ISSN 1313-2970 (online) ISSN 1313-2989 (print)

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RESEARCH ON CHRYSOMELIDAE 8

Edited by
Michael Schmitt, Caroline S. Chaboo, Maurizio Biondi

Donacia crassipes Fabricius, 1775

ZooKeys 856 ♦ 2019
Special Issue

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ZooKeys 856 (Special Issue)

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Cover photo: A copulating pair of *Donacia crassipes* 25.06.2014 near Greifswald, Germany, photo: M. Schmitt.

First published 2019
ISBN 978-954-642-965-0 (paperback)

Pensoft Publishers
12 Prof. Georgi Zlatarski Street, 1700 Sofia, Bulgaria
Fax: +359-2-870-42-82
info@pensoft.net
www.pensoft.net

Printed in Bulgaria, June 2019

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* extended versions of talks presented to the 3rd European Symposium on the Chrysomelidae, Naples, Italy, 5 July, 2018.

ZooKeys 856: 1–2 (2019)
doi: 10.3897/zookeys.856.37027
http://zookeys.pensoft.net

EDITORIAL

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Editorial

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Received 10 June 2019 | Accepted 11 June 2019 | Published 17 June 2019

http://zoobank.org/BAC3F6FE-02C7-4137-ABFC-607B324FB23F

Citation: Schmitt M, Chaboo CS, Biondi M (2019) Editorial. In: Schmitt M, Chaboo CS, Biondi M (Eds) Research on Chrysomelidae 8. ZooKeys 856: 1–2. https://doi.org/10.3897/zookeys.856.37027

Volume 8 of Research on Chrysomelidae (RoC8) presents again examples of the attractiveness and the diversity of Chrysomelidae (sensu lato) as subjects of scientific research. The seven papers included here cover taxonomy, ecology, faunistics as well as phylogenetics. Four of these papers (Geiser, Gikonyo et al., Salvi et al., Wendorff & Schmitt) are extended versions of talks presented to the Third European Symposium on the Chrysomelidae, held on 5 July, 2018, in Naples, Italy within the frame of the

The editors: Caroline S. Chaboo, Maurizio Biondi, Michael Schmitt

11th European Congress of Entomology. Maurizio Biondi (L'Aquila, Italy) and Michael Schmitt (Greifswald, Germany) co-organised the Naples meeting and worked together with Caroline S. Chaboo (Lincoln, NE, USA) in the editorial committee for RoC8.

As with the previous RoC volumes, the team at Pensoft Publishers (Sofia, Bulgaria), especially Yordanka Banalieva, did a wonderful job and made the co-operation of editors and publishers a relaxed and rewarding experience. The editors thank our counterparts at Pensoft for this harmonious collaboration. The editors also thank all authors who submitted their high-quality manuscripts and so made this volume another important contribution towards the science of leaf and seed beetles.

The series of symposia on Chrysomelidae will continue with the 10th International Symposium in Helsinki (Finland) in 2020 and the 4th European Symposium on Crete (Greece) in 2022. The proceedings of these symposia along with submitted papers on Chrysomelidae sensu lato will be published in subsequent volumes of Research on Chrysomelidae, as special issues of ZooKeys.

Michael Schmitt, Caroline S. Chaboo, Maurizio Biondi

ZooKeys 856: 3–25 (2019)
doi: 10.3897/zookeys.856.32462
http://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
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Phylogeography and species distribution modelling of *Cryptocephalus barii* (Coleoptera: Chrysomelidae): is this alpine endemic species close to extinction?*

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Academic editor: *M. Schmitt* | Received 15 December 2018 | Accepted 18 February 2019 | Published 17 June 2019

http://zoobank.org/CBFD99DB-B02F-466E-BFFA-4AFB64136E5D

Citation: Brunetti M, Magoga G, Iannella M, Biondi M, Montagna M (2019) Phylogeography and species distribution modelling of *Cryptocephalus barii* (Coleoptera: Chrysomelidae): is this alpine endemic species close to extinction? In: Schmitt M, Chaboo CS, Biondi M (Eds) Research on Chrysomelidae 8. ZooKeys 856: 3–25. https://doi.org/10.3897/zookeys.856.32462

Abstract

The alternation of glacial and interglacial cycles of the Quaternary period contributed in shaping the current species distribution. Cold-adapted organisms experienced range expansion and contraction in response to the temperature decrease and increase, respectively. In this study, a fragment of the mitochondrial marker COI was used to investigate the phylogeography of *Cryptocephalus barii*, a cold-adapted alpine leaf beetle species endemic of Orobie Alps, northern Italy. The relationships among populations, their divergence time, and the most probable migration model were estimated and are discussed in light of the Pleistocene climate oscillations. Through a species distribution modelling analysis, the current habitat suitability was assessed and the distribution in a future global warming scenario predicted. The main divergence events that led to the actual population structure took place from ~750,000 to ~150,000 years ago, almost following the pattern of the climate oscillations that led to the increase of the connections between the populations during cold periods and the isolation on massifs in warm periods. The most supported migration model suggests that the species survived to past adverse climatic conditions within refugia inside and at the limit of the actual range. The species distribution modelling analysis showed that

* extended versions of a talk presented to the 3rd European Symposium on the Chrysomelidae, Naples, Italy, 5 July, 2018.

** These authors contributed equally.

C. barii is extremely sensitive to air temperature variations, thus the increase of temperature caused by global warming will reduce the suitable areas within the species range, leading to its possible extinction in the next 50 years. *Cryptocephalus barii* is a representative case of how cold adapted and limited distributed species have been and could be affected by climate change, that highlights the implementation of conservation actions.

Keywords
cold-adapted species, endemism, global warming, Italy, Orobie Alps, phylogeography, species distribution models, species extinctions

Introduction

The Quaternary Period, alternating at least seven glacial and interglacial cycles within the last 650,000 years, affected population migration and survival of animals and plants and thus contributed in shaping the current species distribution (Bennett 1990; Davis and Shaw 2001). During this period the average surface temperatures of Earth ranged from ~9 °C to ~16 °C compared to the present ~14 °C (Hansen et al. 2013). How European species adapted to warm and humid environments, both flora and fauna, have passed glacial cycles received a lot of attention in the last decades and it is documented that they survived glacial cycles in restricted areas of refugium represented by Balkan, Italian and Iberian peninsulas, which played a central role for the recolonisation of the temperate regions (e.g., Hewitt 1999, 2000). On the opposite, the interests towards understanding how cold-adapted species overcame glacial ages received limited attention (e.g., Schmitt 2009; Borer et al. 2010; Lohse et al. 2011). Warm- and cold-adapted organisms have shown opposite patterns in response to the decrease of the air temperature: the former shrank the range of distribution towards lower latitude during glacials (e.g., Hewitt 1999, 2000, 2004, 2011), while the latter likely expanded their range in the same periods (e.g., Muster and Berendonk 2006; Mardulyn et al. 2009; Lohse et al. 2011; Martinet et al. 2018). In detail, in the case of cold-adapted species, glacial cycles, associated with a decrease of temperatures, represented periods of range expansion towards lowland with possible contact among populations; when temperatures increased during interglacial periods, they suffered range shrink towards high-altitude lands. After the Last Glacial Maximum, mountainous reliefs of southern Europe (i.e., Balkans, Alps, Apennines, and Pyrenees) have represented the refugia for cold-adapted species, now inhabiting habitats at altitude higher than 1800 meters a.s.l. The interest on cold-adapted species is intended to increase since these taxa, usually consisting of limited and isolated populations, are currently suffering a dramatic shrink of their range, due to the present global warming (e.g., Dirnböck et al. 2011; Jacobsen et al. 2012; Rossaro et al. 2016). In this context, when cold-adapted species are endemic of a limited area, global warming could lead to their extinction (Malcolm et al. 2006; Urbani et al. 2015, 2017). In the last years, conservation policies have increased their effort towards the reduction of the biodiversity loss caused by global warming, but limited attention has been dedicated to the most species rich group of animals, the insects (Dunn 2005; Menéndez 2007).

Italy is an endemic species rich country both in term of flora and fauna (Peruzzi et al. 2014), in particular approximately the 10% of the fauna is composed by endemic species, mainly represented by invertebrates (Minelli et al. 2006). The north of Italy exhibits an especially high number of endemic species, the majority of them inhabit the southern margin of the Alps, where Pleistocenic refuges for cold-adapted species were present (e.g., Carapezza and Faraci 2006; Minelli et al. 2006; Tribsch and Schönswetter 2003; Negro et al. 2008). Besides animals, also plants show a high number of endemic taxa in the southern margin of the Alps (Cerabolini et al. 2004; Casazza et al. 2005; Peruzzi et al. 2014).

In this study we investigate the phylogeography of the alpine endemic leaf beetle *Cryptocephalus barii* Burlini, 1948 (Coleoptera: Chrysomelidae) currently distributed on isolated areas of the southern part of the Alps (Orobie Alps), above 1,800 meters of altitude. The species was described by Burlini in 1948 basing on eight specimens collected in Alben Mount (Burlini 1955) and, beside it, reported also for Pizzo Arera, northern Grigna and Presolana. The species, on the basis of its morphological features, is considered part of *Cryptocephalus sericeus* Linnaeus, 1758 species complex (Sassi 2014), but it is well distinguishable from the other species of the complex especially for the total black external habitus. As well as the majority of the species belonging to *C. sericeus* complex, it feeds on yellow flowers, in particular on *Hieracium tenuiflorum*, *Leontodon autumnalis*, *Telekia speciosissima* (Asteraceae), and *Helianthemum nummularium* (Cistaceae) (Regalin and Redigolo 1993; Sassi 2014). The phylogenetic relationships of the species is controversial; on the basis of nuclear and mitochondrial markers *C. barii* results sister of the *sericeus* – *hypochaeridis* clade (Gómez-Zurita et al. 2012), while on the base of a cladistic analyses performed on morphological characters it is the sister species of *Cryptocephalus atrifrons* Abeille, 1901 due to the presence of an upward plate replacing the lateral margin of the third endophallic sclerite (Sassi 2014).

In this study, through an extensive sampling across the distributional range of the species, we have investigated the phylogeography of *C. barii* in order to define the relationships between the currently isolated populations, estimate their divergence time taking into account Pleistocene climate oscillations, assess the current habitat suitability and predict the distribution of this orophilous and endemic species in a future global warming scenario.

