species were individually assigned. Nineteen of the 23 putative species were distributed to a single terminal node (Fig. 21). The following covariates contributed significantly to the differentiation of species: head marking X- or V-shape (HMXs), tumose external process in abdominal SVIII (ExtPrT1), hind femora with large overlapping spots (FemOS), left paramere rounded or angulate (LP_R), left paramere with apex expanded or flat (LP_CExp), IO:EW, A2–pronotum width ratio (A2:PW), AI uniformly coloured or banded (DarkA1), left paramere short with expanded apex toothed (LP_ST), corium with three or fewer pairs of spots (CorS), denticulate external process in SVIII (ExtPrT2) and A2–head width (A2:HW).

Most of the species, with the exception of *D. epilobii* and *D. tumidifrons*, have a distinct characteristic X-shaped marking on the vertex. The clustering of *D. epilobii* and *D. tumidifrons* (node 4) is likely to be due to the low number of individuals of the latter species in the dataset; however, *D. tumidifrons* is easily differentiated from congeners by external and genitalic characters. *Dicyphus cerastii* and *D. umbertae* were the only two species with a tumose external process in abdominal SVIII (ExtPrT1) (node 3) (Fig. 6F). This is the first time this kind of external process has been reported for *Dicyphus*. *Dicyphus escalerae* was separated from remaining species by the presence of large overlapping spots on the femora (node 4). The shape of the left paramere (angulate or rounded) resulted in two main clusters (node 5). The first cluster includes all species with a long paramere (i.e. *D. bolivari*, *D. baezi*, *D. lindbergi*, *D. maroccanus*, *D. poneli*, *D. rubicundus* and *D. tamaninii*). *Dicyphus baezi* and *D. rubicundus* are separated from remaining species by the flat apex of the left paramere (node 6); these two putative species do not exhibit external morphological differences, neither in the left paramere nor in the aedeagus. *Dicyphus bolivari*, *D. lindbergi*, *D. maroccanus*, *D. poneli* and *D. tamaninii* mixed at terminal nodes 10, 11 and 12. Although these species are aggregated, most of them are differentiated by their external morphology and/or male genitalic characters. For instance, *D. poneli* may be easily separated from *D. bolivari*, *D. lindbergi*, *D. maroccanus* and *D. tamaninii* by the absence of sclerotization on the endosoma and by the presence of large dark spots on the hemelytra (Fig. 5). *Dicyphus bolivari* and *D. maroccanus* are very similar externally to *D. lindbergi* and *D. tamaninii*, but can be

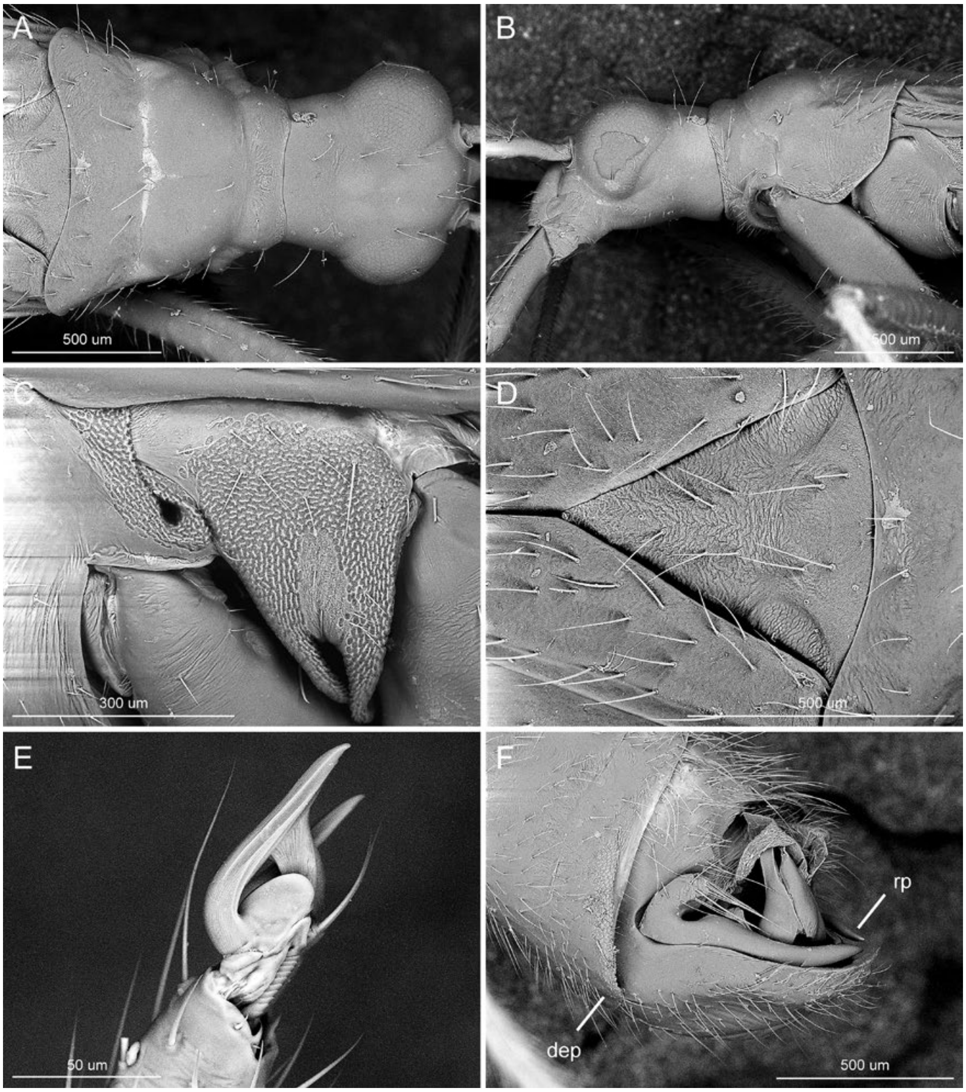

Figure 8. Scanning electron micrographs *D. pallidus*. A, head and pronotum (collar, calli and disk), dorsal view. B, head and pronotum, lateral view. C, external efferent system, metathoracic glands. D, scutelum. E, pretarsus, lateral view. F, genital segment in lateral view, with the denticulated external process (dep) of the VIII abdominal segment, the big left paramere and the small right paramere (rp).

separated from the latter species pair by the number of endosomal sclerites (Figs 12, 14, 22) and length of the left paramere (Figs 9–11). In contrast, *D. bolivari* and *D. maroccanus* cannot be differentiated either by external morphology or by features of the male genitalia. Some species with large endosomal lobal sclerites (e.g. *D. alkannae*, *D. argensis*, *D. constrictus*, *D. hyalinipennis* and *D. stachydis*) were differentiated from *D. flavoviridis* and *D. pallidus* by external characters, such as the presence of a denticulate external process on the left-hand side of abdominal SVIII (ExtPrT2) in the latter pair of species (Figs 7, 8). These processes are substantially different from the hairy tumose proccess of *D. cerastii*/*D. umbertae* and it is the first time they have been reported for *Dicyphus* species. *Dicyphus flavoviridis* and *D. pallidus* are differentiated by the A2:HW ratio (node 20). *Dicyphus alkannae*, *D. argensis*, *D. eckerleini* and *D. josifovi* are grouped at node 23 but can be differentiated by the shape of the left paramere (Figs 9, 10, 23) and the paired endosomal lobal sclerites (Figs 12, 14). Similarly, *D. errans* and *D. caycumensis* are clustered together at node 25, but can be separated by the bigger size of *D. errans* and the A2:PW ratio >1.4 in *D. errans* males (cf. <1.2 in *D. caycumensis*).

Our morphometric analyses demonstrate that body measurements (e.g. A2:PW, DRL:CRL) are useful for clustering groups of *Dicyphus* (*Dicyphus*) species but

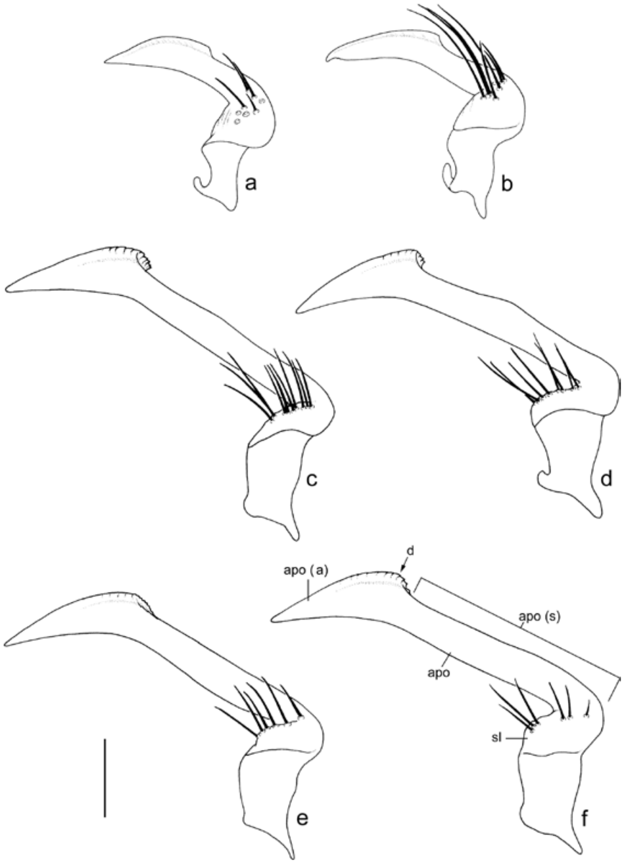

Figure 9. Left paramere. A, *D. alkannae*. B, *D. argensis*. C–F, *D. bolivari*: (C, paratype of *D. bolivari atlanticus*, AMNH_PBI 00208586), (D, Tenerife, Canary Islands, IMIDA_ENT 00000023), (E, paratype of *D. maroccanus*, AMNH_PBI 00208570) and (F, specimen identified as *D. maroccanus*, AMNH PBI 00208574, from the same series of the paratype AMNH_PBI 00208570). Abbreviations: apo, apophysis; apo(a), apex; apo(s), shaft; sl, sensory lobe. Scale bar = 100 ηm.

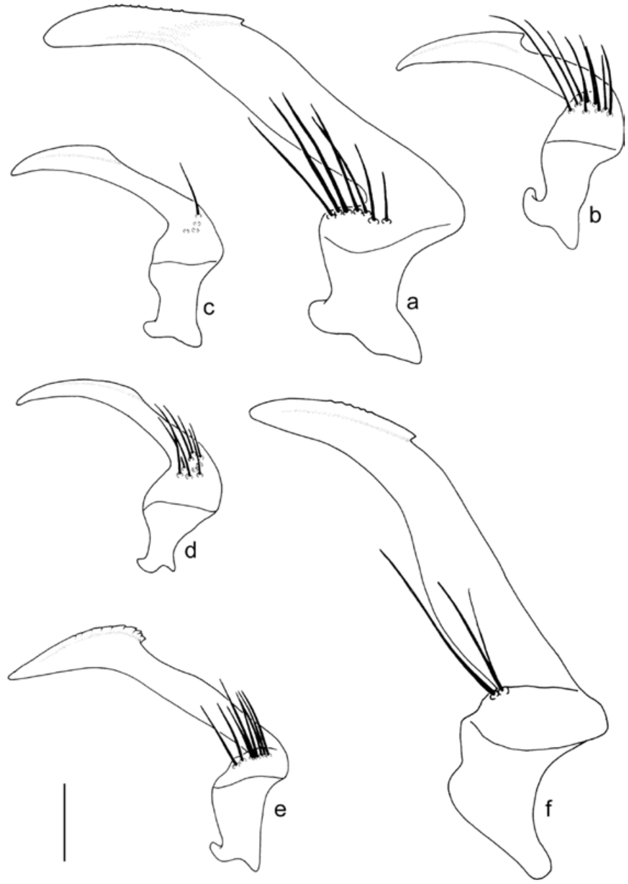

Figure 10. Left paramere. A, *D. flavoviridis*. B, *D. hyalinipennis*. C–D, *D. josifovi*. E, *D. lindbergi*. F, *D. pallidus*. Scale bar = 100 ηm.

are of little use in differentiating species on their own. The discrimination of species using Ctree methods were enhanced when measurements were combined with qualitative characters, including external and genitalic characters. Some external characters, such as the colour-marking of the vertex, the colour of the first antennal segment, the presence of external processes in males and the size of spots on the femora, were all informative. In addition, the shape of the left paramere and the shape and number of endosomal lobal sclerites contributed to species separation.

The combination of morphometric and morphological data resulted in successful discrimination of 20 of 23 *Dicyphus* (*Dicyphus*) species. In contrast, we found the following three species-pairs to be synonymous: *D. maroccanus* and *D. bolivari*, *D. baezi* and *D. rubicundus*, and *D. umbertae* and *D. cerastii* (see Taxonomy section). We had insufficient material of the Iranian species *Dicyphus deylamanus* Linnavuori & Hosseini to implement morphometric methods and inspect the male genitalia; however, the original description is sufficient to uphold it as a distinct species, including its dark coloration and distinct male genitalia (Linnavuori & Hosseini, 1999).

Molecular analysis

The BI and ML analyses resulted in largely overlapping topologies (Figs 24, 25). The parameters used in the RAxML and MrBayes analyses are given in Tables 2 and 3, respectively. *Dicyphus* (*Brachyceraea*) *globulifer* and *D.* (*Brachyceraea*) *albonasutus* are not nested within *Dicyphus* (*Dicyphus*); they are also not recovered as a monophyletic group; however, *Dicyphus* (*Brachyceraea*) paraphyly as shown is likely an artefact of limited taxon sampling. In contrast, *Dicyphus* (*Dicyphus*) is strongly supported as a monophyletic group (BS = 100, PP = 1). In addition, most nodes within *Dicyphus* (*Dicyphus*) are supported by

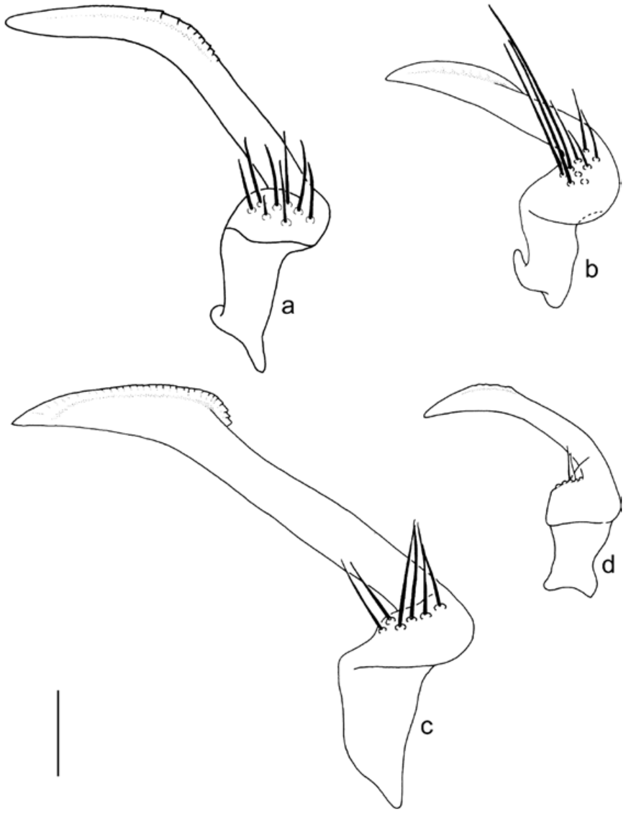

Figure 11. Left paramere. A, *D. rubicundus*. B, *D. stachydis*. C, *D. tamaninii*. D, *D. tumidifrons*. Scale bar = 100 ηm.

high BS and PP values in the ML and BI phylogenies, respectively. Within *Dicyphus* (*Dicyphus*), two major clades were found (Figs 24, 25). Clade A comprises four putative species: *escalerae(baezi,rubicundus) bolivari)*. Clade B comprises 11 species: *(pallidus, flavoviridis)((caycumensis(errans(epilobii,josifovi))) ((cerastii,umbertae)(argensis(stachydis,hyalinipennis)))*. These two clades are corroborated by male genitalic characters, with the endosoma in all three species of clade A possessing fields of spinules and no or small endosomal lobal sclerites. All species of clade B possess two large endosomal lobal sclerites. Our phylogenetic analyses do not support the three species-groups established by Wagner (1951, 1964, 1970) (i.e. *D. pallidus*, *D. errans* and *D. hyalinipennis* species-groups). For example, Wagner's *D. hyalinipennis* species-group includes *D. bolivari*, whereas in our analyses the latter is distant to the other species in his species group, and in clade A. We also found that the remaining species of Wagner's *D. hyalinipennis* species-group are more closely related to his *D. pallidus* and *D. errans* species-groups.

Our two new species, *D. argensis* and *D. caycumensis*, are recognized as discrete taxa, supported by high BS and PP values. *Dicyphus baezi* is placed within the clade that also includes *D. rubicundus*, and within the main clade A. *Dicyphus umbertae* is within the clade of *D. cerastii*, and within the main clade B. Intraspecific variation for *D. escalerae*, *D. flavoviridis*, *D. hyalinipennis*, *D. pallidus* and *D. stachydis* was found in the ML analysis, even though many of the populations sampled are geographically proximate. Within *D. rubicundus* there is differentiation amongst populations that could be explained by their disjunct distribution across the Canary Islands; for example, the populations from Tenerife and La Gomera are geographically proximate and more closely allied than La Palma, the latter being a more distant island. *Dicyphus bolivari* from the Canary Islands and the Iberian Peninsula are in two distinct subclades, each supported by high BS and PP.

Table 2. Parameters of the model used by RAxML in the maximum-likelihood analysis for each of the partitions

Parameter	*COI*	16S	12S
Alpha	0.8375	1.3014	0.7280
Tree-Length:	3.1285	3.1285	3.1285
Rate A<->C	1.8688	0.6506	0.8198
Rate A<->G	8.9798	3.7953	4.2136
Rate A<->T	1.8249	2.3880	1.5607
Rate C<->G	1.6342	0	0.2464
Rate C<->T	17.435	5.0302	5.1503
Rate G<->T	1	1	1

Table 3. Parameters of the model by MrBayes in the Bayesian analysis. PSRF is the potential scale reduction factor

Parameter	Mean	Variance	PSRF
Alpha	0.92087	0.03218	1.00031
Tree length	3.51984	7.54309	1.00080
Rate (A<->C)	0.06757	0.00008	1.00011
Rate (A<->G)	0.29600	0.00047	1.00040
Rate (A<->T)	0.08283	0.00005	0.99996
Rate (C<->G)	0.04939	0.00013	1.00021
Rate (C<->T)	0.44974	0.00057	1.00062
Rate (G<->T)	0.05447	0.00006	0.99952

Genetic distances and species discrimination

Divergence in nucleotide sequences within *Dicyphus* (*Dicyphus*) was below 2.5%. In most cases (132 of 137), distances between individuals within species ranged from 0 to 0.84% (mean = 0.343%, confidence interval (CI) 99% = 0.253–0.433%) (Supporting Information, Table S3, genetic distances). Outliers with sequence divergences >1% were present in *D. epilobii* ($N = 1$),

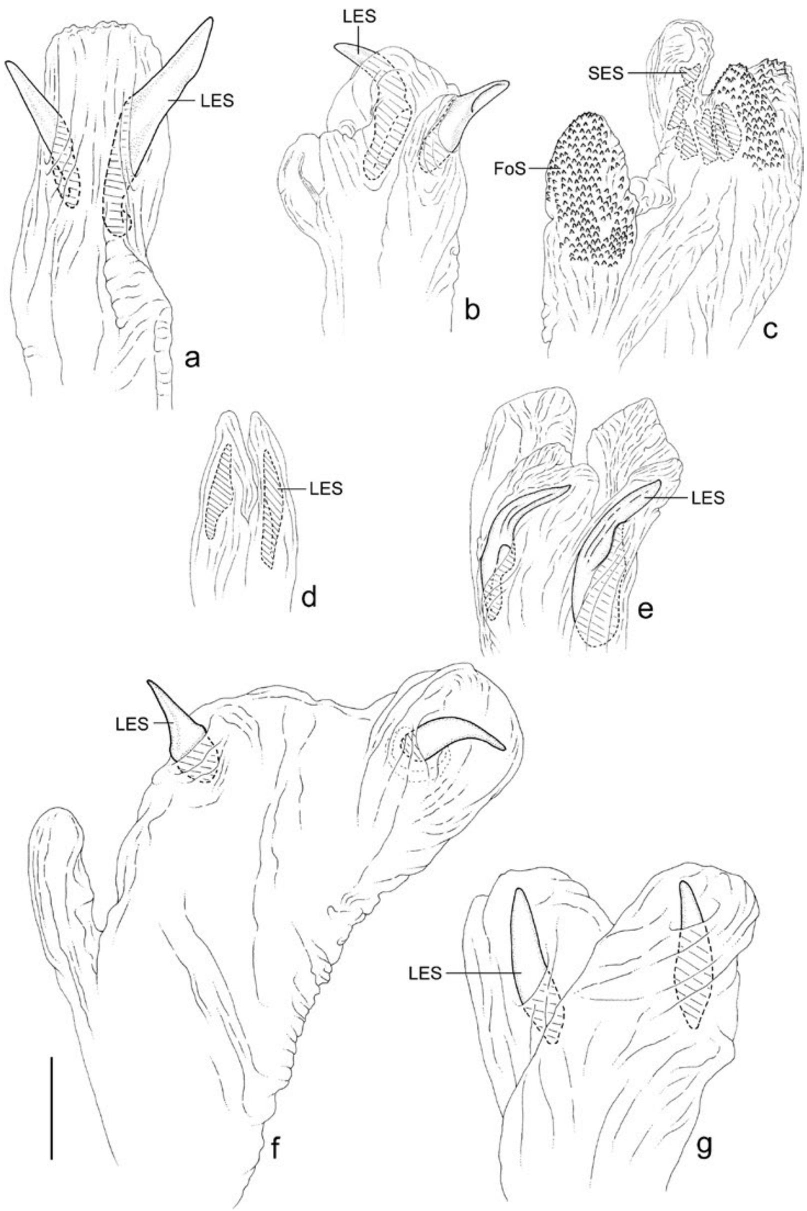

Figure 12. Endosoma. A, *D. alkannae*. B, *D. argensis*. C, *D. bolivari*. D, *D. caycumensis*. E, *D. cerastii*. F, *D. constrictus*. G, *D. eckerleini*. Scale bar = 100 ηm. Abbreviations: FoS, field of spinules; LES, Large endosomal sclerites; SES, small endosomal sclerites.

D. pallidus (*N* = 3) and *D. stachydis* (*N* = 1). The nucleotide divergence between different *Dicyphus* (*Dicyphus*) species was highly variable, ranging from 1.04 to 14.77% (mean = 8.58%, CI 99% = 8.40–8.76%). The divergence between individuals belonging to different dicyphine genera ranged from 19.37 to 28.73% (mean = 25.06%, CI 99% = 24.92–25.19%).

Divergences between nucleotide sequences are informative in the diagnosis of *Dicyphus* (*Dicyphus*) species, with a high degree of confidence. In 96.3% of cases the divergence between sequences within species was below 0.84% and divergence between species was always >1%. These values are similar to the 0–0.86% nucleotide divergences in *COI* sequences reported for other insects, such as Eurytoidae (Hymenoptera) (Zhang, Gates & Shorthouse, 2014). Higher thresholds have been adopted for the discrimination of lepidopteran species (3%) (Hebert *et al.*, 2003a) and mammals (2%) (Avise & Walker, 1999). In the case of *D. epilobii*, the large distance between two specimens may be due to ambiguity in the *COI* sequence. For the other two species with outliers,

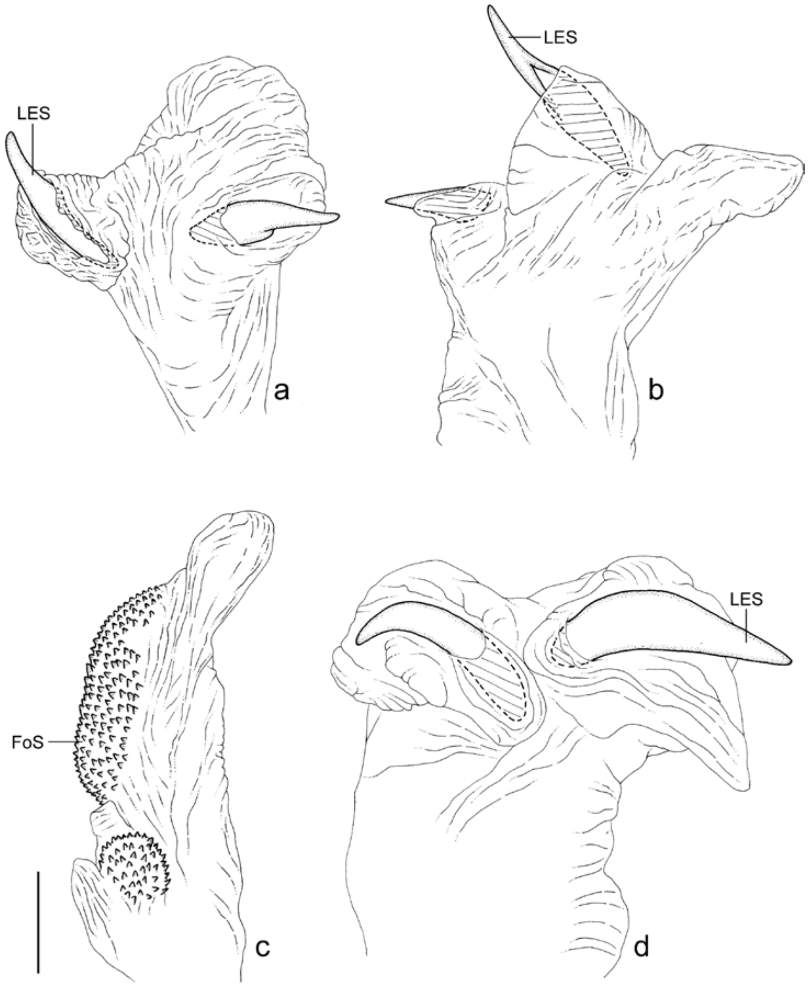

Figure 13. Endosoma. A, *D. epilobii*. B, *D. errans*. C, *D. escalerae*. D, *D. flavoviridis.* Scale bar = 100 ηm. Abbreviations: FoS, field of spinules; LES, large endosomal sclerites.

D. stachydis and *D. pallidus*, all individuals were from neighbouring geographic localities and shorter genetic distances were, therefore, expected. The high intraspecific genetic distances observed in these two species could be due to cryptic species or existence of pseudogenes with higher mutation rates. The nucleotide divergence between *D. baezi* and *D. rubicundus* ranges from 0.322 to 0.441%, which is within the range of variation found within *Dicyphus* species. This is also the case for *D. cerastii* and *D. umbertae*, with divergence ranging from 0.129 to 0.646% (Supporting Information, Table S3). This low nucleotide divergence indicates that specimens putatively identified as *D. baezi* and *D. rubicundus*, as well as those identified as *D. cerastii* and *D. umbertae*, belong to the same species. In some *Dicyphus* species, individuals from disjunct localities are supported by high BS and PP. For example, in the case of *D. bolivari*, all individuals from the Canary Islands and the Iberian Peninsula group into two distinct subclades. Because these individuals are clustered into two subclades, two distinct species could be hypothesized; however, low divergence between individuals across both groups (0–0.58%) indicates conspecificity, with some population differentiation likely due to isolation. Similar genetic differences between populations are expected in other *Dicyphus* (*Dicyphus*) species that are broadly distributed (e.g. *D. cerastii* and *D. errans*). This has been reported for the dicyphine species *M. pygmaeus*, with populations between the Canary Islands and the Iberian Peninsula differentiated due to isolation (Sanchez, La-Spina & Perera, 2012).

Integration of molecular, morphological and molecular partitions

Confidence in identifying *Dicyphus* (*Dicyphus*) species correctly increases when combining

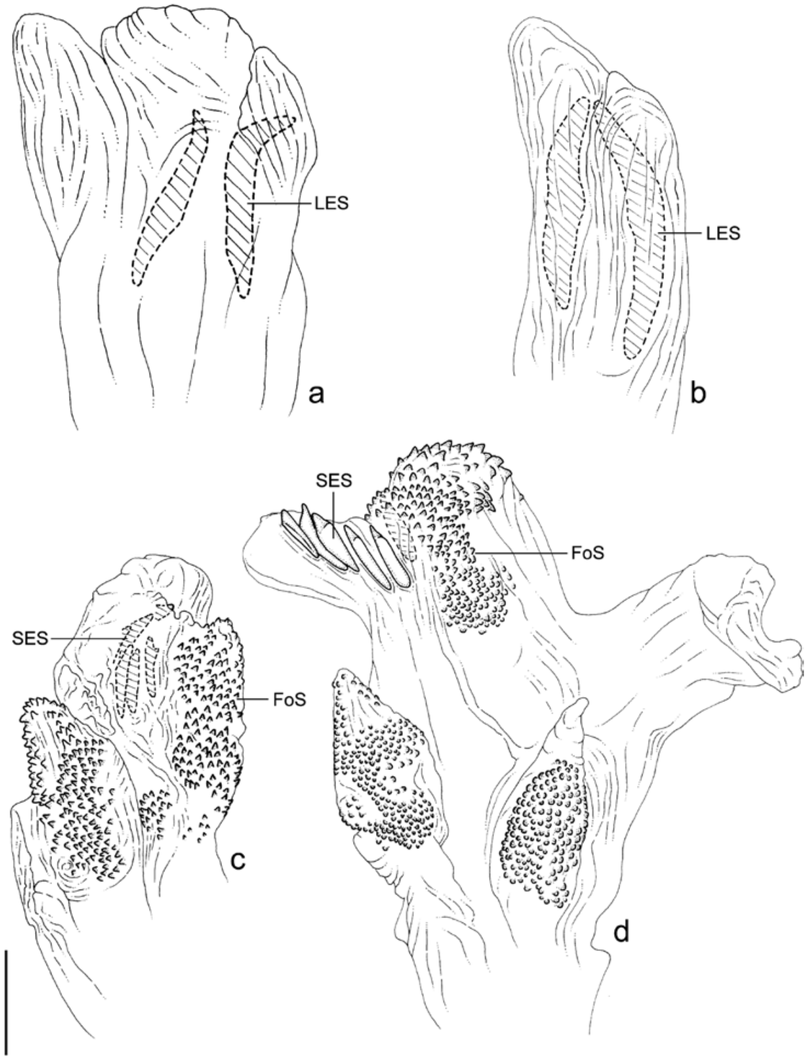

Figure 14. Endosoma. A, *D. hyalinipennis*. B, *D. josifovi*. C–D, *D. lindbergi*. Scale bar = 100 ηm. Abbreviations: FoS, field of spinules; LES, large endosomal sclerites; SES, small endosomal sclerites.

morphological and mtDNA data partitions. The molecular-based phylogenetic analyses showed that *Dicyphus* (*Dicyphus*) species are largely monophyletic, supported by high BS and PP values. Genetic distances within and between species are given as thresholds for the diagnosis of species. In contrast, morphometric data can be used to distinguish groups of species but are not suitable for species diagnostics on their own; when combined with qualitative characters of external and male genitalic morphology they contribute to increasing the level of species discrimination.

Using this iterative approach, we confirm the identity of 21 *Dicyphus* (*Dicyphus*) species, including two new species, from Spain (*D. argensis*) and Turkey (*D. caycumensis*). On the same grounds we consider *D. maroccanus*, *D. baezi* and *D. umbertae* to be junior synonyms of *D. bolivari*, *D. rubicundus* and *D. cerastii*, respectively. We erect *D. baezi* and *D. rubicundus* as synonymous based on phylogenetic analysis, nucleotide divergence, and external and male genitalic morphology. We did not have adequate material of the Moroccan species, *D. maroccanus*, to undertake molecular analysis; nonetheless, we could not differentiate it morphologically from *D. bolivari* and we consider it a junior synonym. As a consequence of integrating these data partitions, we provide the following reclassification of *Dicyphus* (*Dicyphus*), including redescription of previously described species and description of two new species.

TAXONOMY

Dicyphus Fieber

Dicyphus Fieber, 1858: 327 [(original description; type species: *Capsus collaris* Fallén, 1807 = *Dicyphus errans* (Wolf, 1804)]; Carvalho, 1958: 191 (world catalogue); Schuh, 1995: 487 (world catalogue; rejection of subgeneric classification); Cassis (1986): 34 (redescription).

Abibalus Distant, 1909: 521 (original designation; type species – *Abibalus regulus* Distant, 1909, by monotypy); Cassis, 1986: 69 (synonymy).

Bucobia Poppius, 1914: 16 (original designation; type species – *Bucobia gracilis* Poppius, 1914, by monotypy); Cassis, 1986: 69 (synonymy).

Dicyphus (*Dicyphus*) Wagner, 1951: 7 (subgeneric arrangement).

Diagnosis

Dicyphus (*Dicyphus*) is recognized by the following combination of characters: macropters or brachypters; body elongate and parallel-sided; body usually pale brown to stramineous, contrasting with darker markings, usually mid to orange brown, sometimes with red highlighting; body with sparse to moderate distribution of short to elongate hairlike to bristlelike setae, usually semierect; head with a V- or X-shaped dark-brown marking; femora stramineous with brown spotting; pronotum tripartite, with collar long, callosite region well defined and medially confluent; evaporative area extensive, peritreme tongue-shaped; left paramere scythe-shaped, with apophysis short to greatly elongate, and apex usually expanded; aedeagus with multilobed endosomal membrane, often with lobal sclerites or tightly compacted spinules, rarely without sclerotization.

Redescription

Mostly elongate and parallel-sided body; body length: macropterous males 2.91–5.80 mm, brachypterous males 2.04–5.10 mm; macropterous females 3.18–6.02 mm, brachypterous females 2.35–5.67 mm.

Coloration: Body mostly stramineous to yellowish-brown, with dark brown to fuscous and reddish

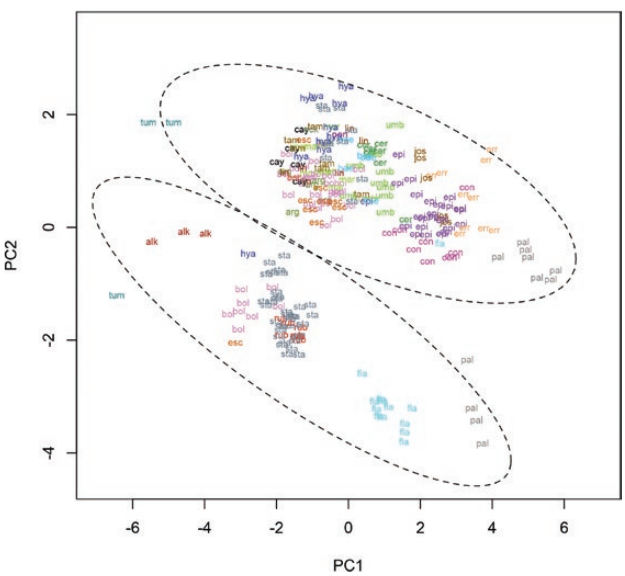

Figure 15. Principal component analysis (PCA) for body measurements of *Dicyphus* (*Dicyphus*) males. Codes used in the graph: *alk, D. alkannae; arg, D. argensis; bae, D. baezi; bol, D. bolivari; cay, D. caycumensis; cer, D. cerastii; con, D. constrictus; eck, D. eckerleini; epi, D. epilobii; err, D. errans; esc, D. escalerae; fla, D. flavoviridis; hya, D. hyalinipennis; jos, D. josifovi; lin, D. lindbergi; mar, D. maroccanus; pal, D. pallidus; pon, D. poneli; rub, D. rubicundus; sta, D. stachydis; tam, D. tamaninii; tum, D. tumidifrons; umb, D. umbertae.* The two ellipses englobe brachypterous (bottom ellipse) and macropterous (upper ellipse) males.

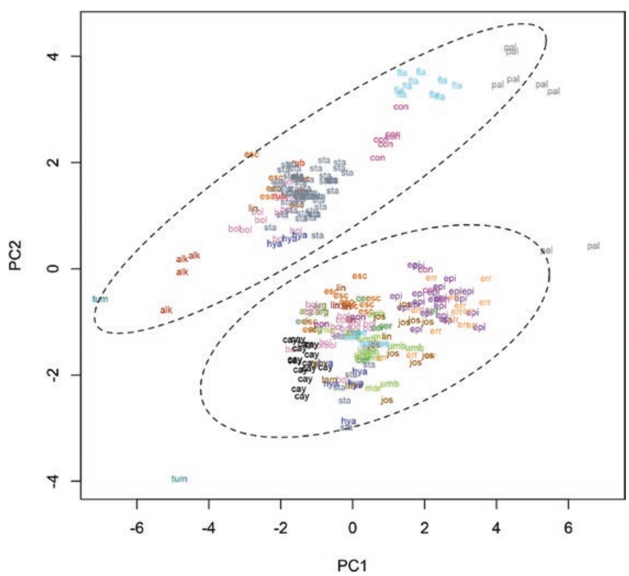

Figure 16. Principal component analysis (PCA) for body measurements of *Dicyphus* (*Dicyphus*) females. Codes used in the graph: *alk, D. alkannae; arg, D. argensis; bae, D. baezi; bol, D. bolivari; cay, D. caycumensis; cer, D. cerastii; con, D. constrictus; dey, D. deylamanus; eck, D. eckerleini; epi, D. epilobii; err, D. errans; esc, D. escalerae; fla, D. flavoviridis; hya, D. hyalinipennis; jos, D. josifovi; lin, D. lindbergi; mar, D. maroccanus; pal, D. pallidus; pon, D. poneli; rub, D. rubicundus; sta, D. stachydis; tam, D. tamaninii; tum, D. tumidifrons; umb, D. umbertae*. The two ellipses englobe brachypterous (upper ellipse) and macropterous (bottom ellipse) females.

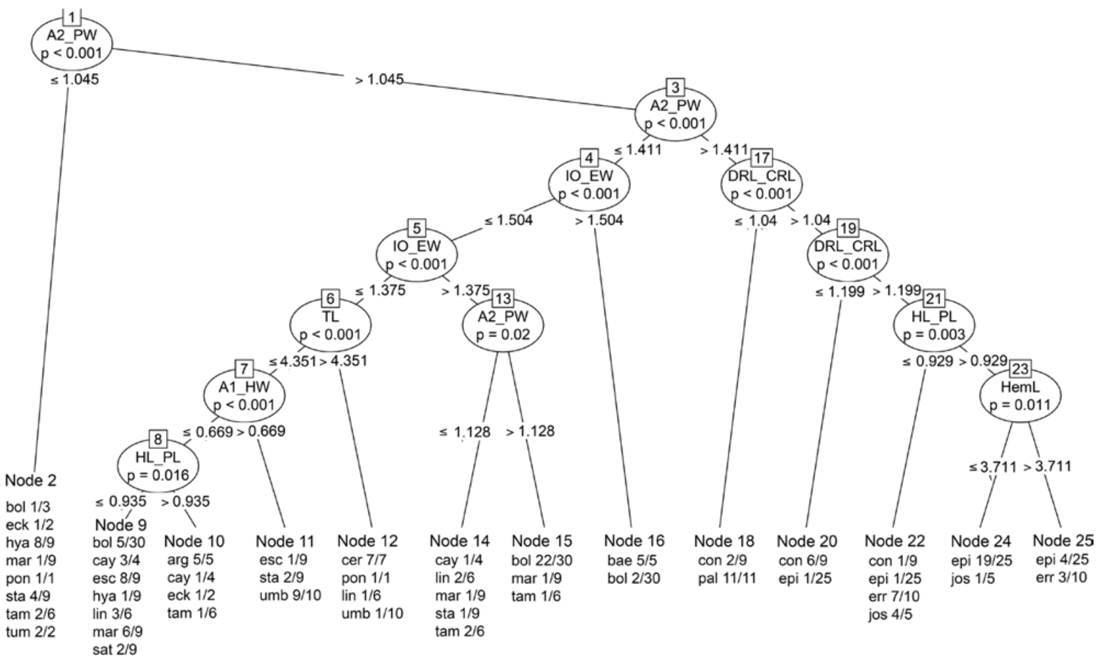

Figure 17. Conditional inference tree (Ctree) using body measurements of *Dicyphus* macropterous males. For each inner node, the Bonferroni-adjusted *P*-values are given. The number of individuals for a given species versus the total number of individuals for such species are displayed at each terminal node. Character abbreviations: A1_HW, ratio A1:head width; A2_PW, ratio between the second antenal segment and the pronotal width; DRL_CRL, ratio disk region length:callosite region length; HemL, hemelitra length; HL_PL, ratio head length:pronotum length; IO_EW, ratio interocular distance:eye witdth; TL, total length. Species abbreviations: alk, *D. alkannae; arg, D. argensis; bae, D. baezi; bol, D. bolivari; cay, D. caycumensis; cer, D. cerastii; con, D. constrictus; eck, D. eckerleini; epi, D. epilobii; err, D. errans; esc, D. escalerae; fla, D. flavoviridis; hya, D. hyalinipennis; jos, D. josifovi; lin, D. lindbergi; mar, D. maroccanus; pal, D. pallidus; pon, D. poneli; rub, D. rubicundus; sta, D. stachydis; tam, D. tamaninii; tum, D. tumidifrons; umb, D. umbertae*.

markings, sometimes more dark brown to fuscous, with paler markings, rarely with both pale and dark colour morphs; dorsum usually polished, more so head and pronotum. *Head:* always with a dark brown to fuscous V- to X-shaped marking on frons+vertex, bounded by paler coloration, usually stramineous to yellow, sometimes orange; clypeus usually pale, sometimes with brown markings, rarely uniformly dark brown; mandibular plate uniformly stramineous; maxillary plate dark brown; gula nearly always pale, rarely dark brown and concolorous with genae. *Pronotum:* collar usually stramineous to whitish, most often translucent, occasionally darker brown highlighting, rarely mostly dark brown; callosite region stramineous with dark brown to fuscous highlighting, sometimes darker overall; disk most often pale, stramineous to yellow, sometimes with orange highlighting, with humeral angles often embrowned, occasionally darker overall. *Mesoscutum:* usually stramineous to orange, often with lateral regions dark brown to fuscous. *Scutellum:* often medially dark brown, sometimes broadly so, rarely more fuscous, lateral regions stramineous, sometimes with orange highlighting; sometimes paler overall, with midline paler brown, with orange or reddish tint. *Hemelytra:* mostly stramineous to yellowish-brown, often translucent; clavus sometimes medially embrowned; corium sometimes with light to dark brown spotting, often with two pairs of larger brown to fuscous spots at corial fracture, apex of endocorium, coupled with dark brown spot at apex of cuneus, sometimes markings more reddish-brown to red; membrane veins usually embrowned, sometimes reddish. *Thoracic pleura and sterna:* propleuron mostly stramineous to light brown with transverse polished dark-brown band; mesobasisternum usually polished dark brown to fuscous, rarely with broad stramineous region laterally; mesepimeron usually stramineous; metepisternum stramineous to brown, sometimes with peritreme contrasting. *Legs:* stramineous to light brown; femora always with two separated rows of small brown spots, rarely with spots larger and subcontiguous; tibiae usually uniformly stramineous to light brown, base rarely with narrow dark-brown annulation; tarsi mostly stramineous with apex embrowned. *Abdomen:* venter often stramineous, with embrownment laterally, sometimes with brown spot posteroventrally on pygophore.