Materials and methods

Sampling, DNA extraction, and PCR amplification

Between 2005 and 2012, different collecting campaigns were organised on mountainous reliefs of the Orobie Alps where the species was already known to be present, viz. Alben, northern Grigna, Presolana, and Arera (Burlini 1955). In addition, in order to investigate the distribution of *C. barii*, additional collecting campaigns were performed on mountainous reliefs surrounding the previous massifs and suitable for the presence of the species (i.e., elevation above 1800 meters and consisting of limestone) (Figure 1).

Collected individuals were labelled with geographic coordinates, date and host plant on which they were found; then preserved in absolute ethanol and stored at –20 °C. With the exception of the Corna Grande population, where only two individuals were collected, seven to ten individuals from each population were selected for the DNA extraction. Total genomic DNA was extracted from each individual through the non-destructive procedure described in Montagna et al. (2013) and purified using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following manufacturer's instructions. The extracted DNA was quantified using NanoDrop2000 spectrophotometer and used as a template for PCR reactions. A fragment of the mitochondrial cytochrome c oxidase subunit I (COI), of approximately 730 bp, was amplified with primer C1-J-2183 / TL2-N-3014 (Simon et al. 1994). PCR were performed in 25 μL reaction mix containing: 1´ GoTaq reaction Buffer (10 mM Tris-HCl at pH 8.3, 50 mM KCl and 1.5 mM $MgCl_2$), 0.2 mM of each deoxynucleotide triphosphate, 0.5 pmol of each primer, 0.6 U of GoTaq DNA Polymerase and 30 ng of DNA. PCR conditions used the following thermal cycle parameters: 3 min at 95 °C followed by 35 cycles of 30 s denaturation at 95 °C, 30 s annealing at 50 °C and 1 min 20 s extension at 72 °C, with a final single extra extension step of 10 min at 72 °C. PCR products were directly sequenced, in both strands, with ABI 3100 Automated Capillary DNA Sequencer (Applied Biosystem, Foster City, CA, USA). The obtained electropherograms were edited and assembled in a consensus sequence using Geneious Pro 5.3. The consensus sequences were deposited in GenBank with accession numbers MK492325-MK492374.

Nucleotide variability, phylogeographic analysis, and divergence time estimation

The obtained 53 COI sequences were aligned using MUSCLE (Edgar 2004) with default parameters. The alignment was checked for reading frame errors and termination codons with MEGA 7 (Kumar et al. 2016). Intra-population and inter-population nucleotide p-distances were calculated with MEGA 7 (Kumar et al. 2016). In order to evaluate correlation between nucleotide and geographic distance matrices, the geographic distances between sampling locations were computed using R software (R Core Team 2016) starting from the latitude and longitude coordinates. Matrices correlation was estimated by Mantel test (Mantel 1967), as implemented in *ade4* R package (Dray and Dufour 2007).

Phylogeographic relationships within *C. barii* were investigated based on Bayesian inference using the software BEAST 2.5.1. (Bouckaert et al. 2014) with the bModelTest module (Bouckaert and Drummond 2017) for the evaluation of the substitution model. In addition, the dataset was tested for strict clock model against the non-clock model using a Bayes factor comparison. The marginal likelihoods of the two models were estimated by the stepping stone method implemented in MrBayes 3.2 (Ronquist et al., 2012), and then compared. According to the criterion reported in Kass and Raftery (1995), the strict clock model was preferred since the difference between the marginal likelihoods of the two models was not significant (p-value > 0.2). We used the alignment partitioned by codon positions, as suggested by preliminary analysis

performed with Partition Finder 2.1.1 (Lanfear et al. 2016), and the strict clock model with a substitution rate set to 0.0177 ± 0.0003 My^{-1} (Papadopoulou et al. 2010), previously used for congeneric species (Montagna et al. 2016).

The tree prior was set using the Constant coalescent Kingman model (Kingman 1982). The analysis was carried out using a random starting tree, running two Markov chains for 100 million generations and sampling every 10,000 generations. Finally, the same analysis was performed sampling from priors only to evaluate the priors that we applied to the various parameters. Convergence was evaluated with Tracer version 1.7.1 (Rambaut et al. 2018), and the two chains were combined with LogCombiner (Drummond et al. 2012), discarding 20% of the trees as burn-in. The combined set of trees was summarised as a maximum clade credibility tree with TreeAnnotator (Drummond et al. 2012).

In order to confirm the rooting position of the tree, we carried out a preliminary phylogenetic reconstruction using an alignment consisting of the haplotype sequences of *C. barii* and orthologous sequences of five species mined from GenBank (i.e., *Cryptocephalus cristula* Dufour, 1843, *Cryptocephalus asturiensis* Heyden, 1870, *Cryptocephalus flavipes* Fabricius, 1781, *Cryptocephalus azurescens* Escalera, 1914 and *Pachybrachis* sp.; accession numbers: HE600320, HE600302, KJ765877, HE600310, HF947529) used as outgroups. In this phylogenetic reconstruction, performed on a dataset of 15 sequences, the tree prior was set using the Yule model (Yule 1925; Gernhard 2008), while other settings were the same of the previous analysis. In order to take into account for introgression and hybridisation phenomena a network of haplotypes was inferred through the minimum spanning network method as implemented in the software PopART 1.7 (Leigh and Bryant 2015).

Gene flow models

We used the coalescent-based program MIGRATE-N 3.7 (Beerli and Palczewski 2010), which estimate past migration rates between populations, to test whether *C. barii* species survived ice ages in situ on ice-free nunataks or on large mountain of refuge at the periphery. It would be obviously impossible to evaluate every possible model of migration so we chose a small set of models in order to test our hypothesis. The following six migration models have been evaluated (Suppl. matreial 1: Figure S1): (A) directional migration from west to east, assuming a colonisation from the west; (B) directional migration from east to west, assuming a colonisation from the east; (C) directional migration from south to north, assuming a colonisation from southern refugia; (D) directional migration from north to south, assuming a colonisation from a possible northern refugium (Pegherolo); (E) a mixed model with colonisation from southern (Grigna) and northern (Presolana) refugia (Lohse et al. 2011); (F) a model, suggested by the phylogenetic analysis, with directional migration from Grigna to Alben, then to Pegherolo and Corna Grande and then to the others (Arera, Concarena and Presolana). We estimated the mutation scaled effective population size $\vartheta = xN_e\mu$ (x = 1, for mitochondrial DNA),

where N_e is the effective population size and μ is the mutation rate, as well as mutation scaled migration rates $M = m/\mu$, where m is the immigration rate per generation. We used the marginal likelihood values approximated with thermodynamic integration to compare models with natural logarithm Bayes factor and to calculate the probability of each model ($P(model_i)=mL(model_i)/\sum_j^n mL(model_j)$; Beerli 2012).

We used the sequence model of Felsenstein (1984) and random starting genealogy. A preliminary analysis was run with parameter values inferred by an F_{st}-based method to obtain ϑ and M estimates that were used as initial values of that parameters in subsequent analysis. Prior distributions for ϑ and M were uniformly distributed with boundaries 0–0.1 and 0–50000, respectively. We performed four independent runs for each analysis, each consisting of a burn-in period of 25 million Markov chain Monte Carlo (MCMC) steps, followed by 100 million steps. Samples were recorded every 5,000 steps, resulting in a total of 20,000 recorded parameter values for each replicate. We used a static heating scheme with four chains with temperatures 1.00, 1.50, 3.00 and 1,000,000, in order to improve the estimation of marginal likelihood (Beerli 2009).

Since the suitable habitat of the species is currently between 1,800 and 2,100 meters of altitude, we hypothesise that during glacials the amount of areas with a suitable habitat increase, thus allowing the formation of corridors connecting the massifs where the species is present. The correspondence between the phylogeography of the species and possible corridors of suitable habitat connecting the different mountainous reliefs was evaluated building maps of the Orobie Alps highlighting areas above a certain altitude by QGIS 3.4.1 software (QGIS Development Team 2009). The average vertical thermal gradient used in this study is of 0.54–0.58 °C every 100 meters, as estimated for Alpine regions by Rolland (2003).

Species Distribution Modelling (SDM)

A dataset of 35 presence localities was generated from GPS-precision field-recorded points for the target species *C. barii*. Nineteen bioclimatic variables were downloaded from the web repository Worldclim.org (Hijmans et al. 2005) at 30" spatial resolution and cut to the extent of the European Alps (sensu Biondi et al. 2013) through the 'Extract by Mask' tool in ArcMap 10.0 (ESRI, 2010). After this process, variables were tested for possible multicollinearity through the 'Band Collection Statistics' tool in ArcMap 10.0 (ESRI, 2010), a correlation matrix was calculated and variables' pairs exceeding the Pearson's r value of 0.85 were discarded (Elith et al. 2006; Iannella et al. 2018a; Iannella et al. 2018b).

For the modelling process, the 'biomod2' package (Thuiller et al. 2016) was used in R environment (R Core Team 2016). In particular, models for current and future climatic conditions were calculated through different sets of variables. Considering that many Global Climate Models (GCMs) are available for future climatic condi-

tions, four GCMs were used in this paper, namely the BCC-CSM-1 (Wu et al. 2014), CCSM4 (Gent et al. 2011), IPSL (Marti et al. 2010) and the MIROC-CHEM (Watanabe et al. 2011). In particular, two scenarios of different radiative forcing were selected to observe the possible differences in conditions of medium and very high increase of radiative forcing, namely the 4.5 and the 8.5, for 2070.

Each species distribution model obtained from the different GCMs was processed through the MEDI algorithm (Iannella et al. 2017), a recent technique used to weight-average different predictions in one single model, thus avoiding predictions from one GCM and/or giving equal weight to models with low performances (see below).

In biomod2, Generalized Linear Models (GLMs, set with type = "quadratic", interaction level = 3), Multiple Adaptive Regression Splines (MARS, set with type = "quadratic", interaction level = 3), Generalized Boosting Model, also known as Boosted Regression Trees (BRT, set with number of trees = 5000, interaction depth = 3, cross-validation folds = 10) and Maxent (MaxEnt, set with maximum iterations = 5000) were selected as single modelling techniques (Phillips et al. 2006). Model was calibrated in current climatic conditions with the BIOMOD_Modelling function; all models' performance were evaluated through the True Skill Statistics (TSS) (Allouche et al. 2006) and the Area Under the Curve (AUC) of the receiver operating characteristic curve (Phillips et al. 2006), with the initial 80% of the occurrence dataset used to calibrate the model and the remaining 20% for the validation. Then, the BIOMOD_EnsembleModelling function was used to obtain Ensemble Model for the target species, with the 'wmean' (weighted mean) algorithm used to merge each single model based on the respective performance scores. The BIOMOD_EnsembleForecasting function was further used to project the calibrated model to future climatic scenarios (Thuiller et al. 2016). A Minimum Convex Polygon (MCP) was generated on the basis of the presence data; all cartographic and spatial processes were managed in ArcMap 10.0 (ESRI, 2010).

Results

Species collection and ecological notes

The extensive sampling campaigns within the Orobie Alps and in neighbouring massifs suitable for the presence of *C. barii* (according with the proposed criteria, Materials and Methods), led to the collection of 60 individuals on eight massifs: the already known Mount Alben, Pizzo Arera, Presolana, and northern Grigna, with the addition of the newly discovered southern Grigna (hereafter reported as Grigna in association with the geographical neighbour northern Grigna), Corna Grande, Pegherolo, and Concarena (Figure 1). The performed extensive collecting campaigns make us to likely exclude the presence of *C. barii* on Mount Legnone, Mount Venturosa, Pizzo dei Tre Signori, Pizzo del Diavolo, and Mount Grona (Figure 1), mountainous reliefs pre-

senting habitat suitable for the species and geographically close to previously known populations. All individuals were collected from mid-July to the end of August at an altitude ranging from 1,601 (only two samples, most likely transported by wind from higher altitudes) to 2,100 meters a.s.l., feeding or mating on *Heliantemum nummularium, Hieracium* spp. or *Telekia speciosissima.* The habitat of collection consists of grassland dominated by *Sesleria coerulea* and *Carex sempervirens* attributable to habitat code *6170 Alpine and subalpine calcareous grasslands* (European Community Habitat's Directive, 92/43/EEC).

Phylogeography, divergence time estimation, and gene flow

DNA was extracted and COI amplified from 53 *C. barii* individuals (Table 1). Intrapopulation and inter-population mean pairwise nucleotide p-distance were 0.00047 (sd = 0.00064) [0–0.0018], and 0.011 (sd = 0.0083) [0.00049–0.024], respectively (Table 2). The population with the highest value of intrapopulation nucleotide p-distance was that of Presolana (0.0018, se = 0.0010), while the lowest values are associated with Alben, Corna Grande, and Grigna (0) (Table 2). Concerning the inter-population p-distance, the highest values were recovered comparing Grigna with other populations (mean p-distance = 0.023, sd = 0.0012), achieving the maximum value of 0.024 (se = 0.0057) when Grigna is compared with Alben, Corna Grande, and Concarena (Table 2). Some individuals collected in Presolana and Arera shared the same COI haplotypes, while all the other populations showed private haplotypes (Figure 2A). Positive correlation between geographic and nucleotide distances was detected by the Mantel test (r = 0.64, p-value = 0.001).

Based on the performed coalescence analysis, almost all the individuals from the same mountainous massif clustered together in monophyletic groups and are supported by high values of Bayesian posterior probability (BPP > 0.85; Figure 2B). However, in some cases, individuals from different massifs grouped together (Figure 2B); in details this phenomenon occurred for Arera and Concarena (two individuals; BPP = 0.92), Arera and Presolana (eight individuals; BPP < 0.5), Presolana and Arera (four individuals; BPP = 0.99) (Figure 2B).

Concerning the estimation of the divergence time among populations, the most ancient split, represented by the separation of Grigna lineage (tree rooted on outgroups) and all the remaining lineages occurred ~724,600 years before present (BP) (95% High posterior density (HPD) 1,140,700–389,900 years BP; BPP = 1) in correspondence with a period of warm climate, probably during the Pastonian or the Günz-Mindel interglacials (Figure 2B). The subsequent split, occurred about 244,700 years BP (95% HPD 417,900–107,500 years BP; BPP = 1) during the Mindel-Riss interglacial, determined the isolation of the Alben population and the next one, even if supported by values of posterior probability < 0.5, corresponded to the separation of Corna Grande-Pegherolo populations from individuals of Arera, Concarena, and Presolana. This last split is dated at about 149,100 years BP (95% HPD 263,900–

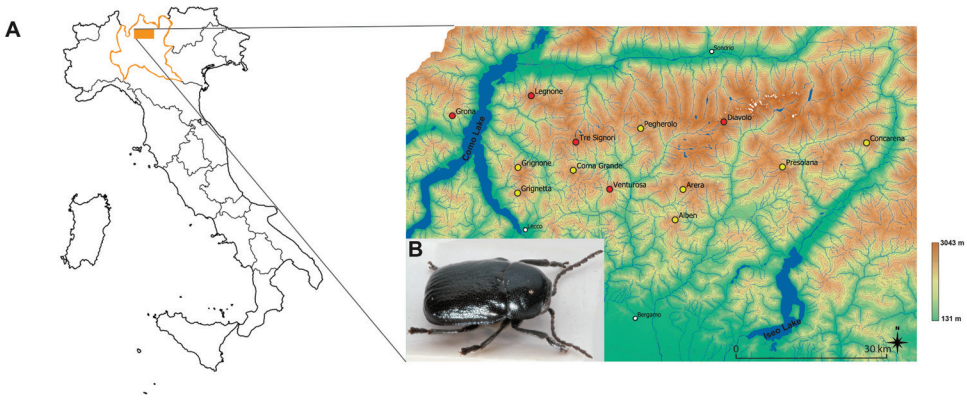

Figure 1. *Cryptocephalus barii* Burlini, 1948 distribution. **A**) Geographic location of the Orobie Alps and *Cryptocephalus barii* distribution. Yellow dots indicate localities where the species was observed, red dots indicate localities investigated with extensive sampling campaigns in which the species was absent (the source map was downloaded from http://www.geoportale.regione.lombardia.it/ and elaborated with QGIS 3.4.1). **B**) *Cryptocephalus barii* picture acquired using a Canon 450D camera; the multilayered micrographs were processed with Zerene Stacker (Richland, WA, USA).

68,900 years BP) corresponding to the Riss-Würm period, during the same interglacial the two populations of Corna Grande and Pegherolo separated one from the other ~87,800 years BP (95% HPD 197,700–24,500 years BP). The remaining populations (Arera, Concarena, and Presolana) diverged during the period from 162,700 to 83,700 years BP.

In order to understand how *C. barii* populations became isolated on different mountainous reliefs, six possible migration models were formalised and tested (Suppl. material 1: Figure S1). Bayes factors, calculated as double the difference of natural log marginal likelihoods (LBF), between two competing models strongly supported the model (E) (LBFs > 5, $Prob_{MODEL\ E} = 0.908$, Figure 3A). In this model, Grigna and Presolana are considered source population, according with the hypothesis that *C. barii* survived ice ages both on ice-free refugia in the inner core of its range and on large mountain of refuge at its southern periphery, with unidirectional gene flow directed toward other populations which instead exchange migrants bidirectionally.

The suitable altitudinal habitat maps, showing the increase of the areas appropriate for the *C. barii* survival and the available corridors connecting the present populations due to the decrease of the temperature, almost perfectly match with the topology achieved by the coalescent and the migration model analyses (Figure 3B–F). Interestingly, the populations inhabiting Arera, Presolana, and Concarena remained connected by habitat suitable for the species even when temperatures are only slightly lower than the present (Figure 3E). This last result is in agreement with the topology achieved by the phylogeographic analyses, where the relationships among these populations should be better represented by a polytomy or a network (BPP < 0.5; Figure 2).

Table 1. Collection localities and host plants of *Cryptocephalus barii* individuals from which the DNA was extracted, and COI amplified. Specimen IDs are reported for sequences obtained during this study, while for sequences already published in Gómez-Zurita et al. (2012) the accession numbers are provided.