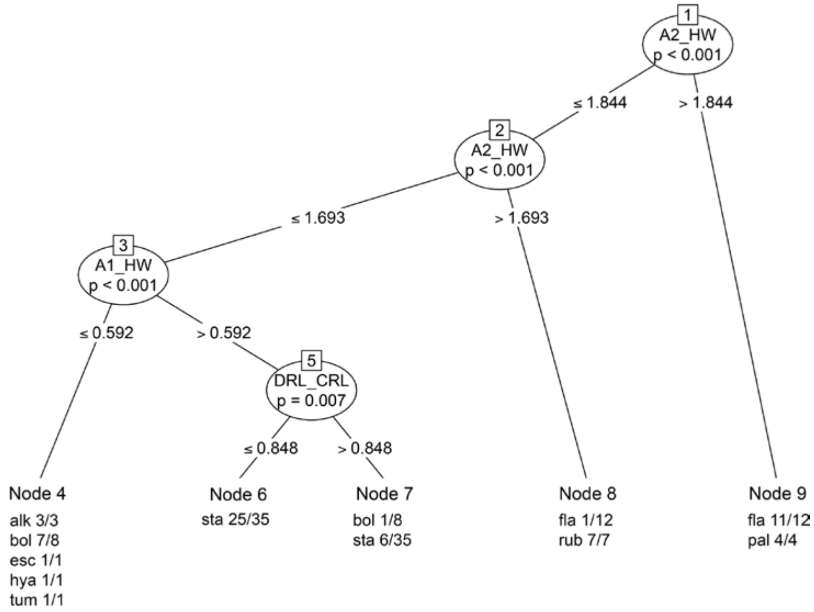

Figure 18. Conditional inference tree (Ctree) using body measurements of *Dicyphus* brachypterous males. For each inner node, the Bonferroni-adjusted *P*-values are given. The number of individuals for a given species versus the total number of individuals for such species are displayed at each terminal node. Character and species abbreviations as in Fig. 17. Additionally, A2_HW, ratio A2:head width.

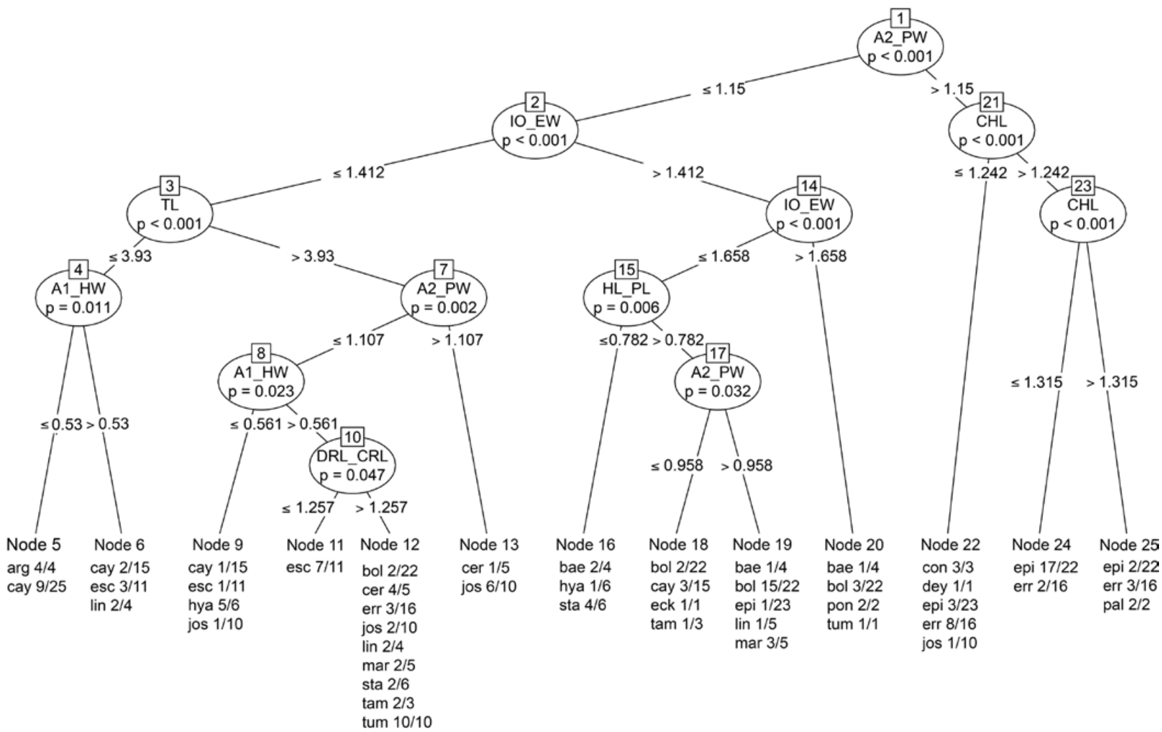

Figure 19. Conditional inference tree (Ctree) using body measurements of *Dicyphus* macropterous females. For each inner node, the Bonferroni-adjusted *P*-values are given. The number of individuals for a given species versus the total number of individuals for such species are displayed at each terminal node. Character and species abbreviations as in Figs 17 and 18. Additionally, CHL, clypeus hemelitra length.

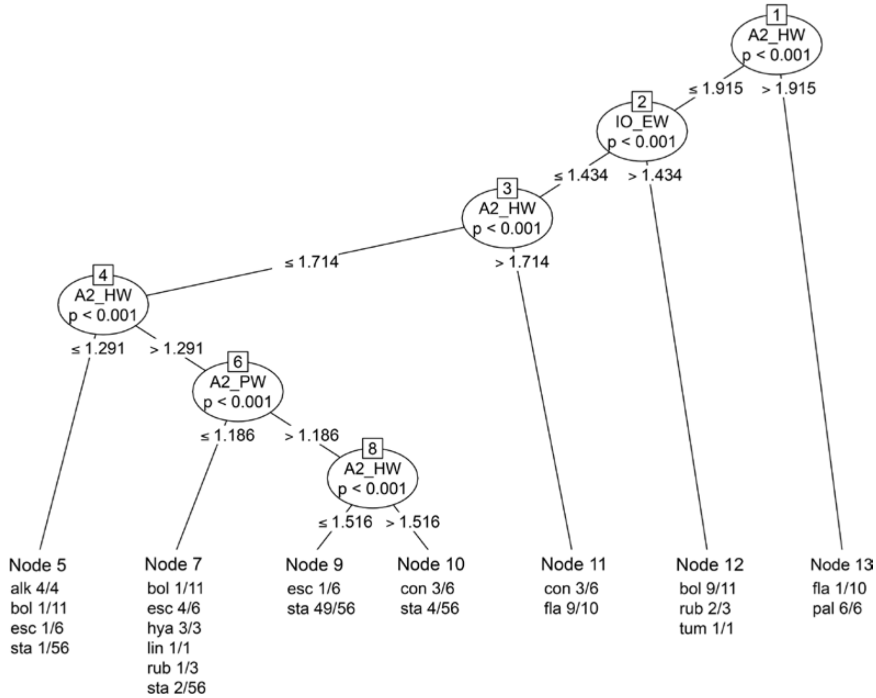

Figure 20. Conditional inference tree (Ctree) using body measurements of *Dicyphus* brachypterous females. For each inner node, the Bonferroni-adjusted *P*-values are given. The number of individuals for a given species versus the total number of individuals for such species are displayed at each terminal node. Character and species abbreviations as in Figs 17, 18 and 19.

Vestiture: Dorsum with sparse to moderate distribution of bristlelike setae, usually longer and more robust on head and pronotum; lateral and ventral regions of body mostly glabrous, with abdominal venter with hairlike setae, more densely distributed posteriorly.

Structure: Head: subpengatonal, usually with eyes enlarged, removed from anterior margin of pronotum by at least width of AII; frons rounded anteriorly, with clypeus visible from above. *Antennae:* usually elongate and thin; AI usually subequal or a little longer than interocular distance; AII usually longer than posterior width of pronotum. *Labium:* usually reaching metacoxae. *Pronotum:* tripartite; collar flattened and long, with anterior margin weakly excavate; calli well-defined, with strongly demarcated posterior margin, usually clearly divided in midline; disk usually longer than callosite region, rarely shorted, with posterior margin excavated, humeral angles rounded. *Thoracic pleura and sterna:* proepimeron weakly depressed; mesobasisternum swollen. *Metathoracic glands:* evaporative areas extensive, reaching near dorsal margin of metepisternum; peritreme tongue-shaped. *Legs:* usually very long, with femora parallel-sided, oval in cross-section, metafemora significantly longer than mesofemora; pretarsi with sublinear claws, large fleshy pseudopulvilli. *Male genitalia:* pygophore mid to large size, weakly asymmetrical; left paramere much larger than right, scythe like, with short tumorose sensory lobe, apophysis short to greatly elongate, with apex spatulate, often with outer margin denticulate; right paramere very small, subcolumnar; phallotheca simple, with broad ventral opening; endosoma with multiple membraneous lobed, usually three lobes, either with a pair of relatively large lobal sclerites, straight to arcuate, symmetrical or asymmetrical, or with field of small lobal sclerites, varying between 2 and 12 in number, closely aggregated, lateral lobes of endosoma often with field of minute spinules. *Female genitalia:* pair of oval sclerotized rings; posterior wall of bursa copulatrix simple and membraneous, without processes or prominent sclerotization.

Remarks

Dicyphus (*Dicyphus*) is differentiated from the other *Dicyphus* subgenera by the shape of the pronotal calli and features of the male genitalia. Wagner (1951) provided a subgeneric key to *Dicyphus* and differentiated the nominotypical subgenus by the large and medially contiguous pronotal calli, the longer and more parallel-sided body and elongate appendages. There are limited external characters that support separation of the subgenera beyond the callosite morphology, although species of *Dicyphus* (*Brachyceraea*) are in general smaller and more rounded in size, and lack the X-/V-shaped marking on the frons+vertex. Also, species of *Dicyphus* (*Dicyphus*) have a distinctive left paramere that is scythe-shaped, which varies in the length of the apophysis and shape (Figs 9–11, 23), and in most cases have a spatulate apex

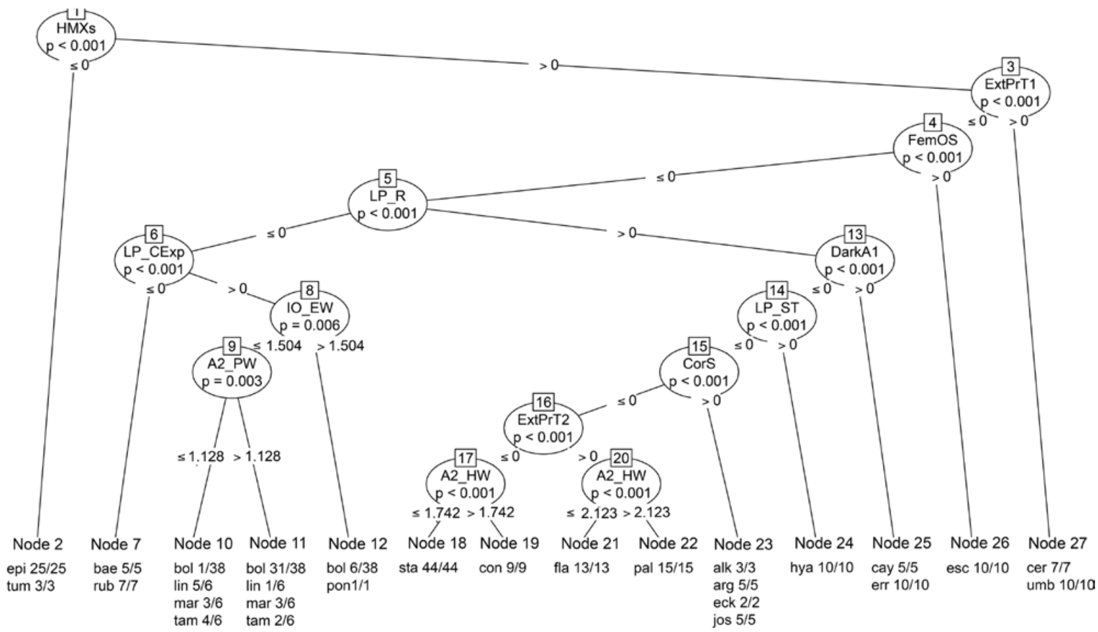

Figure 21. Conditional inference tree (Ctree) for *Dicyphus* males including body measurements, morphological and genitalia characters. For each inner node, the Bonferroni-adjusted *P*-values are given. The number of individuals for a given species versus the total number of individuals for such species are displayed at each terminal node. Species abbreviations as in Fig. 17. Character abbreviations: A2_HW, ratio A2:head width; A2_PW, ratio A2:pronotal width; CorS, corium with three or less pairs of spots; DarkA1, A1 uniformly coloured or banded; ExtProcT1, tumose external process on the left sternal margin of abdominal segment VIII (presence/absence); ExtProcT2, denticulate external process on the left sternal margin of abdominal segment VIII (presence/absence); FemSO, hind femora with or without large overlapping spots; HMXs, vertex marking X or V shape (1/0); IO_EW, ratio interocular distance:eye witdth; LP_CExp, apex of left paramere expanded or flat; LP_R, left paramere rounded or angulate; LP_ST, left paramere short with spatulate apical tooth (acutely joining apophysis) or with other shape.

of the apophysis, which is somewhat flattened in *D. flavoviridis* and *D. pallidus* (Fig. 10).

The genital opening of the pygophore is dorsal in orientation in *Dicyphus*, and does not show any significant variation (Figs 6–8, 26–29). The orientation of the parameres is also consistent at the supraspecific level, with the left paramere larger than the right. The shaft of the left paramere lies parallel to the ventral margin of the genital opening of the pygophore. In contrast, the shape of the left paramere is of primary significance in determining species.

Key to males of species of Dicyphus

The following key is to males only and there are no morphological characters that can readily separate all females of the subgenus. Females can only be identified with confidence by association with males and/or mtDNA sequences. The key has been constructed to allow for the identification of conspecific macropters and brachypters. The following species possess macropterous and brachypterous morphs: *D. alkannae*, *D. bolivari*, *D. constrictus*, *D. escalerae*, *D. flavoviridis*, *D. hyalinipennis*, *D. pallidus*, *D. poneli*, *D. rubicundus* *D. stachydis*, *D. tamaninii* and *D. tumidifrons*. The following species are only known from macropters: *D. argensis*, *D. caycumensis*, *D. cerastii*, *D. deylamanus*, *D. eckerleini*, *D. epilobii*, *D. errans* and *D. josifovi*. Post-couplet 13, end-users will need to investigate the male genitalia, and even then the differences are minor.

Dicyphus alkannae Seidenstucker, 1956

(Figs 9A, 12A, 30, 32)

Dicyphus alkannae Seidenstucker 1956: 145 (original description); Wagner, 1974: 74 (redescription; host plant); Schuh, 1995: 489 (catalogue; full citation); Kerzhner & Josifov, 1999: 21 (Palaearctic catalogue).

Material examined

Turkey: Kayseri, 38.52666°N 35.92805°E, 1490 m, 23–26 May 1995, Seidenstucker, 1♀, paratype (AMNH_PBI 00210746) (MZH), 1♂ (AMNH_PBI 00208540), ex. *Alkanna orientalis* (L.) Boiss (Boraginaceae) (MZH). Ulukischla, 37.54423°N 34.48504°E, 1425 m, 16 May 1955, 22 May 1955, Seidenstücker, 2♀♀ (AMNH_PBI 00208542, AMNH_PBI 00208541), ex. *Alkanna orientalis* (MZH).

CHECKLIST OF *DICYPHUS* (*DICYPHUS*) OF THE WESTERN PALAEARCTIC

D. alkannae Seidenstucker	Turkey, Iran
***D. argensis* sp. nov.**	Iberian Peninsula (Spain).
D. bolivari Lindberg	Canary I., France, Iberian Pen. (Spain), Morocco.
= *D. marocannus* Wagner, new synonymy	
= *D. bolivari atlanticus* Wagner, new synonymy	
***D. caycumensis* sp. nov.**	Turkey
D. cerastii Wagner	Europe
= *D. umbertae* Sanchez & Cassis new synonymy	
D. constrictus (Boheman)	Northern and Central Europe
D. deylamanus Linnavuori & Hosseini	Iran
D. eckerleini Wagner	Europe and Middle East
D. epilobii Reuter	Middle, Central and Northern Europe
D. errans (Wolf)	Europe
D. escalerae Lindberg	Southern and Central Europe
D. flavoviridis Tamanini	France, Italy and Switzerland
D. hyalinipennis (Burmeister)	Europe
D. josifovi Rieger	Crete, Czech Republic, Bulgaria
D. lindbergi Wagner	Crete and Middle East
D. pallidus (Herrich-Schaeffer)	Northern and Central Europe
D. poneli Matocq and Ribes	Madeira Islands
D. rubicundus Blote	Canary Islands
= *D. baezi* Ribes, new synonymy	
D. stachydis Sahlberg	Europe
D. tamaninii Wagner	Europe, northern Africa
D. tumidifrons Ribes	Iberian Peninsula (Spain)

Iran: Tabriz, 38.00590°N 46.42168°E, 1650 m, 21 May 1965, Eckerlein, 3♀♀ (AMNH_PBI 00210747 to AMNH_PBI 00210749), 1♂ (AMNH_PBI 00210751), ex. *Alkanna orientalis* (MZH).

Diagnosis

Dicyphus alkannae is recognized by the following combination of characters: macropterous and brachypterous males (Fig. 30); only brachypterous

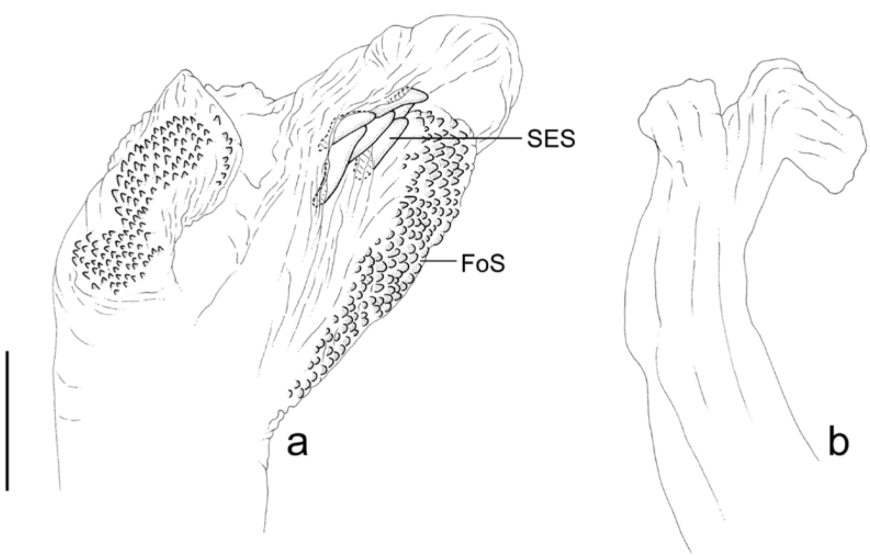

Figure 22. Endosoma. A, D. *tamaninii*. B, D. *tumidifrons*. Scale bar = 100 ηm. Abbreviations: FoS, field of spinules; SES, small endosomal sclerites.

Key to species of *Dicyphus* (*Dicyphus*) from the Western Palaearctic

1. Left sternal process present as expanded flange with denticulate substructure (Figs 7D, 8F)....................2
   – Left sternal process as expanded flange with denticulate substructure absent, SVIII sometimes expanded on left side, with clump of bristlelike setae (Fig. 6F)................ 3
2. AII <2.1× longer than head width; body length 5.00 mm in macropters, 3.65–4.06 mm in brachypters; pygophore without posteroventral brown spot .... *Dicyphus flavoviridis*
   – AII >2.1× longer than head width; body length 5.23–5.80 mm in macropters, 4.34–5.10 mm in brachypters; pygophore with posteroventral brown spot ....*Dicyphus pallidus*
3. Left sternal margin of abdominal SVIII laterally tumose (adjacent to left paramere) (Fig. 6F), with clump of bristlelike setae; apophysis of left paramere short (Fig. 23B); endosomal sclerites asymmetrical and arcuate (Fig. 12E); macropters only .... *Dicyphus cerastii*
   – Left sternal margin of abdominal SVIII laterally not expanded adjacent to left paramere, setae uniformly distributed across segment; apophysis of left paramere short or elongate 4
4. Antennae uniformly black; mandibular plate dark brown to black; macropters only...............................5
   – Either first and/or second antennal segments with medial stramineous region; mandibular plate stramineous; macropters and/or brachypters 6
5. Pronotum with a stramineous midline (Fig. 30); posterior margin of vertex post-X marking stramineous to light brown; endosomal lobal sclerites asymmetrical; body length >5 mm.......... *Dicyphus deylamanus*
   – Pronotum entirely dark brown (Fig. 2); band behind the X-shape mark dark brown; endosomal lobal sclerites symmetrical (Fig. 12D); body length <4 mm ....*Dicyphus caycumensis*
6. Second antennal segment greatly elongate, >1.45× longer than posterior width of pronotum both in macropters and brachypters when present; apophysis of left paramere short; aedeagus with pair of large endosomal lobal sclerites 7
   – Second antennal segment shorter, <1.4× longer than posterior width of pronotum both in macropters and brachypters when present; apophysis of left paramere short or long; aedeagus with or without lobal sclerites 10
7. First antennal segment mostly stramineous, with subbasal and subapical darker annulations (Fig. 2); pronotal disk subequal to a little longer than callosite region, generally <1.2× in macropters; macropters and brachypters... *Dicyphus constrictus*
   – First antennal segment mostly red to reddish brown or dark brown, without evident paler medial part; pronotal disk >1.2× greater than callosite region; macropters only..8
8. Darker species (Fig. 2); second antennal segment mostly dark brown, stramineous medially but narrowly so; first antennal segment red to reddish dark brown; apophysis of left paramere short and robust, spatulate apex expanded (Fig. 23F); paired endosomal lobal sclerites asymmetrical (Fig. 13B); macropters only … ....*Dicyphus errans*
   – Paler species; second antennal segment always broadly stramineous medially, with dark brown subbasal annulation and distally dark brown; first antennal segment reddish. Apophysis of left paramere short, spatulate apex weekly expanded (Figs. 10C–D, 23E) 9
9. Frons+vertex with a short and faint V-shaped brown marking (Fig. 2), not extending to the posterior margin of eyes; endosoma with a pair of medium size (*c*. 1/4 of endosomal length) lobal sclerites weakly asymmetrical (Fig. 13A)...*Dicyphus epilobii*
   – Frons+vertex with a distinct X-shaped dark-brown marking (Fig. 2), extending to the posterior margin of eyes. Endosome with a pair of big (>1/3 of the endosome length) and thick lobal sclerites slightly asymmetrical (Fig. 14B)..*Dicyphus josifovi*
10. Small species (Fig. 5), body length <3.1 mm in macropters, <2.1 mm in brachypters; eyes very small, interocular distance >2× eye width; pale species; endosoma without sclerotization (Fig. 22B); macropters and brachypters..*Dicyphus tumidifrons*
    – Body variable in size, always >3.3 mm in macropters, >2.5 mm in brachypters; eyes moderate to large size; interocular distance <1.7× eye width; pale to dark species; endosoma with sclerotization 11
11. Femora with greatly enlarged dark spots, in irregular two rows, spots very often touching (Fig. 5); first antennal segment entirely dark reddish to dark brown; apophysis of left paramere with broad and recurved apex, outer margin strongly denticulate (Fig. 23G–I); endosoma without small or large lobal sclerites; two endosomal lobes with fields of spinules (Fig. 13C); macropters and brachypters .... *Dicyphus escalerae*

– Femora with two rows of relatively small spots, separated; first antennal segment mostly medially stramineous with red or brown subbasal and subapical annulations, rarely mostly pale red; apophysis of left paramere variable; endosoma with or without lobal sclerites and with or without fields of spinules 12

12. Clavus and corium with uniform distribution of enlarged brown spots (Fig. 5); apophysis of left paramere broad and short; endosoma lacking small or large lobal sclerites, with fields of spinules only; macropters and brachypters .... *Dicyphus poneli*
– Clavus and corium either generally without uniform distribution of enlarged brown spots or at most with small red or brown spots, latter often faint; if enlarged spots present, then left paramere elongate; endosoma always with small or large lobal sclerites, sometimes also with fields of spinules 13

13. Left paramere elongate to greatly elongate (Fig. 9C–F) 14
– Left paramere short (Fig. 9A, B) 17

14. Left paramere with non-expanded apophysis; distal region of apophysis angulate with a serrated outer margin (Fig. 11A); medial lobe of endosoma with 5–11 small lobal sclerites (Fig. 31B); macropters and brachypters. .... *Dicyphus rubicundus*
– Left paramere with apophysis expanded apically 15

15. Left paramere greatly elongate (Fig. 11C), apophysis 530–600 ηm (from outer margin of the base to tip of shaft); medial lobe of endosoma with 2–5 lobal sclerites (Fig. 22A) .... *Dicyphus tamaninii*
– Left paramere moderately elongate (Figs 9C–F, 10E), significantly smaller than *D. tamaninii* (Fig. 11C), apophysis 350–450 ηm; medial lobe of endosoma with 5–12 small lobal sclerites (Figs 12C, 14C–D) 6

16. Endosoma generally with 8–12 small lobal sclerites, rarely 6–7 (Fig. 12C); left paramere moderately elongated (Fig. 9C–F), apophysis 440–450 ηm.... *Dicyphus bolivari*
– Endosoma with five small lobal sclerites (Fig. 14C, D); left paramere elongate (Fig. 10E), apophysis <400 ηm .... *Dicyphus lindbergi*

17. Second antennal segment with proximal 2/3rd stramineous and small apical dark-brown annulation (Fig. 30); endosoma with asymmetrical pair of large lobal sclerites (Fig. 12A).... *Dicyphus alkannae*
– Second antennal segment stramineous medially (Fig. 3), always with basal and apical reddish brown or dark-brown annulations 18

18. Spatulate apex of left paramere with base of outer margin rounded (Fig. 11B); pair of endosomal lobal sclerites near symmetrical, weakly arcuate distally (Fig. 31C); most often with pale body, occasionally very dark; macropters and brachypters .... *Dicyphus stachydis*
– Spatulate apex of left paramere with base of outer margin crested (Figs 9B, 10B, 23D); endosomal lobal sclerites symmetrical to moderately asymmetrical (Figs 12B, G, 14A)....19

19. Spatulate apex of left paramere with a smooth crest (Fig. 23D). Pair of endosomal lobal sclerites straight and symmetrical (Fig. 12G).... *Dicyphus eckerleini*
– Spatulate apex of left paramere with a marked crest (Figs 9B, 10B). Pair of endosomal lobal sclerites arcuate and asymmetrical (Figs 12B, 14A)....20

20. Mostly pale species (Fig. 3); spatulate apex of the left paramere joining the neck of apophysis in an obtuse angle (Fig. 9B); pair of endosomal lobal sclerites moderately large, with right sclerite bended medially and significantly bigger than left (Fig. 12B) macropters only.... *Dicyphus argensis*
– Either pale or dark morphs (Fig. 3); left paramere apophysis angulate, apically, toothed (Fig. 10B); endosomal lobal sclerites elongate, asymmetrical and arcuate at the tip (Fig. 14A); macropters and brachypters .... *Dicyphus hyalinipennis*

females known; small species, brachypterous males 2.40–3.63 mm, brachypterous females 2.88–3.51 mm; AII 0.93× shorter than posterior width of pronotum in brachypters; AII with proximal 2/3 to 3/4 mostly stramineous, apex dark brown; eyes barely removed from anterior margin of pronotum; callosite region and pronotal disk of brachypters subequal in length; propleuron with broad transverse dark brown to fuscous band; clavus, exocorium and endocorium each with a faint red stripe (Fig. 30); apophysis of left paramere short and robust, distally expanded and non-serrated (Fig. 9A); endosoma with two asymmetrical enlarged straight lobal sclerites (Fig. 12A).

Description

Males. Macropters and brachypters (only later examined).

Coloration (Fig. 30): Dorsum mostly stramineous to pale brown, with contrasting dark-brown markings, sometimes with red/orange highlighting. *Head:* frons+vertex with a broad, X-shaped dark-brown marking, sometimes with orange highlighting; clypeus and maxillary plate mostly dark brown; postocular margins of head broadly dark brown to black and shiny; gula and bucculae pale brown. *Antennae:* AI mostly pale brown to stramineous brown, with subbasal brown band and small apical red band; AII proximal 2/3 to 3/4 mostly stramineous, apex dark brown. *Pronotum:* collar white to stramineous, translucent; calli stramineous to pale brown with dark brown highlighting; disk stramineous to pale brown, with humeral angles embrowned. *Thoracic pleura and sterna:* propleuron with transverse dark brown to fuscous band, ventral margin stramineous; metepisternum most often with anterior half dark brown, and posterior half stramineous, including evaporative area. *Mesoscutum:* mesoscutum medially pale brown to orange with lateral margins dark brown. *Scutellum:* lateral angles broadly stramineous with a broad brown stripe along midline, sometimes more broadly stramineous. *Hemelytra:* translucent, mostly pale brown, with red stripes and brown spotting at base of setae; clavus and corium mostly concolorous, with faint red stripe medially on clavus, endocorium and exocorium; apex of exocorium adjacent to costal fracture with prominent dark brown to reddish brown spot; apex of endocorium with obscure dark brown spot; cuneus mostly stramineous to pale brown with apical dark brown to reddish brown spot. *Abdomen:* venter either mostly dark brown to black and shiny, with pale lateral margins, or with banded colour pattern, with contrasting yellow and brown markings.

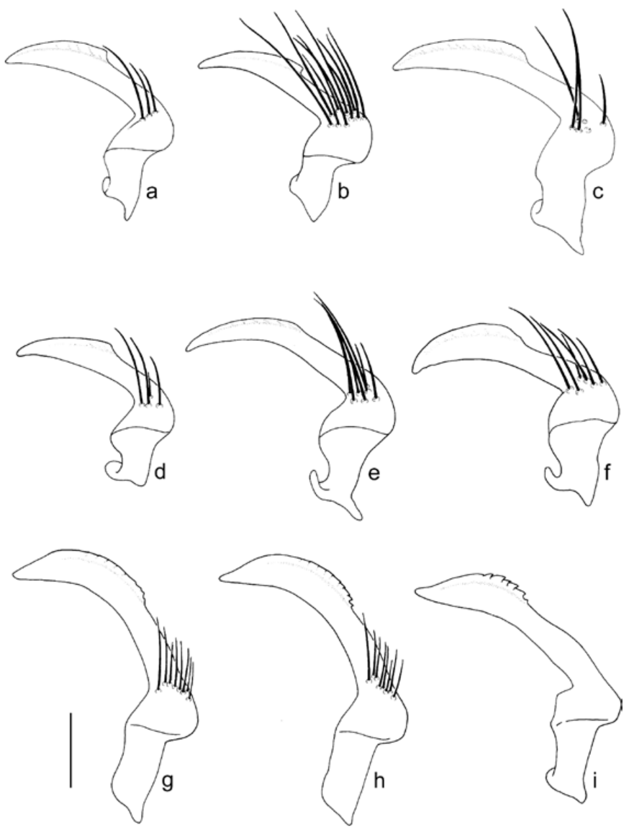

Figure 23. Left paramere. A, *D. caycumensis*. B, *D. cerastii*. C, *D. constrictus*. D, *D. eckerleini*. E, *D. epilobii*. F, *D. errans*. G–I, *D. escalerae*. Scale bar = 100 ηm.

Structure: Head: interocular distance 1.31–1.44× greater than eye width; eyes moderately large, removed from pronotum by distance greater than width of AII in brachypters. *Antennae:* AI short, 0.97–1.14× longer than interocular distance; AII 0.79–0.93× longer than posterior width of pronotum in brachypters. *Pronotum:* disk region 0.93–1.13× longer than the callosite region. *Male genitalia:* left paramere with robust and short apophysis, distantly expanded and non-serrated at outer margin (Fig. 9A); aedeagus with two well-developed endosomal lobes, each with a single elongate sclerite, lobal sclerites asymmetrical (Fig. 12A).

Females. Only brachypterous females known. Coloration, vestiture, texture and structure mostly as in brachypterous males. Interocular distance 1.19–1.38× greater than eye width; AI 0.95–1.12× longer than interocular distance; AII 0.81–0.86× longer than the posterior pronotal width; pronotal disk region 0.85–1.13× the length of the callosite region.

Measurements

See Table 4.

Distribution

Previous to our study, *Dicyphus alkannae* was only reported from Turkey (Seidenstucker, 1956; Kerzhner and Josifov, 1999); we have examined specimens of *D. alkannae* from Turkey and Iran (Fig. 32).

Host plants

Known from *Alkanna orientalis* (L.) Boiss (Boraginaceae) (Seidenstucker, 1956).

Remarks

Dicyphus alkannae was described by Seidenstucker (1956) for a series of specimens from Kayseri, Turkey. Wagner (1970) redescribed the species, assigned it to the nominotypical subgenus and documented its host plant. Although macropters have been documented for males of this species, we were only able to examine brachypters of both sexes, and as such our redescription refers to brachypters only; Wagner (1970) reported the body length range for

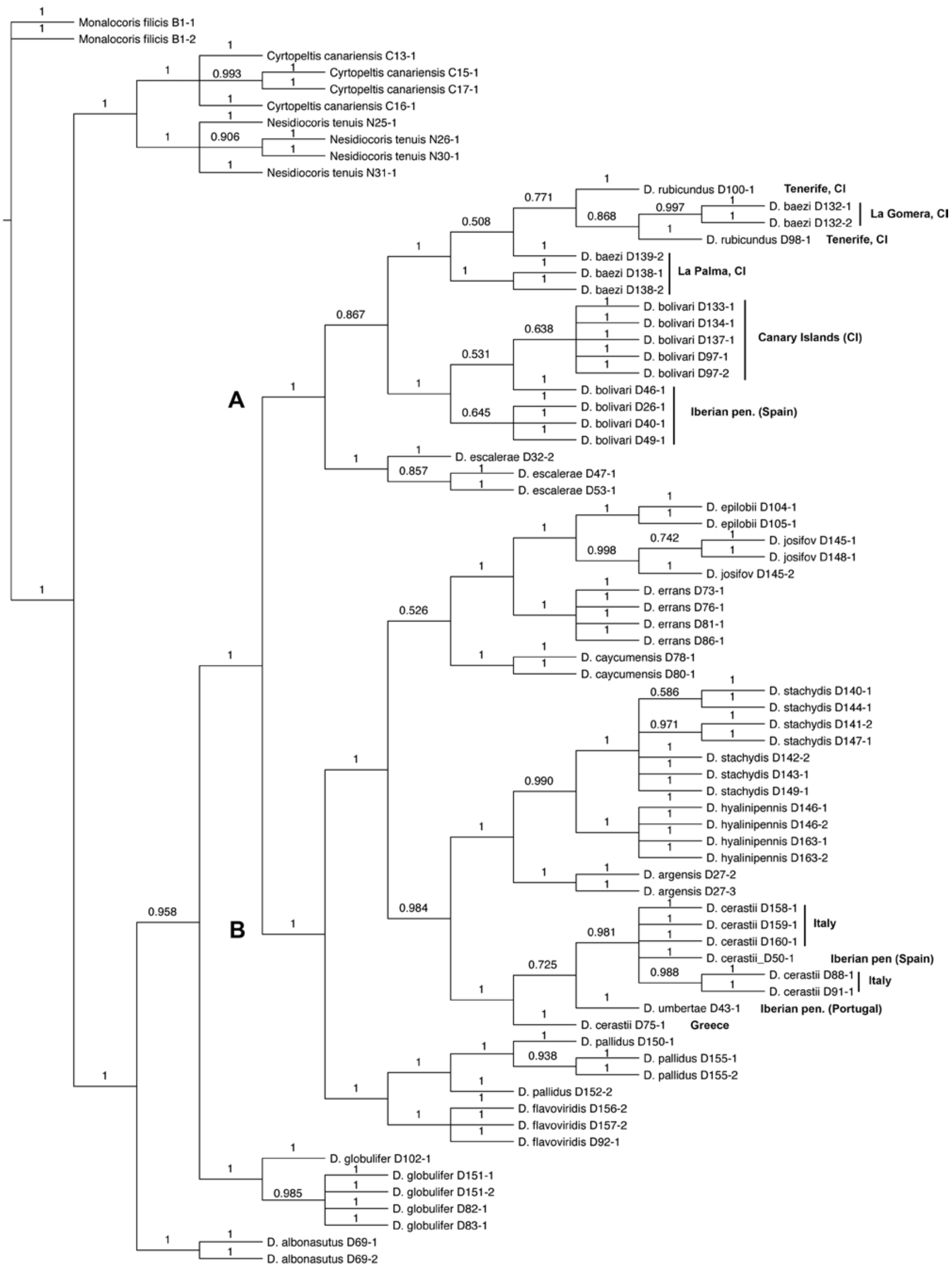

Figure 24. Molecular phylogeny of *Dicyphus* species inferred by Bayesian inference (Mr. Bayes 3.2.6) using sequence data of three mithocondrial genes (*COI*, 16S and 12S). Numbers above the branches are posterior probability (PP) values. Clade A includes all the species possessing fields of spinules and no or small endosomal lobal sclerites; clade B includes al the species with large endosomal lobal sclerites. The geographical origin is indicated whenever specimens from distant procedence were analysed for a given species.

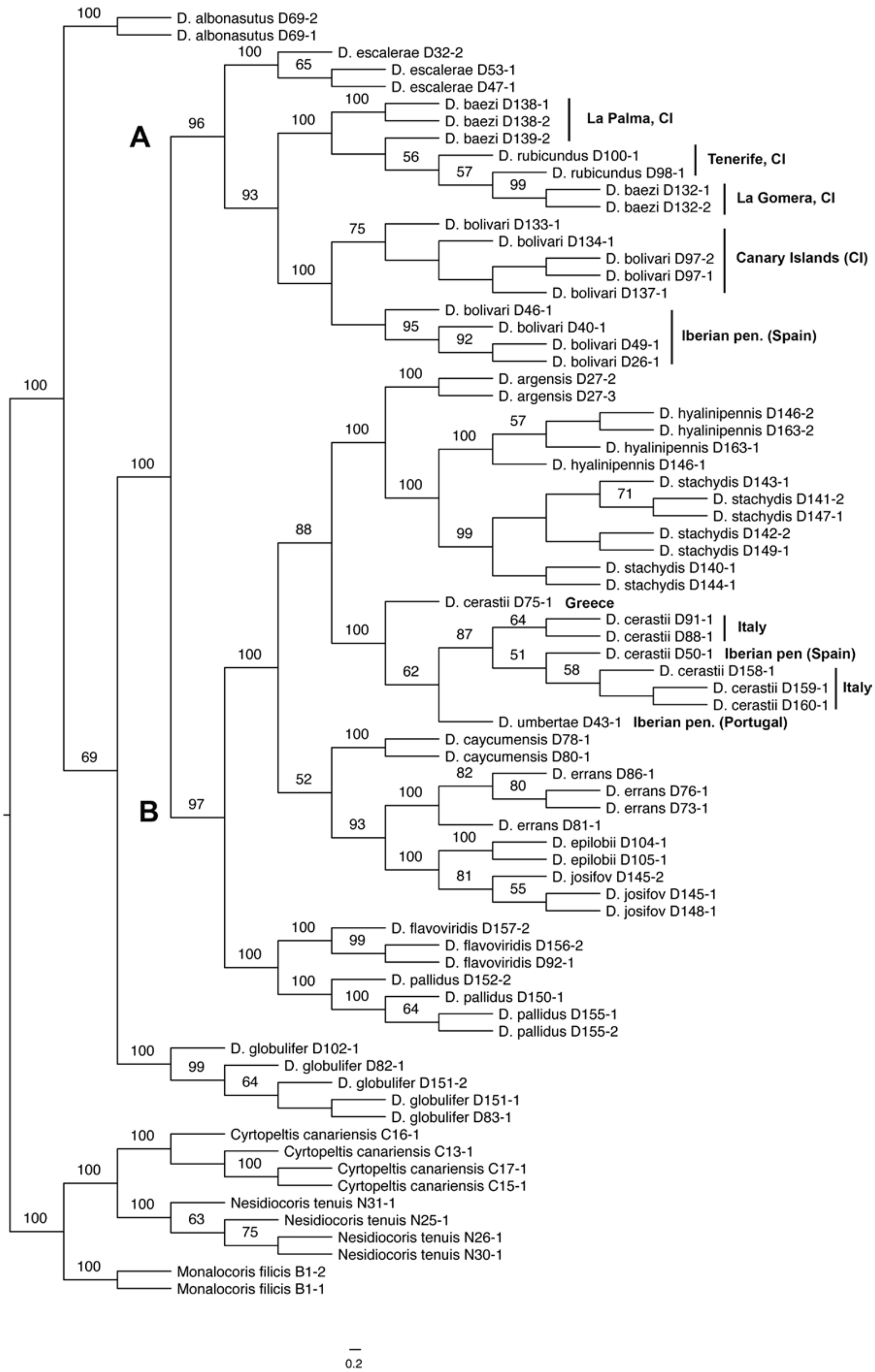

Figure 25. Molecular phylogeny of *Dicyphus* species inferred by maximum likelihood (RAxML) using sequence data of three mithocondrial genes (*COI*, 16S and 12S). Numbers above the branches are bootstrap (BS) values for 1000 replicates (BS > 50). Clade A includes all the species possessing fields of spinules and no or small endosomal lobal sclerites; clade B includes al the species with large endosomal lobal sclerites. The geographical origin is indicated whenever specimens from distant procedence were analysed for a given species.

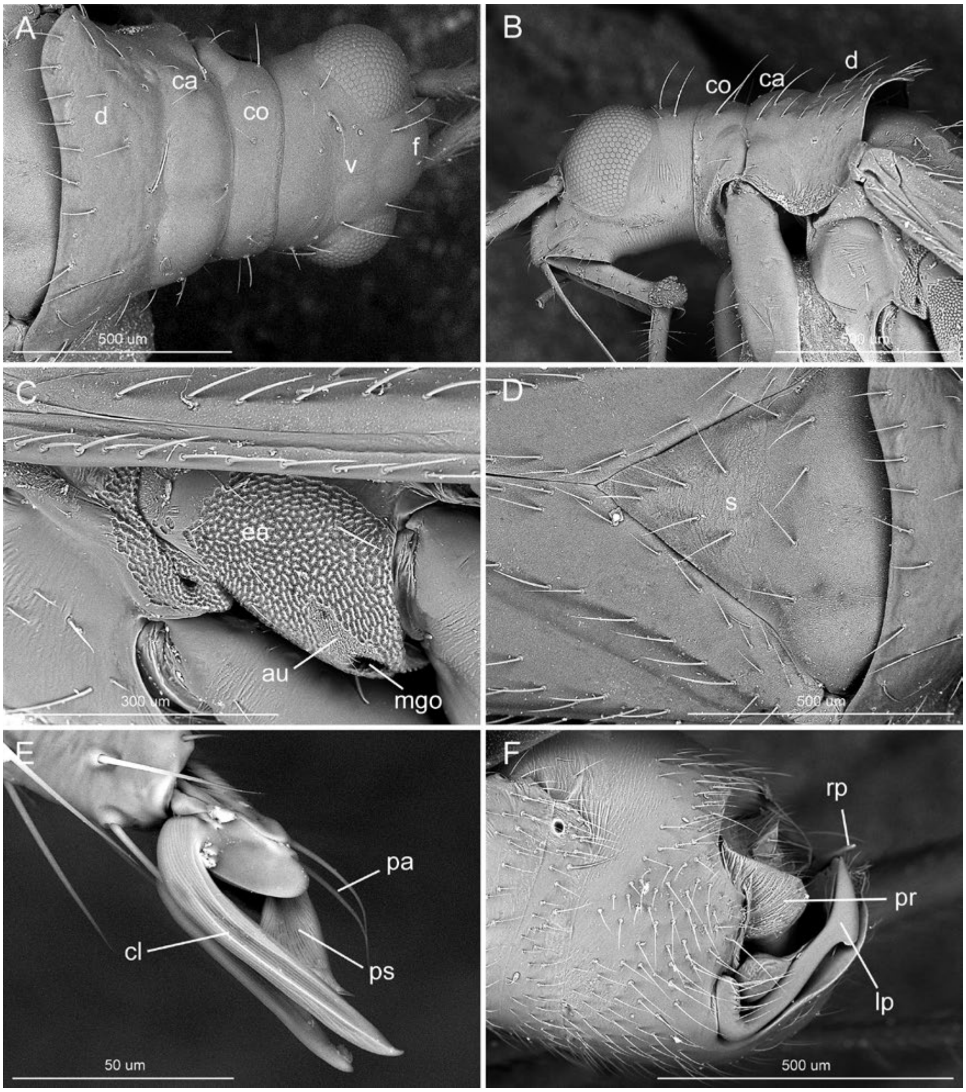

Figure 26. Scanning electron micrographs of *D. bolivari*. A, head and pronotum, dorsal view. B, head and pronotum, lateral view. C, external efferent system, metathoracic glands. D, scutelum (s). E, pretarsus, lateral view. F, genital segment, lateral view. Abbreviations: au, auricle; ca, calli; cl, claw; co, collar; d, disk; ea, evaporatory area; f, frons; lp, left paremere; mgo, metathoracic gland ostiole; pa, paraempodium; pr, proctiger; ps, pseudopulvilli; rp, right paramere; v, vertex.

macropterous males as 3.4–3.5 mm. Wagner (1970) also described the male genitalia, indicating that the lobal sclerites of the 'vesica' are elongate, and longer than the half-length of the aedeagus, and made reference to their asymmetry. We also found the lobal sclerites to be asymmetric, although we found the right varying in length.

Dicyphus alkannae is recognized primarily by characters of the male genitalia, particularly the shape and size of the endosomal lobal sclerites, with both being straight and the left-hand sclerite much larger than the right. There are numerous species that have genital similarities with *D. alkannae* (e.g. *D. argensis*, *D. caycumensis*, *D. cerastii*, *D. eckerleini*, *D. hyalinipennis* and *D. stachydis*), including a short and robust left paramere (Figs 9, 10, 11, 23) and a pair of large endosomal lobal sclerites (Figs 12, 14, 31). The endosomal lobal sclerites of *D. alkannae* are similar to those of *D. eckerleini* (the latter distributed in Turkey, the Lebanon and Iran), being straight, but in the latter species the pair of lobal sclerites are similar in size (Fig. 12A, G). In addition, *D. alkannae* has the AI more stramineous with a red apical annulation (vs. more uniformly red in *D. eckerleini*), the AII is shorter than the posterior width of the pronotum (vs. longer), and the hemelytra have faint red stripes on the clavus and corium (Fig. 30).

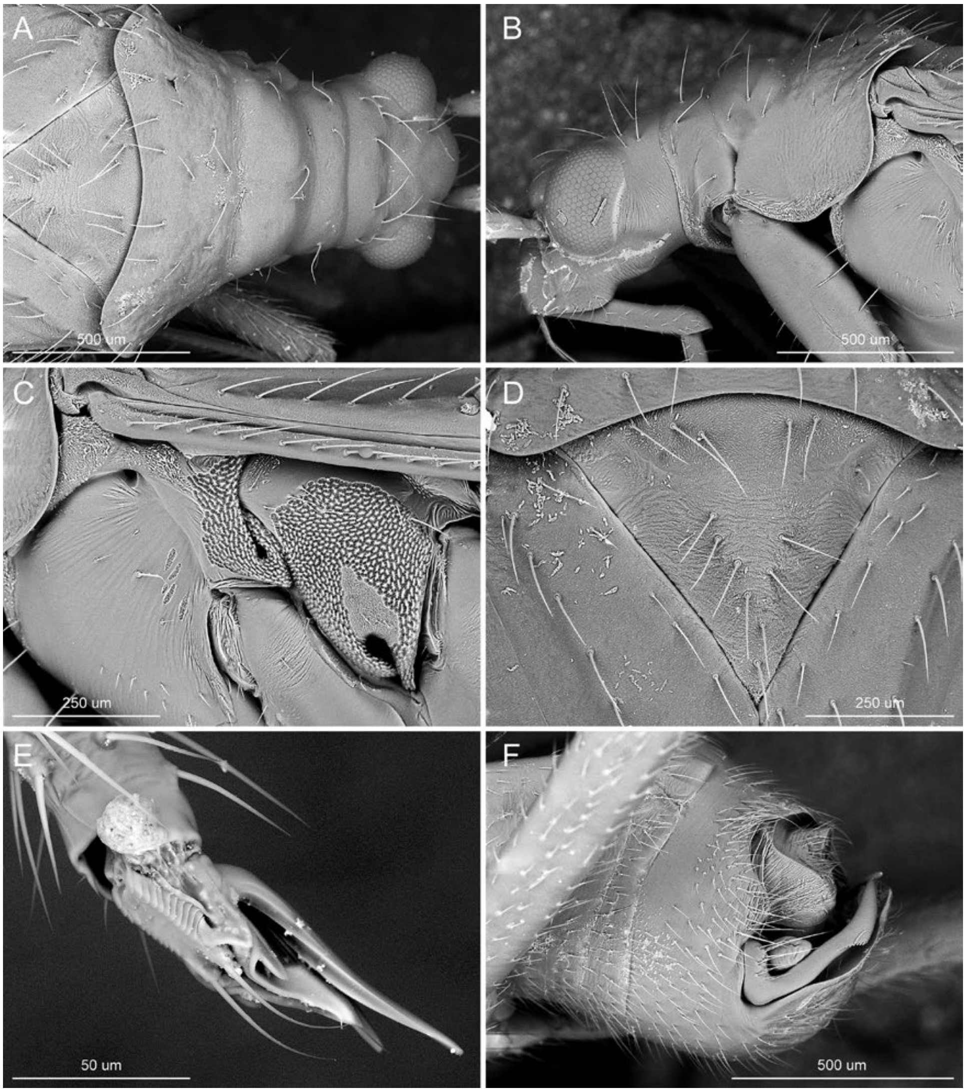

Figure 27. Scanning electron micrographs of *D. rubicundus*. A, head and pronotum dorsal view, with well-defined collar, and callosite and disk region. B, head and pronotum, lateral view. C, external efferent system, metathoracic glands. D, scutelum. E, pretarsus in lateral view, with straight paraempodium below the claws. F, genital segment in lateral view with proctiger, left paramere and the small right paramere visible.

DICYPHUS ARGENSIS SP. NOV.

(FIGS 3, 9B, 12B, 32)

LSID: urn:lsid:zoobank. org:act:673D1FD9-1D63-43C0-A3AF-284996836ADD

Dicyphus cerastii: Sanchez *et al.*, 2006: 288 (misidentification).

Specimens examined

Holotype, Spain: Andalucía, Huelva, Ayamonte, 37.21992ºN 7.38278ºW, 2 Jun 2006, ex. *Solanum lycopersicum* L. (Solanaceae), Sanchez, Martínez & La Spina, ♂ (IMIDA_ENT 00000660) (IMIDA). *Paratypes:* 12♀♀ (IMIDA_ENT 00000662-IMIDA_ENT 00000673), 12♂♂ (IMIDA_ENT 00000649-IMIDA_ENT 00000649, IMIDA_ENT 00000661) (IMIDA). Málaga: Nerja, 36.75808ºN 3.84808ºW, 20 m, 31 May 2006, Sanchez, Martínez & La Spina, 15 adults (♂♂ and ♀♀) (D26), ex. *Cucurbita maxima* Duchesne (Cucurbitaceae) (IMIDA). Murcia: Calasparra, 38.22597ºN 1.69862ºW, 340 m, 21 August 2002, Sanchez, Martínez & La Spina, 26♀♀, 23♂♂ (IMIDA_ENT 00000486-IMIDA_ENT 00000534), ex. *Cucurbita maxima* (IMIDA). Moratalla: Benizar, 38.27489ºN 1.98497ºW, 25 Sep 2002, Sanchez, 13♀♀, 7♂♂ (IMIDA_ENT 00000603-IMIDA_ENT 00000622), ex. *Cucurbita maxima* (IMIDA). Cehegín: Sta. Barbara-Argos, 38.10878ºN 1.78350ºW, 10 Jul

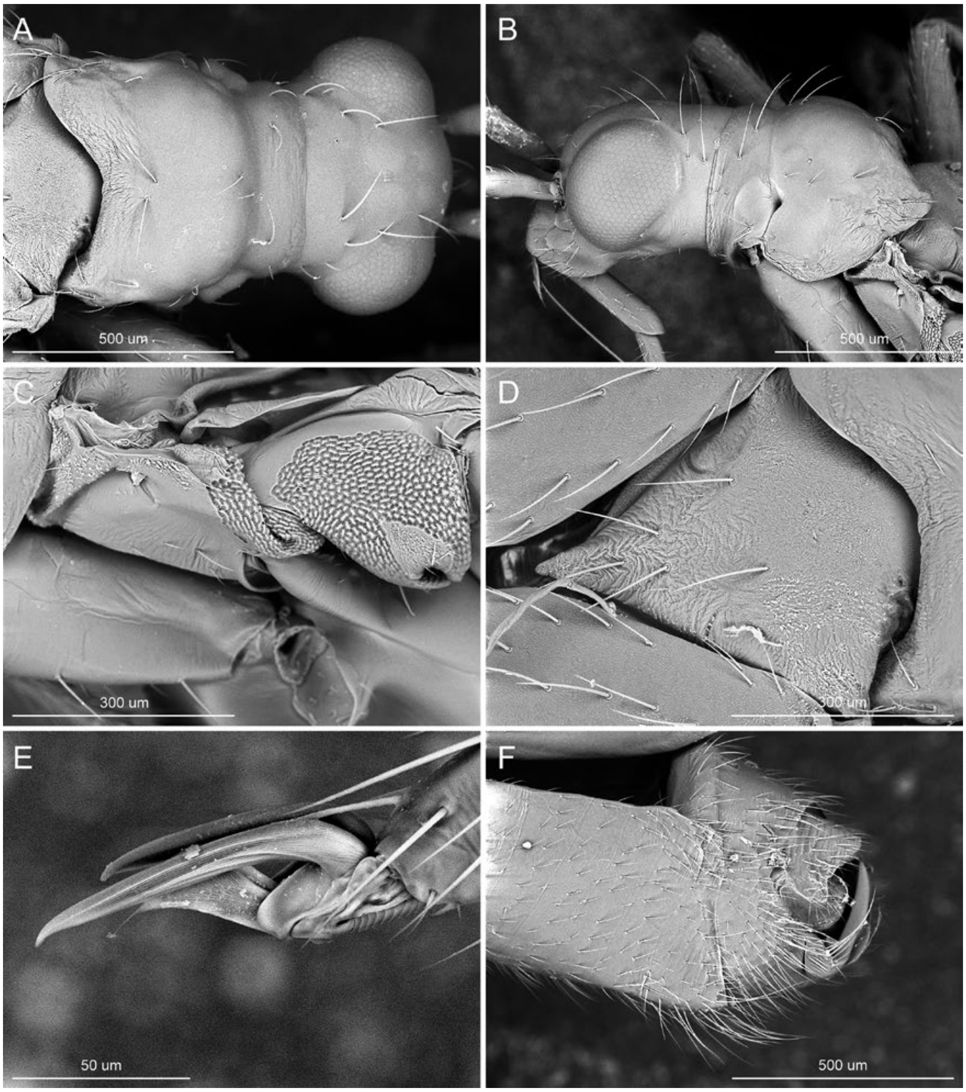

Figure 28. Scanning electron micrographs of *D. stachydis* (brachypter). A, head and pronotum dorsal view, with well-defined collar and calli, and reduced disk region. B, head and pronotum, lateral view. C, external efferent system, metathoracic glands. D, scutelum. E, pretarsus, lateral view. F, genital segment in lateral view with prominent proctiger and left paramere.

2002, Sanchez, 11♀♀, 14♂♂ (IMIDA_ENT 00000623-IMIDA_ENT 00000648), ex. *Cucurbita maxima* (IMIDA). Lorca: 37.64362°N 1.69439°W, 19 Sep 2002, Sanchez, 16♀♀, 12♂♂ (IMIDA_ENT 00000575-IMIDA_ENT 00000602), ex. *Cucurbita maxima* (IMIDA).

Etymology

This species is named after the Argos River in the northwest of Murcia Region, Spain.

Diagnosis

Dicyphus argensis is recognized by the following combination of characters: macropterous males (Fig. 3) and females only; body length, males 3.23–3.91 mm, females 3.82–3.90 mm; pale species; clypeus mostly stramineous; AI mostly pale with subbasal and subapical annulations; AII mostly stramineous with light to dark-brown annulation on distal 1/4 and faint light brown annulation at the base; propleuron with transverse dark-brown band; pygophore with large dark brown spot posteroventrally; left paramere with robust and short smoothly arcuate apophysis (Fig. 9B); aedeagus with three endosomal lobes and a pair of large arcuate lobal sclerites, slightly asymmetrical (Fig. 12B).

Description

Males. Macropters only.

Coloration (Fig. 3): Dorsum mostly pale stramineous to light brown, with wings translucent, with contrasting brown markings, sometimes with minor red/orange highlighting. *Head:* mostly stramineous to pale brown; frons+vertex with a broad, X-shaped

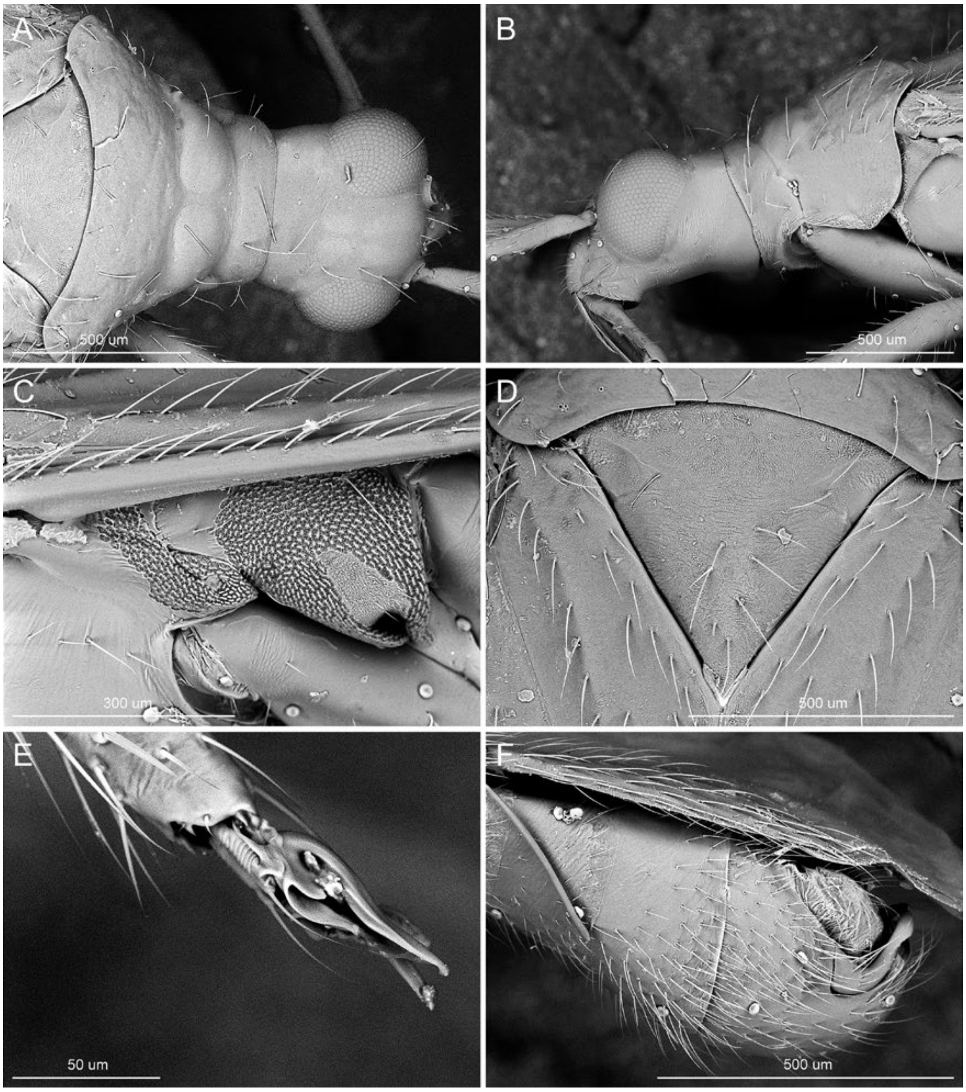

Figure 29. Scanning electron micrographs of *D. hyalinipennis*. A, head and pronotum, dorsal view. B, head and pronotum, lateral view. C, external efferent system, metathoracic glands. D, scutellum. E, pretarsus, lateral view. F, genital segment, lateral view.

dark-brown marking; clypeus mostly stramineous, with dark-brown markings laterally; maxillary plate stramineous to light brown; postocular margins of head broadly dark brown and shiny, extending dorsally towards gula; gula and bucculae stramineous to light brown. *Antennae:* AI medially stramineous to pale brown, with subbasal darker brown band and subapical reddish band, sometimes subapically without red highlighting; AII distinctly stramineous medially, with faint brown subbasal band and light to dark-brown annulation on distal 1/4. *Pronotum:* collar white to stramineous, translucent; calli mostly stramineous, often with minor brown markings adjacent to midline and laterally; disk stramineous to white, translucent, humeral angles narrowly darker brown. *Thoracic pleura and sterna:* propleuron with distinct transverse medium to dark-brown band, ventral margin white to stramineous; mesobasisternum uniformly dark brown, sometimes with red highlighting; mesepimeron uniformly white to stramineous, dull; metepisternum most often bicoloured, anteriorly and posteriorly stramineous, with dull-brown band medially; metepimeron stramineous. *Mesoscutum:* orange with light to dark-brown markings. *Scutellum:* lateral angles broadly stramineous pale with a broad brown stripe along midline. *Hemelytra:* translucent, mostly very light brown, usually with three small brown spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; sometimes with red

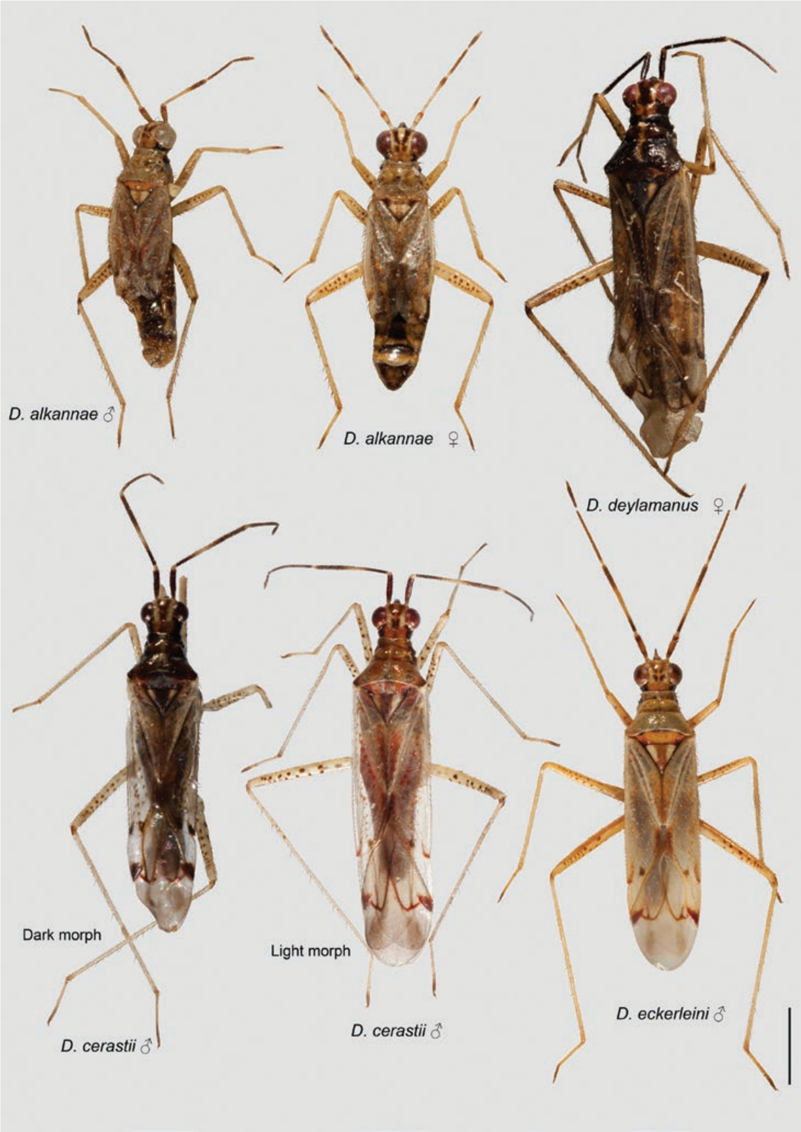

Figure 30. Habitus of *D. alkannae* (male and female), *D. deylamanus*, *D. cerastii* (dark and light morph) and *D. eckerleini*. Scale bar = 1 mm.

highlighting, mostly on clavus and medial margin of endocorium, rarely with red on tip of cuneus and membrane veins. *Abdomen:* venter mostly stramineous, with SII and SIII consistently brown; pygophore mostly stramineous with large brown spot ventrally.

Structure: Head: eyes moderately large, removed from pronotum by distance greater than width of AII; interocular distance 1.15–1.33× greater than eye width. *Antennae:* AI short, 1.34–1.57× longer than interocular distance; AII 1.17–1.25× longer than posterior width of pronotum Disk region 1.20–1.48× longer than the callosite region. *Male genitalia:* left paramere with robust and short apophysis, with outer margin of apex spatulate and inner margin smoothly arcuate (Fig. 9B); aedeagus with three well-developed endosomal lobes, pair of arcuate moderately sized lobal sclerites, slightly asymmetrical (Fig. 12B).

Females. Macropters only. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.12–1.38× greater than eye width. *Antennae:* AI 1.23–1.42× longer than interocular distance; AII 1.01–1.08× longer that the posterior pronotal width. *Pronotum:* disk 1.26–1.47× longer than the callosite region.

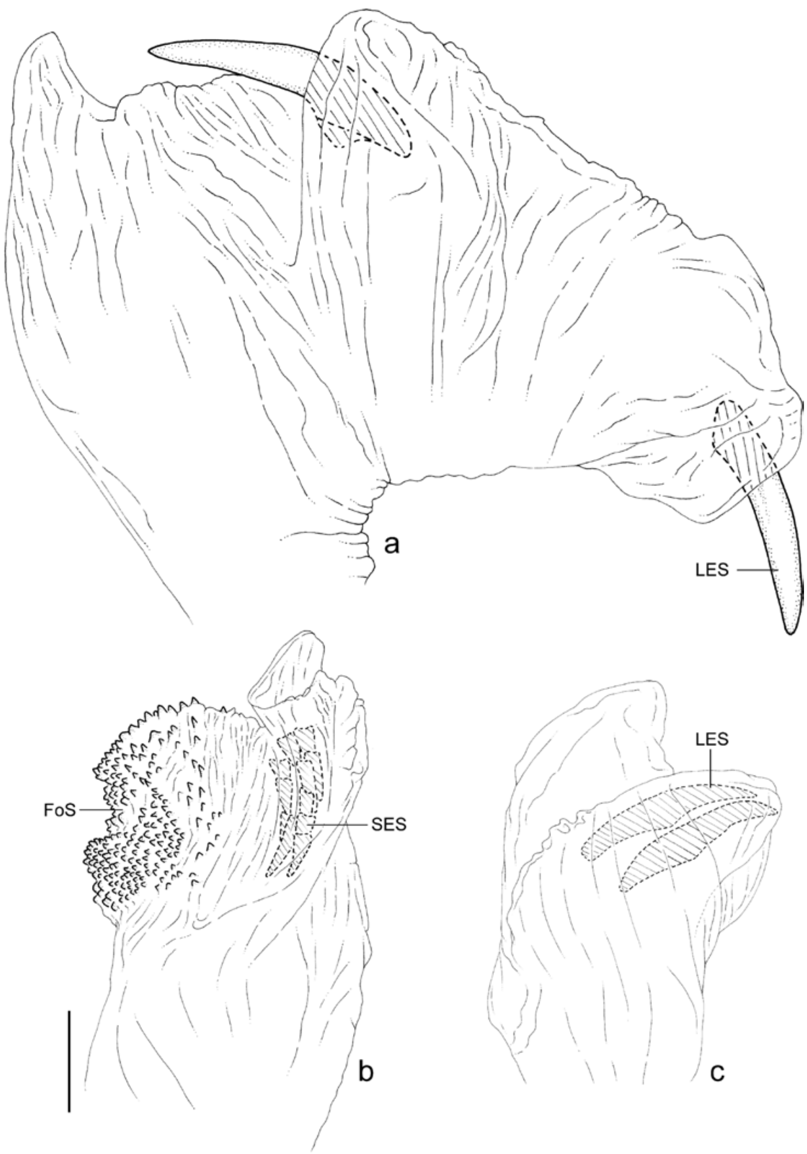

Figure 31. Endosoma. A, *D. pallidus*. B, *D. rubicundus*. C, *D. stachydis*. Scale bar = 100 ηm. Abbreviations: FoS, field of spinules; LES, large endosomal sclerites; SES, small endosomal sclerites.

Measurements
See Table 4.

Distribution
Restricted to southern Spain (Fig. 32).

Host plants
Dicyphus argensis has been found on *Cucurbita maxima* Duchesne (Cucurbitaceae), *Hyosciamus albus* L. (Scrophulariaceae), *Ononis natrix* L. (Fabaceae), *Solanum lycopersicum* L. (Solanaceae) and *Withania frutescens* (L.) Pauquy (Solanaceae).

Remarks
Sanchez *et al.* (2006) redescribed a series of specimens from Spain as *Dicyphus cerastii*, including illustrations of the male and female genitalia. In this same work the authors described a new species of *Dicyphus* from Portugal, naming it *D. umbertae*. Subsequent to this work we were able to examine in detail the type specimens of *D. cerastii*, held in the Zoological Museum, Helsinki, and found that *D. umbertae* is a synonym of *D. cerastii*, and that the material identified as *D. cerastii* were misidentified and represent a new species, which we describe as a new species herein as *D. argensis*.

Table 4. *Dicyphus* (*Dicyphus*) species, body measurements. S, sex (F, female; M, male); M, morph (B, brachypter; M, macropter); N, number of individuals; TL = total length, HL = head length, HW = head width, EW = eye width, IO = interocular distance, AI, AII, AIII, AIV = length of antennal segments I, II, III and IV, respectively, PL = pronotal length, PW = pronotal width, SW = scutellum width, DRL = disk region length, CRL =length of callosite region, HemL =hemelytral length, CHL = clypeus-hemelytral length, TIBL = tibial length.

				Body	Head				Antenna			
Species	S	M	*N*	TL	HL	HW	EW	IO	AI	AII	AIII	AIV
D. alkannae	F	B	7	3.229 ± 0.075	0.527 ± 0.017	0.673 ± 0.014	0.206 ± 0.005	0.261 ± 0.004	0.271 ± 0.009	0.624 ± 0.009	0.431 ± 0.014	0.302 ± 0.010
	M	B	4	3.075 ± 0.360	0.494 ± 0.019	0.620 ± 0.016	0.185 ± 0.006	0.249 ± 0.005	0.259 ± 0.014	0.602 ± 0.026	0.405 ± 0.009	0.284 ± 0.008
D. argensis	F	M	4	3.866 ± 0.018	0.591 ± 0.011	0.637 ± 0.012	0.197 ± 0.007	0.242 ± 0.004	0.328 ± 0.009	0.965 ± 0.016	0.654 ± 0.021	0.328 ± 0.005
	M	M	5	3.596 ± 0.138	0.572 ± 0.017	0.616 ± 0.010	0.193 ± 0.003	0.231 ± 0.006	0.329 ± 0.009	1.020 ± 0.036	0.615 ± 0.021	0.323 ± 0.004
D. bolivari	F	B	11	2.958 ± 0.054	0.594 ± 0.010	0.621 ± 0.004	0.177 ± 0.002	0.266 ± 0.003	0.344 ± 0.006	0.895 ± 0.019	0.558 ± 0.009	0.313 ± 0.011
		M	31	4.140 ± 0.042	0.595 ± 0.005	0.624 ± 0.005	0.179 ± 0.002	0.266 ± 0.003	0.368 ± 0.005	0.988 ± 0.014	0.594 ± 0.008	0.309 ± 0.007
	M	B	10	2.629 ± 0.052	0.562 ± 0.007	0.578 ± 0.005	0.169 ± 0.003	0.240 ± 0.004	0.323 ± 0.004	0.886 ± 0.013	0.541 ± 0.012	0.299 ± 0.005
		M	44	3.910 ± 0.024	0.557 ± 0.004	0.598 ± 0.003	0.175 ± 0.001	0.248 ± 0.001	0.361 ± 0.004	1.045 ± 0.011	0.589 ± 0.008	0.307 ± 0.004
D. caycumensis	F	M	15	3.839 ± 0.044	0.565 ± 0.008	0.648 ± 0.003	0.196 ± 0.002	0.256 ± 0.003	0.335 ± 0.003	0.927 ± 0.010	0.622 ± 0.009	0.293 ± 0.007
	M	M	5	3.618 ± 0.073	0.502 ± 0.010	0.597 ± 0.002	0.184 ± 0.003	0.228 ± 0.005	0.337 ± 0.009	0.981 ± 0.023	0.629 ± 0.016	0.314 ± 0.008
D. cerastii	F	M	18	4.475 ± 0.052	0.643 ± 0.008	0.692 ± 0.004	0.215 ± 0.001	0.263 ± 0.004	0.437 ± 0.007	1.041 ± 0.017	0.731 ± 0.020	0.332 ± 0.007
	M	M	18	4.300 ± 0.044	0.594 ± 0.007	0.648 ± 0.004	0.208 ± 0.002	0.232 ± 0.002	0.444 ± 0.006	1.172 ± 0.008	0.727 ± 0.017	0.329 ± 0.005
D. constrictus	F	B	11	3.866 ± 0.117	0.698 ± 0.010	0.757 ± 0.005	0.241 ± 0.002	0.276 ± 0.004	0.511 ± 0.006	1.292 ± 0.012	0.996 ± 0.021	0.538 ± 0.016
		M	3	4.789 ± 0.012	0.657 ± 0.023	0.734 ± 0.018	0.232 ± 0.008	0.271 ± 0.003	0.516 ± 0.008	1.287 ± 0.015	0.981 ± 0.021	0.441 ± 0.049
	M	M	13	4.607 ± 0.071	0.621 ± 0.008	0.706 ± 0.005	0.229 ± 0.002	0.248 ± 0.002	0.511 ± 0.007	1.540 ± 0.024	0.987 ± 0.022	0.458 ± 0.013
D. deylamanus	F	M	1	4.950	0.669	0.703	0.214	0.275	0.495	1.246	0.902	0.402
D. eckerleini	F	M	1	4.190	0.617	0.624	0.182	0.260	0.329	0.796	0.721	0.343
	M	M	2	4.163 ± 0.022	0.537 ± 0.014	0.630 ± 0.013	0.196 ± 0.006	0.239 ± 0.001	0.361 ± 0.017	0.975 ± 0.041	0.733 ± 0.069	0.361 ± 0.004
D. epilobii	F	M	28	4.826 ± 0.044	0.700 ± 0.007	0.712 ± 0.004	0.210 ± 0.002	0.293 ± 0.003	0.500 ± 0.007	1.259 ± 0.012	0.818 ± 0.013	0.390 ± 0.008
	M	M	28	4.560 ± 0.041	0.646 ± 0.006	0.661 ± 0.004	0.201 ± 0.002	0.260 ± 0.002	0.497 ± 0.006	1.454 ± 0.018	0.825 ± 0.018	0.372 ± 0.008
D. errans	F	M	21	4.798 ± 0.042	0.659 ± 0.011	0.696 ± 0.004	0.217 ± 0.002	0.261 ± 0.002	0.499 ± 0.007	1.264 ± 0.027	0.946 ± 0.029	0.444 ± 0.017
	M	M	11	4.915 ± 0.093	0.625 ± 0.009	0.671 ± 0.005	0.216 ± 0.002	0.239 ± 0.003	0.555 ± 0.010	1.606 ± 0.033	1.023 ± 0.027	0.453 ± 0.009
D. escalerae	F	B	6	3.007 ± 0.072	0.589 ± 0.006	0.680 ± 0.012	0.206 ± 0.005	0.268 ± 0.006	0.398 ± 0.011	0.931 ± 0.030	0.549 ± 0.018	0.319 ± 0.016
		M	11	4.039 ± 0.045	0.602 ± 0.008	0.678 ± 0.006	0.205 ± 0.002	0.269 ± 0.004	0.413 ± 0.007	1.034 ± 0.020	0.581 ± 0.009	0.316 ± 0.006
	M	B	1	2.499	0.518	0.590	0.178	0.234	0.348	0.823	0.490	0.291
		M	10	3.725 ± 0.059	0.537 ± 0.008	0.634 ± 0.006	0.196 ± 0.002	0.241 ± 0.003	0.395 ± 0.007	1.02 ± 0.02	0.551 ± 0.007	0.295 ± 0.012
D. flavoviridis	F	B	10	3.753 ± 0.052	0.782 ± 0.009	0.745 ± 0.004	0.230 ± 0.002	0.286 ± 0.004	0.520 ± 0.009	1.356 ± 0.013	0.970 ± 0.012	0.508 ± 0.008
	M	B	12	3.826 ± 0.040	0.734 ± 0.007	0.719 ± 0.003	0.223 ± 0.002	0.274 ± 0.002	0.524 ± 0.007	1.415 ± 0.02	0.949 ± 0.018	0.514 ± 0.010
		M	1	5.054	0.709	0.723	0.227	0.269	0.516	1.467	0.959	–
D. hyalinipennis	F	B	3	3.322 ± 0.087	0.626 ± 0.022	0.694 ± 0.003	0.203 ± 0.001	0.289 ± 0.001	0.384 ± 0.01	0.933 ± 0.016	0.685 ± 0.032	0.356
		M	7	4.595 ± 0.045	0.603 ± 0.022	0.713 ± 0.006	0.210 ± 0.003	0.291 ± 0.003	0.378 ± 0.007	1.005 ± 0.015	0.660 ± 0.024	0.351 ± 0.005
	M	B	1	2.935	0.524	0.609	0.171	0.267	0.359	0.947	0.543	0.342
		M	11	4.397 ± 0.048	0.602 ± 0.011	0.684 ± 0.005	0.204 ± 0.002	0.276 ± 0.006	0.392 ± 0.006	1.051 ± 0.021	0.661 ± 0.016	0.355 ± 0.007
D. josifovi	F	M	10	4.715 ± 0.035	0.613 ± 0.022	0.713 ± 0.004	0.225 ± 0.002	0.264 ± 0.002	0.440 ± 0.016	1.191 ± 0.018	0.753 ± 0.016	0.350 ± 0.011
	M	M	6	4.446 ± 0.023	0.611 ± 0.009	0.670 ± 0.007	0.212 ± 0.002	0.246 ± 0.005	0.519 ± 0.010	1.506 ± 0.020	0.831 ± 0.016	0.391 ± 0.013
D. lindbergi	F	B	1	2.854	0.555	0.622	0.183	0.255	0.351	0.826	–	–
		M	5	3.984 ± 0.120	0.605 ± 0.02	0.644 ± 0.016	0.193 ± 0.006	0.258 ± 0.008	0.395 ± 0.014	1.033 ± 0.036	0.629	0.277
	M	M	6	4.022 ± 0.173	0.573 ± 0.015	0.614 ± 0.009	0.183 ± 0.004	0.247 ± 0.004	0.379 ± 0.010	1.068 ± 0.043	0.623 ± 0.007	0.296 ± 0.011
D. pallidus	F	B	6	5.037 ± 0.203	0.842 ± 0.013	0.805 ± 0.008	0.245 ± 0.003	0.315 ± 0.003	0.619 ± 0.015	1.782 ± 0.023	1.297 ± 0.029	0.571 ± 0.033

Table 4. *Continued*

				Body	Head				Antenna			
Species	S	M	*N*	TL	HL	HW	EW	IO	AI	AII	AIII	AIV
		M	4	5.975 ± 0.041	0.874 ± 0.024	0.802 ± 0.009	0.241 ± 0.005	0.320 ± 0.003	0.589 ± 0.027	1.762 ± 0.041	1.307 ± 0.075	0.648
	M	B	5	4.649 ± 0.162	0.766 ± 0.009	0.778 ± 0.010	0.239 ± 0.004	0.299 ± 0.004	0.646 ± 0.012	1.913 ± 0.030	1.299 ± 0.032	0.525 ± 0.024
		M	12	5.579 ± 0.058	0.776 ± 0.012	0.768 ± 0.003	0.235 ± 0.002	0.298 ± 0.003	0.660 ± 0.009	1.935 ± 0.014	1.307 ± 0.025	0.549 ± 0.018
D. poneli	F	M	2	4.181 ± 0.153	0.637 ± 0.021	0.618 ± 0.037	0.164 ± 0.015	0.290 ± 0.007	0.396 ± 0.012	0.963 ± 0.075	0.494	0.297
	M	M	1	4.537	0.552	0.608	0.157	0.295	0.405	1.074	0.549	-
D. rubicundus	F	B	3	2.910 ± 0.144	0.586 ± 0.022	0.639 ± 0.006	0.183 ± 0.003	0.274 ± 0.010	0.401 ± 0.006	0.975 ± 0.013	0.645 ± 0.025	0.362 ± 0.005
		M	4	4.367 ± 0.119	0.599 ± 0.011	0.632 ± 0.005	0.177 ± 0.003	0.278 ± 0.005	0.398 ± 0.001	1.006 ± 0.008	0.641 ± 0.013	0.329 ± 0.019
	M	B	7	2.906 ± 0.038	0.583 ± 0.005	0.616 ± 0.006	0.170 ± 0.003	0.276 ± 0.002	0.404 ± 0.004	1.096 ± 0.013	0.651 ± 0.016	0.376 ± 0.010
		M	6	4.380 ± 0.029	0.595 ± 0.015	0.621 ± 0.006	0.174 ± 0.002	0.273 ± 0.001	0.422 ± 0.008	1.157 ± 0.021	0.651 ± 0.024	0.353 ± 0.008
D. stachydis	F	B	63	3.234 ± 0.031	0.601 ± 0.006	0.682 ± 0.003	0.209 ± 0.001	0.263 ± 0.001	0.402 ± 0.003	0.973 ± 0.006	0.731 ± 0.007	0.419 ± 0.006
		M	6	4.453 ± 0.084	0.597 ± 0.008	0.700 ± 0.004	0.205 ± 0.004	0.289 ± 0.009	0.418 ± 0.006	0.981 ± 0.011	0.704 ± 0.017	0.374 ± 0.015
	M	B	46	3.037 ± 0.039	0.584 ± 0.004	0.656 ± 0.003	0.201 ± 0.001	0.253 ± 0.003	0.406 ± 0.003	1.008 ± 0.006	0.709 ± 0.008	0.414 ± 0.007
		M	11	4.301 ± 0.052	0.585 ± 0.009	0.670 ± 0.006	0.201 ± 0.002	0.267 ± 0.006	0.428 ± 0.008	1.080 ± 0.014	0.706 ± 0.019	0.398 ± 0.024
D. tamaninii	F	M	3	4.396 ± 0.112	0.616 ± 0.016	0.679 ± 0.010	0.203 ± 0.005	0.274 ± 0.004	0.382 ± 0.011	1.015 ± 0.043	0.555 ± 0.031	0.282 ± 0.011
	M	M	6	4.081 ± 0.075	0.550 ± 0.014	0.619 ± 0.009	0.183 ± 0.002	0.253 ± 0.006	0.367 ± 0.017	1.010 ± 0.023	0.555 ± 0.018	0.288 ± 0.019
D. tumidifrons	F	B	1	2.349	0.448	0.528	0.102	0.324	0.257	0.573	0.360	0.254
		M	1	3.183	0.486	0.538	0.106	0.326	0.297	0.609	0.384	0.236
	M	B	1	2.044	0.471	0.525	0.107	0.311	0.299	0.644	0.36	0.256
		M	2	2.999 ± 0.093	0.487 ± 0.012	0.515 ± 0.012	0.103 ± 0.001	0.309 ± 0.014	0.253 ± 0.03	0.614 ± 0.014	0.376 ± 0.046	0.245 ± 0.006

				Thorax					Hemelytra		Head-Hem.	Legs
Species	S	M	*N*	PL	PW	SL	DRL	CRL	HemL	CL	CHL	TIBL
D. alkannae	F	B	7	0.516 ± 0.016	0.755 ± 0.008	0.251 ± 0.007	0.194 ± 0.005	0.194 ± 0.009	1.718 ± 0.022	0.326 ± 0.010	0.960 ± 0.021	1.524 ± 0.023
	M	B	4	0.468 ± 0.030	0.700 ± 0.021	0.235 ± 0.015	0.182 ± 0.012	0.182 ± 0.017	1.535 ± 0.051	0.307 ± 0.031	0.917 ± 0.051	1.363 ± 0.038
D. argensis	F	M	4	0.626 ± 0.012	0.920 ± 0.011	0.345 ± 0.009	0.275 ± 0.008	0.199 ± 0.001	3.020 ± 0.048	0.544 ± 0.007	1.061 ± 0.004	2.230 ± 0.045
	M	M	5	0.582 ± 0.014	0.834 ± 0.023	0.322 ± 0.008	0.253 ± 0.007	0.188 ± 0.005	2.881 ± 0.069	0.558 ± 0.024	1.035 ± 0.034	2.243 ± 0.073
D. bolivari	F	B	11	0.602 ± 0.007	0.795 ± 0.012	0.292 ± 0.005	0.210 ± 0.002	0.219 ± 0.003	1.913 ± 0.042	0.289 ± 0.012	1.072 ± 0.018	2.080 ± 0.041
		M	31	0.687 ± 0.008	0.963 ± 0.011	0.365 ± 0.005	0.279 ± 0.004	0.211 ± 0.002	3.188 ± 0.031	0.591 ± 0.006	1.124 ± 0.011	2.267 ± 0.028
	M	B	10	0.560 ± 0.007	0.724 ± 0.006	0.279 ± 0.006	0.185 ± 0.005	0.207 ± 0.006	1.706 ± 0.042	0.253 ± 0.010	0.987 ± 0.010	2.024 ± 0.024
		M	44	0.627 ± 0.004	0.881 ± 0.008	0.338 ± 0.003	0.250 ± 0.002	0.203 ± 0.001	3.027 ± 0.017	0.584 ± 0.005	1.032 ± 0.011	2.284 ± 0.018
D. caycumensis	F	M	15	0.622 ± 0.006	1.020 ± 0.011	0.370 ± 0.005	0.289 ± 0.005	0.181 ± 0.003	3.041 ± 0.024	0.549 ± 0.004	1.057 ± 0.007	2.260 ± 0.047
	M	M	5	0.536 ± 0.008	0.876 ± 0.019	0.332 ± 0.007	0.232 ± 0.007	0.165 ± 0.006	2.839 ± 0.046	0.543 ± 0.014	0.917 ± 0.019	1.992 ± 0.137
D. cerastii	F	M	18	0.742 ± 0.011	1.035 ± 0.015	0.402 ± 0.003	0.308 ± 0.006	0.208 ± 0.003	3.406 ± 0.033	0.618 ± 0.009	1.241 ± 0.016	2.534 ± 0.031
	M	M	18	0.671 ± 0.005	0.915 ± 0.007	0.369 ± 0.006	0.276 ± 0.003	0.195 ± 0.002	3.296 ± 0.038	0.628 ± 0.008	1.135 ± 0.011	2.624 ± 0.023
D. constrictus	F	B	11	0.673 ± 0.007	0.854 ± 0.012	0.350 ± 0.005	0.213 ± 0.005	0.260 ± 0.004	2.267 ± 0.042	0.299 ± 0.013	1.241 ± 0.017	2.910 ± 0.022
		M	3	0.747 ± 0.019	1.032 ± 0.018	0.392 ± 0.014	0.287 ± 0.01	0.238 ± 0.008	3.709 ± 0.043	0.733 ± 0.025	1.227 ± 0.010	2.856 ± 0.030
	M	M	13	0.672 ± 0.008	0.923 ± 0.01	0.373 ± 0.005	0.253 ± 0.004	0.225 ± 0.004	3.607 ± 0.050	0.806 ± 0.013	1.130 ± 0.015	3.056 ± 0.033
D. deylamanus	F	M	1	0.606	1.078	0.459	0.339	0.226	3.779	0.711	1.147	2.713
D. eckerleini	F	M	1	0.567	0.889	0.352	0.269	0.212	3.072	0.513	1.132	1.998
	M	M	2	0.585 ± 0.035	0.890 ± 0.024	0.356 ± 0.010	0.263 ± 0.012	0.178 ± 0.001	3.145 ± 0.062	0.584 ± 0.027	1.044 ± 0.025	2.195 ± 0.029