Collection locality	Specimen id†	Collection date	Latitude	Longitude	E‡	Host plants
Alben	Alb-1	17 Aug 2010	45.8721N	9.7807E	1855	*Helianthemum nummularium*, *Hieracium* sp., *Telekia speciosissima*
	Alb-2	08 Aug 2008	45.8714N	9.7780E	1855	
	Alb-3	08 Aug 2008	45.8714N	9.7780E	1855	
	Alb-4	17 Aug 2010	45.8723N	9.7779E	1855	
	Alb-5	17 Aug 2010	45.8720N	9.7766E	1855	
	Alb-6	17 Aug 2010	45.8727N	9.7766E	1855	
	Alb-7	17 Aug 2010	45.8727N	9.7766E	1855	
	HE600313	17 Aug 2010	45.8713N	9.7787E	1855	
Arera	Are-1	23 Aug2010	45.9263N	9.8013E	1929	*Helianthemum nummularium*, *Hieracium* sp.
	Are-2	23 Aug 2010	45.9176N	9.7952E	1601	
	Are-3	23 Aug 2010	45.9309N	9.8043E	2011	
	Are-4	23 Aug 2010	45.9309N	9.8043E	2011	
	Are-5	23 Aug 2010	45.9336N	9.8029E	2066	
	Are-6	23 Aug 2010	45.9336N	9.8029E	2066	
	Are-7	23 Aug 2010	45.9176N	9.7952E	1601	
	Are-8	23 Aug 2010	45.9263N	9.8044E	1965	
	Are-9	23 Aug 2010	45.9401N	9.8072E	2072	
Corna Grande	Bob-1	30 Jul 2011	45.9618N	9.5206E	1900	*Helianthemum nummularium*
	Bob-2	30 Jul 2011	45.9618N	9.5206E	1900	
Grigna (southern and northern Grigna)	Gri-1	17 Jul 2006	45.9663N	9.3849E	1817	*Hieracium* spp., *Helianthemum nummularium*, *Telekia speciosissima*
	Gri-2	17 Jul 2006	45.9657N	9.3870E	1817	
	HE600311	17 Jul 2006	45.9657N	9.3870E	1817	
	Gri-3	17 Jul 2006	45.9657N	9.3870E	1817	
	Gri-4	24 Jul 2011	45.9219N	9.3763E	1700	
	Gri-5	1 Aug 2005	45.9649N	9.3857E	1817	
	Gri-6	1 Aug 2005	45.9649N	9.3857E	1817	
	Gri-7	1 Aug 2005	45.9649N	9.3876E	1817	
	Gri-8	1 Aug 2005	45.9642N	9.3856E	1817	
	Gri-9	13 Aug 2012	45.9218N	9.3841E	1898	
Pegherolo	Peg-1	26 Aug 2010	46.0375N	9.6929E	2100	*Helianthemum nummularium*
	Peg-2	26 Aug 2010	46.0358N	9.6938E	2100	
	Peg-3	26 Aug 2010	46.0361N	9.6953E	2100	
	Peg-4	20 Jul 2012	46.0351N	9.6940E	2100	
	Peg-5	20 Jul 2012	46.0349N	9.6940E	2100	
	Peg-6	20 Jul 2012	46.0349N	9.6935E	2100	
	Peg-7	20 Jul 2012	46.0348N	9.6943E	2100	
Presolana	Pre-1	11 Aug 2010	45.9696N	10.0435E	2066	*Helianthemum nummularium*, *Hieracium* sp.
	Pre-2	11 Aug 2010	45.9640N	10.0577E	1923	
	Pre-3	11 Aug 2010	45.9640N	10.0577E	1923	
	Pre-4	11 Aug 2010	45.9655N	10.0519E	2002	
	Pre-5	11 Aug 2010	45.9640N	10.0577E	1923	
	Pre-6	11 Aug 2010	45.9640N	10.0577E	1923	
	Pre-7	11 Aug 2010	45.9665N	10.0494E	2031	
	HE600312	11 Aug 2010	45.9665N	10.0494E	1938	
	Pre-8	11 Aug 2010	45.9665N	10.0494E	2031	
	Pre-9	11 Aug 2010	45.9662N	10.0531E	1995	
Concarena	Con-1	09 Sep 2012	46.0044N	10.2735E	1750	*Hieracium tenuiflorum*
	Con-2	09 Sep 2012	46.0044N	10.2735E	1750	
	Con-3	09 Sep 2012	46.0044N	10.2735E	1750	
	Con-4	09 Sep 2012	46.0044N	10.2735E	1750	
	Con-5	09 Sep 2012	46.0044N	10.2735E	1750	
	Con-6	09 Sep 2012	46.0044N	10.2735E	1750	
	Con-7	09 Sep 2012	46.0044N	10.2735E	1750	

Note: †Specimen identifier; ‡Elevation is expressed in meters above sea level.

Table 2. Nucleotide p-distance within and between *Cryptocephalus barii* populations.

Comparison	Nucleotide p-distance†
Alben	0 (0)
Arera	0.00066 (0.00045)
Corna Grande	0 (0)
Grigna (southern Grigna, northern Grigna)	0 (0)
Pegherolo	0.00042 (0.00041)
Presolana	0.0018 (0.0010)
Concarena	0.00042 (0.00040)
Alben – Arera	0.0074 (0.0032)
Alben – Corna Grande	0.0089 (0.0035)
Alben – Grigna	0.024 (0.0056)
Alben – Pegherolo	0.012 (0.0040)
Alben – Presolana	0.0080 (0.0033)
Alben – Concarena	0.0089 (0.0035)
Arera – Corna Grande	0.0045 (0.0026)
Arera – Grigna	0.022 (0.0055)
Arera – Pegherolo	0.0045 (0.0025)
Arera – Presolana	0.00049 (0.00048)
Arera – Concarena	0.0014 (0.0014)
Corna Grande – Grigna	0.024 (0.0058)
Corna Grande – Pegherolo	0.0059 (0.0029)
Corna Grande – Presolana	0.0050 (0.0026)
Corna Grande – Concarena	0.0059 (0.0029)
Grigna – Pegherolo	0.021 (0.0054)
Grigna – Presolana	0.023 (0.0055)
Grigna – Concarena	0.024 (0.0056)
Pegherolo – Presolana	0.0050 (0.0025)
Pegherolo – Concarena	0.0059 (0.0028)
Presolana – Concarena	0.0021 (0.0015)

Note: †Nucleotide p-distance: mean value and standard errors are reported, the latter within in brackets.

Species Distribution Modelling

Concerning the Species Distribution Modelling (SDM) analysis, multicollinearity among the nineteen bioclimatic predictors was prevented by discarding nine variables, keeping as predictors for the modelling process: the mean diurnal range (BIO2); the isothermality (BIO3); the maximum temperature of the warmest month (BIO5); the minimum temperature of the coldest month (BIO6); the mean temperature of the wettest quarter (BIO8); the mean temperature of the driest quarter (BIO9); the annual precipitation (BIO12); the precipitation of the wettest month (BIO13); the precipitation seasonality (BIO15); the precipitation of the driest quarter (BIO17). The corresponding correlation matrix is reported in Suppl. material 2: Table S1. Ensemble Models (EMs) resulted in very high scores of TSS (0.998) and AUC (0.988); the 'wmean' maps resulting show, for current climatic conditions, a predicted suitable area which narrowly encompasses the known distribution range (represented by a Minimum Con-

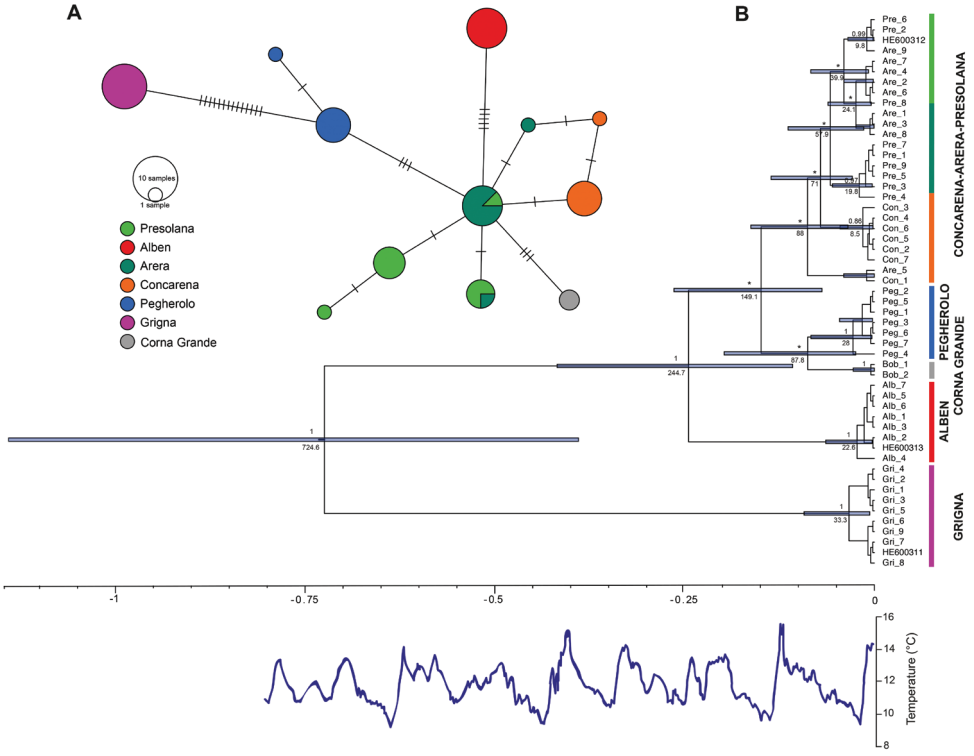

Figure 2. Maximum clade credibility tree and Minimum-spanning haplotype network. **A** Minimum-spanning haplotype network. Each colour represents a *Cryptocephalus barii* population. Circles represent the different haplotypes; their diameter is proportional to the haplotypes abundance. **B** Maximum clade credibility tree. Horizontal blue bars represent 95% HPD age confidence intervals for the nodes. Under the main lineage nodes is reported the divergence time in thousands of years before present. Above the nodes Bayesian posterior probabilities > 0.8 are reported, black asterisks indicate Bayesian posterior probabilities values < 0.80. Vertical coloured bars on the right of the tree indicate monophyletic clades, the colours identify the *C. barii* populations. Under the tree, in blue, the estimated surface temperature for the last 800,000 years (Hansen et al. 2013).

vex Polygon, MCP) (Figure 4A). The suitable climatic conditions are, in fact, strictly limited within *C. barii*'s MCP, with few areas with low suitability in the surrounding mountains, and no suitable areas in the valleys (Figure 4A). The most contributive bioclimatic variables were resulted: BIO3 (34%), BIO17 (27%), and BIO2 (14%).

For future scenarios, the 2070_4.5 predictions resulted in a partial north-eastern shift of the habitat suitability, with an apparent increase of the compatible areas, which however show lower suitability with respect to the current situation (Figure 4B), even in the MCP area (Figure 5). For the 2070_8.5 scenario, a general decrease of suitability is observable, even though a range expansion is predicted; nevertheless, also in this scenario the suitability in the MCP is much lower than the current climatic Ensemble Model (Figure 4C, Figure 5).