Table 4. *Continued*

				Thorax					Hemelytra		Head-Hem.	Legs
Species	S	M	*N*	PL	PW	SL	DRL	CRL	HemL	CL	CHL	TIBL
D. epilobii	F	M	28	0.741 ± 0.009	1.011 ± 0.008	0.391 ± 0.005	0.304 ± 0.003	0.217 ± 0.002	3.738 ± 0.025	0.708 ± 0.008	1.269 ± 0.010	2.797 ± 0.031
	M	M	28	0.644 ± 0.005	0.907 ± 0.008	0.365 ± 0.016	0.267 ± 0.003	0.193 ± 0.002	3.575 ± 0.026	0.700 ± 0.015	1.152 ± 0.014	2.842 ± 0.025
D. errans	F	M	21	0.762 ± 0.009	1.045 ± 0.011	0.419 ± 0.004	0.315 ± 0.005	0.210 ± 0.003	3.744 ± 0.030	0.716 ± 0.011	1.235 ± 0.022	2.782 ± 0.054
	M	M	11	0.705 ± 0.011	0.976 ± 0.013	0.404 ± 0.006	0.28 ± 0.007	0.205 ± 0.003	3.899 ± 0.080	0.824 ± 0.018	1.158 ± 0.018	3.102 ± 0.054
D. escalerae	F	B	6	0.599 ± 0.018	0.8 ± 0.018	0.288 ± 0.006	0.184 ± 0.009	0.226 ± 0.006	1.782 ± 0.067	0.315 ± 0.017	1.080 ± 0.02	2.134 ± 0.069
		M	11	0.702 ± 0.01	0.992 ± 0.008	0.373 ± 0.007	0.264 ± 0.005	0.227 ± 0.005	3.126 ± 0.027	0.613 ± 0.006	1.143 ± 0.02	2.253 ± 0.033
	M	B	1	0.518	0.629	0.228	0.148	0.203	1.353	0.222	0.913	1.869
		M	10	0.619 ± 0.01	0.856 ± 0.016	0.327 ± 0.007	0.232 ± 0.007	0.199 ± 0.004	2.879 ± 0.038	0.564 ± 0.013	1.036 ± 0.023	2.117 ± 0.032
D. flavoviridis	F	B	10	0.809 ± 0.005	0.841 ± 0.009	0.324 ± 0.008	0.211 ± 0.005	0.393 ± 0.006	2.244 ± 0.030	0.403 ± 0.010	1.447 ± 0.013	3.069 ± 0.077
	M	B	12	0.780 ± 0.005	0.823 ± 0.009	0.307 ± 0.005	0.205 ± 0.003	0.389 ± 0.006	2.015 ± 0.014	0.350 ± 0.009	1.360 ± 0.016	3.024 ± 0.038
		M	1	0.896	1.040	0.350	0.298	0.376	3.912	0.888	1.435	3.145
D. hyalinipennis	F	B	3	0.708 ± 0.004	0.860 ± 0.004	0.264 ± 0.018	0.241 ± 0.011	0.259 ± 0.003	2.190 ± 0.06	0.372 ± 0.009	1.168 ± 0.040	2.164 ± 0.032
		M	7	0.793 ± 0.015	1.076 ± 0.015	0.390 ± 0.009	0.348 ± 0.009	0.242 ± 0.007	3.459 ± 0.03	0.695 ± 0.011	1.232 ± 0.014	2.350 ± 0.042
	M	B	1	0.640	0.883	0.290	0.215	0.250	1.951	0.341	0.986	2.275
		M	11	0.762 ± 0.014	1.048 ± 0.019	0.378 ± 0.005	0.327 ± 0.009	0.240 ± 0.005	3.347 ± 0.033	0.716 ± 0.010	1.179 ± 0.015	2.404 ± 0.039
D. josifovi	F	M	10	0.720 ± 0.024	1.067 ± 0.009	0.401 ± 0.009	0.322 ± 0.008	0.211 ± 0.005	3.593 ± 0.040	0.643 ± 0.012	1.233 ± 0.019	2.802 ± 0.034
	M	M	6	0.659 ± 0.021	0.971 ± 0.015	0.389 ± 0.016	0.282 ± 0.005	0.190 ± 0.002	3.504 ± 0.064	0.681 ± 0.029	1.133 ± 0.029	2.918 ± 0.036
D. lindbergi	F	B	1	0.560	0.822	0.264	0.191	0.229	1.701	0.253	1.050	1.960
		M	5	0.717 ± 0.023	0.986 ± 0.031	0.358 ± 0.012	0.296 ± 0.015	0.227 ± 0.005	3.037 ± 0.097	0.57 ± 0.026	1.144 ± 0.034	2.323 ± 0.102
	M	M	6	0.682 ± 0.024	0.965 ± 0.035	0.362 ± 0.016	0.279 ± 0.012	0.220 ± 0.006	3.114 ± 0.109	0.615 ± 0.025	1.048 ± 0.037	2.352 ± 0.086
D. pallidus	F	B	6	0.870 ± 0.011	0.941 ± 0.018	0.381 ± 0.011	0.246 ± 0.007	0.372 ± 0.02	2.397 ± 0.044	0.334 ± 0.019	1.537 ± 0.020	3.648 ± 0.058
		M	4	0.969 ± 0.028	1.201 ± 0.020	0.445 ± 0.029	0.383 ± 0.013	0.358 ± 0.012	4.563 ± 0.053	0.881 ± 0.029	1.660 ± 0.027	3.700 ± 0.058
	M	B	5	0.825 ± 0.015	0.928 ± 0.015	0.386 ± 0.011	0.244 ± 0.011	0.357 ± 0.007	2.375 ± 0.067	0.351 ± 0.025	1.440 ± 0.028	3.727 ± 0.066
		M	12	0.891 ± 0.008	1.136 ± 0.012	0.463 ± 0.008	0.325 ± 0.004	0.332 ± 0.003	4.355 ± 0.027	0.878 ± 0.015	1.466 ± 0.024	3.699 ± 0.041
D. poneli	F	M	2	0.672 ± 0.040	1.081 ± 0.097	0.351 ± 0.024	0.301 ± 0.014	0.261 ± 0.014	3.025 ± 0.036	0.556 ± 0.028	1.157 ± 0.116	2.375 ± 0.195
	M	M	1	0.677	1.064	0.368	0.292	0.224	3.331	0.644	1.206	-
D. rubicundus	F	B	3	0.665 ± 0.019	0.808 ± 0.01	0.282 ± 0.001	0.193 ± 0.011	0.259 ± 0.010	1.758 ± 0.031	0.252 ± 0.006	1.083 ± 0.041	2.249 ± 0.021
		M	4	0.750 ± 0.021	0.996 ± 0.021	0.382 ± 0.009	0.296 ± 0.004	0.239 ± 0.009	3.335 ± 0.055	0.656 ± 0.009	1.192 ± 0.031	2.379 ± 0.028
	M	B	7	0.657 ± 0.009	0.787 ± 0.013	0.293 ± 0.003	0.197 ± 0.003	0.254 ± 0.005	1.771 ± 0.023	0.243 ± 0.008	1.110 ± 0.018	2.424 ± 0.016
		M	6	0.726 ± 0.017	0.997 ± 0.008	0.369 ± 0.007	0.295 ± 0.009	0.246 ± 0.006	3.357 ± 0.028	0.664 ± 0.016	1.167 ± 0.017	2.469 ± 0.033
D. stachydis	F	B	63	0.701 ± 0.004	0.764 ± 0.005	0.283 ± 0.002	0.215 ± 0.002	0.274 ± 0.002	2.057 ± 0.013	0.353 ± 0.004	1.138 ± 0.007	2.293 ± 0.015
		M	6	0.858 ± 0.009	1.078 ± 0.022	0.390 ± 0.011	0.352 ± 0.005	0.257 ± 0.007	3.396 ± 0.076	0.694 ± 0.014	1.205 ± 0.014	2.347 ± 0.023
	M	B	46	0.676 ± 0.004	0.756 ± 0.009	0.279 ± 0.003	0.206 ± 0.002	0.267 ± 0.002	1.905 ± 0.019	0.340 ± 0.005	1.086 ± 0.007	2.247 ± 0.03
		M	11	0.782 ± 0.01	0.993 ± 0.019	0.364 ± 0.009	0.315 ± 0.005	0.244 ± 0.007	3.319 ± 0.048	0.729 ± 0.013	1.151 ± 0.018	2.464 ± 0.057
D. tamaninii	F	M	3	0.730 ± 0.068	1.096 ± 0.027	0.410 ± 0.011	0.329 ± 0.014	0.224 ± 0.007	3.414 ± 0.268	0.719 ± 0.015	1.052 ± 0.112	2.421 ± 0.039
	M	M	6	0.594 ± 0.039	0.921 ± 0.015	0.349 ± 0.011	0.284 ± 0.003	0.211 ± 0.002	3.196 ± 0.057	0.667 ± 0.025	1.058 ± 0.025	2.379 ± 0.016
D. tumidifrons	F	B	1	0.473	0.717	0.217	0.151	0.187	0.683	0.057	0.742	1.428
		M	1	0.629	0.986	0.329	0.293	0.184	2.597	0.492	0.815	1.571
	M	B	1	0.471	0.758	0.217	0.146	0.201	0.693	0.057	0.820	1.500
		M	2	0.506 ± 0.016	0.923 ± 0.021	0.264 ± 0.002	0.236 ± 0.009	0.172 ± 0.011	2.222 ± 0.024	0.469 ± 0.017	0.912 ± 0.027	1.530 ± 0.012

Figure 32. Distribution of the specimens examined: *D. alkannae*, *D. argensis*, *D. bolivari* and *D. caycumensis*.

Dicyphus argensis is very similar to *D. bolivari* but can be readily separated from it by features of the male genitalia. The apophysis of the left paramere of *D. argensis* is very short (vs. elongate in *D. bolivari*) (Fig. 9B, C–F) and the aedeagus has a pair of large and arcuate lobal sclerites and does not possess fields of spinules (vs. multiple small lobal sclerites and fields of spinules) (Fig. 12B, C). Despite these clear differences, there are no external characters that can be used to separate these two species. *Dicyphus argensis* is also very similar to *D. hyalinipennis* and *D. stachydis*, with all three species possessing a relatively short apophysis of the left paramere (Figs 9B, 10B, 11B) and the endosoma has a pair of large lobal sclerites (Figs 12B, 14A, 31C). These three species are also closely related based on mtDNA sequences (Figs 24, 25). *Dicyphus argensis* is smaller than *D. hyalinipennis* and *D. stachydis*, and in contrast to them is known only from macropterous morphs (Fig. 3). Also, the outer margin of the spatulate apex of the apophysis of the left paramere in *D. argensis* is not toothed as in *D. hyalinipennis*, nor smooth as in *D. stachydis* (Figs 9B, 10B, 11B).

Dicyphus bolivari Lindberg, 1934
(Figs 9c–f, 12c, 26, 32, 33)

Dicyphus bolivari Lindberg, 1934: 12 (original description; Spain); Carvalho, 1958: 194 (catalogue); Schuh, 1995: 488 (catalogue; full citation); Kerzhner & Josifov, 1999: 22 (Palaearctic catalogue).

Dicyphus bolivari atlanticus Wagner, 1951: 29 (original description; Canary Islands); new synonymy, this work

Dicyphus maroccanus Wagner 1951: 19 Figs 6, 7, 9 (original description; Morocco); Carvalho, 1958: 198 (catalogue; full citation). Schuh, 1995: 492 (catalogue; full citation); Kerzhner & Josifov, 1999: 23 (catalogue); new synonymy, this work

Material examined

Holotype of Dicyphus bolivari, 1♂, Spain: Andalucia: Sierra Morena: Santa Helena, 38.34284°N 3.53945°W, 762 m, 04–08 Apr 1926, Lindberg, (AMNH_PBI 00208594) (MZH). Type seen.

Holotype of Dicyphus bolivari altanticus, 1♂, Spain: Canary Islands: Tenerife Island: Icod, 28.35°N 16.70°W, 640 m, 09 May 1947, Lindberg, (AMNH_PBI 00208587) (MZH). Type seen.

Other material examined (including paratypes)

Morocco: Amizmiz: Atlas, 31.21888°N 8.23222°W, 980 m, 24–25 May 1926, Lindberg, 4 ♂♂ (AMNH_PBI 00208655, AMNH_PBI 00208656, AMNH_PBI 00208661, AMNH_PBI 00208574), paratype of *Dicyphus maroccanus*, 1♂ (AMNH_PBI 00208570) (MZH); Lindberg, 2♀ (AMNH_PBI 00208647, AMNH_PBI 00208650) (MZH); 24–25 May 1926, Lindberg, 1♂, id. as *Dicyphus maroccanus* (AMNH_PBI 00208642) (MZH). Arround, Atlas ma, 9–12 Jun 1926, Lindberg, 1♂, 1♀ (MZH). Atlas, Arround, 9–12 Jun 1926, Lindberg, paratype of *Dicyphus maroccanus*, 1♂ (AMNH_PBI 00204225) (BMNH). Azrou, Atlas med., 33.435°N 5.22111°W, 1279 m, 24 Jun–2 Jul 1926, Lindberg, 1♂, id. as *Dicyphus maroccanus* (MZH). Marrakech, 31.63722°N 8.01750°W, 453 m, 21–23 May 1926, Lindberg, paratype of *Dicyphus maroccanus*, 1♀ (AMNH_PBI 00208667) (MZH). Moyen Atlas, Aýn-el-Leuh (Azrou), 5 Aug 1959, Eckerlein, 1♂, id. as *Dicyphus maroccanus* (AMNH). Ras-el-Ma, Domaine de. (M. Atlas), 33.43473ºN 5.23189ºW, 483 m, 16 Mar 1961, Meinander, 1♂, id. as *Dicyphus maroccanus* (MZH). Berkane, 34.9211°N 2.3294°W, 179 m, 1♀, id. as *Dicyphus maroccanus* (AMNH_PBI 00209594) (MNHN).

Spain: Canary Islands: Tenerife Island: Puerto de la Cruz, 28.41°N 16.55°W, 53 m, 7–8 May 1947, Lindberg, paratype of *Dicyphus bolivari atlanticus*, 1♀ (AMNH_PBI 00208588) (MZH). Santa Úrsula, 28.43°N 16.49°W, 277 m, 18 May 1947, Lindberg, identified as *Dicyphus bolivari atlanticus*, 1♀ (AMNH_PBI 00208590) (MZH). Santa Úrsula, 28.43°N 16.49°W, 277 m, 18 May 1947, Lindberg, id. as *Dicyphus bolivari atlanticus*, 1♂ (AMNH_PBI 00208575) (MZH); 18 May 1947, Lindberg, id. as *Dicyphus bolivari*, 1♀ (AMNH_PBI 00208589) (MZH). Santa Cruz de Tenerife, 28.47°N 16.25°W, 37 m, 14 Jan 1949, Lindberg, paratypes of *Dicyphus bolivari atlanticus*: 7♂♂ (AMNH_PBI 00208592, AMNH_PBI 00204185, AMNH_PBI 00204186, AMNH_PBI 00208593, AMNH_PBI 00208595-AMNH_PBI 00208597), 1♀ (AMNH_PBI 00208591) (MZH); 4 Apr 1949, Lindberg, paratype of *Dicyphus bolivari atlanticus*, 2♂♂ (AMNH_PBI 00208586, AMNH_PBI 00208597) (MZH). Punta del Hidalgo, ex. *Datura stramonium* L. (Solanaceae), 28.34104ºN 16.19431W, 59 m, 4 March 2004, Sanchez & Martínez-Cascales, 16♂♂, 11♀♀ (IMIDA_ENT 00003056-IMIDA_ENT 00003082) (IMIDA). Punta de Hidalgo, ex. *Datura stramonium*, 28.34169ºN 16.18582W, 59 m, 16 Oct 2008, Sanchez, 6♂♂, 6♀♀ (IMIDA_ENT 00003083-IMIDA_ENT 00003094) (IMIDA). Gran Canaria: Trapiche, ex. *Hyosciamus albus*, 28.0325ºN 15.3219ºW, 91 m, 12 June 2009, Sanchez, 6♂♂, 5♀♀ (IMIDA_ENT 00003083-IMIDA_ENT 00003094) (IMIDA). León: Cistierna, ex. *Epilobium hirsutum* L. (Onagraceae), 42.44593°N 5.0820633°W, 942 m, 4 June 2006, Sanchez, 9♂♂, 11♀♀ (IMIDA_ENT 00000215-IMIDA_ENT 00000234) (IMIDA); Murcia: Cieza, ex. *Cucurbita maxima*, 38.13426ºN 1.24460ºW, 231 m, 12 Sept 2002, Sanchez, 5♂♂, 8♀♀ (IMIDA_ENT 00000235-IMIDA_ENT 00000247) (IMIDA); Cehegín, ex. *Epilobium hirsutum*, 38.06152ºN 1.47397ºW, 544 m, 10 Jul 2002, Sanchez, 9♂♂, 12♀♀ (IMIDA_ENT 00000025-IMIDA_ENT 00000044, IMIDA_ENT 00000047) (IMIDA); Cataluña: Barcelona: Cabrils, 41.525112ºN 2.367061ºE, C. Castañé, ♂♂ and ♀♀ (D167 and D168) (IMIDA); Gerona: Alt Emporda, Castelló d'Empuries: Santa Fe, 42.2ºN, 3.07ºE, 5 m, 22 May 1983, ex. *Hyosciamus albus*, J. Ribes, 1 ♂, 1 Adult sex unknown (Jordi Ribes Collection). Navarra: Garralda, 42.9ºN, 1.2ºW, 846 m, 20 Jul 1983, J. Ribes, 2 ♂♂ (Jordi Ribes Collection).

Diagnosis
Dicyphus bolivari is recognized by the following combination of characters: macropterous and brachypterous males (Fig. 33) and females; body length, males 3.58–4.21 mm in macropters and 2.52–2.90 mm in brachypters; females 3.76–4.73 mm in macropters and 2.69–3.21 mm in brachypters. Pale species (Fig. 33); clypeus mostly stramineous; AI and AII mostly stramineous, with subbasal and subapical dark-brown annulations; left paramere with moderately robust and long apophysis, inner margin of shaft angulated (Fig. 9C–F); aedeagus with three endosomal lobes, medial lobe with generally 8–12 small endosomal lobal sclerites, rarely 6–7 sclerites, lateral lobes densely spinulate (Fig. 12C).

Redescription
Males. Macropters and brachypters known (Fig. 33).

Coloration (Fig. 33): Dorsum mostly stramineous with light to dark-brown markings, plus orange/red highlighting. *Head:* mostly stramineous to orange, frons+vertex with a short, reddish-brown to dark brown X-shaped marking, not extending beyond posterior margin of eyes; clypeus stramineous with medium brown highlighting, occasionally more extensive embrownment; mandibular plates stramineous; maxillary plate embrowned; vertex orange; postocular margins of head orange medium brown; gula and bucculae yellow. *Antennae:* AI medially, basally and apically stramineous, with subbasal and subapical reddish brown annulations; AII mostly stramineous, with distal 1/3rd dark brown, narrowly and faintly brown at base; AIII and AIV concolorous, uniformly dark brown. *Pronotum:* collar stramineous, translucent; callosite region mostly stramineous with variable embrownment; disk stramineous, translucent, sometimes humeral angles embrowned. *Thoracic pleura and sterna:* propleuron stramineous with weak embrownment, ventral margin whitish; mesobasisternum medium brown; mesepimeron and metepisternum, including evaporative areas, stramineous to whitish. *Mesoscutum:* mostly orange, with faint embrownment. *Scutellum:* lateral angles broadly pale stramineous to whitish with narrow brown stripe along midline. *Hemelytra:* translucent,

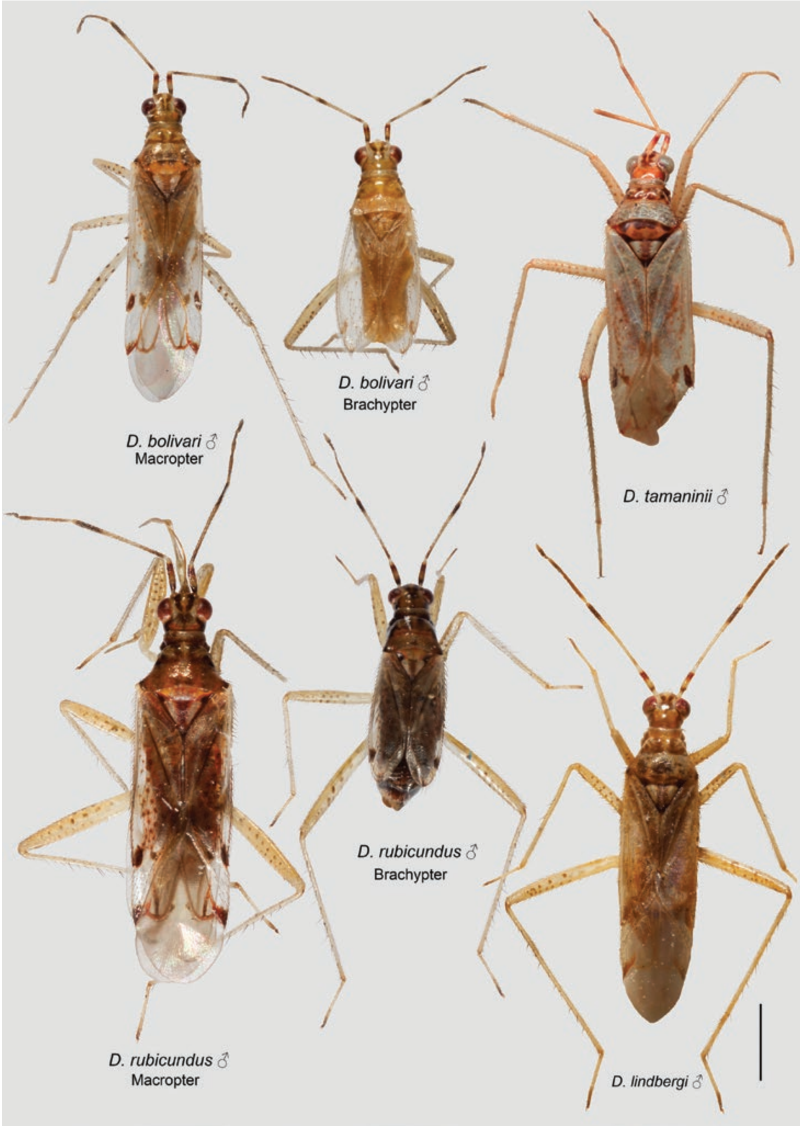

Figure 33. Habitus of *D. bolivari* (macropter and brachypter), *D. tamaninii*, *D. rubicundus* (macropter and brachypter), *D. lindbergi*. Scale bar = 1 mm.

mostly stramineous with medium brown to reddish brown markings/highlighting; with three pairs of medium brown to reddish brown markings, each pair at corial fracture, apex of endocorium and tip of cuneus; membrane veins embrowned. *Abdomen:* venter uniformly stramineous.

Structure: Head: interocular distance 1.21–1.62× greater than eye width in macropters, 1.23–1.62× in brachypters. *Antennae:* AI short, 1.16–1.67× longer than interocular distance in macropters, 1.23–1.63× in brachypters; AII 1.03–1.30× longer than posterior width of pronotum in macropters, 1.08–1.32× in brachypters. *Pronotum:* disk region 1.05–1.41× longer than the callosite region in macropters and 0.71–1.13× in brachypters. *Male genitalia:* left paramere apophysis moderately robust and long, with shaft angulated, with subapical excavation on outer margin, spatulate apex weakly denticulate on outer margin (Fig. 9C–F); aedeagus with three endosomal lobes, medial lobe with generally 8–12 small endosomal lobal sclerites, rarely 6–7 sclerites, lateral lobes densely spinulate (Fig. 12C).

Females. Macropters and brachypters known. Coloration, vestiture, texture and structure mostly as in males. Abdominal venter pale yellowish green. Interocular distance 1.22–1.70× greater than eye width in macropters, 1.38–1.64× in brachypters; AI 1.16–1.58× longer than interocular distance in macropters, 1.20–1.38× in brachypters; AII

0.94–1.11× longer than the of posterior pronotal width in macropters, 1.03–1.24× in brachypters. Disk region 1.05–1.55× longer than the calli region in macropters, 0.89–1.01× in brachypters.

Measurements

See Table 4.

Distribution

We examined specimens that we identified as *D. bolivari* from Morocco, the Iberian Peninsula (Spain) and Canary Islands (Fig. 32). Wagner (1970) reported *D. bolivari bolivari* from southern France, Iberian Peninsula (Spain) and Corsica, and *D. bolivari atlanticus* from the Canary Islands (Tenerife, Gran Canaria). Wagner (1970) and Mollá *et al.* (2010) reported *Dicyphus maroccanus* from Morocco and Spain, respectively. The new synonymies that we propose in this work extends the distribution of *D. bolivari* to North Africa, and establishes its broad distribution in the western Mediterranean region (Fig. 32).

Host plants

We found *D. bolivari* on *Datura stramonium* L. (Solanaceae), *Hyosciamus albus* and *Solanum lycopersicum*, *Epilobium hirsutum* L. (Onagraceae), *Lagenaria siceraria* (Molina) Standley (Cucurbitaceae) and *Ononis natrix*. Wagner (1964, 1970) stated that *D. bolivari* lives on *E. hirsutum*. Wagner (1970) also reported that Eckerlein found *D. maroccanus* on *Digitalis atlantica* Pomel (Scrophulariaceae).

Remarks

See also Remarks' section for *D. argensis*. Lindberg (1934) described *Dicyphus bolivari* from specimens collected on herbs on the bank of a stream near the train station in Santa Helena (Sierra Morena, Jaen, Spain) in April, 1926. He dedicated this species to the Spanish entomologist Ignacio Bolivar. Wagner (1951) examined specimens of the type material, sent to him by Lindberg, and described the male genitalia of a paratype. He also compared Spanish *D. bolivari* specimens with Lindberg material from the Canary Islands, and established the latter as a new subspecies (*D. bolivari atlanticus*), with the nominotypical subspecies restricted to the Iberian Peninsula. In the same work, Wagner (1951) described *Dicyphus maroccanus* as a new species, from four males and two females, collected by Lindberg in Morocco (Atlas-Amismiz-and Marrackech) in May/June, 1926, placing it in the *hyalinipennis* species group. He stated that *D. maroccanus* was very closely related to *D. tamaninii*, with the two species differing in the shape of the left paramere, and the number and size of the lobal sclerites of the endosoma. He also compared *D. maroccanus* and *D. bolivari* and concluded that, despite their similar structure and ratios of body measurements, the former species could be separated by the longer body length, second and fourth antennomeres and hind tibiae.

We examined the types of *D. bolivari*, *D. bolivari altanticus* and *D. maroccanus*, and in all cases found no differences in the male genitalia or external features. In this work, we propose new synonymies for *D. bolivari*, *D. bolivari altanticus* and *D. maroccanus*. In our phylogenetic analyses, specimens from the Iberian Peninsula and the Canary Islands are clustered separately (Figs 24, 25), but the genetic distances alone do not justify the ongoing recognition of the subspecies *D. bolivari*. Although we did not have access to fresh specimens from Morocco, we find no morphological basis for the maintenance of *D. maroccanus* as a valid species, and relegate it to a junior synonym of *D. bolivari*.

DICYPHUS CAYCUMENSIS SP. NOV.

(FIGS 2, 12D, 23A, 32, 34)

LSID: urn:lsid:zoobank.org:act: 35527B6B-0785-4713-B2AF-DEF83071D51F

Material examined

Holotype. ♂ (IMIDA_ENT 00000200), Caycuma in the region of Zonguldak, Turkey; 41.4297°N 32.0775°E; ex. *Solanum lycopersicum*, Sanchez and Cassis coll. (IMIDA). Paratypes 4♂♂, 15♀♀ (IMIDA_ENT 00000201, IMIDA_ENT 00000248-IMIDA_ENT 00000266) (IMIDA). Same location and host plant as holotype (IMIDA).

Etymology

This species is named after the village of Caycuma in Turkey where the species was collected.

Diagnosis

Dicyphus caycumensis is recognized by the following combination of characters: macropterous males and females (Fig. 2); body length, males 3.37–3.80 mm, females 3.52–4.12 mm; body with head, pronotum, thoracic pleura and abdomen mostly shiny black, remainder stramineous to translucent pale grey; antennae mostly dark brown to black, AII uniformly so; pronotum short, a little shorter than head length; AII a little longer than posterior width of pronotum in males and subequal in females; left paramere with short and robust apophysis (Fig. 23A); aedeagus with two large straight endosomal lobal sclerites, subequal in size (Fig. 12D).

Description

Males. Macropters only known.

Coloration (Fig. 2): Dorsum mostly dark brown to black, with minor stramineous markings. *Head:* frons+vertex shiny with a X-shaped black marking, with lateral regions and midline stramineous, sometimes with minor orange highlighting; posterior region of head black; postocular margins broadly black; clypeus, maxillary plate and bucculae black; mandibular plate stramineous; gula mostly black with either a broad yellow stripe or a pair of yellow stripes either side of midline. *Antennae:* mostly fuscous to black; AI and AII dark brown to black; AIII and AIV entirely dark brown to black. *Pronotum:* collar black and shiny; calli shiny, dark brown to black, narrowly yellow-brown medially; disk shiny, black with midline white to stramineous. *Thoracic pleura and sterna:* propleuron black, anterior half of ventral margin whitish; mesobasisternum uniformly shiny black; mesepimeron whitish; metepisternum and metathoracic glands dull black. *Mesoscutum:* uniformly black. *Scutellum:* dull black with anterolateral angles white. *Hemelytra:* translucent, with faint pale-yellow hue, usually with three small dark-brown to fuscous spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; corium also with minor brown spots, often associated with setae; membrane veins embrowned. *Abdomen:* venter either uniformly fuscous to black, or mostly black with medial region stramineous.

Structure: Head: interocular distance 1.13–1.42× greater than eye width. *Antennae:* AI short, 1.24–1.64× longer than interocular distance; AII 1.06–1.19× longer than posterior width of pronotum. *Pronotum:* disk region 1.28–1.52× the callosite region. *Male genitalia:* genital opening of pygophore oval, without tergal processes; left paramere with robust and short apophysis, with outer margin of apex spatulate (Fig. 23A); aedeagus with two well-developed endosomal lobes, each with a straight and distally tapered sclerites; lobal sclerites subequal in size (Fig. 12D).

Females. Macropters only known. Coloration, vestiture, texture and structure mostly as in males. Body length 3.52–4.12 mm; interocular distance 1.16–1.53× greater than eye width; AI 1.24–1.49× longer than interocular distance; AII 0.86–0.95× longer than the posterior pronotal width. Pronotal disk 1.39–1.88× than the callosite region.

Measurements

See Table 4.

Distribution

Collected in the village of Caycuma, in the Zonguldak region of Turkey (Fig. 32).

Host plants

Dicyphus caycumensis was collected on *Cucurbita maxima* and *Solanum lycopersicum*.

Remarks

We describe *Dicyphus caycumensis* **sp. nov.** as new to science, recognizing its similarity to dark morphs of *D. cerastii* in shape, coloration and vestiture. *Dicyphus caycumensis* can be distinguished from the *D. cerastii* by its shorter and darker body, AII is uniformly dark brown to black (cf. medially stramineous in *D. cerastii*) (Figs 2, 30), the absence of a sternal process on the left side abdominal SVIII (Figs 6F, 34F), and the endosomal lobal sclerites are straight (cf. arcuate) (Fig. 12D, E). We compared *D. caycumensis* with specimens of two other Turkish species, *D. alkannae* and *D. eckerleini*, and found them to be consistently separated by the much darker dorsum, including the head (Figs 2, 30), as well as differences in the male genitalia (Figs 9A,12A, D, G, 23A, D). Both *D. alkannae* and *D. caycumensis* have asymmetrical endosomal lobal sclerites, but is more pronounced in the former species (Fig. 12A, D). In comparison, *Dicyphus eckerleini* has symmetrical endosomal lobal sclerites (Fig. 12G).

Dicyphus cerastii Wagner 1951
(Figs 6, 12e, 23b, 30, 35)

Dicyphus cerastii Wagner, 1951: 13 (original description); Schuh, 1995: 489 (world catalogue); Kerzhner & Josifov, 1999: 22 (Palaearctic catalogue)

Dicyphus umbertae Sanchez & Cassis, 2006: 288 (original description); new synonymy, this work

Material examined

Croatia: Lastovo: Dalmatia, 42.76810ºN 16.90080ºE, 51 m, 11 May 1948, Novak, 1 ♀Female, Paratype (AMNH_PBI 00208556) (MZH).

Italy: Torino: Giaveno: Prafiel, 45.03144ºN 7.28472ºE, 1003 m, 25 Ago 2009, ex. Compositae, Sanchez, 5♀♀ (IMIDA_ENT 00000546-IMIDA_ENT 00000550), 5♂♂ (IMIDA_ENT 00000551-IMIDA_ENT 00000555) (IMIDA).

Greece: Crevena: Xirolimni, 40.29801ºN 21.65455ºE, 757 m, 15 Jun 2007. ex. Lamiaceae, 1♂ and nymphs (D75) Sanchez & Cassis.

Portugal: Estremoz, 38.84222°N, 7.59908°W, ex. *Hyosciamus albus*, Sanchez & Pennaroli, 10 Sept 2004, 1♂ holotype of *D. umbertae*, 2♂♂, 1♀♀ paratypes of *Dicyphus umbertae* (IMIDA). Carrapateira, 37.19250ºN, 8.89944W, ex. *Solanum lycopersicon*, Sanchez & Pennaroli, 12 Sept 2004, 2♂♂, 2♀♀ paratypes of *D. umbertae* (IMIDA). Leiria: Albergaria, 39.74500ºN 8.89111ºW, 86 m, 01 Jun 1959, Lindberg, 1 adult sex unknown, (AMNH_PBI 00208599) (MZH), 1 adult sex unknown, (AMNH_PBI 00208602), 1♀ (AMNH_PBI 00208600), 1♀ (AMNH_PBI 00208600) (MZH). Porto: Gerez, 41.24888ºN 8.40416ºW, 246 m, 31 May 1959, Lindberg, 1♀ (AMNH_PBI 00208598), 1♂ (AMNH_PBI 00208603) (MZH). Faro: Ameixial, 37.36813ºN 7.96977ºW, 417 m, 2 Jun 2006, Sanchez, ex. *Solanum*

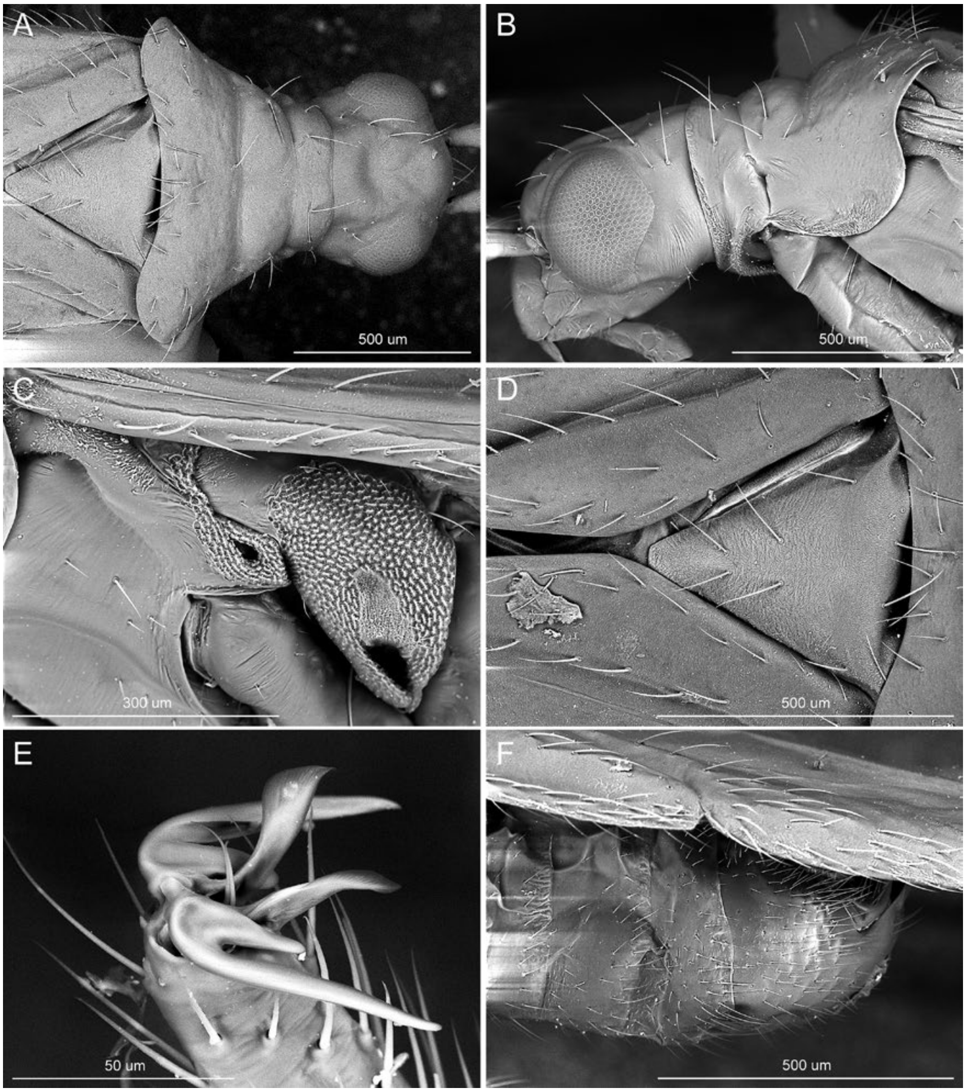

Figure 34. Scanning electron micrographs of *D. caycumensis*. A, head and pronotum dorsal view, with well-defined collar, and callosite and disk region. B, head and pronotum, lateral view. C, external efferent system, metathoracic glands. D, scutelum. E, pretarsus in lateral view, with well-visible membranous pseudopulvilli between the claws. F, genital segment, lateral view.

lycopersicum, 2♂♂ (IMIDA_ENT 00000049, IMIDA_ENT 00000082), 3♀♀ (IMIDA_ENT 00000078, IMIDA_ENT 00000079, IMIDA_ENT 00000080) (IMIDA); Alto Alentejo: Castelo de Vide, 39.41423°N 7.45396°W, 606 m, 3 June 2006, ex. *Solanum lycopersicum*, Sanchez, 5♂♂ (IMIDA_ENT 00000087, IMIDA_ENT 00000088, IMIDA_ENT 00000048, IMIDA_ENT 00000089, IMIDA_ENT 00000094), 5♀♀ (IMIDA_ENT 00000090, IMIDA_ENT 00000091, IMIDA_ENT 00000092, IMIDA_ENT 00000084, IMIDA, IMIDA_ENT 00000086) (IMIDA). Portalegre: 39.29672°N 7.42848°W, 468 m, 3 Jun 2006, ex. *Solanum lycopersicum*, Sanchez, 3♂♂ (IMIDA_ENT 00000081, IMIDA_ENT 00000083, IMIDA_ENT 00000085), 2♀♀ (IMIDA_ENT 00000076, IMIDA_ENT 00000077) (IMIDA).

Spain: Huesca: Torla, Bujaruelo, 42.70722°N, 0.12004°W, 1300 m, 6 Jun 2016, ex. *Ononis natrix*, Sanchez & La Spina, 1 ♂ (D50-1), 1 adult, sex unknown (D50-2) (IMIDA). Cataluña: Barcelona: Montseny: Santa Fe, 41.77°N, 2.46°E, 2 Oct 2002, Ribes, 1♂, 1♀ (Jordi Ribes Collection).

Turkey: Izmir: Smyrna: Mont Jamanl., 38.431°N 27.146°E, Sahlberg, 1♀, paratype (AMNH_PBI 00208601) (MZH).

Ukraine: Eupatoria, Tavricheskaya Government: 45.19045°N 33.36687°E, 0 m, 24 Jul 1967, 1♂ paratype of *Dicyphus cerastii* (AMNH_PBI 00208585) (MZH); 20 Aug 1907, Yakovlev, 1 ♀ (AMNH_PBI

00210777) (ZISP); 22 Aug 1907, Yakovlev, 1♀ (AMNH_PBI 00210778) (ZISP). Crimea: Opolznevoe (Kikeneiz), S. coast of Crimea: 44.41012°N 33.94303°E, 423 m, 14 Aug 1926, Kiritshenko, 1♀ (AMNH_PBI 00210779) (ZISP); 22 Aug 1926, Kiritshenko, 1♀ (AMNH_PBI 00210780) (ZISP); 4 Sep 1926, Kiritshenko, 2 ♀♀ (AMNH_PBI 00210781, AMNH_PBI 00210783), 3♂♂ (AMNH_PBI 00210782, AMNH_PBI 00210784, AMNH_PBI 00210785) (ZISP), 6 Aug 1926, Kiritshenko, 1♀ (AMNH_PBI 00341226) (ZISP). Nikitskiy Botanical Gardens: 44.51142°N 34.23251°E, 157 m, 12 Jul 1951, Loginova, 2♂♂ (AMNH_PBI 00341227, AMNH_PBI 00341228) (ZISP).

Diagnosis

Dicyphus cerastii is recognized by the following combination of characters: macropterous males and females. Body length 3.84–4.65 mm in males, 4.17–4.79 mm in females. Orange-brown or dark-brown morphs (Fig. 30); macropterous males and females; AI mostly reddish to dark brown; AII subequal to a little longer in length to posterior width of pronotum; AII with medial pale annulation; hemelytra with three pairs of markings (endocorial spot almost obsolete in paler morph); male abdominal SVIII with prominent tumose sternal process on left side (Fig. 6F); apophysis of left paramere robust and short with spatulate apex toothed (Fig. 23B); aedeagus with two arcuate lobal sclerites, lobal sclerites asymmetrical (Fig. 12E).

Redescription

Males. Macropters only known.