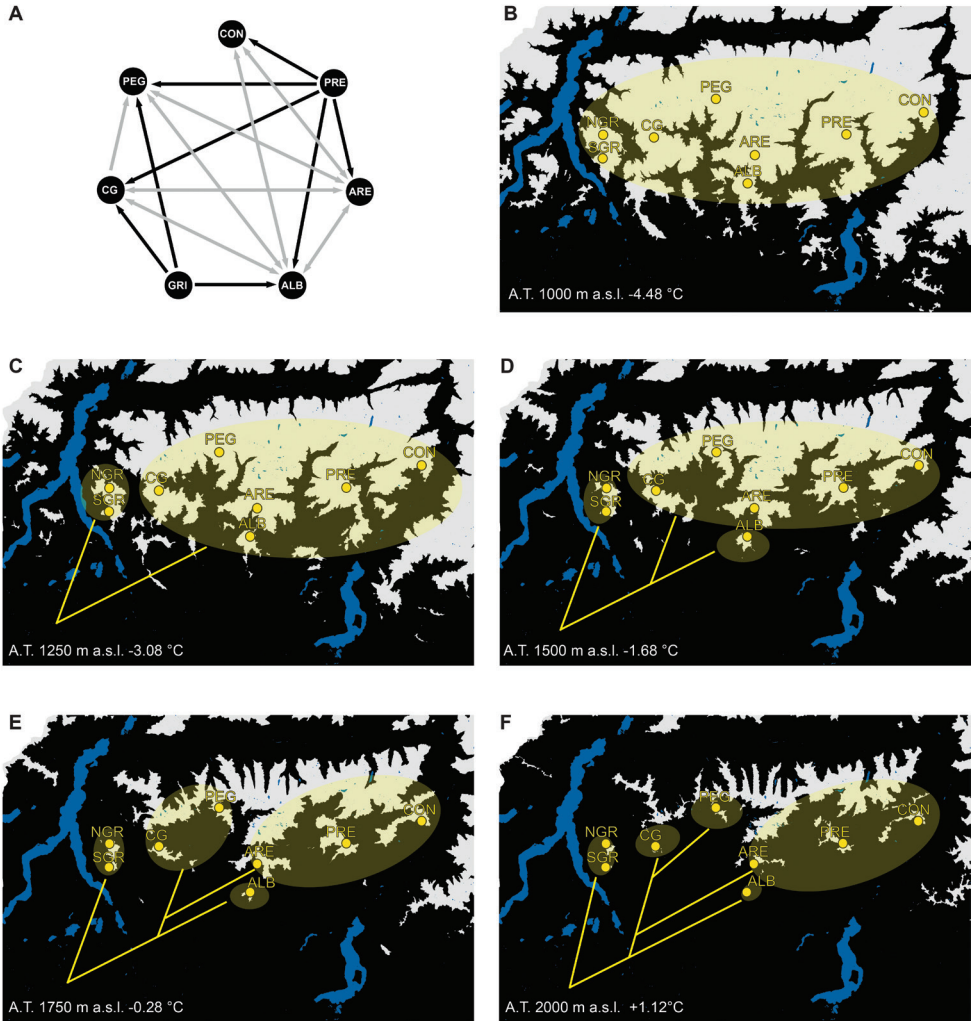

Figure 3. Most likely migration model and altitudinal habitat maps reporting suitable area for the presence of the species during cold periods. **A** Most likely migration model. Arrows indicate unidirectional flows (in black) and bidirectional flows (in gray) between populations. **B–F** Suitable altitudinal habitat maps. In light grey are reported the areas suitable for the presence of the species above a certain altitudinal threshold; the yellow ellipses are schematic drawing of *Cryptocephalus barii* populations; dendrograms showing the divergence events among populations, according to the tree in Fig. 1, are superimposed on the maps. At the bottom left of each map are reported: the minimum elevation at which climatic conditions are suitable for the presence of *Cryptocephalus barii* (inferred from present knowledge) corresponding to the altitudinal threshold used to draw the suitable areas, and the corresponding estimates of temperature variation in respect to the present. Abbreviations: A.T. = altitudinal threshold; CON = Concarena; PRE = Presolana; ARE = Arera; ALB = Alben; GRI = Grigna; NGR = northern Grigna; SGR = southern Grigna; CG = Corna Grande; PEG = Pegherolo.

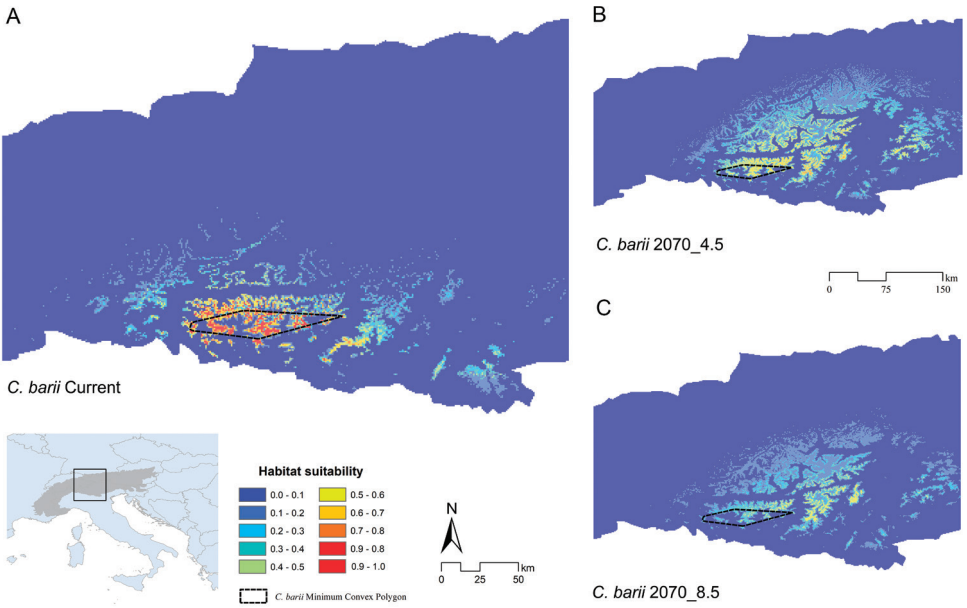

Figure 4. Predicted suitability for *Cryptocephalus barii* for current and future climatic conditions. Predicted suitability resulting from the Ensemble Modelling process performed over bioclimatic variables for *Cryptocephalus barii*, with the Minimum Convex Polygon built on the species' presence sites for **A** current **B** 2070 – 4.5 scenario of radiative forcing, and **C** 2070 – 8.5 scenario of radiative forcing.

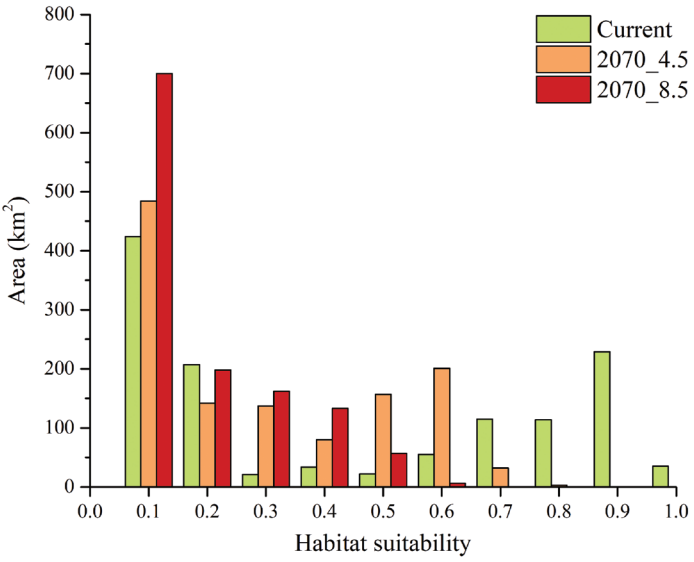

Figure 5. Changes in habitat suitability for *Cryptocephalus barii*. Histogram reporting classes of habitat suitability calculated within the Minimum Convex Polygon built on *Cryptocephalus barii* presence sites through Ensemble Modelling process. Areas calculated for current and future climatic conditions (2070, 4.5 and 8.5 scenarios) are reported, respectively, in green, orange and red.

Discussion

With this study the presence of the species is discovered on four mountainous reliefs from which it was never sampled before, thus extending its previous distribution towards the north (Pegherolo), east (Concarena), and south (southern Grigna). Since during the collecting campaigns the species has been searched also on suitable areas outside the previously known species range and it was not detected, we can be confident in supporting the fact that the species is nowadays confined in a limited area between the Como (on west) and Iseo (on east) lakes, corresponding to the glacial paleochannels of Adda and Oglio glaciers. The actual range of *C. barii* is limited to mountainous and geographically isolated calcareous reliefs of Orobie Alps, thus presenting a patchy distribution similar to that of an insular species inhabiting an archipelago. Regarding populations size, we observed that the most vigorous populations are those of northern Grigna (Circo di Moncodeno), Alben, Presolana, and Arera; while, those of southern Grigna, Pegherolo, Corna Grande, and Concarena inhabit a surface restricted area and consist of a limited number of individuals.

Species distribution modelling analyses showed that the most contributing variables retained as predictors are the mean diurnal range, the isothermality and the precipitation of the driest quarter. As other insect species associated with high altitude (Urbani et al. 2017), also *C. barii* shows a significant habitat suitability inversely proportional to the increase of isothermality values, indicating a high sensitivity to large and instable fluctuations in temperature. At present the habitat suitability within the current estimated range of the species (identified with MCP) is high, while in the case of the tested future scenarios the habitat suitability within the MCP suffered a decrease. Noteworthy, it has been predicted an increase of the compatible areas even if associated with low-intermediate values of habitat suitability, with a partial north-eastern shift of suitable areas. The results of our phylogeographic analyses showed a strong population structure, in accordance with previous studies on congeneric species, where a limited gene flow between populations were observed even when geographic distances are short (Piper and Compton 2003). Personal observations (M Montagna) on *C. barii* adult behaviour (individuals feeding or mating on a host plant once disturbed return back on it within few minutes) suggest a limited movement ability. These aspects, in association with the presence of biogeographical barriers, viz. the Como Lake on west, the Valtellina on north and the Val Camonica on east, delimiting the actual species range, let us to conclude that the possibility of the species to disperse and colonise new suitable areas within 50 years has to be considered highly improbable.