Coloration: Dark-brown morph (Fig. 30): dorsum mostly dark brown to black, with contrasting stramineous markings. *Head:* frons+vertex shiny with a X-shaped dark marking, with lateral regions and midline stramineous, sometimes with minor orange highlighting; posterior region of head mostly orangish yellow, with medial embrownment; clypeus dark, sometimes a little paler medially; mandibular plate stramineous; gula dark brown with broad stramineous to yellow stripe. *Antennae:* mostly dark brown; AI dark brown, with extremities narrowly yellow to stramineous; AII mostly dark brown with broad medial stramineous band, extremities yellow to stramineous; AIII mostly dark brown, with base yellow to stramineous; AIV dark brown. *Pronotum:* collar dark and shiny, with medial stramineous spot; calli shiny, dark brown with minor yellow stripe, midline broadly yellow to stramineous; disk mostly shiny dark brown, obscurely yellow to stramineous medially. *Thoracic pleura and sterna:* propleuron black, ventral margin whitish to stramineous; mesobasisternum uniformly shiny dark brown; mesepimeron whitish; metepisternum and MTG dull dark brown. *Mesoscutum:* dark brown, with lateral regions orangish. *Scutellum:* dull dark-brown with anterolateral angles stramineous. *Hemelytra:* translucent, mostly very light brown usually with three small dark-brown spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; endocorium and clavus with brown spotting. *Abdomen:* venter variable in colour, either uniformly dark brown or stramineous medially with lateral regions dark brown; tergites more uniformly

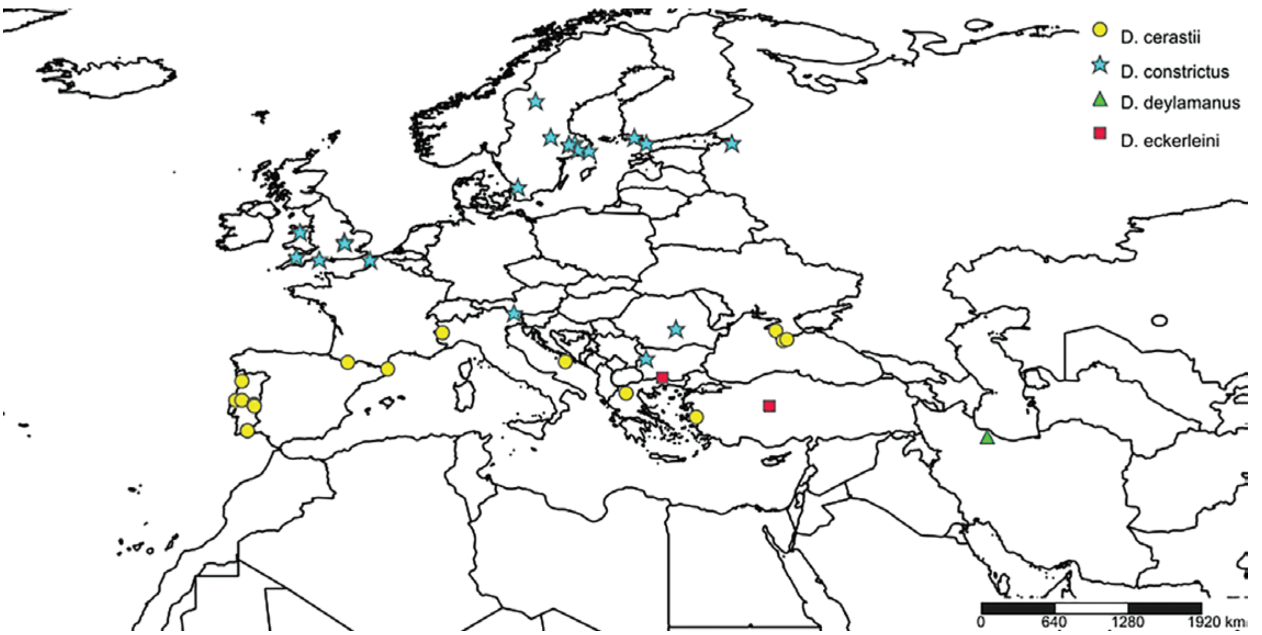

Figure 35. Distribution of the specimens examined: *D. cerastii*, *D. constrictus*, *D. deylamanus* and *D. eckerleini*.

dark brown. *Orange-Brown Morph* (Fig. 30)*:* dorsum mostly pale orange brown, with wings translucent, with contrasting reddish brown markings, sometimes with minor red/orange highlighting. *Head*: mostly pale orange-brown; frons+vertex also with a narrow, X-shaped dark-brown marking; clypeus, mandibular and maxillary plates mostly medium brown; postocular margins broadly medium brown and shiny, extending dorsally towards gula; gula and bucculae broadly yellow to stramineous. *Antennae:* AI mostly red to reddish brown, with extremities yellow to stramineous; AII distinctly banded, base and medial region stramineous, contrasting with small subbasal and distal 1/3rd reddish to medium brown; AIII mostly reddish to medium brown with small basal stramineous band; AIV reddish to medium brown. *Pronotum:* collar white to stramineous, translucent; calli and disk mostly pale brown, sometimes with pale red highlighting; humeral angles narrowly darker brown. *Thoracic pleura and sterna:* propleuron pale orange-brown, with pleural suture darker brown, ventral margin white to stramineous; mesobasisternum uniformly medium brown and shiny; mesepimeron uniformly white to stramineous, dull; metepisternum pale orange brown, peritreme darker than evaporative area. *Mesoscutum:* uniformly pale orange brown, sometimes with red highlighting. *Scutellum:* medially pale orange brown, lateral angles stramineous. *Hemelytra:* translucent, mostly very light brown usually with three small light-brown to red-brown spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; endocorium and clavus with red spotting. *Abdomen:* venter mostly pale orange-brown, with SII and SIII consistently brown; pygophore concolorous with pregenital venter, without large brown spot ventrally.

Structure: Head: interocular distance 0.97–1.25× greater than eye width. *Antennae:* AI short, 1.73–2.25× longer than interocular distance. *Pronotum:* AII 1.20–1.39× longer than posterior width of pronotum. *Male genitalia:* males with left sternal tumose process on abdominal SVIII (Fig. 6F); left paramere robust and short apophysis, with outer margin of apex spatulate and toothed; setae of sensory lobe very long, reaching distally beyond 1/2 length of spatulate region (Fig. 23B); aedeagus with three well-developed endosomal lobes, two of the lobes with a single arcuate moderately sized sclerite each (Fig. 12E).

Females. Macropters only known. Coloration, vestiture, texture and structure mostly as in males. *Head*: interocular distance 1.06–1.37× greater than eye width. *Antennae:* AI 1.55–1.98× longer than interocular distance; AII 0.95–1.18× longer than posterior pronotal width. *Pronotum:* disk 1.26–1.72× longer than callosite region.

Measurements

See Table 4.

Distribution

We examined specimens of this species from Portugal, northern Spain, northern Italy, Croatia and Greece (Fig. 35). Kerzhner & Josifov (1999) also documented this species from Albania, Andorra, Bosnia, Bulgaria, France, Macedonia, Portugal and the Ukraine.

Host plants

We collected *D. cerastii* on *Solanum lycopersicum* and unidentified plant species belonging to the Lamiaceae and Asteraceae in Greece and Italy, respectively. *Dicyphus cerastii* has also been recorded from *Salvia glutinosa* L. (Lamiaceae) and *Digitalis grandiflorum* Miller (Scrophulariaceae) (Ingegno *et al.*, 2008), *Cerastium virescens* L. and *Cerastium arvense* L. (Caryophyllaceae) (Wagner, 1964, 1970).

Remarks

Wagner (1951) described *D. cerastii* from specimens collected in Croatia and Crimea (Nova collector) and Turkey (Sahlberg collector), placing it in the *hyalinipennis* species-group. He stated that *D. cerastii* was very similar to *D. hyalinipennis*, with the latter distinguished by the narrower vertex, larger eyes, longer second antennomere, broader pronotum, longer hind tibiae, darker pronotum and head, and, above all, by the morphology of the male genitalia. Wagner (1951) pointed out that *D. cerastii* differed from *D. stachydis* by having longer antennae and legs, a narrower vertex, shorter fourth antennomere and genital morphology. Compared to Wagner (1951), we found that the measurements' characters that he highlighted overlap between the above three species, and concluded that the fine details of the male genitalia are the most reliable morphological characters for differentiating them. We are in agreement with Wagner (1951) that *D. cerastii* and *D. errans* have a similar dark colour and elongate body, and that the males of the two species can be separated by the length of the second antennomere (Table 4).

See *D. argensis* remarks for synonymy of *D. umbertae* with *D. cerastii*. *Dicyphus cerastii* varies greatly in colour, with dark and pale morphs known (Fig. 30), and as a result can be easily misidentified. Males of this species are, however, readily differentiated from congeners by the presence of a left abdominal SVIII process (Fig. 6F), which is unlike that found in *D. flavoviridis* and *D. pallidus* (Figs 7D, 8F). This is the first time external processes in pregenital abdominal segments have been reported for *Dicyphus* species. The function of these processes is unknown but it is quite likely that they intervene at mating.

Dicyphus constrictus (Boheman, 1852)
(Figs 2, 12F, 23C, 35)

Capsus constrictus Boheman 1852: 74 (original description).
Dicyphus (*Dicyphus*) *constrictus*: Carvalho, 1958: 195 (world catalogue); Schuh, 1995: 489 (world catalogue); Kerzhner & Josifov, 1999: 22 (Palaearctic catalogue).
Dicyphus constrictus eduardi Josifov & Nikolay, 2008: 99 (original description)

Material examined
Austria: Carnische Alp., 1♂ (AMNH_PBI 00208576), 1♀ (AMNH_PBI 00208577) (MZH).

Bulgaria: Brese, 43.01666°N 23.21666°E, 795 m, 24 Jul 1997, Horvath, 1♂ (AMNH_PBI 00213948) (HNHM).

Finland: Ekero, 60.02 N 23.32, 4♂♂ (AMNH-PBI 00209469), 4♀♀, 1♂ (AMNH-PBI 00209470), 4♀♀, 1♂ (AMNH-PBI 00209471), 22 July 1917, Hakan Lindberg. Pargas, 60.30129ºN 22.30243ºE, 2 m, Horvath, 1♀ (AMNH_PBI 00213947) (HNHM); Horvath, 1 adult sex unknown (AMNH_PBI 00213946) (HNHM).

France: Nord-Pas de Calais: Boulogne-sur-Mer, 50.72555°N 1.61472°E, Oct 1983, 2 adults sex unknown (AMNH_PBI 00209578, AMNH_PBI 00209579) (MNHN).

Poland: Mielnik, 52.33108ºN 23.04596ºE, 141 m, 17 Jun 1987, Gorczyca, *Salicion albae* (habitat), 2 adults sex unknown (AMNH_PBI 00206847, AMNH_PBI 00206848) (AMNH).

Romania: Sinaia, 45.33083°N 25.55527°E, 793 m, Aug 1960, Sienkiewicz, 1 adult sex unknown (AMNH_PBI 00206845) (AMNH).

Sweden: Jamtlands: Frösön, 63.16666°N 14.58194°E, 305 m, 27 Jul 1941, Ossiannilsson, 2♀♀ (AMNH_PBI 00212498, AMNH_PBI 00212499) (MZLU). Frösön, 63.16666°N 14.58194°E, 299 m, 27 Jul 1941, Ossiannilson, 1 adult sex unknown (AMNH_PBI 00206843) (AMNH); 16 Aug 1942, Ossiannilsson, 1 adult sex unknown (AMNH_PBI 00206841) (AMNH). Sýter, 60.34555°N 15.75833°E, 172 m, 02 Sep–04 Sep 1944, Ossiannilsson, 1 adult sex unknown (AMNH_PBI 00206844) (AMNH). Scania: Fagelsang, 56.417350°N, 13.192663°E, 67 m, 26 Jul 1939, Ossiannilsson, 3♀♀ (AMNH_PBI 002124954♂ AMNH_PBI 00212497) (MZLU), 1 adult sex unknown (AMNH_PBI 00206842) (AMNH), 1♂ (AMNH_PBI 00212494) (MZLU). Stockholm: Stockholm: Ekerý: Drottningholm, 59.32472°N 17.889341°E, 14 m, 19 Aug 1940, Kemner, 1♀ (AMNH_PBI 00212503) (MZLU). Nysýtra, Oxdjupet tr., 59.74194°N 17.17194°E, 14 m, 27 Aug 1975, Ossiannilsson, 1♂ (AMNH_PBI 00212504) (MZLU). Uppsala: Ultuna, 59.85805°N 17.64444°E, 170 m, 15 Aug 1939, Kemner, 2♀♀ (AMNH_PBI 00212500, AMNH_PBI 00212501) (MZLU).

United Kingdom: England: Bedford: Renhold, 52.1625°N 0.4025°E, 56 m, 04 Aug 1975, Leston, 2 adults sex unknown (AMNH_PBI 00206849, AMNH_PBI 00206850) (AMNH). Bedfordshire: Rowney Warren, 52.05054°N 0.35944°W, 73 m, 12 Aug 1975, Leston, 1 adult sex unknown (AMNH_PBI 00206851) (AMNH). Devon: Torrington, 50.95194°N 4.13666°E, 96 m, 13 Jul 1957, 4 adults sex unknown (AMNH_PBI 00204187-AMNH_PBI 00204188, AMNH_PBI 00204190 AMNH_PBI 00204191) (BMNH). Dorset: Lulworth: Bransgore: Christchurch, 50.754769ºN 2.346513ºW, 15 m, G. C. C., 1 adult sex unknown (AMNH_PBI 00204245) (BMNH). Snowdonia, Aug 1912, Butler, 1 adult sex unknown (AMNH_PBI 00204189) (BMNH).

Diagnosis
Dicyphus constrictus is recognized by the following combination of characters: macropterous and brachypterous males (Fig. 2) and females. Body length 4.26–4.99 mm in macropterous males; body length reported by Wagner (1970) for brachypterous males 3.6–4.4 mm; 4.77–4.80 mm in macropterous and 3.38–4.36 mm in brachypterous females; pale body with contrasting dark-brown markings (Fig. 2); corium usually with less than three pairs of spots; AI mostly stramineous with subbasal and subapical brown annulations, latter often pale; interocular distance greater than eye width in macropters, subequal in brachypters; AI greatly elongate, *c*. 2× interocular distance; AII >1.5× longer than posterior width of pronotum in males, 1.20× in females; shiny dark-brown band on propleuron short, not extending beyond posterior margin of callosite region; callosite region generally >2× longer than collar along midline; disk region generally <1.2× longer than callosite region along midline; apophysis of left paramere robust and short (Fig. 23C); endosoma with three membraneous lobes, with pair of large weakly arcuate endosomal lobal sclerites (Fig. 12F).

Redescription
Males. Macropters and brachypters known (only macropters examined).

Coloration (Fig. 2): Dorsum mostly stramineous, with contrasting dark-brown markings, without red highlighting. *Head:* frons+vertex with a broad, X-shaped dark-brown to fuscous marking; clypeus dark brown, with lateral margins sometimes paler; mandibular plates stramineous; maxillary plates dark brown; posteromedial region of vertex yellowish brown to orange; postocular margins of head shiny dark brown; gula and bucculae stramineous. *Antennae:* AI mostly stramineous, with subbasal and subapical medium-brown annulations, extreme tip sometimes whitish, sometimes more broadly red; AII mostly stramineous, with narrow medium brown annulation, and distal 1/4 medium brown, sometimes with tip whitish; AIII base stramineous, remainder medium brown; AIV uniformly medium brown. *Pronotum:* collar white to stramineous, translucent, sometimes darker laterally; calli pale orange to light brown with lateral darker markings extending to propleuron; disk stramineous pale brown, sometimes translucent, humeral angles darker brown. *Thoracic pleura and sterna:* mostly stramineous to light pale brown, with short transverse shiny dark-brown marking, mostly anterior, not extending beyond posterior margin of callosite region in lateral view; mesobasisternum uniformly medium brown, almost shiny; mesepimeron and metepisternum stramineous, sometimes with evaporative area embrowned. *Mesoscutum:* mostly yellow to orange, sometimes with embrownment. *Scutellum:* lateral angles stramineous with a broad yellow to orange stripe along midline. *Hemelytra:* translucent, mostly very light brown, usually with less than three pairs of obscure pale reddish brown to light-brown spots, at corial fracture, middle of apical margin of endocorium, and tip of cuneus generally obsolete; corium and clavus without red or brown spotting medially; membrane veins brown, without red highlighting. *Abdomen:* venter mostly stramineous. region of pronotum glossy; pronotal disk dull; hemelytra dull and translucent.

Structure: Head: interocular distance 1.02–1.21× greater than eye width in macropters. *Antennae:* AI 1.88–2.25× longer than interocular distance in macropters; AII 1.52–1.80× longer than posterior width of pronotum in macropters. *Male genitalia:* apophysis of left paramere robust and short, spatulate apex moderately long, with outer margin rounded, without teeth (Fig. 23C); aedeagus with three well-developed endosomal lobes, with two large weakly arcuate lobal sclerites (Fig. 12F).

Females. Macropters and brachypters known. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.12–1.25× greater than eye width in macropterous and 1.05–1.25× greater that eye width in brachypterous females; *Antennae:* AI 1.87–1.95× longer than interocular distance in macropters, 1.68–2.03× in brachypters; AII 1.21–1.27× longer than posterior pronotal width in macropters, 1.45–1.59× in brachypters. *Pronotum:* disk region 1.15–1.27× longer than callosite region in macropters, 0.69–0.96× in brachypters.

Measurements

See Table 4.

Distribution

Kerzhner & Josifov (1999) reported that *D. constrictus* is broadly distributed in the Western Palaearctic, from Ireland in the west to Azerbaijan in the east, and from Norway in the north and possibly as far south as Italy. We confirmed the identity of this species from Bulgaria, Czech Republic, Germany, France, Finland, Italy, Poland, Romania, Sweden, Switzerland, the Netherlands and the United Kingdom. The distribution map for these latter records are given in Fig. 35.

Host plants

Dicyphus constrictus has been collected on *Aconitum* sp. (Ranunculaceae), *Lychnis* sp. (Caryophyllaceae), *Galeopsis* sp. (Lamiaceae), *Melandrium* sp. (Caryophyllaceae), *Stachys silvatica* L. (Lamiaceae), *Salvia* sp. (Lamiaceae) and *Urtica* sp. (Urticaceae) (Wagner, 1964, 1974; Wachmann, Melber & Deckert, 2004). Josifov & Simov (2008) described a new subspecies of *D. constrictus* (*D. constrictus eduardi*), and reported its association with *Geranium sylvaticum* L. and *Geranium macrorrhyzum* L. (Geraniaceae) in karstic habitats.

Remarks

Dicyphus constrictus is a moderately sized and pale species, with limited darker markings on the dorsum. It is best characterized by the elongate first and second antennomeres, with the latter significantly longer than the posterior width of the pronotum in males and brachypterous females. This species is very similar to *D. epilobii* and *D. josifovi* and it is differentiated from them by: the more stramineous first antennomere (cf. reddish) (Fig. 2), the larger spatulate region of the apophysis of the left paramere (Figs 23C, 10C–D, 23E) and the smaller endosomal lobal sclerites (Figs 12F, 13A, 14B). *Dicyphus constrictus* specimens, particularly, can have a dark-brown band on the propleuron and X-shaped marking on the frons+vertex. However, we examined specimens of *D. epilobii* (see AMNH_PBI00219764) that are darker than the other two species, and could only be separated by the more uniformly reddish first antennal segment. Wagner (1951) placed *D. constrictus* within his *pallidus* species-group, which included species (i.e. *D. pallidus*, *D. flavoviridis* and *D. constrictus*) with AII >1.5× longer than the posterior width of the pronotum in males and the callosite region *c*. 2× longer than collar width. All the males of *D. constrictus* that we measured had the AII:posterior width of pronotum >1.5×, but in some individuals the ratio of the callosite region:collar width is <2×, overlapping with *D. errans* and *D. epilobii*. We predict that

D. constrictus will group within the *errans* clade when mtDNA sequence data becomes available.

Josifov & Simov (2008) described a new subspecies, *Dicyphus constrictus eduardi*, from Bulgaria based on morphometric characters. The authors remarked that previous Bulgarian records of *Dicyphus constrictus* are those of the new subspecies. We did not examine specimens of the new subspecies and were thus unable to test its validity. Matocq & Streito (2013) described a dark morph of *D. constrictus* that differs with the stramineous specimens we have described in the present work.

Dicyphus deylamanus Linnavuori & Hosseini, 1999 (Figs 30, 35)

Dicyphus deylamanus Linnavuori & Hosseini, 1999: 156 (original description).

Material examined

Iran: Gilan, Deylaman, 36.88599°N 49.9085°E, 1431 m, 16 Aug 1998, Hosseini & Linnavuori, 1♀ paratype (UNSW_ENT00026529) (College of Agriculture, Rasht, Iran).

Diagnosis

Dicyphus deylamanus is recognized by the following combination of characters: macropterous males and females only known; large species, body length 5.0–5.25 mm in males, 4.75–5.0 mm in females (Linnavuori & Hosseini, 1999). Only one female examined. Extensively dark species (Fig. 30), with most of head, including clypeus, mandibular and maxillary plates, genae and gula shiny black; frons+vertex with broad X-shaped black marking bounded by stramineous lateral regions; antennae mostly dark brown to black, with base and apices of AI and base of AII narrowly stramineous; pronotum nearly all black, aside from pale yellow midline on collar and callosite region; thoracic pleura mostly black, with ventral margin of propleura and evaporative bodies bounding metathoracic spiracle stramineous; mesoscutum and scutellum with midline broadly dark brown to black, with lateral angles of latter stramineous; hemelytra bicoloured, with clavus, endocorium and tip of cuneus dark brown, exocorium mostly stramineous three pairs of dark-brown spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; membrane veins embrowned; aside from two rows of black spots on femora, legs also with base of tibiae narrowly dark brown to black; female abdominal venter shiny dark brown to black. Left paramere moderately long with spatulate region not greatly expanded and tapered; endosoma with two large, asymmetrical and weakly arcuate lobal sclerites (Linnavuori & Hosseini, 1999).

Measurements

See Table 4.

Distribution

Know only to Iran (Linnavuori & Hosseini, 1999) (Fig. 35).

Host plants

Known from *Stachys* sp. (Lamiaceae) (Linnavuori & Hosseini, 1999).

Remarks

Linnavuori & Hosseini (1999) described *Dicyphus deylamanus* from a single location in northeastern Iran. The authors compared this species and the western Palaearctic species *D. errans*, highlighting the shared black thorax and antennae of the Iranian species and occasional specimens of *D. errans*. In the material we examined, we found that *D. deylamanus* is always darker. Furthermore, the near black lateral and ventral facies of the head of *D. deylamanus* are unlike any other *Dicyphus* species known to us, and reminds us of the near black head of the Indian species, *Dicyphus regulus* Distant. We were able to observe a female paratype from the University of Rasht, Iran (courtesy of Reza Hosseini), upon which we based much of the above diagnosis, supplemented with details from the original description. We concur with Linnavuori & Hosseini (1999) that *D. deylamanus* is a distinct species.

Dicyphus eckerleini Wagner, 1963 (Figs 12G, 23D, 30, 35)

Dicyphus eckerleini Wagner, 1963: 59 (original description); Schuh, 1995: 489 (world catalogue); Linnavuori & Hosseini, 1999: 158 (Iran); Kerzhner & Josifov, 1999: 22 (Palaearctic catalogue).

Material examined

Bulgaria: Rhodopene, 41.5°N 24.5°E, 1960, M. Josivof, 1♂ (AMNH_PBI 00206764) AMNH, 1♀ (UNSW_ENT 00045428), 1♂ (UNSW_ENT 00045427) (HNHM).

Diagnosis

Dicyphus eckerleini is recognized by the following combination of characters: only macropterous males and females; body length 4.14–4.19 mm in males, 4.19 mm in females; interocular distance longer than eye width; AI mostly red in males, more stramineous medially in females; AI elongate, *c.* 1.5× longer than interocular distance; AII length subequal to posterior width of pronotum; shiny dark-brown band on propleuron short, not extending beyond posterior margin of callosite region; callosite region >1.8× longer than collar along midline; pronotal disk region *c.* 1.5× longer than callosite region; apophysis of left paramere robust and short (Fig. 23D); endosoma with two membraneous lobes, each with weakly arcuate spicule, lobal sclerites similar size (Fig. 12G).

Redescription
Males. Macropters only known.

Coloration (Fig. 30): Dorsum mostly light yellowish brown, with contrasting dark-brown markings. *Head:* frons+vertex with a short X-shaped reddish brown marking; clypeus dark brown; mandibular plates stramineous; posteromedial region of vertex yellowish brown to orange; postocular margins of head shiny dark brown; gula and bucculae mostly brown. *Antennae:* AI mostly red, with subbasal brown annulation, tip stramineous; AII with base narrowly whitish, dark-brown annulation on proximal and distal 1/3rd, with medial stramineous band, sometimes with red highlighting. *Pronotum:* collar white to stramineous, sometimes darker laterally; calli pale orange to light brown with dusty darker markings medially; disk stramineous to whitish. *Thoracic pleura and sterna:* propleura stramineous with transverse medium to dark-brown band, with ventral margin whitish; mesobasisternum uniformly medium brown, shiny; mesepimeron stramineous; metepisternum dull light brown. *Mesoscutum:* mostly dark orange-brown, sometimes little paler laterally. *Scutellum:* lateral angles broadly stramineous with a broad dark reddish brown stripe along midline. *Hemelytra:* translucent, mostly very light brown, usually with three pairs of obscure red spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; membrane veins mostly red. *Abdomen:* venter mostly medium brown with stramineous highlighting.

Structure: Head: interocular distance 1.19–1.26× greater than eye width in macropters. *Antennae:* AI 1.45–1.58× longer than interocular distance in macropters; AII 1.02–1.17× longer than posterior width of pronotum in macropters. *Pronotum:* callosite region *c.* 1.8× longer than collar; calli short; pronotal disk *c.* 1.5× longer than callosite region. *Male genitalia:* left paramere with robust and short apophysis (Fig. 23D); aedeagus with two well-developed endosomal lobes, each lobe with a weakly arcuate endosomal lobal sclerites subequal in size (Fig. 12G).

Females. Macropters only known. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.43× greater than eye width. *Antennae:* AI 1.27× longer than interocular distance; AII 0.90× longer than posterior pronotal width. *Pronotum:* disk region 1.27× longer than the calli region.

Measurements
See Table 4.

Distribution
Wagner (1963) originally described *Dicyphus eckerleini* from Turkey. Wagner (1970) subsequently documented it from Bulgaria and Lebanon, and Kerzhner & Josifov (1999) reported it from Syria. This species has also been documented from Iran (Linnavuori & Hosseini, 1999) and Italy (Tavella & Goula, 2001). We examined material from Bulgaria (Fig. 35).

Host plants
Known from *Cirsium* sp. (Asteraceae), *Epilobium hirsutum*, *Galeopsis tetrahit* L. (Lamiaceae) and *Geranium* spp. (Geraniaceae) (Wagner, 1970; Tavella & Goula, 2001).

Remarks
See Remarks' section of *Dicyphus alkannae. Dicyphus eckerleini* is grouped in our taxonomic key with species that have a pair of large endosomal lobal sclerites and the apophysis of the left paramere is robust and short. Externally, this species is very similar to *D. argensis* and *D. hyalinipennis* (Fig. 3), and we differentiate it from these two species by its symmetry of the endosomal lobal sclerites (Figs 12B, G, 14A). Wagner (1963) separated *D. eckerleini* on the basis of morphometric characters, but we found his characters to overlap in many species of his *hyalinipennis* species group. We lacked mtDNA sequence data for *D. eckerleini* and have maintained it as a distinct species based on the endosomal lobal sclerites.

Dicyphus epilobii Reuter, 1883
(Figs 2, 13A, 23E, 36)

Dicyphus epilobii Reuter, 1883: 52 (original description); Carvalho, 1958: 156 (world catalogue); Schuh, 1995: 490 (world catalogue) Kerzhner & Josifov, 1999: 22 (Palaearctic catalogue).

Material examined
Austria: Neustadt, May 1872, 1 adult sex unknown (AMNH_PBI 00213952) (HNHM).

Bulgaria: Plovdiv: Asenovgrad, 42.01337°N 24.87844ºE, 227 m, 29 Sep 1961, Josifov, 1 adult sex unknown (AMNH_PBI 00210765) (ZISP); 1♀, (Not laballed) (RAS).

France: Bonneville, 4 Sep 1989, Duverger, 1 adult sex unknown (AMNH_PBI 00209583) (MNHN).

Italy: Monfalcone, 45.84555°N 13.53277°E, 84 m, 1885, Kensch, 1 adult sex unknown (AMNH_PBI 00213953) (HNHM). Piemonte: Torino: Caluso, 45.31278ºN 7.83889ºE, 291 m, ex. *Epilobium hirsutum*, 1 Aug 2008, Sanchez, 2♂♂, 2♀♀(IMIDA_ENT 00000163-IMIDA_ENT 00000166); Coazze (Giaveno), 45.04667ºN 7.30722ºE, 631 m, ex. *Epilobium hirsutum*, 15 Aug 2008, Sanchez, 2♂♂, 2♀♀ (IMIDA_ENT 00000159-IMIDA_ENT 00000162). Liguria: Orco Feglino, 44.21250ºN 8.32555ºE, 127 m, ex. *Epilobium hirsutum*, 13 Aug 2008, Sanchez, 2♂♂, 2♀♀(IMIDA_ENT 00000167-IMIDA_ENT 00000170).

Netherlands: Zuid-Holland: Nieuwkoop, 52.15361°N 4.78333°E, 15 Aug 1951, Lindberg, 2♂♂ (AMNH_PBI 00209450, AMNH_PBI 00209452), 3♀♀ (AMNH_PBI 00209444, AMNH_PBI 00209451, AMNH_PBI 00209453) (MZH). Henmstede, 52.35277°N 4.62138°E, 2 m, 28 Jul 1953, Meurer, 1 adult sex unknown (AMNH_PBI 00206885) (AMNH). Wageningen, Gelderland, 51.5804ºN 5.3949W, 291 m, ex. *Epilobium hirsutum*, 21 July 2006, Sanchez, 6♂♂, 6♀♀ (IMIDA_ENT 00000353-IMIDA_ENT 00000365).

Sweden: Hýsselholm: Ignaberga, 56.12305°N 13.83166°E, 49 m, 29 Jul 1932, Kemner, 4♀♀ (AMNH_PBI 00206877) (AMNH). Lund: ýstra Mýllavýgen, 55.66361°N 13.35694°E, 50 m, 21 Jul 1989, Danielsson, 3 adults sex unknown (AMNH_PBI 00212439-AMNH_PBI 00212441) (MZLU). Brunnby, 59.83083°N 13.53277°E, 31 m, 2 Aug 1962, Ossiannilsson, 2 adults sex unknown (AMNH_PBI 00212437, AMNH_PBI 00212438) (MZLU). Karlskrona, 56.16055°N 15.58666°E, 18 Jul 1972, Gyllensvard, 1 adult sex unknown (AMNH_PBI 00212442) (MZLU). Kýrret, 57.45472°N 11.92694°E, 7 m, 6 Aug 1950, Tjeder, 1 adult sex unknown (AMNH_PBI 00212443) (MZLU). Kývlinge, 55.79166°N 13.11027°E, 13 m, 30 Jul 1938, 1 adult sex unknown (AMNH_PBI 00212444) (MZLU). Simrishamn: Vitemölla, 55.69888°N 14.20666°E, 4 m, 24 Jul 1947, 1 adult sex unknown (AMNH_PBI 00212436) (MZLU); 25 Jul 1947, 2 adults sex unknown (AMNH_PBI 00212434, AMNH_PBI 00212435) (MZLU). Västergötland: Rävlunda: Having, 55.71667ºN 14.15000°E, 26 Jul 1959, Gyllensvard, 2♂♂ (AMNH_PBI 00206876) (AMNH).

United Kingdom: England: Bedford: Maulden Wood beds, 52.032118°N 0.437167°W, 67 m, 24 Jul 1975, Leston, 1♂ (AMNH_PBI 00206880) (AMNH). Renhold, 52.1625°N 0.4025°E, 56 m, 21 Jul 1975, Leston, 1♂ (AMNH_PBI 00206882) (AMNH); Flitwick Moor Beds, 52.004604°N 0.497946ºW, 80 m, 5 Aug 1975, Leston, 1♂, (AMNH_PBI 00206879) (AMNH); 13 Aug 1975, Leston, 1♂ (AMNH_PBI 00206883) (AMNH); Leston, 1♂, (AMNH_PBI 00206881) (AMNH). Buckinghamshire: Chiltern Hills, Aylesbury, 51.78916°N 0.71694°E, 170 m, 16 Aug 1915, 1 adult sex unknown (AMNH_PBI 00206884) (AMNH). Hertfordshire: Rickmansworth, 51.63861°N 0.46916°E, 53 m, 1 Aug 1948, Leston, 1 adult sex unknown (AMNH_PBI 00206878) (AMNH). London: Buckham, S. of London, 51.14904ºN 0.97869ºW, 107 m, 30 Jul 1951, Lindberg, 2♂♂ (AMNH_PBI 00209447, AMNH_PBI 00209454) (MZH).

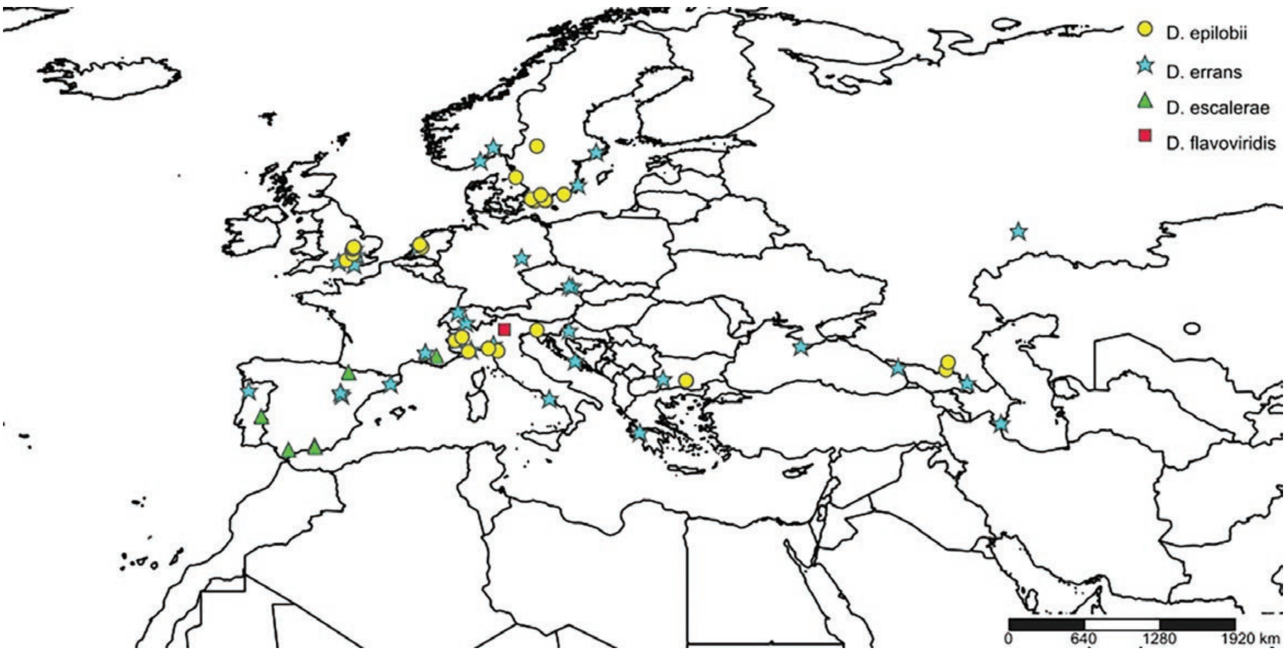

Figure 36. Distribution of the specimens examined: *D. epilobii*, *D. errans*, *D. escalerae* and *D. flavoviridis*.

Diagnosis

Dicyphus epilobii is recognized by the following combination of characters: macropters only; body length 4.14–4.93 mm in males and 4.30–5.23 mm in females; pale body with minor reddish brown to light brown markings (Fig. 2); frons+vertex with a V-shaped medium brown marking, sometimes marking very faint; AI mostly broadly red, sometimes with narrow darker brown annulation; interocular distance longer than eye width in macropters in both sexes; AI elongate, >1.4× interocular distance in both sexes; AII >1.4× longer than posterior width of pronotum in males, raging 1.0–1.4× in females; callosite region <1.9× longer than collar along midline; disk >1.2× longer than callosite region along midline in both sexes; apophysis of left paramere moderately elongate, with spatulate region weakly expanded, outer margin without ornamentation (Fig. 23E); endosoma with three membraneous lobes, the two lateral lobes with a weakly arcuate sclerite each (Fig. 13A).

Redescription

Males. Macropters only known.

Coloration (Fig. 2): Dorsum mostly stramineous, often with medium brown markings. *Head:* frons+vertex with a V-shaped medium-brown marking, sometimes marking very faint, posterior region of head often more orangish yellow; postocular margins either stramineous or with medium-brown band extending to lateral regions of gula; clypeus, maxillary plate and bucculae usually medium brown, sometimes with stramineous highlighting, rarely more stramineous generally; mandibular plate stramineous; gula mostly stramineous. *Antennae:* bicoloured; AI mostly pale red, sometimes with darker reddish brown annulation subbasally, apex stramineous; AII mostly stramineous, with short subbasal and elongate distal medium brown annulations, with base narrowly stramineous; AIII and AIV mostly medium brown, usually with base of AIII narrowly stramineous. *Pronotum:* collar whitish, sometimes translucent; calli stramineous to yellow, without contrasting brown markings; disk stramineous with whitish highlighting, often translucent, humeral angles rarely weakly embrowned. *Thoracic pleura and sterna:* propleuron mostly stramineous, sometimes with whitish highlighting, sometimes with medium-brown marking medially on anterior half; mesobasisternum uniformly orange brown to light brown, rarely darker brown; mesepimeron whitish to stramineous; metepisternum and MTG stramineous. *Mesoscutum:* uniformly stramineous to orange. *Scutellum:* anterolateral angles stramineous, with orange to orangish brown midline. *Hemelytra:* translucent, with faint pale stramineous hue, usually with three small reddish brown to dark brown spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; clavus sometimes with reddish highlighting; medial margin of endocorium post-commissure often narrowly red to reddish brown; corium also with minor red to reddish brown spots, often associated with setae; membrane veins reddish or brown. *Abdomen:* venter either uniformly stramineous to light brown, sometimes lateral regions of basal segments weakly embrowned.

Structure: Head: interocular distance 1.02–1.63× greater than eye width in macropters. *Antennae:* AI elongated, 1.68–2.18× longer than interocular distance in macropters; AII 1.42–1.74× longer than posterior width of pronotum in macropters. *Pronotum:* callosite region 1.47–2.04× longer than collar; calli short; pronotal disk 1.20–1.57× longer than callosite region. *Male genitalia:* genital opening of pygophore oval, without tergal processes; apophysis of left paramere moderately elongate, with spatulate region weakly expanded, outer margin without ornamentation (Fig. 23E); aedeagus with three well-developed endosomal lobes, lateral lobes each with a weakly arcuate lobal sclerites subequal in size (Fig. 13A).

Females. Macropters only known. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.16–1.64× greater than eye width. *Antennae:* AI 1.44–1.88× longer than interocular distance; AII 1.14–1.36× longer than posterior pronotal width. *Pronotum:* disk region 1.25–1.51× longer than callosite region.

Measurements

See Table 4.

Distribution

Distributed in Central Europe and Italy (Wagner 1964, Kerzhner & Josifov (1999). We examined specimens of *D. epilobii* from Austria, Bulgaria, France, Italy, The Netherlands, Sweden and the United Kingdom (Fig. 36).

Host plants

Dicyphus epilobii is known from *Epilobium hirsutum* and *Cucubalus* sp. (Caryophyllaceae) (Wagner, 1964). Ehanno (1960, 1968) also documented *D. epilobii* from *Mercurialis annua* L. (Euphorbiaceae) and *Urtica* sp. (Urticaceae) (see also Schuh 1995). Ingegno *et al.* (2008) collected *D. epilobii* on *Antirrhinum majus L.* (Scrophulariaceae), *Calendula officinalis* L. (Asteraceae), *Circaea lutetiana* (L.) Georgi (Onagraceae), *Digitalis grandiflorum*, *E. hirsutum*, *Galeopsis tetrahit* and *Geranium pyrenaicum Burm.* (Geraniaceae).

Remarks

See also Remarks' section for *D. constrictus* and *D. josifovi*. The specimens of *D. epilobii* that we examined exhibited considerable variation in the darker markings that contrast with the stramineous ground colour. Most specimens we observed are mostly pale, and the V-shaped brown marking on the head and the transverse brown band on the propleuron are often very faint. This could be interpreted as an artefact of specimen preservation; however, we discount this as we have collected fresh material that have a pale hue. Regardless, the presence of a broadly reddish AI in this species is found in all specimens that we examined. This consistently differentiates *D. epilobii* from *D. constrictus*. In addition, *D. epilobii* is only known from macropterous males and females, whereas *D. constrictus* is also represented by brachypterous males and females. In the taxonomic key above, *D. epilobii* is keyed out in the same couplet as *D. errans*, where the latter species is generally darker, including most of AII, the shaft of the left paramere is more expanded (cf. weakly expanded in *D. epilobii*) (Fig. 23E, F), and the endosomal lobal sclerites are asymmetrical (cf. subequal in *D. epilobii*) (Fig. 13A, B). *Dicyphus epilobii* is also very similar to *D. josifovi*, although the pale yellow colour of *D. epilobii* contrasts with the olivaceous green of *D. josifovi* (Fig. 2). The differences in the genitalia are minor; the apophysis of the left paramere is a little more expanded in *D. epilobii* than in *D. josifovi* (Figs 10C–D, 23E), and the pair lobal sclerites are straighter in *D. epilobi* than in *D. josifovi* (Figs 13A, 14B). In spite of these minor morphological differences, the two species clustered independently in the phylogenetical analyses (Figs 24, 25).

Dicyphus errans (Wolff, 1804)
(Figs 2, 13b, 23f, 36)

Gerris errans Wolff, 1804: 161 (original description).
Capsus collaris Fallén, 1807: 103 (original description); Herrich-Schaeffer (1836): 52 (synonymy).
Capsus collaris longicollis Fallén, 1829: 125 (original description; subspecies).
Dicyphus errans: Carvalho, 1958: 196; Schuh, 1995: 490 (catalogue); Kerzhner & Josifov, 1999: 22 (Palaearctic catalogue).

Material examined
Azerbaijan: Between Dzhoni and Tuli: Talysh: Lenkoranskiy uezd: 38.75371ºN 48.84988ºE, 20 m below sea level, 31 Jul 1931, Varshalovich, 1♀ (AMNH_PBI 00341222) (ZISP).

Bulgaria: Kjustendil: Rila: Rila, silva frond., 42.12722°N 23.13361°E, 550 m, 6 Aug 1939 12 Aug 1939, Lindberg, 1♀ (AMNH_PBI 00208615) (MZH). Morava, 43.50833°N 25.14972°E, 154 m, 21 Sep 1943, Stehlik, 1 adult sex unknown (AMNH_PBI 00206900) (AMNH); 21 Sep 1943, Stehlik, 1 adult sex unknown (AMNH_PBI 00206898) (AMNH); 21 May 1944, Stehlik, 1 adult sex unknown (AMNH_PBI 00206899) (AMNH); 12 Sep 1948, Stehlik, 1 adult sex unknown (AMNH_PBI 00206901) (AMNH).

Croatia: Split, 43.50666°N 16.44222°E, 13 m, 20 Jul 1954, Hellén, 2♀♀ (AMNH_PBI 00208617, AMNH_PBI 00208627) (MZH). Zagreb, 45.815°N 15.97833°E, 242 m, 30 Sep 1983, 1 adult sex unknown (AMNH_PBI 00213955) (HNHM).