A geographic structure characterising *C. barii* populations was first confirmed by the positive correlation between geographic and nucleotide distances resulting from the Mantel test, even if based on a single mitochondrial marker. Indeed, most of the populations are characterised by private COI haplotype and only Presolana and Arera partially share haplotypes (Figure 2A). Furthermore, the reciprocal monophyly that characterise most of the populations analysed (Figure 2), even those geographically close such as Alben and Arera or Grigna and Corna Grande, suggests that such popula-

tions have been isolated from each other for a quite long period of time, and that the present population structure was only marginally affected by the last glaciation and by the Holocene climate optimum occurred between 9,000 and 5,000 years before present (Mayewski et al. 2004). The estimated time of divergence, even adopting a general nucleotide substitution rate, suggests that most of the divergence events largely predate the last glacial maximum in the Alps occurred approximately 26,500–23,500 years BP (Ivy-Ochs et al. 2008; Monegato et al. 2007). The isolation of the populations on separate mountains, occurred during warm periods when the species followed its optimal climate towards the higher quotes, was probably caused by ancient glacial cycles (from more than 1 million years ago to about 100,000 years BP). The last glacial cycle seems to have had limited effect in shaping the species population structures. Furthermore, the isolation of Grigna population (724,600 years BP) from the other populations largely predate the subsequent splits, represented by the divergence of Alben population (244,700 years BP) and Corna Grande-Pegherolo populations (149,100 years BP). The long-term isolation of the Grigna population is also supported by its high average nucleotide distance from other populations (0.0228 ± 0.0056), a value that is above the interspecific threshold inferred for the subfamily of Cryptocephalinae (1% nucleotide distance, Magoga et al. 2018). Grigna, Alben, Corna Grande and Pegherolo seem to be well isolated from other populations, while Arera, Presolana and Concarena, resulting not monophyletic and sharing haplotypes, are not genetically isolated. In detail, Arera and Presolana share two haplotypes and two COI sequences from Arera and Concarena cluster together in coalescent tree. This fact suggests the possibility that gene flow between these three populations occurred in the last 90,000 years.

The long-term isolation and the high average nucleotide distance from other populations inferred for individuals collected from Grigna seem to counteract with the migration model that has been selected as the most probable (Figures 2, 3A), indeed this model considers Grigna and Presolana as source population from which re-colonisation towards other mountains begun. At the same time, Presolana has the highest haplotype diversity and it is highly connected with at least two other populations (Concarena and Arera) making it justified to suppose that this could have act as a refugium during Holocene interglacials characterised by an increase of the temperature. Further analyses, based on the use of innovative approaches such as RAD (Restriction site Associated DNA) sequencing, have to be adopted in order to shed light on the past demography of this species and elucidate the mode and time of the migration processes occurred among populations.

Conclusions

In this study, through an extensive sampling the comprehensive distribution of *C. barii*, species endemic of Orobie Alps, was defined. As expected, the population genetic structure of this cold adapted species was strongly affected by Pleistocene climate oscillations; in fact the observed phylogeographic patterns reflect population connections and isolation during cold and warm periods, respectively. Even if the obtained

results are based on a single mitochondrial marker and not on the whole mitochondrial genome or part of the nuclear genome, the correspondence between presence of corridors among populations predicted at different temperatures and the observed genetic variability, let us to be confident about the accuracy of COI in phylogeographic pattern reconstruction, at least in the analysed case. This result further confirms the possibility to exploit the huge amount of COI sequences developed through DNA barcoding and DNA metabarcoding studies in the last 15 years, not only for DNA taxonomy purpose but also for phylogeography and genetic conservation ones.

The reduction of *C. barii* habitat suitability predicted within 50 years because of global warming, in association with the presence of biogeographic barriers that prevent the species dispersion, open the possibility that *C. barii* will be extinct during this time span. This prediction, in association with the observed low population size, the isolation of populations and the limited area of occupancy of the species prompt us to propose the inclusion of *C. barii* in the IUCN Red List as vulnerable or superior category, thus requiring urgent conservation actions pursued by Natural Parks and environmental agencies.

The case of *C. barii* can be representative of the cold adapted species, both animals and plants, currently present in the Alpine arc and inhabiting high altitude environments. Such species can be considered habitat specialists and the spatial extent of areas with suitable characteristics will be strongly reduced in the next years due to global warming. Beside the decrease in term of biodiversity, caused by the possible species extinctions, the impact on ecosystems, produced by the loss of these habitats, is currently unknown.

Acknowledgements

The authors sincerely acknowledge Davide Sassi for his help in the collection activity; in addition, we would like to thank the reviewers for their thoughtful comments and efforts towards improving our manuscript. The study was partially supported by funds assigned to MM by Parco delle Orobie Bergamasche contract ML 18 (22nd February 2011) and 438 (9th March 2011) and by MIUR Fondo per il finanziamento delle attività base di ricerca FFABR 2017.

References

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43: 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x

Beerli P, Palczewski M (2010) Unified framework to evaluate panmixia and migration direction among multiple sampling locations. Genetics 185(1): 313. https://doi.org/10.1534/genetics.109.112532

Beerli P (2009) How to use MIGRATE or why are Markov chain Monte Carlo programs difficult to use. In: Bertorelle G, Bruford MW, Hauffe HC, Rizzoli A, Vernesi C (Eds) Population genetics for animal conservation. Cambridge University Press, 39–77. https://pdfs.semanticscholar.org/461c/8ac05e3e75592348d3f875dde154327fd32d.pdf

Beerli P (2012) Migrate documentation. Florida State University, Tallahassee, 119 pp. http://popgen.sc.fsu.edu/migratedoc.pdf

Bennett KD (1990) Milankovitch cycles and their effects on species in ecological and evolutionary time. Paleobiology 16(1): 11–21. https://doi.org/10.1017/S0094837300009684

Borer M, Alvarez N, Buerki S, Margraf N, Rahier M, Naisbit RE (2010) The phylogeography of an alpine leaf beetle: Divergence within *Oreina elongata* spans several ice ages. Molecular Phylogenetics and Evolution 57(2): 703–709. https://doi.org/10.1016/j.ympev.2010.08.017

Bouckaert RR, Drummond AJ (2017) bModelTest: Bayesian phylogenetic site model averaging and model comparison. BMC evolutionary biology 17(1): 42. https://doi.org/10.1186/s12862-017-0890-6

Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu CH, Xie D, Suchard MA, Rambaut A, Drummond AJ (2014) BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS computational biology 10(4): e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Burlini M (1948) Nuove specie di *Cryptocephalus* italiani. Memorie Museo civico di Storia naturale di Verona 1: 211–229

Burlini M (1955) Revisione dei *Cryptocephalus* italiani e della maggior parte delle specie di Europa (Col. Chrysomelidae). Memorie della Società Entomologica Italiana, 287 pp.

Carapezza A, Faraci F (2006) Insecta Heteroptera Leptopodidae, Saldidae, Miridae (partim), Tingidae. In: Stoch F (Ed.) Checklist and distribution of the Italian fauna: 10,000 terrestrial and inland water species. Memorie del Museo Civico di Storia Naturale di Verona – 2. Serie. Sezione Scienze della Vita, Verona, 304 pp.

Casazza G, Barberisa G, Minuto L (2005) Ecological characteristics and rarity of endemic plants of the Italian Maritime Alps. Biological Conservation 123: 361–371. https://doi.org/10.1016/j.biocon.2004.12.005

Cerabolini B, De Andreis R, Ceriani RM, Pierce S, Raimondi B (2004) Seed germination and conservation of endangered species from the Italian Alps: *Physoplexis comosa* and *Primula glaucescens*. Biological Conservation 117: 351–356. https://doi.org/10.1016/j.biocon.2003.12.011

Davis MB, Shaw RG (2001) Range shifts and adaptive responses to Quaternary climate change. Science 292(5517): 673–679. https://doi.org/10.1126/science.292.5517.673

Dirnböck T, Essl F, Rabitsch W (2011) Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biology 17(2): 990–996. https://doi.org/10.1111/j.1365-2486.2010.02266.x

Dray S, Dufour AB (2007) The ade4 package: implementing the duality diagram for ecologists. Journal of statistical software 22(4): 1–20. https://doi.org/10.18637/jss.v022.i04

Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian phylogenetics with BEAUti and the BEAST 1.7. Molecular biology and evolution 29(8): 1969–1973. https://doi.org/10.1093/molbev/mss075

Dunn RR (2005) Modern insect extinctions, the neglected majority. Conservation biology 19(4): 1030–1036. https://doi.org/10.1111/j.1523-1739.2005.00078.x

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic acids research 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Elith J, Graham CH, Anderson RP, Dudík M, Ferrier S, Guisan A, Hijmans JR, Huettmann F, Leathwick RJ, Lehmann A, Li J, Lohmann GL, Loiselle AB, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton McCJ, Townsend Peterson A, Phillips JS, Richardson K, Schachetti-Pereira R, Schapire RE, Soberòn J, Williams S, Wisz SM, Zimmermann EN, Araújo M (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29: 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x

ESRI (2010) ArcMap 10.0. ESRI, Redlands, California. http://desktop.arcgis.com/en/arcmap/

Felsenstein J (1984) Distance methods for inferring phylogenies: a justification. Evolution 38(1): 16–24. https://doi.org/10.1111/j.1558-5646.1984.tb00255.x

Gent PR, Danabasoglu G, Donner LJ, Holland MM, Hunke EC, Jayne SR, Lawrence DM, Neale RB, Rasch PJ, Vertenstein M (2011) The community climate system model version 4. Journal of Climate 24: 4973–4991. https://doi.org/10.1175/2011JCLI4083.1

Gernhard T (2008) The conditioned reconstructed process. Journal of theoretical biology 253(4): 769–778. https://doi.org/10.1016/j.jtbi.2008.04.005

Gómez-Zurita J, Sassi D, Cardoso A, Balke M (2012) Evolution of *Cryptocephalus* leaf beetles related to *C. sericeus* (Coleoptera: Chrysomelidae) and the role of hybridization in generating species mtDNA paraphyly. Zoologica Scripta 41(1): 47–67. https://doi.org/10.1111/j.1463-6409.2011.00500.x

Hansen J, Sato M, Russell G, Kharecha P (2013) Climate sensitivity, sea level and atmospheric carbon dioxide. Philosophical Transactions of the Royal Society A 371(2001): 20120294. https://doi.org/10.1098/rsta.2012.0294

Hewitt GM (1999) Post-glacial re-colonization of European biota. Biological journal of the Linnean Society 68(1–2): 87–112. https://doi.org/10.1111/j.1095-8312.1999.tb01160.x

Hewitt GM (2000) The genetic legacy of the Quaternary ice ages. Nature 405(6789): 907. https://doi.org/10.1038/35016000

Hewitt GM (2004) Genetic consequences of climatic oscillations in the Quaternary. Philosophical Transactions of the Royal Society B: Biological Sciences 359(1442): 183–195. https://doi.org/10.1098/rstb.2003.1388