Czech Republic: Moravia: Vladislav, 49.21027°N 15.98888°E, 389 m, 27 Aug 1946, Stehlik, 1♀ (AMNH_PBI 00206890) (AMNH). CSR Morava: Udoli: Chvojnice, 49.14128ºN 16.23650ºE, 320 m, 21 Sep 1943, Stehlik, 1♂ (AMNH_PBI 00206898), 1♀ (AMNH_PBI 00206900) (AMNH).

France: Vaucluse: Lafare: Lafare, 44.14638°N 5.05222°E, 166 m, 19 Sep 1965, Carayon, 3 adults sex unknown (AMNH_PBI 00209584-AMNH_PBI 00209586) (MNHN).

Greece: Peloponnisos: Road Patras–Pirgou km 9, 38.0728°N 21.3752°E, 52 m, ex. *Solanum nigrum* L (Solanaceae), 10 Jun 2007, Sanchez & Cassis, 5♂♂, 5♀♀ (IMIDA_ENT 00000476-IMIDA_ENT 00000485) (IMIDA).

Georgia: Sokhumi (Sukhum): Chernomorskaya Government, 43.00153ºN 41.023415ºE, 8 m, 31 Oct 1927, Zimin, 1♀ (AMNH_PBI 00210755) (ZISP). Lagodekhi: Zakatal'skiy okrug: Tiflis Government, 41.81863°N 46.278131°E, 434 m, 21 Oct 1896, Mlokosevich, 1♂ (AMNH_PBI 00210758) (ZISP); Lagodekhi: Zakatal'skiy okrug: Tiflis Government, 41.81863°N 46.278131°E, 434 m, 21 Oct 1896, Mlokosevich, 1♀ (AMNH_PBI 00210759) (ZISP).

Germany: Sachsen: Leipziger Land: Leipzip, 51.33944°N 12.37111°E, 110 m, 1♀ (AMNH_PBI 00208616) (MZH).

Italy: Campania: Positano, 45.41611°N 7.61667°E, 37 m, 7 Aug 1925, El. Miram, 1 adult sex unknown (AMNH_PBI 00210757) (ZISP). Piemonte: Torino: Pont Canavese, 45.2458ºN 7.3700ºE, 426 m, ex. *Lagenaria* sp., 1 Aug 2006, Sanchez & Pennaroli, 3♂♂, 3♀♀ (IMIDA_ENT 00000387-IMIDA_ENT 00000392); ex. *Solanum lycopersicum*, 1 Aug 2006, Sanchez & Pennaroli, 2♂♂, 4♀♀ (IMIDA_ENT 00000387-IMIDA_ENT 00000392) IMIDA. Villarbasse, 45.04500ºN 7.46500ºE, 396 m, ex. *Cucurbita maxima*, 6 Aug 2006, Sanchez & Pennaroli, 2♂♂, 4♀♀ (IMIDA_ENT 00000387-IMIDA_ENT 00000392) IMIDA. Parma: Parma, 44.75667ºN

10.23278°E 105 m, ex. *Solanum nigrum*, 18 Aug 2008, Sanchez & Pennaroli, 3♂♂, 3♀♀ (IMIDA_ENT 00000393-IMIDA_ENT 00000398) IMIDA. Liguria: Sanda, 44.36889°N 8.52833°E, 230 m, ex. *Solanum nigrum*, 11 Aug 2008, Sanchez, 3♂♂, 3♀♀ (IMIDA_ENT 00000399-IMIDA_ENT 00000404) (IMIDA).

Netherlands: Zuid-Holland: Leiden, 52.16083°N 4.49000°E, 3 m, 15 Sep 1950, Lindberg, 3 adults sex unknown (AMNH_PBI 00208610, AMNH_PBI 00208620, AMNH_PBI 00208623) (MZH).

Norway: Aust-Agder: Risor, 58.71638°N 9.23055°E, 52 m, 24 Sep 1913, Warloe, 1♂ (AMNH_PBI 00208622) (MZH). Buskerud: Drammen, 59.74500°N 10.21333°E, 11 m, 24 Aug 1924, Warloe, 1 adult sex unknown (AMNH_PBI 00208626) (MZH).

Portugal: Porto, Gerez, 41.24888°N 8.40416°W, 246 m, 31 May 1959, Lindberg, 1♂ (AMNH_PBI 00208604), 1♂ (AMNH_PBI 00208605) (MZH).

Romania: Tulcea: Greci, 54.19138°N 28.25055°E, 47 m, 2 Jul 1954, Sienkiewicz, 1 adult sex unknown (AMNH_PBI 00206773) (AMNH).

Russia: Samara Prov.: Krasnaya Glinka, 25 km of Samara: 53.38972°N 50.17286°E, 76 m, 24 Jul 1896, Lubischev, 1♀, (AMNH_PBI 00210756) (ZISP).

Spain: Cataluña: Barcelona: Montseny, 41.760°N 2.395°E, 510 m, 23 Sep 1989, Silfverberg, 2♂♂ (AMNH_PBI 00208563, AMNH_PBI 00208612) (MZH). Teruel: Calamocha, 40.91972°N 1.30528°W, 900 m, ex. *Solanum lycopersicum*, 7 June 2006, Sanchez, 5♂♂, 5♀♀ (IMIDA_ENT 00000365-IMIDA_ENT 00000374). Zaragoza: Daroca, 41.108611°N 1.41417°W, 797 m, ex. *Solanum lycopersicum*, 7 June 2006, Sanchez, Martínez & La Spina, 2♂♂, 4♀♀ (IMIDA_ENT 00000455-IMIDA_ENT 00000460) (IMIDA).

Sweden: Kalmar: Oland: Borgholm, 56.87916°N 16.65583°E, 9 m, 5 Sep 1944, Ossiannilsson, 1 adult sex unknown (AMNH_PBI 00212514) (MZLU). Stockholm: Bergianska trädgården: Bergianska trädgården, 59.369825°N 18.046053°E, 4 Sep 1940, Ossiannilsson, 5 adults sex unknown (AMNH_PBI 00212507-AMNH_PBI 00212511) (MZLU); 1♀ (AMNH_PBI 00206893) (AMNH); 1♂ (AMNH_PBI 00206894) (AMNH); 29 Aug 1940, Ossiannilson, (AMNH_PBI 00208613) (MZH), 1 adult sex unknown, (AMNH_PBI 00212512), 1♂ (AMNH_PBI 00208619) (MZH), 1 adult sex unknown, (AMNH_PBI 00212512) (MZLU). Uppsala: Uppsala: Berg. Trýdg, 29 Aug 1940, Ossiannilsson, 1♂ (AMNH_PBI 00208619), 1♀ (AMNH_PBI 00208613) (MZH). Flottsund, 9 Sep 1961, Ossiannilsson, 1 adult sex unknown (AMNH_PBI 00212513) (MZLU).

Switzerland: Solothurn: Lebern: Solothurn, 47.20694°N 7.53305°E, 365 m, Jul 1953, Lindberg, 2♀♀ (AMNH_PBI 00208624, AMNH_PBI 00208628) (MZH). Wallis: Friesch, 46.40305°N 8.13472°E, 1050 m, 13 Jul 1953, Lindberg, 1♀ (AMNH_PBI 00208618) (MZH).

Ukraine: Crimea: Sevastopol, 44.61027°N 33.62722°E, 188 m, 26 Sep 1910, Pliginskiy, 1 adult sex unknown (AMNH_PBI 00213954) (HNHM).

United Kingdom: England: Hertfordshire: Boxhill, S of London, 51.76333°N 0.47°E, 131 m, 21 Jul 1951, Lindberg, 1 adult sex unknown (AMNH_PBI 00208611) (MZH). Boxhill, pr. London, 51.76333°N 0.47°E, 131 m, 2 Oct 1955, Lindberg, 1 adult sex unknown (AMNH_PBI 00208621) (MZH). London: Hampstead Heath, 51.56583°N 0.16055°W, 87 m, 17 Jun 1949, Leston, 1♂ (AMNH_PBI 00206888) (AMNH). Romsey: Kents Oak: Awbridge, 51.01722°N 1.54555°E, 82 m, 1962, 1 adult sex unknown (AMNH_PBI 00204247) (BMNH). West Sussex.: Broadwater For., 50.828768°N 0.374083°W,10 m, 26 Jun 1949, Leston, 1♀, (AMNH_PBI 00206889) (AMNH). Shefford, 52.03833°N 0.33277°W, 40 m, 26 Aug 1975, Leston, 1♀ (AMNH_PBI 00206895), 1♂ (AMNH_PBI 00206896), 1♂ (AMNH_PBI 00206897) (AMNH).

Diagnosis

Dicyphus errans is recognized by the following combination of characters: macropters only; body length 4.58–5.54 mm in males and 4.40–5.14 mm in females; most often with dark head and pronotum; frons+vertex with X-shaped dark-brown marking bounded by stramineous and orange coloration, occasionally with head and pronotum generally paler (Fig. 2); AI–AIV mostly dark brown, with AI more reddish brown, occasionally with AII medially light brown; AI long, >2× than interocular distance in males; AII elongate, >1.45× longer than posterior width of pronotum in males; pronotal disk >1.2× longer than callosite region in both sexes; left paramere with short apophysis, spatulate apex expanded (Fig. 23F); aedeagus with three endosomal lobes, with left lateral lobe with small weakly arcuate lobal sclerite, medial lobe with larger weakly arcuate lobal sclerite (Fig. 13B).

Redescription

Males. Macropters only known.

Coloration (Fig. 2): Body variable in colour, with head and pronotum ranging from more stramineous/light brown to dark brown, with darker morph more common. *Dark morph: Head:* frons+vertex mostly dark brown to approaching black, with contrasting yellow markings narrowly placed adjacent to eyes, with a X-shaped dark-brown marking, contiguous with broad dark-brown band along posterior margin of head, sometimes paler medially, yellowish to orangish brown; lateral margins of postocular region dark brown to near black, extending to lateral regions of gula; clypeus, maxillary plate and bucculae usually dark brown, bucculae sometimes narrowly stramineous ventrally; mandibular plate stramineous; gula mostly dark brown to black, sometimes with midline narrowly stramineous; AI mostly shiny dark reddish brown, with apex narrowly stramineous, sometimes with darker annulation subbasally; AII–AIV mostly dark brown, sometimes with base of AII more reddish brown, apex of AIII with narrow stramineous tip, generally with medial region of AII faintly stramineous. *Pronotum:* mostly shiny dark brown, with midline sometimes narrowly stramineous, callosite region occasionally paler brown with orange tinge. *Thoracic pleura and sterna:* pleura, including mesobasisternum, mostly shiny dark brown, with metepisternum duller; mesepimeron stramineous. *Mesoscutum:* dull dark-brown, laterally with stramineous to orange tinge. *Scutellum:* anterolateral angles stramineous, with midline broadly dull dark-brown. *Hemelytra:* translucent, pale greyish to stramineous colour, with three small dark-brown spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus, spots sometimes with red infusion; clavus sometimes with faint embrownment; medial margin of endocorium post-commissure sometimes with faint reddish brown highlighting; corium sometimes with minor red-brown to medium-brown spots, often associated with setae; membrane veins mostly brown, sometimes with reddish tinge. *Abdomen:* venter variable, from uniformly medium to dark brown, to mostly stramineous with lateral embrownment on basal segments, pygophore shiny medium to dark brown. *Pale morph:* mostly as in dark morph, but with head and pronotum more uniformly stramineous to light brown, with X-marking on frons+vertex less extensive, posterior margin of head stramineous to orange.

Structure: Head: interocular distance 0.99–1.23× greater than eye width. *Antennae:* AI 2.03–2.70× longer than interocular distance; AII long, 1.47–1.78× longer than posterior width of pronotum. *Pronotum:* callosite region 1.7–2.41× longer than collar; calli short; pronotal disk 1.24–1.50 mm longer than callosite region. *Male genitalia:*left paramere with robust and short apophysis, spatulate apex expanded (Fig. 23F); aedeagus with three well-developed endosomal lobes, left lateral lobe with a small lobal sclerite, medial lobe with larger weakly arcuate lobal sclerite (Fig. 13B).

Females. Macropters only known. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.07–1.32× than eye width. *Antennae:* AI length 1.70–2.12× interocular distance. AII 1.01–1.36× longer than posterior pronotal width. *Pronotum:* disk 1.32–1.80× longer than callosite region.

Measurements
See Table 4.

Distribution
Kerzhner & Josifov (1999) report this species as widespread in Europe (Fig. 36; only specimens examined).

Host plants
Dicyphus errans has a very wide range of host plants. Wagner (1964) reported this species on *Silene* sp. (Caryophyllaceae), *Ononis natrix* and *Salvia* sp. (Lamiaceae). We found *D. errans* on *Cucurbita maxima* Duchesne and *Lagenaria siceraria*, *Solanum lycopersicum* and *Solanum nigrum* and *Epilobium hirsutum*. Additionally, *D. errans* has been reported on *Chenopodium* sp. (Chenopodiaceae), *Geranium robertianum* L. and *Geranium rotundifolium* L. (Geraniaceae), *Hieracium* sp. (Asteraceae), *Polygonum persicaria* L. (Polygonaceae), *Salvia glutinosa* and *Stachys sylvatica* L. (Lamiaceae), *Silene alba* (Miller) Krause and *Silene dioica* (L.) Clairv. (Caryophyllaceae) and *Urtica dioica* L. (Urticaceae) (Tavella & Goula, 2001; Ingegno *et al.*, 2008), *Geranium macrorrhizum* L. (Geraniaceae) (Josifov 1974), *Mercurialis annua* and *Viburnum tinus* L. (Caprifoliaceae) (Ehanno, 1960) (see also Schuh 1995), *Lavatera* sp. (Malvaceae), *Parietaria officinalis* L. and *Urtica* sp., *Amaranthus* sp. (Amaranthaceae), *Dittrichia viscosa* (L.) Greuter, *Erigeron annuus* (L.) Persoon and *Sonchus* sp. (Asteraceae), and *Cistus monspeliensis* L. and *Cistus salvifolius* L. (Cistaceae) (Alomar, Goula & Albajes, 1994).

Remarks
See Remarks' section for *Dicyphus epilobii*. *Dicyphus errans* and *D. epilobii* are very similar in general structure and size but differ in coloration, with *D. errans* darker than *D. epilobii*. The X-shaped marking on the head, the transverse brown band on the propleuron and most of AII are brown to dark brown in *D. errans* (cf. faint in *D. epilobii*) (Fig. 2). The two species may be differentiated by the morphology of the genitalia: the left paramere is more robust in *D. errans* than in *D. epilobii* (Fig. 23E, F) and the endosomal lobal sclerites are asymmetrical in *D. errans* and subequal in *D. epilobii* (Fig. 13A, B). *Dicyphus errans* is similar in coloration to the dark morph of *D. cerastii* (Figs 2, 30). However, these two species are easily differentiated by: the more elongate AII (>1.45× posterior width of pronotum)

in males of *D. errans* (cf. shorter in *D. cerastii*), the absence of a left-side process on abdominal SVIII in males of *D. errans* (cf. presence of sternal process in *D. cerastii*; Fig. 6F), and the endosomal lobal sclerites are asymmetrical and barely arcuate in *D. errans* (cf. similar size with one sclerite strongly arcuate in *D. cerastii*) (Figs 12E, 13B).

Dicyphus escalerae Lindberg, 1934
(Figs 5, 13C, 23G–I, 36)

Dicyphus escalerae Lindberg, 1934: 11 (original description); Wagner, 1951: 29 (redescription); Carvalho, 1958: 197 (world catalogue); Schuh, 1995: 490 (world catalogue); Kerzhner & Josifov, 1999: 22 (Palaearctic catalogue).

Materials examined

France: Vaucluse: Lafare, 44.14681ºN 5.05144ºE, 169 m, 3 May 1998, Matocq, 2♂♂ (UNSW_ENT 00026530), 10 May 2006, 1♂ (UNSW_ENT 00026531) (MNHN).

Spain: Granada: Monachil: Sierra Nevada, 37.09305°N 3.39416°E, 2256 m, 21–24 Jul 1926, Lindberg, Holotype, 1♂ (AMNH_PBI 00208614), 1♂ (AMNH_PBI 00208557), 1♀ (AMNH_PBI 00208629) (MZH). Granada: Capileira, 36.96438ºN 3.36043ºW, 1436 m, ex. *Antirrhinum hispanicum* Chavannes (Scrophulariaceae), 31 May 2006, Sanchez, Martínez & La Spina, 4♂♂, 6♀♀ (IMIDA_ENT 00000445-IMIDA_ENT 00000454) (IMIDA). Cadiz: Grazalema, 36.75972ºN 5.36556W, 812 m, ex. *Antirrhinum graniticum* Rothmaler (Scrophulariaceae), 1 June 2006, Sanchez, Martínez & La Spina, 5♂♂, 10♀♀ (IMIDA_ENT 00000061-IMIDA_ENT 00000075). Huesca: Canal de Berdún, 42.64194ºN 0.80194ºW, 700 m, ex. *Antirrhinum* sp. (Scrophulariaceae), 6 June 2006, Sanchez, Martínez & La Spina, 4♂♂, 1♀ (IMIDA_ENT 00000050-IMIDA_ENT 00000054) (IMIDA).

Portugal: Portalegre: Portalegre, 39.29194°N 7.44083°W, 590 m, ex. *Antirrhinum* sp. (Scrophulariaceae), 3 June 2006, Sanchez, Martínez & La Spina, 1♂♂, 5♀♀ (IMIDA_ENT 00000055-IMIDA_ENT 00000060).

Diagnosis

Dicyphus escalerae is recognized by the following combination of characters: macropters and brachypters in both sexes; moderately sized species, macropterous males 3.48–4.05 mm, brachypterous males 2.5 mm, macropterous females 3.79–4.31 mm, brachypters females 2.79–3.33 mm; AI *c.* 1.5× longer than interocular distance in macropterous males, a little shorter in brachypters; AII *c.* 1.2× longer than posterior width of pronotum in macropters, *c.* 1.3× longer in brachypters. AII <1.7× shorter than head width. AI mostly dark brown; corium with dense distribution of brown spots and three brown to dark-brown spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; femora with large brown overlapping spots in both sexes (Fig. 5); left paramere small and moderately thickened, with spatulate apex denticulate proximally (Fig. 23G–I); endosoma with spinules only, no lobal sclerites present (Fig. 13C).

Redescription

Males. Macropters and brachypters known.

Coloration (Fig. 5): Dorsum light pale with extensive dark-brown markings, sometimes with red/orange highlighting. *Head:* frons+vertex with a broad, X-shaped dark-brown marking; clypeus and maxillary plate mostly dark brown to black; postocular margins of head broadly dark brown to black and shiny; gula stramineous. *Antennae:* AI dark brown with tip reddish, base narrowly stramineous; AII mostly dark brown with broad medial annulation. *Pronotum:* collar white to stramineous, translucent; calli stramineous to pale brown with dark-brown highlighting; disk stramineous to pale brown, with extensive brown markings laterally on humeral angles. *Thoracic pleura and sterna:* propleuron uniformly dark brown, with ventral margin whitish; mesepimeron and metepisternum stramineous, including evaporative area. *Mesoscutum:* broadly dark brown intermixed with extensive yellowish brown markings. *Scutellum:* angles broadly whitish with a broad dark brown stripe along midline. *Hemelytra:* translucent, mostly pale brown, with brown spotting at base of setae on clavus; clavus with faint embrownment; apex of exocorium adjacent to costal fracture with prominent dark-brown to reddish brown spot; apex of endocorium with obscure dark brown spot; cuneus mostly stramineous to pale brown with apical dark-brown to dark reddish brown spot; membrane veins mostly dark brown, sometimes with reddish highlighting. *Legs:* spots on femora greatly enlarged and blending. *Abdomen:* venter mostly stramineous, with basal sternites and lateral regions dark brown; pygophore bicoloured, dark brown and stramineous.

Structure: Head: interocular distance 1.19–1.29× longer than eye width in macropters and 1.31× in brachypters. *Antennae:* AI 1.52–1.77× longer than interocular distance in macropters and 1.49× in brachypters; AII 1.11–1.25× longer than posterior width of pronotum in macropters, 1.31× in brachypters. *Pronotum:* pronotal disk subequal 0.93–1.43× than callosite region in macropters and 0.73× in brachypters. *Male genitalia:* left paramere apophysis short and moderately thickened, with spatulate apex denticulate posteriorly (Fig. 23G–I); aedeagus with three well-developed endosomal lobes, without endosomal lobal sclerites, two lobes with dense distribution of spinules (Fig. 13C).

Females. Macropters and brachypters known. Coloration, vestiture, texture and structure mostly as in males. Female abdominal venter mostly stramineous, with basal sternites dark brown laterally. *Head:* interocular distance 1.19–1.39× longer than eye width in macropters and 1.20–1.41× in brachypters. *Antennae:* AI length 1.38–1.60× longer than interocular distance in macropterous and 1.42–1.56× in brachypterous females. AII 0.96–1.11× longer than posterior pronotal width in macropters and 1.11–1.23× in brachypters. *Pronotum:* disk 0.98–1.34× longer than callosite region in macropters, 0.70–0.87× in brachypters.

Measurements

See Table 4.

Distribution

This species was originally described from Spain and subsequently reported from Italy, Corsica and France (Tamanini, 1956; Hollier & Matocq, 2004; Ingegno *et al.*, 2008), Germany (Heckmann & Rieger, 2001), Switzerland (Hollier & Matocq, 2004; Rabitsch, 2008) and the Czech Republic (Hradil, 2011). We collected *D. escalerae* in Portugal and Spain (Grazalema, Sierra Nevada, The Pyrenees) and examined specimens from France (Fig. 36).

Host plants

This species has been frequently reported on *Antirrhinum majus* (Ehanno, 1987; Simon, 1995; Tavella & Goula, 2001; Hollier & Matocq, 2004; Ingegno *et al.*, 2008). We collected *D. escalerae* on *Antirrhinum hispanicum* Chavannes (Scrophulariaceae) and *Antirrhinum graniticum* Rothmaler (Scrophulariaceae).

Remarks

Lindberg (1934) originally described *Dicyphus escalerae* from specimens collected in Sierra Nevada (Spain), naming it after the Spanish entomologist Manuel Martínez de la Escalera. Wagner (1951) examined part of the type series and provided the first description of the male genitalia. The brachypters of *D. escalerae* are similar in appearance to the Turkish species *D. alkannae* and to the Madeiran species *D. poneli* (Figs 5, 30). They differ by the presence of large brown femoral spots in *D. escalerae* (cf. smaller spots, never merged in *D. alkannae* and *D. poneli*). *Dicyphus escalerae* also differs from *D. alkannae* by the dark-brown AI (cf. mostly stramineous medially in *D. alkannae*), and AII with brown annulations basally and distally (cf. more stramineous overall with reddish brown apex). *Dicyphus escalerae* can be readily differentiated from *D. poneli* and the other congeners by the characteristic shape and denticulation of the left paramere (Fig. 23G–I).

Dicyphus flavoviridis Tamanini, 1949
(Figs 4, 7, 10A, 13D, 36)

Dicyphus flavoviridis Tamanini, 1949: 2, figs. 3–5 (original description); Carvalho, 1958: 197 (world catalogue); Schuh, 1995: 491 (world catalogue); Kerzhner & Josifov, 1999: 23 (Palaearctic catalogue)

Materials examined

Italy: Trentino: Yal Lagarina, 45.89972°N 11.06083°E, 417 m, 7 Oct 1934, Daiano, 1 adult sex unknown (MZLU). Piemonte: Torino: Giaveno: Maddalena Frazione, 45.02917°N 7.30361°E, 762 m, ex. *Rubus* sp., 25 Aug 2009, Sanchez, 8♂♂, 5♀♀ (IMIDA_ENT 00000130-IMIDA_ENT 00000140, IMIDA_ENT 00000195, IMIDA_ENT 00000196), ex. *Stachys silvatica*, 25 Aug 2009, Sanchez, 5♂♂, 5♀♀ (IMIDA_ENT 00000171-IMIDA_ENT 00000180) (IMIDA).

Diagnosis

Dicyphus flavoviridis is recognized by the following combination of characters: macropters and brachypters in both sexes (Tamanini, 1956): moderately sized species, macropterous males 5.05 mm, brachypterous males 3.65–4.06 mm, brachypterous females 3.56–4.02 mm (no macropterous females examined); body mostly pale yellowish green, with few darker markings (Fig. 4); clypeus mostly pale yellowish green, with anterior embrownment; propleuron with weak brown transverse band; mesobasisternum at least partly pale yellowish green; cuneus apically dark reddish brown; AI mostly pale yellowish green with subbasal dark-brown annulation and subapical red annulation; AI long, *c.* 2× longer than interocular distance in both macropterous and brachypterous males; AII 1.41× longer than posterior width of pronotum in macropterous males, 1.48–1.88× longer in brachypterous males; pronotal disk shorter than callosite region in macropterous (0.79×) and brachypterous (0.48–0.63×) males; callosite region *c.* 3× longer than collar width at middle line in both macropterous and brachypterous males; corium without spots; left side of posterior margin of male abdominal sternite SVIII with sclerotized flange-like process on left side with denticulate substructure (Fig. 7D); pygophore without posteroventral brown spot left paramere elongate and robust, with caplike apex denticulate margin (Fig. 10A); endosoma with two lobes, with pair of large asymmetrical moderately arcuate lobal sclerites (Fig. 13D).

Redescription

Males. Macropterous and brachypterous morphs examined.

Coloration (Fig. 4): Dorsum mostly stramineous to pale yellowish green with limited brown markings. *Head:* mostly stramineous to pale yellowish green; frons+vertex with X-shaped dark-brown marking, not extending beyond posterior margin of eyes; anterior region of clypeus and maxillary plate embrowned; postocular margins of head with narrow transverse brown band, sometimes reduced to brown spot adjacent to eye. *Antennae:* AI mostly stramineous, with base narrowly whitish, subbasal dark-brown annulation and subapical red annulation; AII mostly stramineous with subbasal narrow dark-brown annulation, apical 1/4 dark brown. *Pronotum:* collar and callosite region stramineous to pale green-yellowish, with medial regions of each callus sometimes embrowned; disk transparent, mostly pale yellowish green to whitish green. *Thoracic pleura and sterna:* propleuron pale yellowish green, with medium-brown transverse band; mesobasisternum pale yellowish green, sometimes dark brown medially and with dark-brown spot dorsolaterally; mesepimeron and metepisternum including evaporative areas pale yellowish green. *Mesoscutum:* broadly stramineous to pale yellowish green. *Scutellum:* lateral angles broadly pale stramineous to yellowish green with brown stripe along midline. *Hemelytra:* translucent, mostly pale yellowish green without brown spotting associated with setae or large brown spots distally on corium, sometimes exocorium paler; cuneus pale yellowish green, sometimes whitish, with apex dark reddish brown in macropters; membrane fumose in macropters; apex of wings in brachypters paler approaching white, with faint red spot apically. *Abdomen:* venter uniformly pale yellowish green; posterior margin of left side of SVIII black; pygophore with posteroventral brown spot.

Structure: Head: interocular distance 1.19× greater than eye width in macropters, 1.15–1.31× in brachypters. *Antennae:* AI 1.92× longer than interocular distance in macropters, in 1.76–2.09× brachypters; AII 1.41× longer than posterior width of pronotum in macropters, 1.48-1.88× longer in brachypters. *Pronotum:* pronotal disk 0.79× longer than the callosite region in macropters, 0.48–0.63× in brachypters; callosite region 3.05–4.06× longer than collar width at middle line in macropters and 2.96× longer in brachypters. *Abdomen:* posterior margin of left side of SVIII with heavily sclerotized flange-like expansion process with denticulate substructure (Fig. 7D). *Male genitalia:* left paramere apophysis robust and elongate, with caplike apex, with minutely denticulate margin, proximal shaft weakly sinuate (Fig. 10A); aedeagus with two well-developed endosomal lobes, each lobe with large moderately arcuate endosomal lobal sclerites, lobal sclerites asymmetrical (Fig. 13D).

Females. Only brachypters examined. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.14–1.41× longer than eye width in brachypters. *Antennae:* AI 1.65–2.01× longer than interocular distance in brachypters; AII 1.51–1.71× longer than posterior pronotal width in brachypters. *Pronotum:* disk 0.45–0.69× in brachypters; callosite region 2.63–3.37× longer than collar width at middle line in brachypters. *Abdomen:* venter pale yellowish green.

Measurements
See Table 4.

Distribution
Dicyphus flavoviridis is distributed in northern Italy (Tavella & Goula, 2001; Ingegno *et al.*, 2008) (Fig. 36, material examined); it has also been reported from France (Matocq & Streito, 2013) and Switzerland (Kerzhner & Josifov, 1999).

Host plants
Dicyphus flavoviridis has a broad host range: Calamintha nepeta (L.) Savi (Lamiaceae), *Circaea lutetiana*, *Hieracium* sp., *Epilobium hirsutum*, *Galeopsis tetrahit*, *Geranium pyrenaicum*, *Geranium robertianum*, *Geranium rotundifolium*, *Geum molle* Vis. et Pančić (Rosaceae), *Ononis repens* L. (Fabaceae), *Salvia glutinosa*, *Silene alba*, *Silene dioica*, *Solanum nigrum*, *Stachys sylvatica* (Tavella & Goula, 2001; Ingegno *et al.*, 2008). We also collected this species on *Rubus* sp. (Rosaceae).

Remarks
Wagner (1951) placed *Dicyphus flavoviridis* within his *pallidus* species group, by the AII >1.5× longer than posterior width of pronotum in males and the callosite region *c.* 2× longer than collar width. In comparison to Wagner (1951, 1964), we found that the AII: posterior width of pronotum ratio in males was sometimes shorter (macropters: 1.41; brachypters: 1.48–1.88×) and the callosite region: collar ratio was always >2.9× both in macropters and brachypters. The external and genitalic morphology of *D. flavoviridis* are very similar to those of *D. pallidus*, with both possessing a left-side abdominal SVIII process (Figs 7D, 8F), the left paramere apophysis is robust and elongate (Fig. 10A, F), and the endosomal lobal sclerites are large (Figs 13D, 31A).

Dicyphus flavoviridis also has a smaller body than *D. pallidus* (macropterous males: 5.05 mm in *D. flavoviridis* cf. 5.22–5.75 mm in *D. pallidus*; brachypterous males: 3.65–4.05 mm in *D. flavoviridis* cf. 4.34–5.10 mm in *D. pallidus*). In addition, AII:head to width ratio is smaller in *D. flavoviridis* (<2.13) than in *D. pallidus* (>2.14). *Dicyphus flavoviridis* can also be differentiated from *D. constrictus*, *D. epilobii*, *D. errans* and *D. josifovi* by the callosite region:collar ratio *c.* 3× longer in macropterous and brachypterous males, the presence of a denticulate abdominal SVIII process (Fig. 7D), and the left paramere apophysis robust and elongate, with a caplike apex (Fig. 10A). This is the first time the abdominal SVIII process has been reported for this species.

Dicyphus hyalinipennis (Burmeister, 1835) (Figs 3, 10b, 14a, 29, 38)

Dicyphus hyalinipennis Burmeister, 1835: 268 (original description); Carvalho, 1958: 197 (world catalogue); Schuh, 1995: 492 (catalogue); Kerzhner & Josifov, 1999: 23 (Palaearctic catalogue).

Material examined

Armenia: Marz: Between Avan and Ozhervezh and Nork, 40.21119ºN 44.556618ºE, 1244 m, 8 Nov 1939, Rikhter, 1 ♀(AMNH PBI 00210791) (ZISP).

Austria: Niederosterreich: Viena, 48.20916°N 16.37277°E, 184 m, 1♂ (AMNH_PBI 00208646) (MZH).

Bulgaria: Sofija-Grad: Sofý, 42.71027°N 23.32361°E, 673 m, 1♀ (AMNH_PBI 00213972) (HNHM); Sep 1928, Biro, 1♂ (AMNH_PBI 00213973) (HNHM); Sep 1928, Biro, 1♀ (AMNH_PBI 00213971) (HNHM). Bulgarien, 42.73361°N 25.48555°E, 472 m, 10 Oct 1966, Josifov, 1♀ (AMNH_PBI 00209593) (MNHN). Reg. inf. m. Vitos, 05 Aug 1939, Lindberg, 1♂ (AMNH_PBI 00208640) (MZH).

Czech Republic: Moravia: Jihomororavsky: Radejov, Kutky Deer Park, 48.8415ºN 17.3545ºE, 357 m, 16 Aug 2009, ex. *Hyosciamus niger* L. (Scrophulariaceae), Sanchez, Kment & Pennaroli, 2♂♂ (IMIDA_ENT 00000540, IMIDA_ENT 00000543), 2♀♀ (IMIDA_ENT 00000537-IMIDA_ENT 00000541); ex. *Atropa belladonna* L. (Solanaceae), 1♂ (IMIDA_ENT 00000191), 1♀ (IMIDA_ENT 00000192), 1♂, 4♀♀ (IMIDA_ENT 00000210-IMIDA_ENT 00000214) (IMIDA).

Germany: Bayern: Coburg: Coburgo, 50.2575°N 10.96583°E, 305 m, 10 Oct 1949, Eckerlein, 1♀ (AMNH_PBI 00212492) (MZLU). Hýrnleins-grund, 50.26888°N 10.94250°E, 328 m, 10 Oct 1949, Eckerlein, 1♂ (AMNH_PBI 00212493) (MZLU).

Hungary: Gant: Výrteskozma: Fýni-Výlgy, 47.46138°N 18.46027°E, 257 m, 07 Jul 1961, Murai É., 1♂ (AMNH_PBI 00213974) (HNHM).

Russia: Krasnovar: Krasnovar, 45.039267°N 38.987221ºE, 34 m, Oct. 1926, Telenga, 1♂ (AMNH PBI 00210789), 1♀ (AMNH PBI 00210790), 1♀ (AMNH_PBI 00341135) (ZISP); 30 Oct 1939, Resaca, 1♀ (AMNH PBI 00210792) (ZISP).

Spain: Madrid: Valsalva rp, 40.54055°N 3.75194°E, 640 m, 28 Mar 1926, Lindberg, 1♂ (AMNH_PBI 00208568) (MZH).

Diagnosis

Dicyphus hyalinipennis is recognized by the following combination of characters: macropters and brachypters in both sexes; body length 4.10–4.61 mm in macropterous males, 2.94 mm in brachypterous males; body length 4.47–4.77 mm in macropterous females, 3.18–3.48 mm in brachypterous females; pale and dark morphs (Fig. 3); always with frons+vertex with dark brown X-shaped marking; clypeus embrowned, with stramineous highlighting; mandibular plate stramineous; maxillary plates dark brown; propleuron with prominent shiny dark-brown transverse band; AI short, mostly stramineous to orange, with subbasal brown and subapical red stramineous annulations; AII mostly stramineous with subbasal and distal 1/4 brown annulations; corium with three light- to dark-brown spots, at corial fracture, middle of apical margin of endocorium and tip of cuneus; pygophore without large posteroventral brown spot; left paramere apophysis robust and short, with base of spatulate apex toothed (joining the apophysis in an acute angle) (Fig. 10B), aedeagus with two endosomal lobes, with pair of large asymmetrical, arcuate endosomal lobal sclerites (Fig. 14A).

Redescription

Males. Macropters and brachypters examined.

Coloration: Stramineous and dark morphs present (Fig. 3). *Stramineous morph. Head:* mostly stramineous to pale yellowish green; frons+vertex with a short, X-shaped dark-brown marking, not extending beyond posterior margin of eyes; clypeus mostly dark brown with stramineous highlighting, sometimes paler overall; and maxillary plate embrowned; postocular margins of head with transverse brown band. *Antennae:* AI stramineous, with base narrowly whitish, subbasal dark-brown annulation and subapical red annulation; AII mostly stramineous with subbasal narrow dark-brown annulation, apical 1/4 dark brown. *Pronotum:* collar and disk whitish to stramineous; callosite region stramineous to pale green-yellowish, with medial regions of each callus sometimes embrowned. *Thoracic pleura and sterna:* propleuron pale stramineous, with medium to dark-brown transverse band; mesobasisternum dark brown, sometimes paler stramineous; mesepimeron and metepisternum including evaporative areas

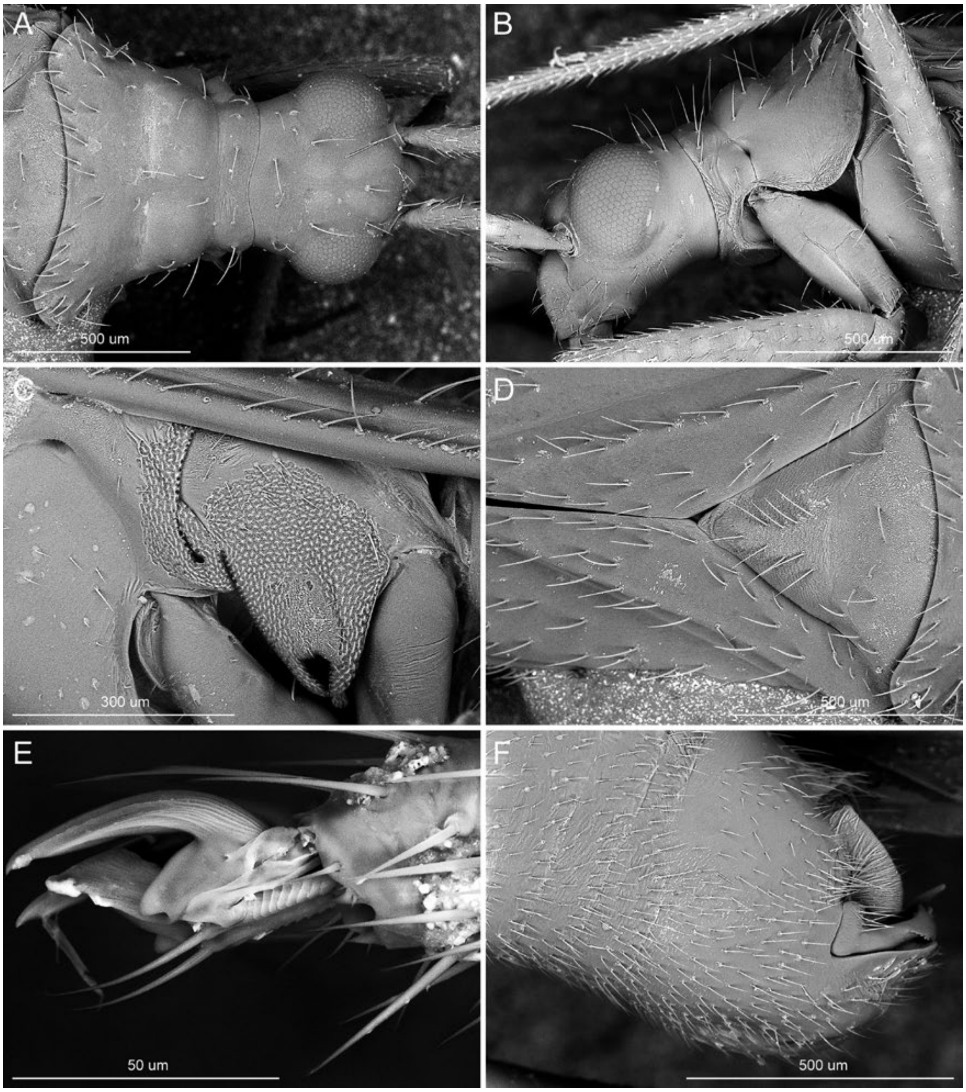

Figure 37. Scanning electron micrographs of *D. escalerae*. A, head and pronotum dorsal view, with well-defined collar, and callosite and disk region. B, head and pronotum, lateral view. C, external efferent system, metathoracic glands. D, scutelum. E, pretarsus in lateral view, with straight paraempodium below the claws. F, genital segment in lateral view with proctiger and left paramere visible.

pale yellowish green. *Mesoscutum:* broadly orange, sometimes with lateral angles embrowned. *Scutellum:* lateral angles broadly pale stramineous to yellowish with brown stripe along midline. *Hemelytra:* translucent, mostly pale stramineous, sometimes with brown or red spotting associated with setae on corium; three pairs of faint red to brown spots, on corial fracture, apex of endocorium, and tip of cuneus; apex of wings in brachypters paler with faint red and brown spot apically. *Abdomen:* venter stramineous intermixed with brown highlighting. *Dark morph*. Mostly as in pale morph, with lateral facies of head, lateral regions of collar, callosite region and pronotal disk, medial and lateral regions of mesoscutum and lateral regions of abdominal sterna dark brown.

Structure: Head: interocular distance 1.21–1.58× greater than eye width in macropters, 1.56× in brachypters. *Antennae:* AI 1.28–1.54× longer than interocular distance in macropters, 1.34× in brachypters; AII 0.89–1.08× longer that the posterior width of pronotum in macropters, 1.07× longer in brachypters. *Pronotum:* pronotal disk 1.20–1.67× the callosite region in macropters, 0.86× in brachypters. *Male genitalia:* left paramere apophysis robust and short, with base of spatulate apex toothed (joining the

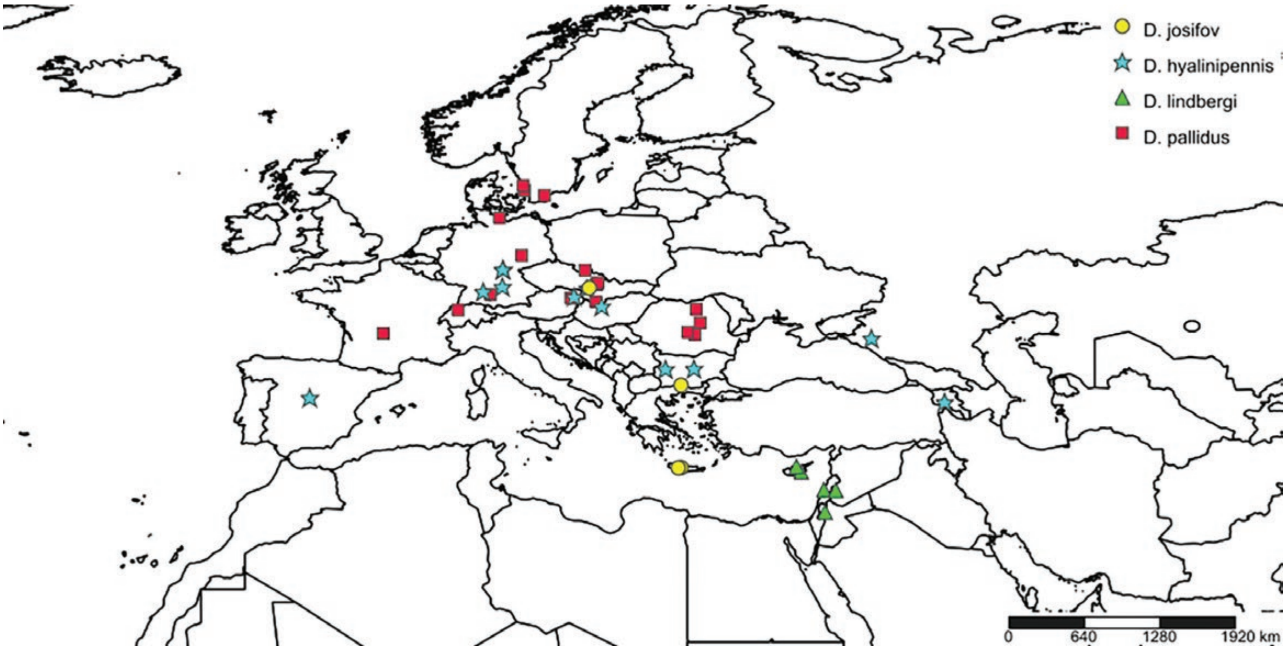

Figure 38. Distribution of the specimens examined: *D. hyalinipennis*, *D. josifovi*, *D. lindbergi* and *D. pallidus*.

apophysis neck in an acute angle) (Fig. 10B); aedeagus with two well-developed endosomal lobes, each lobe with large moderately arcuate lobal sclerite, lobal sclerites asymmetrical (Fig. 14A).

Females. Macropters and brachypters examined. Coloration, vestiture, texture and structure mostly as in males; pale and dark morphs known. Female abdominal venter stramineous with dark-brown markings in pale morphs, more uniformly dark brown in dark morphs. *Head:* interocular distance 1.33–1.53× than eye width in macropters, 1.41–1.43× in brachypters. *Antennae:* AI 1.21–1.40× longer than interocular distance in macropters, 1.28–1.40× in brachypters; AII 0.89–0.97× length of posterior pronotal width in macropters, 1.04–1.11× in brachypters. *Pronotum:* disk 1.22–1.79× longer than callosite region in macropters, 0.87–0.99× in brachypters.

Measurements

See Table 4.

Host plants

Wagner (1951, 1974) reported *D. hyalinipennis* from four host plant species: *Atropa bella-donna*, *Epilobium* sp., *Hyosciamus niger*, *Ononis natrix*, *Senecio viscosa* L. (Asteraceae). Wagner (1951) stated that *D. hyalinipennis* lives on *A. bella-donna*, whereas *D. stachydis* lives on *Stachys sylvatica*. In contrast, we have collected both of these *Dicyphus* species on *A. bella-donna*.

Distribution

We examined material of *D. hyalinipennis* from Austria, Bulgaria, Czech Republic, France, Germany, Hungary and Spain (Fig. 38). Kerzhner & Josifov (1999) report this species from many European and North African countries, as well as Turkey and Iraq, and possibly Azerbaijan. However, we have observed that many specimens identified as *D. hyalinipennis* in collections have been misidentified, and we are uncertain of the distributional range of this species.

Remarks

See Remarks' section of *D. argensis* and *D. eckerleini*. *Dicyphus hyalinipennis* is very similar in appearance to *D. stachydis* in size and coloration (Fig. 3). Wagner (1951) stated that both species are very closely related and can be easily confused. He reported differences in the ratio between the antennal segments and other characters; however, we found these characters had no discriminating value. We agree with Wagner (1951) that the morphology of the male genitalia provides a reliable means for differentiating the above two species. The apophysis of the left paramere is robust and short in both species, but lacks a notch at the base of the spatulate apex in *D. stachydis* (Figs 10B, 11B). Both species have a pair of large endosomal lobal sclerites, which are weakly arcuate and symmetrical in *D. stachydis*, but are strongly asymmetrical in *D. hyalinipennis*, with one of them almost straight and the other strongly bent apically (Figs 14A, 31C). Also, in the materials we examined, wing polymorphism is far less common in *D. hyalinipennis*.

DICYPHUS JOSIFOVI RIEGER, 1995
(FIGS 2, 10C–D, 14B, 38)

Dicyphus josifovi Rieger, 1995: 80 (original description); Kerzhner & Josifov, 1999: 23 (catalogue).

Material examined

Czech Republic: Velka Nad Velickou: Jihomoravsky, 48.88056°N 17.51806°E, 274 m, ex. *Epilobium hirsutum*, 16 Aug 2009, Sanchez, Pennaroli & Kment, 6♂♂, 4♀♀ (IMIDA_ENT 00000181-IMIDA_ENT 00000190) (IMIDA).

Diagnosis

Dicyphus josifovi is recognized by the following combination of characters: macropters only. Body length 4.35–4.51 mm in males and 4.56–4.90 mm in females; body mostly pale with dark-brown markings on head and thoracic pleura (Fig. 2); collar and pronotal disk whitish to whitish stramineous, contrasting with brown callosite region; mesoscutum mostly orange; AI elongate, mostly red; AII mostly stramineous, with apical 1/3rd brown; AII >1.5× longer than pronotum width in males; pronotal callosite region 1.35–1.57× longer than disk in males, 1.31–1.71× in females; left paramere narrow and short apophysis, weakly expanded distally (Fig. 10C–D); aedeagus with two endosomal lobes, each lobe with moderately long, weakly arcuate lobal sclerites (Fig. 14B).

Redescription

Males.

Coloration: Dorsum mostly stramineous with orange and dark-brown markings, sometimes with red highlighting (Fig. 2). *Head:* mostly stramineous to whitish, with contrasting markings; frons+vertex with a moderately long X-shaped dark reddish brown marking extending to level of posterior margin of eyes; clypeus dark-brown; mandibular plates stramineous; maxillary plate with faint embrownment; vertex orangish yellow; postocular margins of head dark brown, extending to genae; gula and bucculae stramineous. *Antennae:* fuscous; AI mostly red, with subbasal narrow dark reddish brown annulation, base and apices stramineous to whitish dark-brown on the base; AII medially pale, with basal and distal 1/3rd dark brown; AIII and AIV concolorous, uniformly dark brown, mostly with base of AIII narrowly stramineous. *Pronotum:* collar and pronotal disk whitish to whitish stramineous, translucent; callosite region mostly brown, rarely darker posterolaterally; humeral angles weakly embrowned. *Thoracic pleura and sterna:* propleuron mostly shiny dark brown with ventral margin stramineous; mesobasisternum broadly shiny dark brown; mesepimeron and metepisternum including evaporative areas stramineous, sometimes with peritreme dark brown. *Mesoscutum:* mostly orange, with faint embrownment. *Scutellum:* lateral angles broadly pale stramineous to whitish with narrow brown stripe along midline. *Hemelytra:* translucent, mostly stramineous with medium-brown to reddish brown markings/highlighting; with three pairs of medium-brown to reddish brown markings, each pair at corial fracture, apex of endocorium and tip of cuneus, latter more reddish; membrane veins embrowned to reddish. *Abdomen:* venter mostly stramineous, pygophore sometimes with brown markings.

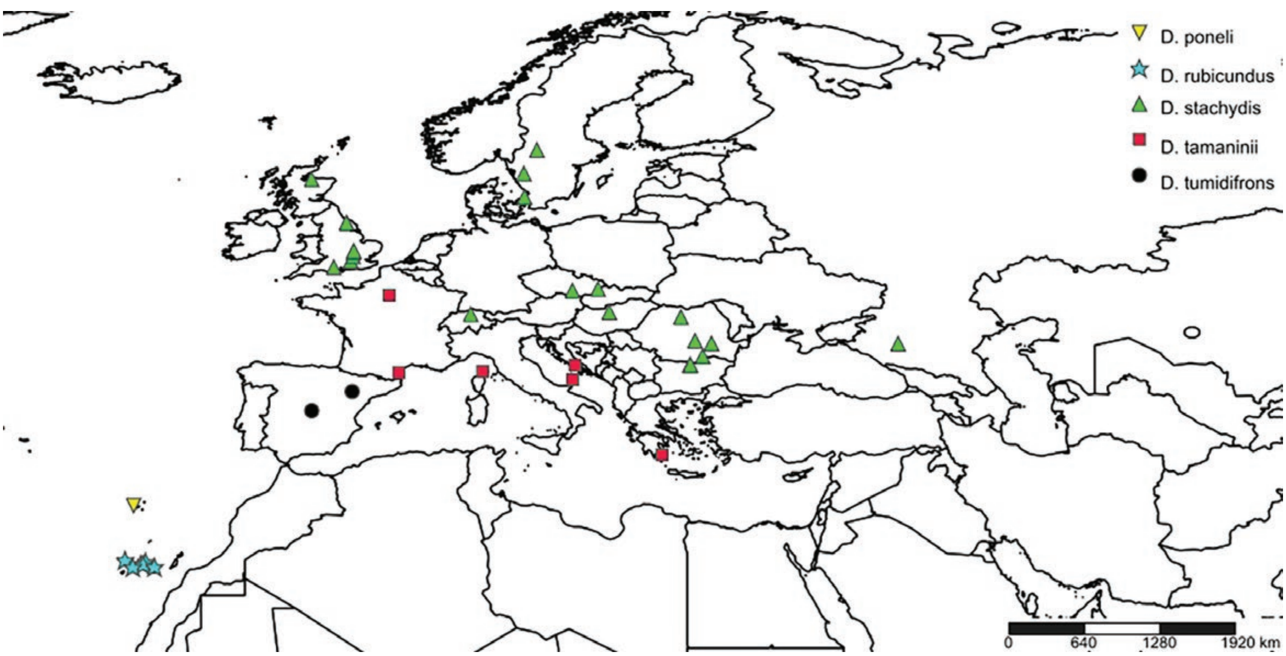

Figure 39. Distribution of the specimens examined: *D. poneli*, *D. rubicundus*, *D. stachydis*, *D. tamaninii* and *D. tumidifrons*.

Structure: Head: interocular distance 1.05–1.24× greater than eye width. *Antennae:* AI long, 1.99–2.23× longer than interocular distance; AII 1.50–1.62× longer than posterior width of pronotum. *Pronotum:* disk 1.35–1.57× longer than callosite region. *Male genitalia:* left paramere apophysis narrow and short, with shaft weakly arcuate, apex narrowly expanded (Fig 10C–D); aedeagus with two endosomal lobes, each lobe with moderately long endosomal lobal sclerites; lobal sclerites subequal in size, near symmetrical and weakly arcuate (Fig. 14B).

Females. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.11–1.26× longer than eye width. *Antennae:* AI 1.47–1.82× longer than interocular distance. AII 1.02–1.20× longer than posterior pronotal width. *Pronotum:* disk 1.31–1.71× longer than callosite region. *Abdomen:* venter pale yellowish green.

Measurements
See Table 4.

Distribution
Rieger (1995) described *Dicyphus josifovi* from Crete and also reported it from Bulgaria. In this work, we report this species for the first time from the Czech Republic (Fig. 38).

Host plants
We collected *Dicyphus josifovi* from *Epilobium hirsutum*.

Remarks
Rieger (1995) remarked that *Dicyphus josifovi* and *D. epilobii* differ in the shape and size of the endosomal lobal sclerites and left paramere, with the apex of the apophysis of the latter more expanded in *D. epilobii*. We concur that these two species are very similar, although the pale-yellow colour of *D. epilobii* contrasts with the olivaceous green of *D. josifovi* (Fig. 2). We found that differences in the left paremere are minor, with the apophysis only a little less expanded in *D. josifovi* (Figs 10C–D, 23E). We also observed only minor differences in the shape and size of the endosomal lobal sclerites, being a little more arcuate in *D. josifovi* (Figs 13A, 14B). We opted to maintain *D. josifovi* and *D. epilobii* as valid species based on differences in the molecular phylogeny (Figs 24, 25) and the above minor genitalic features.

DICYPHUS LINDBERGI WAGNER, 1951
(FIGS 10E, 14C–D, 33, 38)

Dicyphus lindbergi Wagner, 1951: 17 (original description); Carvalho, 1958: 198; Schuh, 1995: 492 (catalogue; full citation); Kerzhner & Josifov, 1999: 23 (Palaearctic catalogue).

Materials examined
Cyprus: Larnaca: Larnaca, 34.91666°N 33.63611°E, 7 m, 25 Jun 1939 01 Jul 1939, Lindberg, paratype of *Dicyphus lindbergi* 1♀ (AMNH_PBI 00208676) (MZH). Ayios Hilarion, 35.31250°N 33.28333°E, 545 m, 7 Jun 1939, Lindberg, paratype of *Dicyphus lindbergi*, 1♂ (AMNH_PBI 00204222) (BMNH), paratype of *Dicyphus lindbergi*, 1♂ (AMNH_PBI 00208569), paratypes of *Dicyphus lindbergi*, 2♀♀ (AMNH_PBI 00208673, AMNH_PBI 00208675) (MZH). Lapithos, 13 Jun 1939, Lindberg, paratype of *Dicyphus lindbergi*, 1♀ (AMNH_PBI 00208670) (MZH). Larnaka, 34.91666°N 33.63611°E, 6 m, 01 Jul 1939, Lindberg, paratype of *Dicyphus lindbergi*, 1♀(AMNH_PBI 00204221) (BMNH). Ayios Hilarion, 35.3125°N 33.28333°E, 545 m, 7 Jun 1939, Lindberg, 2♂♂, 2♀♀, identified as *Dicyphus lindbergi* (MZH).

Lebanon: Saida: Sidon, 33.55707°N 35.37295°E, 11 m, 28 Apr 1962, *Hyosciamus albus*, Eckerlein, 1♂ (AMNH_PBI 00206719) (AMNH).

Syria: Damascus, 33.51381°N 36.27653°E, 692 m, 1952, Seidenstücker, 1♂ (AMNH_PBI 00341137), 1♀(AMNH_PBI 00341138) (ZISP).

West Bank: Cisjordania: Jerico, 31.85698°N 35.46057°E, –255 m, Sahlb., 1♂ (identified as *Dicyphus bolivari*, AMNH_PBI 00208567) (MZH).

Diagnosis
Dicyphus lindbergi is recognized by the following combination of characters: only macropterous males known (Wagner, 1970), macropterous and brachypterous females; body length 3.62–4.57 mm in macropterous males, 3.72–4.44 mm in macropterous females and 2.85 mm in brachypterous females. Body stramineous with dark-brown markings and orange/red highlighting; AI stramineous with subbasal and subapical reddish brown annulations; AII mostly stramineous, with distal 1/3rd dark brown, narrowly and faintly brown at base (Fig. 33); disk 1.05–1.24× longer than callosite region in males; left paramere with moderately elongate apophysis, with outer margin of shaft sinuate (Fig. 10E); aedeagus with three endosomal lobes, medial lobe with five small endosomal lobal sclerites, outer lobes densely spinulate (Fig. 14C, D).

Redescription
Males.

Coloration (Fig. 33): Dorsum mostly stramineous with light to dark-brown markings, plus orange/red highlighting. *Head:* mostly stramineous to orange, with a broad, frons+vertex with a short, X-shaped reddish-brown marking, not extending beyond posterior margin of eyes; clypeus stramineous with medium-brown highlighting; mandibular plates stramineous; maxillary plate embrowned; vertex orange; postocular margins of head orange medium brown; gula and bucculae yellow. *Antennae:* AI medially, basally and apically stramineous, with subbasal and subapical reddish brown annulations; AII mostly stramineous, with distal 1/3rd dark brown, narrowly and faintly brown at base; AIII and AIV concolorous, uniformly dark brown. *Pronotum:* collar stramineous, translucent; callosite region mostly stramineous with variable embrownment; disk stramineous, translucent, sometimes humeral angles embrowned. *Thoracic pleura and sterna:* propleuron stramineous with weak embrownment, ventral margin whitish; mesobasisternum medium brown; mesepimeron and metepisternum, including evaporative areas, stramineous to whitish. *Mesoscutum:* mostly orange, with faint embrownment. *Scutellum:* lateral angles broadly pale stramineous to whitish with narrow brown stripe along midline. *Hemelytra:* translucent, mostly stramineous with medium brown to reddish brown markings/highlighting; with three pairs of medium brown to reddish brown markings, each pair at corial fracture, apex of endocorium and tip of cuneus; membrane veins embrowned. *Abdomen:* venter uniformly stramineous.

Structure: Head: interocular distance 1.27–1.48× greater than eye width. *Antennae:* AI short, 1.46–1.68× longer than interocular distance; AII 1.05–1.24× longer than posterior width of pronotum. *Pronotum:* disk 1.05–1.24× longer than callosite region. *Male genitalia:* left paramere apophysis moderately elongate, with shaft weakly sinuate, with subapical excavation on outer margin, spatulate apex weakly denticulate on outer margin (Fig. 10E); aedeagus with three endosomal lobes, medial lobe with five small endosomal lobal sclerites, lateral lobes densely spinulate (Fig. 14C, D).

Females. Macropters and brachypters examined. Body length 3.72–4.44 mm in macropters females and 2.85 mm in brachypters. Coloration, vestiture, texture and structure mostly as in males. Female abdominal venter pale yellowish green. *Head:* interocular distance 1.18–1.46× greater than eye width in macropterous females, 1.39× in brachypters. *Antennae:* AI 1.39–1.68× longer than interocular distance in macropters, 1.38× in brachypters; AII 0.99–1.11× longer than posterior pronotal width in macropters, 1.01× in brachypters. *Pronotum:* disk 1.20–1.48× longer than callosite region in macropters, 0.83× in brachypters.

Measurements
See Table 4.

Distribution
We have examined specimens of *Dicyphus lindbergi* from Cyprus, Lebanon and Cisjordania (Fig. 38). This species is known also in Syria (Wagner, 1970).

Host plants
Collected on *Hyosciamus albus* and *Hyosciamus aureus* L. (Scrophulariaceae) (Wagner, 1951).

Remarks
Also see *D. bolivari* remarks. Wagner (1951) based his description of *D. lindbergi* on materials collected by H. Lindberg in Cyprus in 1939. Wagner (1951) placed *D. lindbergi* in the *hyalinipennis* species-group and differentiated it by the morphology of the genitalia. *Dicyphus lindbergi* and *D. bolivari* are very similar in shape and colour (Fig. 33), and the former species can only be confidently separated by the apophysis of the left paramere being shorter (Figs 9C–F, 10 E) and the fewer small endosomal lobal sclerites (N = 5 cf. N = 6–12) (Figs 12C, 14C, D). Based on these genitalic features, we predict that *Dicyphus lindbergi* will group in the *bolivari–rubicundus* clade and not in the *hyalinipennis* species-group of Wagner (1951).

Dicyphus pallidus Herrich-Schaeffer, 1836 (Figs 4, 8, 10F, 31A, 38)

Dicyphus pallidus Herrich-Schaeffer, 1836: 51 (original description); Carvalho, 1958: 198 (world catalogue); Schuh, 1995: 493 (world catalogue); Kerzhner & Josifov, 1999: 23 (Palaearctic catalogue).

Material examined
Austria: Niederosterreich: Mýdling: Wienerwald, 48.09722°N 16.10972°E, 415 m, 13 Aug 1960, Lindberg, 1♀ (AMNH_PBI 00209455) (MZH).

Bulgaria : Kjustendil: Rila, silva frond., 42.12722°N 23.13361°E, 550 m, 6-12 Aug 1939, Lindberg, 1♂ (AMNH_PBI 00208571) (MZH).

Czech Republic: Jeseniky, 50.22722°N 17.19277°E, 1350 m, 1 Aug 1948, Stehlik, 1 adult sex unknown (AMNH_PBI 00206740) (AMNH). Zlinsky: Potec: Plosciny Mountain, 49.13944ºN 18.06000ºE, 639 m, 17 Aug 2009, ex. *Salvia glutinosa*, Sanchez, Kment & Pennaroli, 3♂♂, 3♀♀ (IMIDA_ENT 00000193, IMIDA_ENT 00000194, IMIDA_ENT 00000461, IMIDA_ENT 00000464). Valasske Klobouky, 49.27611ºN 18.18194ºE, 450 m, 17 Aug 2009, ex. *Stachys sylvatica*, Sanchez, Kment & Pennaroli, 2♂♂, 2♀♀ (IMIDA_ENT 00000470-IMIDA_ENT 00000473) (IMIDA). Nedasov: Kanoury Reserve, 49.0822ºN 18.0336ºE, 619 m, 18 Aug 2009, ex. *Stachys alpina* L. (Lamiaceae), Sanchez, Kment & Pennaroli, 2♀♀ (IMIDA_ENT 00000474, IMIDA_ENT 00000475) (IMIDA).

France: Lafare, 44.14638°N 5.05222°E, 166 m, Jul 1985, Carayon, 1 adult sex unknown (AMNH_PBI 00209592) (MNHN). St. Augustin, 45.42138°N 1.84194°E, 534 m, 26 Jun 1994, Matile, 2 adults sex unknown (AMNH_PBI 00209590, AMNH_PBI 00209591) (MNHN).

Germany: Sachsen: Leipziger Land: Leipzip, 51.33944°N 12.37111°E, 110 m, 1♂ (AMNH_PBI 00208706) (MZH). Schleswig-Holstein: Ostholstein: Kirchný, 54.2050N 10.68055°E, 106 m, 22 Jul 1932, Wagner, 1♂ (AMNH_PBI 00208715) (MZH). Ulm, 48.39944°N 9.99638°E, 473 m, 17 Jul 1994, Hüeber, 1 adult sex unknown (AMNH_PBI 00213965) (HNHM).

Netherlands: Gravestein, 23 Jun 1946, Geutem, 1♂ (AMNH_PBI 00208711) (MZH).

Romania: Cirtisoara, 16 Aug 1958, Sienkiewicz, 1 adult sex unknown (AMNH_PBI 00206739) (AMNH). Carpathes: Brosteni Molday, 47.25083°N 25.66444°E, 1007 m, 1 adult sex unknown (AMNH_PBI 00204218) (BMNH). Sinaia Valachie, 45.50277°N 25.02500°E, 2136 m, Montandon, 1 adult sex unknown (AMNH_PBI 00206736) (AMNH), 1 adult sex unknown (AMNH_PBI 00213967) (HNHM). Sinaia, 45.33083°N 25.55527°E, 793 m, Jul 1955, Sienkiewicz, 1♂ (AMNH_PBI 00206732) (AMNH); Jul 1955, Sienkiewicz, 2♂♂ (AMNH_PBI 00206733) (AMNH); 20 Sep 1957, Sienkiewicz, 1 adult sex unknown (AMNH_PBI 00206734) (AMNH). Tusnad, 46.22916°N 25.95222°E, 689 m, Jonesett, 2♂♂, 1♀ (AMNH_PBI 00206737) (AMNH).

Slovakia: Kamenicny: Balvany, 47.83027°N 18.02055°E, 108 m, 4 Aug 1956, Mihalyi, 1 adult sex unknown (AMNH_PBI 00213964) (HNHM).

Sweden: Kristianstad: Lyngby, 55.89277°N 14.11444°E, 16 m, 1 Aug 1939, Kemner, 2 adults sex unknown (AMNH_PBI 002124864, AMNH_PBI 00212488) (MZLU). Arild, 56.27°N 12.58138°E, 35 m, 29 Aug 1939, Kemner, 1 adult sex unknown (AMNH_PBI 00212489) (MZLU). Brunnby, 56.24888°N 12.56694°E, 20 m, 24 Jul 1961, Ossiannilsson, 2 adults sex unknown (AMNH_PBI 00212484, AMNH_PBI 00212485), 1 adult sex unknown (AMNH_PBI 00212483) (MZLU). Hýlsingborg, 28 Jul 1939, Kemner, 2♂♂ (AMNH_PBI 00206724, AMNH_PBI 00206725), 1♀ (AMNH_PBI 00206726) (AMNH), 1 adult sex unknown (AMNH_PBI 00212490) (MZLU); 28 Jul 1939, Kemner, 2 adults sex unknown (AMNH_PBI 00212478, AMNH_PBI 00212479) (MZLU). Kullaberg, 56.6425°N 12.48972°E, 19 Sep 1963, Tjeder, 2 adults sex unknown (AMNH_PBI 00212480, AMNH_PBI 00212481) (MZLU); 24 Jul 1968, Andersson, 1 adult sex unknown (AMNH_PBI 00212482) (MZLU).

Switzerland: Solothurn: Lebern: Solothurn, 47.20694°N 7.53305°E, 365 m, 2 Jul 1953, Lindberg, 1♂ (AMNH_PBI 00208708) (MZH); 9 Jul 1953, Lindberg, 2♂♂ (AMNH_PBI 00208699, AMNH_PBI 00208707) (MZH).

Serbia: Ruplje, Sep 1902, Horváth, 1 adult sex unknown (AMNH_PBI 00213966) (HNHM).

Diagnosis

Dicyphus pallidus is recognized by the following combination of characters: macropters and brachypters in both sexes; body length 5.23–5.80 mm in macropterous males, 4.34–5.10 mm in brachypterous males, 5.93–6.02 mm in macropterous females, 4.49–5.67 mm in brachypterous females. AII 2.14× longer than head width. AII–pronotal width ratio >1.5 in males. Pronotal disk *c.* 1× shorter than callosite region in males. Callosite region >2.5× longer than collar width at middle line in males and >2.4× longer in females. Body mostly stramineous, including most of head aside from dark X-shaped marking on frons+vertex and postocular margins of head; thorax and hemelytra mostly pale, whitish, stramineous and pale orange, with dark markings posterolaterally on callosite region and mesoscutum in brachypters; AI greatly elongate, mostly reddish brown with base and apex stramineous; AII mostly stramineous to light brown, darker distally (Fig. 4); posterior margin of left side of SVIII with heavily sclerotized flange-like expansion process with denticulate substructure (Fig. 8F); pygophore with posteroventral brown markings; left paramere greatly elongate with short cap-like spatulate apex (Fig. 10F); aedeagus with pair of large, symmetrical, weakly arcuate endosomal lobal sclerites (Fig. 31A).

Description

Males. Macropters and brachypters examined.

Coloration (Fig. 4): Dorsum mostly stramineous with pale orange dark-brown markings, sometimes with red highlighting. *Head:* mostly stramineous with posterior margin behind eyes pale orange; frons+vertex with a moderately long X-shaped dark reddish brown marking, incomplete posteriorly, extending to level of posterior margin of eyes; clypeus stramineous, sometimes weakly embrowned; mandibular and maxillary plates, gula and bucculae stramineous; postocular margins of head narrowly dark brown. *Antennae:* AI mostly brown, with base and apex stramineous, sometimes paler towards base; AII mostly stramineous, sometimes with faint embrownment basally and distally; AIII and AIV concolorous, stramineous to weakly brown. *Pronotum:* collar and pronotal disk whitish to whitish stramineous, translucent; callosite region mostly stramineous, rarely with faint embrownment in macropters, commonly with dark-brown markings posterolaterally in brachypters. *Thoracic pleura and sterna:* mostly stramineous, with ventral margin of propleuron and mesepimeron more whitish, sometimes medial region of mesobasisternum also whitish. *Mesoscutum:* mostly stramineous to light brown, with dark-brown spots laterally in brachypters. *Scutellum:* lateral angles broadly pale stramineous to whitish with midline a little darker. *Hemelytra:* translucent, most often uniformly stramineous, macropters sometimes with faint brown markings at corial fracture, apex of endocorium and tip of cuneus; membrane veins mostly brown, occasionally reddish; brachypters without markings. *Abdomen:* venter stramineous, pygophore with posteroventral brown markings in macropters and brachypters.

Structure: Head: interocular distance 1.15–1.42× greater than eye width in macropters, 1.19–1.31× in brachypters. *Antennae:* AI 1.88–2.41× longer than interocular distance in macropters, 2.03–2.39× in brachypters; AII long, 1.56–1.83× longer than posterior width of pronotum in macropters, 1.87–2.17× in brachypters. *Pronotum:* disk 0.90–1.04× longer than callosite region in macropters, 0.59–0.77× in brachypters; callosite region 2.62–3.03× longer than collar width at middle line in macropters and 2.70–3.22× longer in brachypters. *Male genitalia:* posterior margin of left side of SVIII with heavily sclerotized flange-like process with denticulate substructure (Fig. 8F); left paramere greatly elongate and robust, apophysis weakly sinuate; spatulate apex weakly expanded and short (Fig. 10F); aedeagus with three endosomal lobes, medial lobe and right side lobe each with a weakly arcuate endosomal lobal sclerites, symmetrical and of equal size (Fig. 31A).

Females. Macropters and brachypters examined. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.27–1.40× greater than eye width in macropters, 1.22–1.32× in brachypters. *Antennae:* AI 1.67–1.97× longer than interocular distance in macropters, 1.85–2.11× in brachypters; AII 1.38–1.53× longer than posterior pronotal width in macropters, 1.84–1.99× in brachypters. *Pronotum:* disk 1.03–1.11× longer than callosite region in macropters, 0.54–0.81× in brachypters; callosite region 2.50–2.92× longer than collar width at middle line in macropters and 2.96–3.37× in brachypters.

Measurements

See Table 4.

Distribution

Dicyphus pallidus is broadly distributed in northern Europe (Fig. 38). See Kerzhner & Josifov (1999) for a complete list of countries. Linnavuori & Hosseini (1999) also reported this species from Iran.

Host plants

We have collected this species on *Salvia glutinosa*, *Stachys sylvatica* and *Stachys alpina*. *Dicyphus pallidus* has been reported on *Epilobium* sp. and *Geranium* sp. (Tamanini, 1956; Wagner, 1964; Linnavuori & Hosseini, 1999).

Remarks

Also see *Dicyphus flavoviridis* remarks. *Dicyphus pallidus* is the largest species of *Dicyphus* (*Dicyphus*). Wagner (1951) erected it as the nominate species of his *pallidus* species-group, based on the ratio of the AII:posterior width and the callosite region:collar width. This species is similar in external structure (Fig. 4) and the morphology of the genitalia to *D. flavoviridis* (Figs 10A, F, 13D, 31A). Both species possess a left side abdominal SVIII process (Figs 7D, 8F), elongate left paramere (Fig. 10A, F) and two endosomal lobal sclerites that are of similar size and weakly arcuate (Figs 13D, 31A). The molecular phylogenetic analysis yielded separation of these two species (Figs 24, 25), which is congruent with the above morphological characters. *Dicyphus pallidus* is readily differentiated from *D. constrictus*, *D. epilobii*, *D. errans* and *D. josifovi* by the abdominal SVIII process (Fig. 8F) and the shape of the left paramere (Figs 10, 23). This is the first time this structure is reported for *D. pallidus*.

Dicyphus poneli Matocq & Ribes, 2004 (Figs 5, 39)

Dicyphus poneli Matocq & Ribes, 2004: 43 (original description).

Material examined

Paratypes. Portugal: Madeira Islands: Clifts between Ribeira de Janela and Seixtal, 32.82638ºN 17.15584ºW, 5 m, Jul 2001, Ponel, 1♂ (UNSW_ENT 00026526), 1♀ (UNSW_ENT 00026527), 1♀ (J. Ribes, personal collection).

Diagnosis

Dicyphus poneli is recognized by the following combination of characters: only macropterous males known, macropterous and brachypterous females (Matocq & Ribes, 2004); only macropters examined in both sexes. Body length 4.54 mm in macropters males, 4.03–4.33 mm in macropters females; mostly stramineous to light brown, with extensive dark brown spots and larger markings on dorsum, with posterior margin of head and mesoscutum orange (Fig. 5); clypeus orange with minor embrownment; maxillary plates dark brown; callosite region with dark markings; AI with subbasal and subapical dark reddish brown markings, paler medially; AII mostly stramineous to light orange-brown, with subbasal and apical dark-brown annulations; AIII pale orange; AIV dark brown; hemelytra with extensive dark brown spotting on corium and clavus associated with setae, larger dark-brown markings on corial fracture, apex of endocorium and tip of cuneus. Apophysis of left paramere moderately robust and elongated; aedeagus with spinules, without enlarged endosomal lobal sclerites (Matocq & Ribes, 2004).

Redescription

Males. One macropterous male examined.

Structure: Body length 4.54 mm. *Head:* interocular distance 1.88× greater than eye width. *Antennae:* AI 1.37× longer than interocular distance in macropters; AII 1.01× longer than posterior width of pronotum. *Pronotum:* disk 1.30× longer than callosite region. *Male genitalia:* apophysis of left paramere moderately robust and elongated; aedeagus with spinulations, without enlarged endosomal lobal sclerites (Matocq & Ribes, 2004).

Females. Only macropters examined, 4.03–4.33 mm. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.66–1.89× than eye width. *Antennae:* AI 1.36–1.37× longer than interocular distance; AII 0.88–0.90× longer than posterior pronotal width. *Pronotum:* disk 1.15–1.16× longer than callosite region.

Measurements

See Table 4.

Distribution

Restricted to Madeira, Portugal (Matocq & Ribes, 2004) (Fig. 39).

Host plants

Unknown.

Remarks

Matocq & Ribes (2004) described *Dicyphus poneli* from three localities in Madeira, Portugal. They documented male and female specimens, including macropters and brachypters (reported as submacropters) and immatures. They described the male and female genitalia, including illustrations of the parameres and the aedeagus. We were able to observe several paratypes of this species and confirm its validity. Our redescription of this species is brief to accommodate our own observations. Matocq & Ribes (2004) did not observe endosomal lobal sclerites, which is typical for *Dicyphus* (*Dicyphus*) species of the Western Palaearctic. This species also has distinct colour patterning of the antennae, as well as extensive brown spotting on the hemelytra, including the clavus. In terms of its affinities, this species is likely allied to *D. escalerae* (Fig. 5). See also remarks for this latter species.

Dicyphus rubicundus Blöte, 1929
(Figs 11A, 27, 31B, 33, 39)

Dicyphus rubicundus Blöte, 1929: 163 (original description); Carvalho, 1958: 194 (world catalogue); Wagner, 1974: 80; Schuh, 1995: 494 (world catalogue); Ribes & Ribes, (1997): 163–166 (redescription); Kerzhner & Josifov, 1999: 23 (Palaearctic catalogue).

Dicyphus baezi Ribes, 1983: 67 (original description); Kerzhner & Josifov, 1999: 21 (Palaearctic catalogue), new synonymy, this work.

Material examined

Paratype of *Dicyphus baezi*, 1♂, *Spain:* Canary Islands: Gomera Island: Meriga, 28.1°N 17.2°W, 15 Aug 1977, Baez (J. Ribes, personal collection).

Spain: Canary Islands: Gran Canaria: Moya (Near Galdar), ex. *Aeonium virgineum* Webb & Christ (Crassulaceae), 28.14194ºN 15.57500ºW, 34 m, 14 Apr 2007, Sanchez, 5♂♂, 5♀♀ (IMIDA_ENT 00000415-IMIDA_ENT 00000424). La Gomera: El Cedro, ex. *Aeonium subplanum* Praeger (Crassulaceae), 28.12778ºN 17.21527ºW, 800 m, 12 Apr 2007, Sanchez, 5♂♂, 5♀♀(IMIDA_ENT 00000435-IMIDA_ENT 00000444). La Palma: Lomo de Mestres: San Pedro de Peña Alta, ex. *Aeonium palmense* Webb ex Christ (Crassulaceae), 28.66556ºN 17.80889ºW, 747 m, 10 June 2009, Sanchez, 11♂♂, 8♀♀ (IMIDA_ENT 00000111-IMIDA_ENT 00000129). Tenerife: Icod el Alto, ex. *Aeonium canariensis* (L) Webb & Berth (Crassulaceae), 28.31754ºN 16.42396ºW, 660 m, 10 Apr 2008, Sanchez, 5♂♂, 5♀♀ (IMIDA_ENT 00000405-IMIDA_ENT 00000414); 14 Oct 2008, Sanchez, 9♂♂, 6♀♀ (IMIDA_ENT 00000338-IMIDA_ENT 00000352); Las Mercedes–Taganana road, ex. *Aeonium canariensis*, 28.53333ºN 16.25500ºW, 820 m, 15 Oct 2008, Sanchez, 12♂♂, 6♀♀ (IMIDA_ENT 00000315-IMIDA_ENT 00000332); Los Realejos–Icod road, ex. *Aeonium canariensis*, 28.38000ºN 16.59861ºW, 516 m, 16 October 2008, Sanchez, 23♂♂, 17♀♀ (IMIDA_ENT 00000267-IMIDA_ENT 00000306) (IMIDA).

Diagnosis

Dicyphus rubicundus is recognized by the following combination of characters: macropters and brachypters in both sexes; body length 4.29–4.45 mm in macropterous males, 2.76–3.04 mm in brachypterous males, 4.15–4.69 mm in macropterous females, 2.70–3.19 mm in brachypterous females; body stramineous to brown, with dark-brown markings (Fig. 33); frons+vertex with dark brown X-shaped marking; clypeus mostly stramineous; mandibular plate stramineous; maxillary plates dark brown; thorax brown, with dark markings posterolaterally on callosite region and mesoscutum; brown markings on corial fracture, apex of endocorium and tip of cuneus in macropters; hemelytra mostly pale, whitish, stramineous, generally with dark spots at base of setae; AI short, mostly stramineous to brown, with subbasal and subapical dark reddish brown annulations; AII mostly stramineous with subbasal brown annulation and distal 1/4 dark brown; pygophore with large posteroventral brown spot; left paramere apophysis greatly elongate and strongly recurved, with shaft not expanded and outer margin minutely denticulate proximally (Fig. 11A); aedeagus with three endosomal lobes, medial lobe with 5–11 small lobal sclerites, lateral lobes densely spinulate (Fig. 31B).

Redescription
Males. Macropters and brachypters examined.

Coloration (Fig. 33): Dorsum mostly brown with darker markings, plus orange/red highlighting. *Head:* frons+vertex with a X-shaped dark-brown marking, extending to posterior margin of eyes; vertex orange; postocular margins of head orange medium brown; gula and bucculae stramineous; clypeus stramineous with medium-brown highlighting dorsally; mandibular plates stramineous; maxillary plate embrowned. *Antennae:* AI with subbasal and subapical dark reddish brown annulations, stramineous to light brown medially; AII mostly stramineous, with subbasal annulation and distal 1/4 dark brown; AIII and AIV concolorous, uniformly light to medium brown; antennae often paler overall in brachypters, with AII sometimes without brown markings, or faint at most, and AIII and AIV paler brown to stramineous. *Pronotum:* collar variable from stramineous to brown, translucent; callosite region with variable embrownment; disk stramineous, humeral angles embrowned. *Thoracic pleura and sterna:* propleuron most often with shiny dark brown transverse band, ventral margin stramineous overall, with reddish highlighting, more so in some brachypters; mesobasisternum most often medium brown, sometimes bicoloured with light reddish brown mottling; mesepimeron whitish to stramineous; metepisternum varying from mostly medium brown to brown intermixed with stramineous highlighting. *Mesoscutum:* mostly orange, with faint embrownment laterally, darker reddish brown laterally in some brachypters. *Scutellum:* lateral angles broadly pale stramineous to whitish with dark reddish brown stripe along midline. *Hemelytra:* translucent, mostly stramineous with medium-brown to reddish brown markings/highlighting, generally with dark spots at base of setae; with three pairs of medium-brown to reddish brown markings, each pair at corial fracture, apex of endocorium and tip of cuneus; membrane veins embrowned; mostly translucent with two pairs of faint brown spots distally in brachypters. *Abdomen:* venter mostly stramineous, with basal sternites and lateral regions of pregenital sternites dark brown, sometimes with red or orange highlighting; pygophore mostly stramineous, with anterior embrownment and large dark-brown spot posteroventrally.

Structure: Head: interocular distance 1.52–1.63× greater than eye width in macropters, 1.55–1.76× in brachypters. *Antennae:* AI 1.49–1.66× longer than interocular distance in macropters, 1.39–1.51× in brachypters; AII 1.11–1.25× longer than posterior width of pronotum in macropters, 1.35–1.44× in brachypters. *Pronotum:* disk 1.04–1.37× longer than callosite region in macropters, 0.74–1.37× in brachypters. *Male genitalia:* left paramere apophysis greatly elongate and strongly recurved distally, shaft straight and not expanded, with outer margin minutely denticulate proximally (Fig. 11A); aedeagus with three endosomal lobes, medial lobe with 5–11 small endosomal lobal sclerites, lateral lobes densely spinulate (Fig. 31B).

Females. Macropters and brachypters examined. Coloration, vestiture, texture and structure mostly as in males. *Head*; interocular distance 1.47–1.68× longer than eye width in macropters, 1.36–1.60× in brachypters. *Antennae:* AI 1.39–1.48× longer than interocular distance in macropters, 1.42–1.53× in brachypters; AII length 0.96–1.07× posterior pronotal width in macropters, 1.18–1.26× longer in brachypters. *Pronotum:* disk 1.15–1.32× longer than callosite region, 0.70–0.81× in brachypters.

Measurements
See Table 4.

Distribution
Endemic to the Canary Islands. The species was known to La Gomera, and Tenerife (Ribes, 1981; Ribes & Ribes, 1997). We have collected *D. rubicundus* in these two islands and report it for the first time to the island of La Palma (Fig. 39).

Host plants
We collected *D. rubicundus* on *Aeonium canariensis* (L.) Webb & Berth (Crassulaceae), *Aeonium palmense* Webb ex. Christ (Crassulaceae), *Aeonium subplanum* Praeger (Crassulaceae) and *Aeonium virgineum* Webb & Christ (Crassulaceae).

Remarks
Blöte (1929) described *D. rubicundus* from a single specimen collected in Lagunetas (Gran Canaria, Canary Islands), mistaking a brachypterous male as a female. Ribes & Ribes (1997) pointed out this *lapsus* and redescribed the species, including a description of the male genitalia. Ribes & Ribes (1981) had also previously described *Dicyphus baezi* from two

macropterous males as a new Canarian species, without recognizing that these specimens were macropters of *D. rubicundus*. Based on our new collections from the Canary Islands, we found that macropters and brachypters are commonly encountered in the same population, their male genitalia being indistinguishable and the mtDNA sequences identical or very similar. On these attributes, we synonymize *D. rubicundus* and *D. baezi*.

Dicyphus rubicundus is generally darker and has a longer body than *D. bolivari* (Fig. 33). These two species are best separated by the shape of the apophysis of the left paramere, with *D. rubicundis* possessing a more elongate apophysis, which is strongly recurved apically and not expanded (Figs 9C–F, 11A). The aedeagus of these two species is very similar, with both possessing two densely spinulate endosomal lateral lobes, and the medial lobe has a tightly packed of small lobal sclerites, which vary intraspecifically (Figs 12C, 31B).

Dicyphus stachydis Sahlberg, 1878 (Figs 3, 11b, 28, 31c, 39)

Dicyphus stachydis Sahlberg, 1878: 29 (original description); Carvalho, 1958: 200 (world catalogue); Schuh, 1995: 495 (world catalogue); Kerzhner & Josifov, 1999: 23 (Palaearctic catalogue).

Dicyphus stachydis wagneri Tamaninii, 1956: Tamanini (1956) (original description; subspecies).

Materials examined

Bulgaria: Morava, 43.50833°N 25.14972°E, 154 m, 21 May 1944, Stehlik, 4 adults sex unknown (AMNH); 21 May 1944, Stehlik, 1 adult sex unknown (AMNH).

Hungary: Budapest: Jýnos h., 47.49972°N 19.03916°E, 136 m, 2 Apr 1916, Györffy, 1 adult sex unknown (HNHM); 1 Oct 1929, Biro, 1 adult sex unknown (HNHM).

Czech Republic: Zlinsky: Valasske: Klobouky, 49.0816ºN 18.0117ºE, 450 m, 17 Aug 2009, ex. *Stachys silvatica*, Sanchez, Kment & Pennaroli, 8 ♂♂ (IMIDA_ENT 0000093, IMIDA ENT0000095, IMIDA_ENT 0000096, IMIDA_ENT 0000097, IMIDA_ENT 0000101, IMIDA_ENT 0000105, IMIDA_ENT 0000106, IMIDA_ENT 0000110), 8♀♀ (IMIDA_ENT 00000098-IMIDA_ENT 00000100, IMIDA_ENT 00000104, IMIDA_ENT 00000108, IMIDA_ENT 00000674-IMIDA_ENT 00000676). Zlinksy: Valasske: Klobouky: Kralovec Mountain, 49.07574ºN 18.01595ºE, 589 m, 17 Aug 2009, ex. *Atropa bella-donna*, Sanchez, Kment & Pennaroli, 11♂♂, 7♀♀ (IMIDA_ENT 00000141-IMIDA_ENT 00000158), 5♂♂, 3♀♀ (IMIDA_ENT 00000202-IMIDA_ENT 00000209) (IMIDA).