Hewitt GM (2011) Quaternary phylogeography: the roots of hybrid zones. Genetica 139(5): 617–638. https://doi.org/10.1007/s10709-011-9547-3

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International journal of climatology 25: 1965–1978. https://doi.org/10.1002/joc.1276

Iannella M, Cerasoli F, Biondi M (2017) Unraveling climate influences on the distribution of the parapatric newts *Lissotriton vulgaris meridionalis* and *L. italicus*. Frontiers in Zoology 14: 55. https://doi.org/10.1186/s12983-017-0239-4

Iannella M, Cerasoli F, D'Alessandro P, Console G, Biondi M (2018a) Coupling GIS spatial analysis and Ensemble Niche Modelling to investigate climate change-related threats to the

Sicilian pond turtle *Emys trinacris*, an endangered species from the Mediterranean. PeerJ 6: e4969. https://doi.org/10.7717/peerj.4969

Iannella M, D'Alessandro P, Biondi M (2018b) Evidences for a shared history for spectacled salamanders, haplotypes and climate. Scientific reports 8: 16507. https://doi.org/10.1038/s41598-018-34854-1

Ivy-Ochs S, Kerschner H, Reuther A, Preusser F, Heine K, Maisch M, Kubik PW, Schlüchter C (2008) Chronology of the last glacial cycle in the European Alps. Journal of Quaternary Science 23(6–7): 559–573. https://doi.org/10.1002/jqs.1202

Jacobsen D, Milner AM, Brown LE, Dangles O (2012) Biodiversity under threat in glacier-fed river systems. Nature Climate Change 2(5): 361. https://doi.org/10.1038/nclimate1435

Kass RE, Raftery AE (1995) Bayes factors. Journal of the American Statistical Association 90: 773–795. https://doi.org/10.2307/2291091

Kingman JF (1982) On the genealogy of large populations. Journal of applied probability 19(A): 27–43. https://doi.org/10.2307/3213548

Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular biology and evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2016) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34(3): 772–773. https://doi.org/10.1093/molbev/msw260

Leigh JW, Bryant D (2015) POPART: full-feature software for haplotype network construction. Methods in Ecology and Evolution 6(9): 1110–1116. https://doi.org/10.1111/2041-210X.12410

Lohse K, Nicholls JA, Stone GN (2011) Inferring the colonization of a mountain range – refugia vs. nunatak survival in high alpine ground beetles. Molecular Ecology 20(2): 394–408. https://doi.org/10.1111/j.1365-294X.2010.04929.x

Magoga G, Sahin DC, Fontaneto D, Montagna M (2018) Barcoding of Chrysomelidae of Euro-Mediterranean area: efficiency and problematic species. Scientific reports 8(1): 13398. https://doi.org/10.1038/s41598-018-31545-9

Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah LEE (2006) Global warming and extinctions of endemic species from biodiversity hotspots. Conservation biology 20(2): 538–548. https://doi.org/10.1111/j.1523-1739.2006.00364.x

Mantel N (1967) The detection of disease clustering and a generalized regression approach. Cancer research 27(2 Part 1): 209–220. http://cancerres.aacrjournals.org/content/27/2_Part_1/209.short

Mardulyn P, Mikhailov YE, Pasteels JM (2009) Testing phylogeographic hypothesis in euro-siberian cold-adapted leaf beetle with coalescent simulations. Evolution 63(10): 2717–2729. https://doi.org/10.1111/j.1558-5646.2009.00755.x

Marti O, Braconnot P, Dufresne JL, Bellier J, Benshila R, Bony S, Brockmann P, Cadule P, Caubel A, Codron F (2010) Key features of the IPSL ocean atmosphere model and its sensitivity to atmospheric resolution. Climate Dynamics 34: 1–26. https://doi.org/10.1007/s00382-009-0640-6

Martinet B, Lecocq T, Brasero N, Biella P, Urbanová K, Valterová I, Cornalba M, Gjershaug JO, Michez D, Rasmont P (2018) Following the cold: geographical differentiation between interglacial refugia and speciation in the arcto-alpine species complex *Bombus monticola* (Hymenoptera: Apidae). Systematic Entomology 43(1): 200–217. https://doi.org/10.1111/syen.12268

Mayewski PA, Rohling EE, Stager JC, Karlén W, Maasch KA, Meeker LD, Meyerson EA, Gasse F, van Kreveld S, Holmgren K, Lee-Thorp J, Rosqvist G, Rack F, Staubwasser M, Schneider RR, Steig EJ (2004) Holocene climate variability. Quaternary Research 62: 243–255. https://doi.org/10.1016/j.yqres.2004.07.001

Menéndez R (2007) How are insects responding to global warming? Tijdschrift voor Entomologie 150: 355–365. https://www.nev.nl/pages/publicaties/tve/cat/info.php?artikelid=2501

Minelli A, Ruffo S, Stoch F (2006) Endemism in Italy. In: Stoch F (Ed.) Checklist and distribution of the italian fauna: 10.000 terrestrial and inland water species. Memorie del Museo Civico di Storia Naturale di Verona – 2. Serie. Sezione Scienze della Vita, Verona, 304 pp.

Monegato G, Ravazzi C, Donegana M, Pini R, Calderoni G, Wick L (2007) Evidence of a two-fold glacial advance during the last glacial maximum in the Tagliamento end moraine system (eastern Alps). Quaternary Research 68(2): 284–302. https://doi.org/10.1016/j.yqres.2007.07.002

Montagna M, Sassi D, Giorgi A (2013) *Pachybrachis holerorum* (Coleoptera: Chrysomelidae: Cryptocephalinae), a new species from the Apennines, Italy, identified by integration of morphological and molecular data. Zootaxa 3741(2): 243–253. https://doi.org/10.11646/zootaxa.3741.2.3

Montagna M, Kubisz D, Mazur MA, Magoga G, Ścibior R, Kajtoch Ł (2016). Exploring species-level taxonomy in the *Cryptocephalus flavipes* species complex (Coleoptera: Chrysomelidae). Zoological Journal of the Linnean Society 179(1): 92–109. https://doi.org/10.1111/zoj.12445

Muster C, Berendonk TU (2006) Divergence and diversity: lessons from an arctic-alpine distribution (*Pardosa saltuaria* group, Lycosidae). Molecular Ecology 15(10): 2921–2933. https://doi.org/10.1111/j.1365-294X.2006.02989.x

Negro M, Casale A, Migliore L, Palestrini C, Rolando A (2008) Habitat use and movement patterns in the endangered ground beetle species, *Carabus olympiae* (Coleoptera: Carabidae). European Journal of Entomology 105: 105–112. https://doi.org/10.14411/eje.2008.015

Papadopoulou A, Anastasiou I, Vogler AP (2010) Revisiting the insect mitochondrial molecular clock: the mid-Aegean trench calibration. Molecular Biology and Evolution 27(7): 1659–1672. https://doi.org/10.1093/molbev/msq051

Peruzzi L, Conti F, Bartolucci F (2014) An inventory of vascular plants endemic to Italy, Phytotaxa 168 (1): 001–075. https://doi.org/10.11646/phytotaxa.168.1.1

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecological Modelling 190: 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026

Piper RW, Compton SG (2003) Subpopulations of *Cryptocephalus* beetles (Coleoptera: Chrysomelidae): geographically close but genetically far. Diversity and distributions 9(1): 29–42. https://doi.org/10.1046/j.1472-4642.2003.00163.x

QGIS Development Team (2009) QGIS Geographic Information System. Open Source Geospatial Foundation http://qgis.osgeo.org

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 10: https://doi.org/10.1093/sysbio/syy032

Regalin R, Redigolo E (1993) Ritrovamento di *Cryptocephalus* (s. str.) *barii* Burlini, 1948 (Coleoptera Chrysomelidae) sul Monte Grigna Settentrionale e note ecologiche. Bollettino di Zoologia agraria e di Bachicoltura, Series II 25(2): 259–263.

Rolland C (2003) Spatial and seasonal variations of air temperature lapse rates in Alpine regions. Journal of Climate 16(7): 1032–1046. https://doi.org/10.1175/1520-0442(2003)016<1032:SASVOA>2.0.CO;2

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. https://doi.org/10.1093/sysbio/sys029

Rossaro B, Montagna M, Lencioni V (2016) Environmental traits affect chironomid communities in glacial areas of the Southern Alps: evidence from a long-lasting case study. Insect Conservation and Diversity 9(3): 192–201. https://doi.org/10.1111/icad.12157

Sassi D (2014) Taxonomic remarks, phylogeny and evolutionary notes on the leaf beetle species belonging to the *Cryptocephalus sericeus* complex (Coleoptera: Chrysomelidae: Cryptocephalinae). Zootaxa 3857(3): 333–378. https://doi.org/10.11646/zootaxa.3857.3.2

Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the entomological Society of America 87(6): 651–701. https://doi.org/10.1093/aesa/87.6.651

Schmitt T (2009) Biogeographical and evolutionary importance of the European high mountain systems. Frontiers in Zoology 6: 9. https://doi.org/10.1186/1742-9994-6-9

Thuiller W, Georges D, Engler R (2016) biomod2: Ensemble platform for species distribution modeling. R package version 3.3–7 http://CRAN.R-project.org/package=biomod2

Tribsch A, Schönswetter P (2003) Patterns of endemism and comparative phylogeography confirm palaeoenvironmental evidence for Pleistocene refugia in the Eastern Alps. Taxon 52: 477–497. https://doi.org/10.2307/3647447

Urbani F, D'Alessandro P, Frasca R, Biondi M (2015) Maximum entropy modeling of geographic distributions of the flea beetle species endemic in Italy (Coleoptera: Chrysomelidae: Galerucinae: Alticini). Zoologische Anzeiger 258: 99–109. https://doi.org/10.1016/j.jcz.2015.08.002

Urbani F, D'Alessandro P, Biondi M (2017) Using Maximum Entropy Modeling (MaxEnt) to predict future trends in the distribution of high altitude endemic insects in response to climate change. Bulletin of Insectology 70: 189–200. http://www.bulletinofinsectology.org/pdfarticles/vol70-2017-189-200urbani.pdf