Romania: Bistrita, 47.13361°N 24.49277°E, 360 m, Aug 1952, 13 adults sex unknown (AMNH). Buzan, 45.22277°N 26.72138°E, 122 m, Aug 1953, 2 adults sex unknown (AMNH). Comana, 43.89833°N 28.30500°E, 106 m, 28 Jun 1953, 1 adult sex unknown (AMNH); 18 May 1954, Sienkiewicz, 1 adult sex unknown (AMNH). Sinaia, 45.33083°N 25.55527°E, 793 m, Jul 1955, 1 adult sex unknown (AMNH); 13 Sep 1957, Sienkiewicz, 1 adult sex unknown (AMNH); 13 Sep 1957, Sienkiewicz, 1 adult sex unknown (AMNH); 20 Sep 1957, Sienkiewicz, 1 adult sex unknown (AMNH); 18 Aug 1959, Cant., 1 adult sex unknown (AMNH); 26 Aug 1960, Sienkiewicz, 1 adult sex unknown (AMNH); 11 Sep 1962, Sienkiewicz, 1 adult sex unknown (AMNH).

Russia: Krasnodar Terr.: Novokubansk [Kubanskaya St.] nr Armavir, 45.11167ºN 41.01828ºE, 153 m, 8 Jul 1934, Zimin, 2♂♂ (AMNH_PBI 00341233, AMNH_PBI 00341235), 3♀♀ (AMNH_PBI 00341231, AMNH_PBI 00341232, AMNH_PBI 00341234) (ZISP).

Sweden: Alingsas: Kullen, 58.04166°N 12.53833°E, 102 m, 29 Aug 1939, Kemner, 2 adults sex unknown (MZLU); 29 Aug 1959, 1 adult sex unknown (AMNH). Hýganý: Arild, 56.27000°N 12.58138°E, 35 m, 29 Aug 1939, Kemner, 1 adult sex unknown (MZLU). Arild, 56.27000°N 12.58138°E, 35 m, 29 Aug 1939, 1 adult sex unknown (AMNH). Brunnby, 59.83083°N 13.53277°E, 31 m, 28 Aug 1964, Ossiannilsson, 2 adults sex unknown (MZLU). Vg., Kinnekulle, 1 Jul 1928, Lindberg, 1 adult sex unknown (MZLU). Skane Lan: Arild, 56.27000°N 12.58138°E, 35 m, 20 Aug 1937, Lindberg, 4♂♂ (MZH).

Switzerland: Uetliberg, 47.35222°N 8.48750°E, 870 m, 9 Jun 1953, Lindberg, 1♂, 1♀ (MZH).

United Kingdom: England: Bedford: Renhold, 52.16305°N 0.4025°W, 56 m, 9 Aug 1935, Leston, 4 adults sex unknown (AMNH). Bedfordshire: Maulden wood, 52.02888°N 0.44500°W, 81 m, 08 Aug 1935, Leston, 1 adult sex unknown (AMNH). Berkshire: Silwood Park, Ascot, 51.4126°N 0.63659°W, 62 m, 23 Apr 1953, Southwood, 1 adult sex unknown (AMNH). Dorset: Cranborne, Wimborne, 50.91833°N 1.92250°W, 66 m, 12 Oct 1935, P.H., 1 adult sex unknown (BMNH). Hertfordshire: Boxhill, 51.76333°N 0.47000°W, 131 m, 2 Oct 1955, Lindberg, 1 adult sex unknown (MZH). York: Kirkbymoorside, 54.28777°N 0.95944°W, 139 m, Jessop, 1 adult sex unknown (BMNH); 11 Sep 1982, Jessop, 1 adult sex unknown (BMNH). Springwood, 54.27444°N 0.93444°W, 88 m, 11 Sep 1982, Jessop, 1 adult sex unknown (BMNH). Well, 25 Jun 1988, 1 adult sex unknown (BMNH); 20 Oct 1988, 1 adult sex unknown (BMNH). Scotland: Morayshire: Forres, 57.61111°N 3.61055°W, 106 m, 1 adult sex unknown (AMNH). Scotia, 55.95°N 3.2°W, 31 m, 3♂♂, 2♀♀ (MZH).

Diagnosis
Dicyphus stachydis is recognized by the following combination of characters: macropters and brachypters in both sexes; body length 4.02–4.51 mm in macropterous males, 2.09–3.52 mm in brachypterous males, 4.07–4.68 mm in macropterous females, 2.85–3.81 mm in brachypterous females; body mostly stramineous and orange, with dark-brown markings (Fig. 3); frons+vertex with dark brown X-shaped marking, reaching posteromedial angle of eyes; clypeus mostly stramineous, with dorsal and ventral embrownment; mandibular plate stramineous; maxillary plates dark brown; propleuron with prominent shiny dark-brown transverse band; faint brown markings on corial fracture and tip of cuneus in macropters; AI short, mostly stramineous, with subbasal and subapical red stramineous annulations, latter sometimes more reddish brown; AII mostly stramineous with subbasal brown annulation and distal 1/4 brown; left paramere apophysis robust and short, with weakly expanded spatulate apex, outer margin smooth (Fig. 11B); aedeagus with three endosomal lobes, and two large, symmetrical, weakly arcuate lobal sclerites (Fig. 31C).

Redescription
Males. Macropters and brachypters examined.

Coloration (Fig. 3): Dorsum mostly stramineous with dark-brown markings, sometimes with orange/red markings or highlighting, rarely more intensely dark brown. *Head:* mostly stramineous, frons+vertex with a short, X-shaped dark-brown marking, extending to posteromedial angles of eyes; vertex orange; postocular margins of head orange; gula and bucculae stramineous; clypeus stramineous with medium brown highlighting dorsally; mandibular plates stramineous; maxillary plate embrowned. *Antennae:* AI mostly stramineous, with faint subbasal and darker subapical reddish brown annulations, sometimes annulations faint; AII mostly stramineous, with subbasal annulation and distal 1/4 dark brown; AIII and AIV concolorous, uniformly light to medium brown; antennae often paler overall in brachypters, with AII sometimes without brown markings, or faint at most, and AIII and AIV paler brown to stramineous. *Pronotum:* collar whitish to stramineous, translucent; callosite region mostly stramineous, sometimes with variable embrownment, occasionally with two or three dark brown spots laterally in macropters and brachypters; disk stramineous, humeral angles embrowned. *Thoracic pleura and sterna:* propleuron most often with shiny dark-brown transverse band, sometimes not extending to the propleural suture, ventral margin whitish, sometimes more stramineous overall, with reddish highlighting, more so in some brachypters; mesobasisternum most often medium brown, sometimes bicoloured with lateral regions stramineous; mesepimeron whitish to stramineous; metepisternum varying from mostly medium brown to brown intermixed with stramineous highlighting, peritreme sometimes dark brown. *Mesoscutum:* mostly orange to stramineous, with faint embrownment laterally. *Scutellum:* lateral angles broadly pale stramineous with pale orange brown stripe along midline. *Hemelytra:* translucent, mostly stramineous to pale brown; with costal fracture and tip of cuneus with pale brown to reddish brown markings in macropters. *Abdomen:* venter mostly stramineous to whitish.

Structure: Head: interocular distance 1.11–1.51× greater than eye width in macropters, 1.04–1.54× in brachypters. *Antennae:* AI 1.42–1.84× longer than interocular distance in macropters, 1.39–1.87× in brachypters; AII length 0.96–1.21× posterior width of pronotum in macropters, 1.09–1.49× in brachypters. *Pronotum:* disk 1.11–1.49× longer than callosite region in macropters, 0.58–0.95× in brachypters. *Male genitalia:* left paramere apophysis robust and short, with apex weakly spatulate, with outer margin smooth, setae of sensory lobe greatly elongate (Fig. 11B); aedeagus with three endosomal lobes, with pair of large, moderately arcuate endosomal lobal sclerites (Fig. 31C).

Females. Macropters and brachypters examined. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.15–1.62× greater than eye width in macropters, 1.12–1.42× in brachypters. *Antennae:* AI 1.33–1.56× longer than interocular distance in macropters, 1.37–1.82× in brachypters; AII 0.84–1.01× greater than posterior pronotal width in macropters, 1.10–1.42× longer in brachypters. *Pronotum:* disk 1.27–1.56× longer than callosite region in macropters, 0.65–0.99× in brachypters.

Measurements
See Table 4.

Distribution

This species is common in central Europe. See Kerzhner & Josifov (1999) for a complete list of countries. We have examined specimens from Bulgaria, Czech Republic, Romania, Russia, Sweden, Switzerland and the United Kingdom (Fig. 39).

Host plants
Dicyphus stachydis has been reported on *Circaea* sp., *Digitalis* sp., *Galeopsis* sp. and *Geranium* sp. (Wagner, 1964, 1970). We collected *D. stachydis* on *Atropa belladonna*, *Stachys sylvatica* and *Stachys alpina*.

Remarks

Also see *D. hyalinipennis* remarks. *Dicyphus stachydis* is a generally paler species and is difficult to distinguish from *D. hyalinipennis*, *D. bolivari* and *D. argensis* externally (Figs 3, 33). The male genitalia are the most reliable characters for separating these species. The aedeagus differs significantly between *D. stachydis* and *D. bolivari*, with the former species possessing a pair of large endosomal lobal sclerites (cf. a cluster of very small endosomal lobal sclerites on the medial endosomal lobe *D. bolivari*) (Figs 12C, 31C). Also, they differ in the shape of the apophysis of the left paramere, which is very short in *D. stachydis* (cf. elongate in *D. bolivari*) (Figs 9C–F, 11B). *Dicyphus stachydis*, *D. hyalinipennis* and *D. argensis* share a robust and short left paramere (Figs 9B, 10B, 11B) and two well-developed endosomal lobal sclerites (Figs 12B, 14A, 31C). *Dicyphus stachydis* differs from the latter two species by the lack of a notch at the base of the spatulate apex and the symmetrical and weakly arcuate endosomal lobal sclerites. The separation of these species is corroborated by the molecular phylogeny, where all of the above four species are differentiated (Figs 24, 25).

Tamanini (1956) described a new subspecies, *Dicyphus stachydis wagneri*, with a European meridional distribution (southern France and Italy), based on more prominent eyes, darker coloration, the more abundant and elongate setae of the sensory lobe of the left paramere, and the larger endosomal lobal sclerites. As in the case of *D. constrictus*, we did not have access to the type material of this subspecies and have not assessed its validity.

DICYPHUS TAMANINII WAGNER, 1951
(FIGS 11C, 22A, 33, 39)

Dicyphus tamaninii Wagner, 1951: 16 (original description); Carvalho, 1958: 200 (world catalogue); Schuh, 1995: 495 (world catalogue); Kerzhner & Josifov, 1999: 24 (Palaearctic catalogue).

Material examined

Croatia: Palagruza, 42.39222°N 16.25833°E, 19 May 1949, Novak, paratypes 2♂♂ (AMNH_PBI 00208572, AMNH_PBI 00208652), 1♀ (AMNH_PBI 00208653) (MZH). Split, Dalmatia, 43.50000°N 16.43333°E, Novak, paratype, 1♀ (AMNH_PBI 00208651) (MZH). Palagruza, 42.39222ºN 16.25833ºE 19 May 1949, Novak, 1♂, (UNSW_ENT 00026528).

France: París: Seine, 48.8ºN 2.3ºE, 100 m, 23 Nov 2006, ex. *Erigeron canadensis* (L.) Cronquist (Asteraceae), Matocq & Derzhansky, 1♂, (AMNH_PBI00209595) (MNHN); Audi: Leucate, 42.91030°N 3.02816°E, 23 m, 1 Jun 1991, Pericart & Matocq, 1 ♀ (AMNH_PBI00209596) (MNHN).

Corsica: Haute Corse: Barcaggio, Bord de mer, 43.00616ºN 9.40129ºE, 5 m, 24 Nov 1999, Matocq, 1 ♂ (AMNH_PBI00209598) (MNHN).

Greece: Laconie: Monemvassia: 36.68760°N 23.05603ºE, 24 m, 5 May 1998, Magnien, Péricart & Matocq, 1♂ (AMNH_PBI00209597) (MNHN).

Diagnosis

Dicyphus tamaninii is recognized by the following combination of characters: macropters and brachypters in both sexes (Wagner, 1951); body length 3.92–4.29 mm in macropterous males, 4.17–4.53 mm in macropterous females; Wagner (1951) reported body length for brachypterous males (3.0–3.2 mm) and females (3.7–4.4 mm). Body stramineous with dark-brown markings, orange markings, sometimes with red highlighting (Fig. 33); dark brown X-shaped marking on frons+vertex not extending beyond medial angles of eyes; AI stramineous with reddish brown subbasal and subapical annulations; AII mostly stramineous, with apical 1/3rd dark brown; vertex and mesoscutum mostly orange; AI 1.22–1.70× longer than interocular distance in macropterous males; AII 1.01–1.21× longer than posterior width of pronotum in macropterous males; left paramere with moderately robust and elongate apophysis, with spatulate crest narrow and elongate (Fig. 11C); aedeagus with three endosomal lobes, with medial lobe with two to five small lobal sclerites, lateral lobes spinulate (Fig. 22A).

Redescription

Males.

Coloration (Fig. 33): Dorsum mostly stramineous with orange and dark brown to fuscous markings, sometimes with red highlighting. *Head:* mostly stramineous with contrasting markings; frons+vertex with a X-shaped reddish-brown marking, reaching the medial angle of eyes; clypeus dark brown highlighting; mandibular plates stramineous; maxillary plate dark brown; vertex orange; postocular margins of head orange broadly dark brown; gula and bucculae yellow. *Antennae:* AI mostly stramineous, with subbasal and subapical dark reddish brown annulations; AII mostly stramineous, with distal 1/3rd dark brown, narrowly and faintly brown at base; AIII and AIV concolorous, uniformly dark brown. *Pronotum:* collar whitish, translucent; callosite region mostly stramineous with variable embrownment; disk stramineous, translucent, sometimes humeral angles embrowned. *Thoracic pleura and sterna:* propleuron stramineous with dark brown transverse band, ventral margin whitish; mesobasisternum dark brown; mesepimeron whitish; metepisternum including brown evaporative areas mostly stramineous, sometimes with patches of medium to dark brown. *Mesoscutum:* mostly orange, with embrownment laterally. *Scutellum:* lateral angles broadly pale stramineous to whitish with narrow brown stripe along midline. *Hemelytra:* mostly stramineous with medium-brown to reddish brown markings/highlighting, including red to reddish brown spotting on exocorium associated with setal bases; with three pairs of medium-brown to reddish brown markings, each pair at corial fracture, apex of endocorium and tip of cuneus; membrane veins embrowned to sometimes red. *Abdomen:* venter mostly stramineous, often with faint medium brown banding laterally on pregenital sternites, sometimes with dark brown patches on pygophore.

Structure: Only macropters examined. *Head:* interocular distance 1.27–1.47× greater than eye width. *Antennae:* AI 1.22–1.70× longer than interocular distance; AII 1.01–1.21× longer than posterior width of pronotum. *Pronotum:* disk 1.27–1.40× longer than callosite region. *Male genitalia:* left paramere apophysis moderately robust and elongate, with shaft weakly sinuate, with spatulate weakly denticulate on outer margin (Fig. 11C); aedeagus with three endosomal lobes, medial lobe with two to five small endosomal lobal sclerites, lateral lobes densely spinulate (Fig. 22A).

Females. Only macropters examined. Body length 4.17–4.53 mm. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 1.28–1.42× than eye width. *Antennae:* AI 1.29–1.48× longer than interocular distance; AII 0.88–0.97× shorter than pronotum width. Disk 1.41–1.52× longer than callosite region. *Abdomen:* venter mostly stramineous, with faint brown markings laterally on pregenital sternites.

Measurements
See Table 4.

Distribution
We have examined specimens of *D. tamaninii* from Croatia, France and Greece (Fig. 33). Wagner (1951) reported the species to countries in the Mediterranean area: Croatia, Italy and Tunisia. Kerzhner & Josifov (1999) added Bosnia Hercegovina and Israel to the list, although it is quite likely that some of these records are misidentifications.

Host plants
Wagner (1974) reported *D. tamaninii* from *Hyosciamus niger*. Alomar *et al.* (1994) gave an extensive list of host plants belonging to multiple families: Amaranthaceae (*Amaranthus* sp.), Asteraceae (*Calendula arvensis* (Vaill.) L., *Erigeron annuus*, *Centaurea* sp. *Galactites tomentosa* Moench, *Sonchus* sp., *Dittrichia viscosa*), Boraginaceae (*Borago officinalis* L., *Cynoglossum* sp.), Chenopodiaceae (*Atriplex* sp.), Cistaceae (*Cistus monspeliensis* and *Cistus salvifolius*), Euphorbiaceae (*Euphorbia* sp., *Mercurialis* sp.), Geraniaceae (*Geranium* sp.), Malvaceae (*Lavatera* sp.), Solanaceae (*Solanum nigrum*), Rubiaceae (*Galium* sp.) and Urticaceae (*Parietaria officinalis* and *Urtica* sp.). Matocq & Derzhansky collected *D. tamaninii* on *Erigeron canadensis* (L.) Cronquist (Asteraceae) (this work).

Remarks
Wagner (1951) described *D. tamaninii* from specimens collected by P. Novak in Croatia between 1945 and 1949. Wagner placed *D. tamaninii* in his *hyalinipennis* species-group and stated that it was very close to *D. stachydis*. *Dicyphus tamaninii* belongs to a group of species that possess an elongate apophysis of the left paramere and the endosoma has only small lobal sclerites (also *D. rubicundus* and *D. bolivari*). However, *D. tamaninii* has a significantly longer apophysis of the left paramere (530–600 ηm) than *D. rubicundus* (425–430 ηm) and *D. bolivari* (440–450 ηm) (Figs 9C–F, 11A). These three species are similar externally, although in general *D. rubicundus* is darker (Fig. 33). *Dicyphus rubicundus* is endemic to the Canary Islands and is found only on *Aeonium* spp., whereas *D. tamaninii* is not. In contrast, the body size and external characters of *D. bolivari* and *D. tamaninii* strongly overlap, and species separation is based on differences in the male genitalia, especially the size of the left paramere and the number of endosomal lobal sclerites.

DICYPHUS TUMIDIFRONS RIBES, 1997
(FIGS 5, 11D, 22B, 39)

Dicyphus tumidifrons Ribes, 1997: 27 (original description, Ribes, Blaco-Zumeta & Ribes, 1997); Kerzhner & Josifov, 1999: 24 (Palaearctic catalogue).

Materials examined
Spain: Madrid: Aranjuez, 40.03194°N 3.60305°W, 509 m, 28 Jul 1999, de la Rosa, 1♂ paratype (AMNH_PBI 00206669). Zaragoza: Pina de Ebro, 41.48883ºN 0.52696ºW, 159 m, 18 Jun 1989, ex. *Lavatera triloba* L. (Malvaceae), Ribes, 1♀ paratype (AMNH_PBI 00341236) (ZISP), 1♀ 1♂ paratypes (J. Ribes, personal collection).

Diagnosis
This species is recognized by the following combination of characters: macropterous and brachypterous morphs; small species, body length 2.91–3.09 mm in macropterous males, 2.04 mm in brachypterous males, 3.18 mm in macropterous females, 2.35 mm in brachypterous females; body generally pale yellow, with very few dark markings (Fig. 5); AII shorter than width of posterior margin of pronotum; left paramere

small, arcuate, with outer margin minutely denticulate (Fig. 11D); endosoma without sclerotization (Fig. 22B).

Redescription
Males. Macropters and brachypters examined.

Coloration (Fig. 5): Body whitish to stramineous, with minor brown markings; pronotum, thoracic pleura and sterna, mesoscutum, scutellum and abdominal venter uniformly stramineous. *Head:* mostly stramineous, with whitish markings adjacent to medial margin of eyes; frons + vertex with a faint V-shaped brown marking, reaching middle of eye at most; clypeus, bucculae, lateral plates, gula and postocular margins stramineous. *Antennae:* AI and AII mostly stramineous, with weak subapical reddish annulation on AI, apex of AII with faint red annulation; AIII and AIV pale brown. *Hemelytra:* stramineous, with faint reddish brown spotting at base of setae; faint brown markings on corial fracture, apex of endocorium and tip of cuneus, sometimes with weak red highlighting yellow translucent, with six dark spots, two on each coria and one on the cuneus; membrane non stained, veins pale yellow. *Legs:* yellow with brown spotting on femora; third tarsal segment fuscous.

Structure: Head: interocular distance 2.84–3.17× greater than eye width in macropters, 2.89× in brachypters. *Antennae:* AI short, 0.69–0.96× greater than interocular distance in macropters, 0.96× in brachypters; AII 0.64–0.70× longer than posterior width of pronotum in macropters, 0.85× in brachypters. *Pronotum:* disk 1.35–1.41× longer than callosite region in macropters, 0.73× in brachypters. *Male genitalia:* left paramere apophysis short and strongly recurved, with weakly expanded spatulate apex, with outer margin denticulate (Fig. 11D); endosoma without sclerotization (Fig. 22B).

Females. Macropters and brachypters examined. Coloration, vestiture, texture and structure mostly as in males. *Head:* interocular distance 3.08× greater than eye width in macropters, 3.16× in brachypters. *Antennae:* AI 0.91× longer than of interocular distance in macropters, 0.79× in brachypters; AII length 0.62× longer than posterior pronotal width in macropters, 0.80× in brachypters. *Pronotum:* disk 1.59× longer than callosite region in macropters, 0.81× in brachypters.

Measurements
See Table 4.

Distribution
This species is only known from Spain (Ribes *et al.*, 1997) (Fig. 39).

Host plants
Known from *Lavatera triloba* L. (Malvaceae) (Ribes *et al.*, 1997).

Remarks
Ribes (Ribes *et al.*, 1997) described *D. tumidifrons* from Zaragoza, Spain. We had the opportunity to examine five specimens of this species, and confirm it as a valid species. This species is highly autapomorphic, having very small eyes and a correspondingly broad interocular distance. It is also easily distinguished from all other Western Palaearctic species of *Dicyphus* by the absence of sclerotization on the endosoma. Ribes *et al.* (1997) indicated that it was difficult to place *D. tumidifrons* in the species-groups of Wagner (1951), and regarded the left paramere as atypical for the *D. hyalinipennis* species-group. We have examined specimens of African *Dicyphus* species from Uganda that also lack on sclerotization in the endosoma, but these taxa are much larger than *D. tumidifrons*.

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REFERENCES

Abbas S, Pérez-Hedo M, Colazza S, Urbaneja A. 2014. The predatory mirid *Dicyphus maroccanus* as a new potential biological control agent in tomato crops. *BioControl* **59:** 565–574.

Albajes R, Alomar O, Gullino ML, Van Lenteren JC. 1999. Current and potential use of polyphagous predators. In: Albajes, R., Gullino, M.L., van Lenteren J.C eds. *Integrated pest and disease management in greenhouse crops*. Dordrecht (The Netherlands): Kluwer Academic Publishers, 265–275.

Alomar O, Goula M, Albajes R. 1994. Mirid bugs for biological control: identification, survey in non-cultivated winter plants, and colonization of tomato fields. *IOBC/WPRS Bulletin* **17:** 217–217.

Alomar O, Goula M, Albajes R. 2002. Colonisation of tomato fields by predatory mirid bugs (Hemiptera: Heteroptera) in northern Spain The ecology of field margins in European farming systems. *Agriculture, Ecosystems & Environment* **89:** 105–115.

Arnó J, Castañé C, Riudavets J, Gabarra R. 2010. Risk of damage to tomato crops by the generalist zoophytophagous predator *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae). *Bulletin of Entomological Research* **100:** 105–115.

Avise JC, Walker D. 1999. Species realities and numbers in sexual vertebrates: perspectives from an asexually transmitted genome. *Proceedings of the National Academy of Sciences of the United States of America* **96:** 992–995.

Blöte HC. 1929. Hemiptera. *Contributions to the knowledge of the fauna of the Canary-Islands*. Tijdschrift voor Entomologie, **72:** 161–168.

Boheman CH. 1852. Nya svenska Hemiptera. *Öfversigt af Kongliga Vetenskapsakademiens Förhandlingar* **9:** 65–80.

Burmeister H. 1835. *Handbuch der Entomologie. Zweiter Band. Erste Abtheilung-Rhynchota*. Berlin: Theod. Chr. Friedr. Enslin.

Calvo J, Blockmans K, Stansly PA, Urbaneja A. 2009. Predation by *Nesidiocoris tenuis* on *Bemisia tabaci* and injury to tomato. *Biocontrol* **54:** 237–246.

Carvalho JCM. 1958. A catalogue of the Miridae of the world. Part III. Arquivos do Museu Nacional. *Rio de Janeiro* **47:** 161 pp.

Carvalho P, Mexia A. 2000. First approach on the potential role of *Dicyphus cerastii* Wagner (Hemiptera: Miridae), as natural control agent in Portuguese greenhouses. *IOBC/WPRS Bulletin* **23:** 261–264.

Cassis G. 1986. *A systematic study of the subfamily Dicyphinae (Heteroptera, Miridae)*. PhD Thesis, Oregon State University. University Microfilms International, Ann. Arbor.

Cassis G. 2008. The *Lattinova* complex of Austromirine plant bugs (Hemiptera: Heteroptera: Miridae: Orthotylinae). *Proceedings of the Entomological Society of Washington* **110:** 845–939.

Cassis G, Schuh RT. 2012. Systematics, biodiversity, biogeography, and host associations of the Miridae (Insecta: Hemiptera: Heteroptera: Cimicomorpha). *Annual Review of Entomology* **57:** 377–404.

Castañé C, Alomar O, Goula M, Gabarra R. 2004. Colonization of tomato greenhouses by the predatory mirid bugs *Macrolophus caliginosus* and *Dicyphus tamaninii*. *Biological Control* **30:** 591–597.

Castañé C, Arnó J, Gabarra R, Alomar O. 2011. Plant damage to vegetable crops by zoophytophagous mirid predators. *Biological Control* **59:** 22–29.

Castañé C, Agustí N, Arnó J, Gabarra R, Riudavets J, Comas J, Alomar O. 2012. Taxonomic identification of *Macrolophus pygmaeus* and *Macrolophus melanotoma* based on morphometry and molecular markers. *Bulletin of Entomological Research* **93:** 179–185.

Ceglarska EB. 1999. *Dicyphus hyalinipennis* Burm. (Heteroptera: Miridae): a potential biological control agent for glasshouse pests in Hungary. *IOBC/WPRS Bulletin* **22:** 33–36.

Dayrat B. 2005. Towards integrative taxonomy. *Biological Journal of the Linnean Society* **85:** 407–415.

DeSalle R, Egan MG, Siddall M. 2005. The unholy trinity: taxonomy, species delimitation and DNA barcoding. *Philosophical Transactions of the Royal Society of London. Series B, Biological sciences* **360:** 1905–1916.

Distant WL. 1909. Descriptions of Oriental Capsidae. *Annals and Magazine of Natural History* **8:** 509–523.

Ehanno B. 1960. Contribution a la connaissance des Insectes Héteroptères Miridae Armoricains (2e note). *Bulletin de la Societe scientifique de Bretagne* **35:** 313–324.

Ehanno B. 1968. Hémiptères Miridae interessants recoltes en *Cahiers des Naturalistes* **24:** 45–51.

Ehanno B. 1987. *Les Hétéroptères Mirides de France. Tome Il-A : Inventaire et syntheses écologiques*. Paris : Secrétariat de la Faune et de la Flore, I–X, **97:** 647 pp.

Fallén CF. 1807. Monographia Cimicum Sveciae. *C. G. Proft, Hafniae*: 123 pp.

Fallén CF. 1829. *Hemiptera Sueciae. Sectio prior. Hemelytrata*. Gothorum, Londini.

Fieber FX. 1858. Criterien zur generischen Theilung der Phytocoriden (Capsini aut.). *Wiener Entomologische Monatschrift* **2:** 289–388.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3:** 294–299.

Gabarra R, Castañé C, Bordas E, Albajes R. 1988. *Dicyphus tamaninii* as a beneficial insect and pest in tomato crops in Catalonia, Spain. *Entomophaga* **33:** 219–228.

Gillespie D, McGregor R, Sanchez JA, VanLaerhoven S, Quiring D, Roitberg B, Foottit R, Schwartz M, Shipp

L, Vicent C, Goettel MS, Lazarovits G. 2007. An endemic omnivorous predator for control of greenhouse pests. In: Vicent C, Goettel MS, Lazarovits G, eds. *Biological control: a global perspective*. Wallingford, UK: CABI, 128–135.

Hebert PDN, Cywinska A, Ball SL, deWaard JR. 2003a. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B: Biological Sciences* **270:** 313–321.

Hebert PDN, Ratnasingham S, de Waard JR. 2003b. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society of London B: Biological Sciences* 270(Suppl.): S96–S99.

Heckmann R, Rieger C. 2001. Wanzen aus Baden-Württemberg – Ein Beitrag zur Faunistik und Ökologie der Wan-zen in Baden-Württemberg (Insecta, Heteroptera). *Carolinea* **59:** 81–98.

Herrich-Schaeffer GAW. 1836. Die wanzenartigen Insecten. *C. H. Zeh, Nurnberg*.

Hollier J, Matocq A. 2004. *Dicyphus escalerae* Lindberg, 1934 (Hemiptera: Miridae), a plant-bug species new for Switzerland. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **77:** 333–335.

Hothorn T, Hornik K, Zeileis A. 2006. Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics* **15:** 651–674.

Hradil K. 2011. Faunistic records from the Czech Republic. *Klapalekiana* **47:** 261–2262.

Ingegno BL, Goula M, Navone P, Tavella L. 2008. Distribution and host plants of the genus *Dicyphus* in the Alpine valleys of NW Italy. *Bulletin of Insectology* **61:** 139–140.

Ingegno BL, Pansa MG, Tavella L. 2011a. Plant preference in the zoophytophagous generalist predator *Macrolophus pygmaeus* (Heteroptera: Miridae). *Biological Control* **58:** 174–181.

Ingegno BL, Pansa MG, Tavella L. 2011b. Plant preference in the zoophytophagous generalist predator *Macrolophus pygmaeus* (Heteroptera: Miridae). *Biological Control* **58:** 174–181.

Ingegno BL, Ferracini C, Gallinotti D, Alma A, Tavella L. 2013. Evaluation of the effectiveness of *Dicyphus errans* (Wolff) as predator of *Tuta absoluta* (Meyrick). *Biological Control* **67:** 246–252.

Ingegno BL, La-Spina M, Jordan MJ, Tavella L, Sanchez JA. 2016. Host plant perception and selection in the sibling species *Macrolophus melanotoma and Macrolophus pygmaeus* (Hemiptera: Miridae). *Journal of Insect Behavior* **29:** 117–142.

Josifov M, Simov N. 2008. Contribution to the taxonomy of *Dicyphus constrictus* (Boheman, 1852) (Heteroptera : Miridae). *Historia Naturalis Bulgaria* **19:** 99–110.

Katoh K, Toh H. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* **9:** 286–298.

Katoh K, Kuma K, Toh H, Miyata T. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* **33:** 511–518.

Kerzhner IM, Josifov M. 1999. Cimicomorpha II: Miridae. In: Aukema B, Rieger C, eds. *Catalogue of the Heteroptera of the Palaearctic Region*. The Netherlands: Wageningen, 577.

Kocher TD, Thomas WK, Meyer A, Edwards SV, Pääbo S, Villablanca FX, Wilson AC. 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the United States of America* **86:** 6196–200.

Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33:** 1870–1874.

Lanfear R, Calcott B, Ho SY, Guindon S. 2012. Partitionfinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* **29:** 1695–1701.

Lindberg H. 1934. Inventa entomologica itineris Hispanici et Maroccanni quod a. 1926 fecerunt Harald et Hakan Lindberg. XX. *Spanien Gesammelte Miriden*: **4:** 1–23.

Linnavuori R, Hosseini R. 1999. On the genus *Dicyphus* (Heteroptera: Miridae, Dicyphinae) in Iran. *Acta Universitatis Carolinae Biologica* **43:** 155–162.

Martínez-Cascales JI, Cenis JL, Cassis G, Sanchez JA. 2006a. Species identity of *Macrolophus melanotoma* (Costa 1853) and *Macrolophus pygmaeus* (Rambur 1839) (Insecta: Heteroptera: Miridae) based on morphological and molecular data and bionomic implications. *Insect Systematics & Evolution* **37:** 385–404.

Martínez-Cascales JI, Cenis JL, Sanchez JA. 2006b. Differentiation of *Macrolophus pygmaeus* (Rambur 1839) and *Macrolophus melanotoma* (Costa 1853) (Heteroptera: Miridae) based on molecular data. *Bulletin IOBC/WPRS* **29:** 223–227.

Matocq A, Ribes J. 2004. Un nouveau *Dicyphus* de l'île de Madère (Heteroptera, Miridae, Bryocorinae, Dicyphini). *Revue Français d'Entomologie* **26:** 43–46.

Matocq A, Streito JC. 2013. Données sur trois espèces d'Hétéroptères nouvelles pour la France (Hemiptera Miridae et Anthocoridae). *L'Entomologiste* **69:** 3–7.

Mehrparvar M, Madjdzadeh SM, Arab NM, Esmaeilbeygi M, Ebrahimpour E. 2012. Morphometric discrimination of black legume aphid, *Aphis craccivora* Koch (Hemiptera: Aphididae), populations associated with different host plants. *North-Western Journal of Zoology* **8:** 172–180.

Mollá O, Alonso M, Montón H, Beitia F, Verdú MJ, González-Cabrera J, Urbaneja A. 2010. Control Biológico de *Tuta absoluta*. Catalogación de enemigos naturales y potencial de los míridos depredadores como agentes de control. *Phytoma España* **217:** 42–46.

Nei M, Kumar S. 2000. *Molecular evolution and phylogenetics*. New York: Oxford University Press.

Palumbi SR. 1996. Nucleic acids II: the polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK, eds. *Molecular systematics*. Sunderland: Sinauer Associates, 205–247.

Perdikis D, Lykouressis D. 2000. Effects of various items, host plants, and temperatures on the development and survival of *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae). *Biological Control* **17:** 55–60.

Perdikis DC, Lykouressis DP. 2004. *Myzus persicae* (Homoptera: Aphididae) as suitable prey for *Macrolophus* *pygmaeus* (Hemiptera: Miridae) population increase on pepper plants. *Environmental Entomology* **33:** 499–505.

Perdikis D, Favas C, Lykouressis D, Fantinou A. 2007. Ecological relationships between non-cultivated plants and insect predators in agroecosystems: the case of *Dittrichia viscosa* (Asteraceae) and *Macrolophus melanotoma* (Hemiptera: Miridae). *Acta Oecologica* **31:** 299–306.

Pérez-Hedo M, Urbaneja-Bernat P, Jaques JA, Flors V, Urbaneja A. 2015. Defensive plant responses induced by *Nesidiocoris tenuis* (Hemiptera: Miridae) on tomato plants. *Journal of Pest Science* **88:** 543–554.

Poppius B. 1914. Die Miriden der Äthiopischen Region II -Macrolophinae, Heterotominae, Phylinae. *Acta Societatis Scientiarum Fennicae* **43:** 136 pp.

R-Development-Core-Team. 2015. *A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rabitsch W. 2008. Alien true bugs of Europe (Insecta: Hemiptera: Heteroptera). *Zootaxa* **44:** 1–44.

Reuter OM. 1883. The British species of *Dicyphus*. *Entomologist's Monthly Magazine* **20:** 49–53.

Ribes J. 1981. Nuevos datos sobre heterópteros de las Islas Canarias. *Micellània Zoològica* **7:** 67–74.

Ribes J, Blasco-Zumeta J, Ribes E. 1997. Heteróptera de un sabinar de *Juniperus thurífera* L. en los Monegros, Zaragoza. *Monografias de la Sociedad Entomológica Aragonesa*: 1–127.

Rieger C. 1995. Zwei neue Miriden von de Insel Kreta (Heteroptera). *Entomologische Berichten* **55:** 79–82.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic biology* **61:** 539–542.

Ruiz C, Lanfranco D, Carrillo R, Parra L. 2014. Morphometric variation on the cypress aphid *Cinara cupressi* (Buckton) (Hemiptera: Aphididae) associated to urban trees. *Neotropical Entomology* **43:** 245–251.

Sahlberg J. 1878. Bidrag till Nordvestra Sibiriens Insektfauna, Hemiptera-Heteroptera. *Kungliga Svenska Vetenskapsakademiens Handlingar* **16:** 1–39.

Sanchez JA. 2008. Factors influencing zoophytophagy in the plantbug *Nesidiocoris tenuis* (Heteroptera: Miridae). *Agriculture and Forest Entomology* **10:** 70–80.

Sanchez JA. 2009. Density thresholds for *Nesidiocoris tenuis* (Heteroptera: Miridae) in tomato crops. *Biological Control* **51:** 493–498.

Sanchez JA, Lacasa A. 2008. Impact of the zoophytophagous plant bug *Nesidiocoris tenuis* (Heteroptera: Miridae) on tomato yield. *Journal of Economic Entomology* **101:** 1864–1870.

Sanchez JA, Gillespie DR, McGregor RR. 2004. Plant preference in relation to life history traits in the zoophytophagous predator *Dicyphus hesperus*. *Entomologia Experimentalis et Applicata* **112:** 7–19.

Sanchez JA, Martínez-Cascales JI, Cassis G. 2006. Description of a new species of *Dicyphus* Fieber (Insecta: Heteroptera: Miridae) from Portugal based on morphological and molecular data. *Insect Systematics & Evolution* **37:** 281–300.

Sanchez JA, Spina ML, Perera OP. 2012. Analysis of the population structure of *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae) in the Palaearctic region using microsatellite markers. *Ecology and Evolution* **2:** 3145–3159.

Sanchez JA, del Amor FM, Flores P, López-Gallego E. 2016. Nutritional variations at *Nesidiocoris tenuis* feeding sites and reciprocal interactions between the mirid and tomato plants. *Journal of Applied Entomology* **140:** 161–173.

Schlick-Steiner BC, Steiner FM, Seifert B, Stauffer C, Christian E, Crozier RH. 2010. Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology* **55:** 421–438.

Schuh RT. 1995. *Plant bugs of the world (Insecta: Heteroptera: Miridae): systematic catalog, distributions, host list and bibliography.* New York: The New York Entomological Society.

Schuh RT, Slater JA. 1995. *True bugs of the world (Hemiptera: Heteroptera). Classification and natural history*. Ithaca, New York: Comstock Publications Associates.

Schuh RT, Weirauch C, Wheeler WC. 2009. Phylogenetic relationships within the Cimicomorpha (Hemiptera: Heteroptera): a total-evidence analysis. *Systematic Entomology* **34:** 15–48.

Seidenstucker G. 1956. Ein neuer *Dicyphus* aus Kleinasien (Heteroptera-Miridae). *Revue de la Faculté des sciences de l'Université d'Istanbul (B)* **21:** 14–148.

Simon H. 1995. Nachweis von *Dicyphus escalerai* Lindberg, 1934 (Heteroptera: Miridae) in Mitteleuropa. *Fauna und Flora Rheinland-Pfalz* **8:** 53–63.

Sites JW, Marshall JC. 2004. Operational criteria for delimiting species. *Annual Review of Ecology, Evolution, and Systematics* **35:** 199–227.

Stamatakis A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics (Oxford, England)* **30:** 1312–1313.

Stonedahl GM. 1988. Revision of the mirine genus *Phytocoris* Fallén (Heteroptera: Miridae) for western North America. *Bulletin of the American Museum of Natural History* **198:** 1–88.

Tamanini L. 1949. La presenza del *Dicyphus pallidus* H. Sch. in Italia e descrizione di una nuova specie (Hem. Het. Miridae). *Pubblicazione della Societa Museo Civico in Rovereto* **12:** 12 pp.

Tamanini L. 1956. Alcune osservazioni sui *Dicyphus* italiani e loro distribuzione (Heteroptera: Miridae). *Memorie della Societa Entomologica Italiana* **35:** 14–22.

Tan AM, Gillespie RG, Oxford GS. 1999. Paraphyly of the *Enoplognatha ovata* group (Araneae, Theridiidae) based on DNA sequences. *The Journal of Arachnology* **27:** 481–488.

Tavella L, Goula M. 2001. Dicyphini collected in horticultural areas of north-western Italy (Heteroptera Miridae). *Bollettino di Zoologia Agraria e di Bachicoltura* **33:** 93–102.

Wachmann E, Melber A, Deckert J. 2004. *Die Tierwelt Deutschlands. Begründet 1925 von Friedrich Dahl. 75*. Teil. Keltern: Goecke & Evers.

Wagner E. 1951. Zur Systematik der Gattung, *Dicyphus* (Hem. Het., Miridae). *Soc. Scient. Fenn. Comm. Biol.* **12:** 12–35.

Wagner E. 1963. *Dicyphus eckerleini* nov. spec., eine neue Miriden-Art aus dem ostlichen Mittelmeerraum (Hem. Het.). *Zeitschrift der Arbeitsgemeinschaft Österreichischer Entomologen* **15:** 59–61.

Wagner E. 1964. Hétéroptères miridae. *Faune de France* **67:** 589 pp.

Wagner E. 1970. Die Miridae Hahn, 1831, des Mittelmeerraumes und der Makaronesischen Inseln (Hemiptera: Heteroptera). *Entomologische Abhandlungen* **37:** 1–484.

Wagner E. 1974. Die Miridae Hahn, 1831, des Mitelmeerraumes und der Makaronesischen Inseln (Hemiptera, Heteroptera). Vol 1. *Entomologische Abhandlungen* **37** Suppl.: 484 pp.

Wagner E, Weber HH. 1978. Die Miridae Hahn 1831 des Mittelmeerraumes und der Makaronesischen Inseln (Hemiptera, Heteroptera). *Nachtrge zu den Teil* 1–3. *Entomologische Abhandlungen herausgegeben vom staatlichen Museum für Tierkunde Dresde* **42:** 96 pp.

Wilke AB, Christe Rde O, Multini LC, Vidal PO, Wilk-da-Silva R, de Carvalho GC, Marrelli MT. 2016. Morphometric wing characters as a tool for mosquito identification. *PLoS ONE* **11:** e0161643.

Wolff JF. 1804. Icones Cimicum descriptionibus illustratae. *J. J. Palm, Erlangae*.

Yeates DK, Seago A, Nelson L, Cameron SL, Joseph L, Trueman JWH. 2011. Integrative taxonomy, or iterative taxonomy? *Systematic Entomology* **36:** 209–217.

Zhang YM, Gates MW, Shorthouse JD. 2014. Testing species limits of Eurytomidae (Hymenoptera) associated with galls induced by *Diplolepis* (Hymenoptera : Cynipidae) in Canada using an integrative approach. *The Canadian Entomologist* **146:** 321–334.

SUPPORTING INFORMATION

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Table S1. Body measurements of males and females of *Dicyphus (Dicyphus)* species. Direct measurements: HW, head width; HL, head length; EyeW, Eye width; IO, interocular distance; A1, A1 length; A2, A2 length; A3, A3 length; A4, A4 length; CW, collar width; PCL, collar length; CRL, callosite region length; DRL, disk length; PW, pronotum width; PL, pronotum length; SW, scutelum width; SL, scutelum length; CL, Cuneo length; HemL, hemelitral length; TIBL, tibial length; FL, femur length, CHL, clypeus-hemelytral length; TL, total length. Ratios: A1:IO, A1 length:interocular distance; A1:HW, A1 length:head width; A2:PW, A2 length:pronotum width; A2:HW, A2 length:head width; IO:EW, interocular distance:eye width; HL:PL, head length:pronotum length; DRL:CRL, disk length:callosite region length; CRL:PCL, callosite region length:collar length.

Table S2. Body measurements of males and qualitative characters of *Dicyphus (Dicyphus)* species used in the Ctree analyses. Body measurements and ratios codes as in Table S1. For qualitative codes see Ctree analyses in the methodology section.

Table S3. Genetic distances [Kimura-two-parameter (K2P)] between the specimens used in the molecular analyses: *Dicyphus (Dicyphus)* species and outgroups.