Watanabe S, Hajima T, Sudo K, Nagashima T, Takemura T, Okajima H, Nozawa T, Kawase H, Abe M, Yokohata T (2011) MIROC-ESM 2010: Model description and ba-

sic results of CMIP5-20c3m experiments. Geoscientific Model Development 4: 845. https://doi.org/10.5194/gmdd-4-1063-2011

Wu T, Song L, Li W, Wang Z, Zhang H, Xin X, Zhang Y, Zhang L, Li J, Wu F, Liu Y, Zhang F, Shi X, Chu M, Zhang J, Fang Y, Wang F, Lu Y, Liu X, Wei M, Liu Q, Zhou W, Dong M, Zhao Q, Ji J, Li L, Zhou M (2014) An overview of BCC climate system model development and application for climate change studies. Journal of Meteorological Research 28(1): 34–56. https://doi.org/10.1007/s13351-014-3041-7

Yule GU (1925) A mathematical theory of evolution, based on the conclusions of Dr. JC Willis, FR S. Philosophical Transactions of the Royal Society B 213(402–410): 21–87. https://doi.org/10.1098/rstb.1925.0002

Supplementary material 1

Migration models tested in this study using Migrate-n E) Most likely migration model

Authors: Matteo Brunetti, Giulia Magoga, Mattia Iannella, Maurizio Biondi, Matteo Montagna

Data type: statistical model

Explanation note: Arrows indicate unidirectional flows (in black) and bidirectional flows (in gray) between populations. Abbreviations: con = Concarena; pre = Presolana; are = Arera; alb = Alben; gri = Grigna; cg = Corna Grande; peg = Pegherolo.

Link: https://doi.org/10.3897/zookeys.856.32462.suppl1

Supplementary material 2

Correlation matrix built among the 19 candidate predictors downloaded from the online repository Worldclim.org.

Authors: Matteo Brunetti, Giulia Magoga, Mattia Iannella, Maurizio Biondi, Matteo Montagna

Data type: statistical data

Explanation note: Variables showing a Pearson's $|r| > 0.85$ are highlighted in yellow and were discarded from the model building process.

Link: https://doi.org/10.3897/zookeys.856.32462.suppl2

ZooKeys 856: 27–50 (2019)
doi: 10.3897/zookeys.856.32388
http://zookeys.pensoft.net

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To be or not to be a synonym – revision of the *Donacia clavareaui-fukiensis* complex (Coleoptera, Chrysomelidae, Donaciinae)*

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Academic editor: *M. Schmitt* | Received 13 December 2018 | Accepted 12 February 2019 | Published 17 June 2019

http://zoobank.org/779E3481-B7AD-40C8-A5F4-AAD52DAD60ED

Citation: Geiser E (2019) To be or not to be a synonym – revision of the *Donacia clavareaui-fukiensis* complex (Coleoptera, Chrysomelidae, Donaciinae). In: Schmitt M, Chaboo CS, Biondi M (Eds) Research on Chrysomelidae 8. ZooKeys 856: 27–50. https://doi.org/10.3897/zookeys.856.32388

Abstract

The East Palaearctic species *Donacia clavareaui* Jacobson, 1906 and *Donacia fukiensis* Goecke, 1944 have been confused for decades. Finally, *D. fukiensis* was synonymized with *D. clavareaui* by Askevold (1990) but he could not examine the type series of *D. fukiensis* because it was stored in an inaccessible collection. Cong and Yu (1997) re-established *D. fukiensis* as a distinct species, also without direct access to the type series. The synonymization by Askevold (1990) was applied in the identification key of Palaearctic Chrysomelidae (Warchalowski 2010) and the Catalogue of Palaearctic Chrysomelidae (Silfverberg 2010). Because the type series of *D. fukiensis* is now accessible, it has been possible to proof that *D. fukiensis* is a distinct species, and a lectotype has been established from the series of seven syntypes. *Donacia kweilina* Chen, 1966 and *D. mediohirsuta* Chen, 1966, which were split from the mixture of *D. clavareaui* and *D. fukiensis*, are now also synonymized with *D. clavareaui*, because their characters are the same or within the variation range of the characters of *D. clavareaui*. Furthermore, a distribution map is provided with the reliable records known to date.

Keywords

China, Fujian, East Palaearctic, *Donacia clavareaui*, *Donacia fukiensis*, *Donacia kweilina*, *Donacia mediohirsuta*, identification key, lectotype, Museum Frey, reed beetles, synonym, taxonomy

* extended versions of a talk presented to the 3rd European Symposium on the Chrysomelidae, Naples, Italy, 5 July, 2018.

Introduction

The East Palaearctic species of *Donacia clavareaui* Jacobson, 1906, *D. fukiensis* Goecke, 1944, *D. kweilina* Chen, 1966, and *D. mediohirsuta* Chen, 1966 all have in common that their pronotum is pubescent while their elytra are glabrous. All other East Palaearctic *Donacia* species have either hairs on both pronotum and elytra or no hairs.

Although the first descriptions of *D. clavareaui* and of *D. fukiensis* are very detailed (see Appendix 1, 2) it is not possible to distinguish these two species with the described characters alone. Worse, each description leads to *D. clavareaui* and to *D. fukiensis* without any contradiction. Therefore many misidentifications occurred, especially in specimens from China. Subsequently in the identification key of Gressitt and Kimoto (1961) only *D. fukiensis* was considered to occur in China, which resulted in further identification errors. Chen (1966) split *D. kweilina* and *D. mediohirsuta* from this mixture. Askevold (1990) synonymized *D. fukiensis* with *D. clavareaui*. Cong and Yu (1997) re-established *D. fukiensis* as a distinct species, but in the main comprehensive books on Palaearctic Chrysomelidae (Warchalowski 2010, Silfverberg 2010) *D. fukiensis* is still considered to be synonymous with *D. clavareaui*. These problems arose because the syntype series was neither accessible to Askevold nor to Cong and Yu. Today, the type series of *D. fukiensis* is stored at the Natural History Museum in Basel and it has been possible at last to examine it.

Materials and methods

Abbreviations of collections

ASIZ Academia Sinica, Institute of Zoology, Beijing, China
CASC California Academy of Science, San Francisco
CMIC Natural History Museum and Institute Chiba, Japan
GBIF Global Biodiversity Information Facility, https://www.gbif.org/
IBNM Ibaraki Nature Museum, Japan
ISAC coll. IS Askevold, Florida
NHMB Natural History Museum Basel, Switzerland
NHMW Natural History Museum Vienna, Austria
NSMK National Science Museum of Korea, Daejeon, South Korea
MNHN Muséum National d'Histoire Naturelle, Paris
SDEI Senckenberg German Entomological Institute, Müncheberg, Germany
USNM United States National Museum, Washington D.C., US
ZSMC Zoological State Collection, Munich, Germany

Type specimens

***Donacia clavareaui* Jacobson, 1906**

Type locality. Russia: Buryatia, Kjachta, 50°21'N, 106°27'E

Holotype. MNHN EC2130: ♂ "Kjachta Siberie par Götzelmann [Clavareau's handwriting]/Donacia clavareaui TYPE Jacob. [Clavareau's handwriting]/TYPE [red, added by N Berti]/Museum Paris coll. H. Clavareau 1932/ Donacia clavareaui Jac. ♂ typ. G. Jacobson det."

Photograph of type specimen examined. https://science.mnhn.fr/institution/mnhn/collection/ec/item/ec2130?listIndex=1&listCount=6 [26.11.2018]

***Donacia fukiensis* Goecke, 1944**

Type locality. China: Fukien [Fujian], Kuatun [≈10 km NNE of Shaowu], 27°24'N, 117°24'E, 2300 m a.s.l.

Lectotype (here designated to fix the identity of the species). NMB-FREY0000001: ♂ "Kuatun (2300m) 27,40 n. Br. 117,40 ö. L.; J. Klapperich [leg.] 7.5.1938 (Fukien)". NHMB in coll. Frey (Figs 1, 2)

Paralectotypes. 3 ♂, ♀♀ 7.5.1938, 3 ♂♂, ♀ 27.04.1938 (other data same as lectotype) (Fig. 3: ♀ from 7.5.1938 of this series)

Goecke did not designate a single type specimen; his description derives from seven syntypes, which are the specimens mentioned above. All of them are stored in the NHMB in coll. Frey.

***Donacia kweilina* Chen, 1966**

Type locality. China: Guangxi, Kweilin, 25°16'55"N, 110°17'11"E.

Holotype. ♂, allotype: ♀, paratypes: 47 ♂♂, ♀♀ "Kwangsi: Kweilin (April-May, 1952)"

The type specimens are kept in ASIZ except for two paratypes in ISAC.

***Donacia mediohirsuta* Chen, 1966**

Type locality. China: Yunnan, Shishong-Baana (Xishuangbanna), 22°1'N, 100°48'E, 1200 m a.s.l.

Holotype. ♀ "Yunnan: Shishong-Baana, 15.5.1958"

The type specimen is retained in ASIZ.

Table 1. List of specimen records of *Donacia clavareaui*, *D. fukiensis*, *D. kweilina* and *D. mediohirsuta*

Species	Location	Lat.–Long.	Province	Country	Date	Qty	Legit	Determinavit	Coll.	Source
D. clavareaui	Kjachta	50°21.00'N; 106°27.00'E	Transbaikalia, Republic of Buryatia	Russia	–	1	Götzelmann	det. G. Jacobson 1906	MNHN	Photograph of type specimen (website MNHN)
	no details	–	Primorski krai (no more details)	Russia	–			det. Hayashi and Shiyake	–	Hayashi & Shiyake 2004, Bienkowski 2014
	a 30 km Suchebatora (= Süchbaatar)	50°14'N; 106°12'E	Selenge	Mongolia	–	1		det. L. Medvedev vid. E. Geiser 2018	ZSMC	specimen examined
	Mitanda, Katsuta	36°22'N; 140°33'E	Ibaraki-ken, Honshu	Japan	09.03.1988	10	Y. Narita	det. Y. Narita	IBNM	Narita 1991
	Urizura	36°30'N; 140°27'E	Ibaraki-ken, Honshu	Japan	09.01.1991	12	Y. Narita	det. Y. Narita	IBNM	Narita 2003
	Mito-shi	36°26.67'N; 140°26.18'E	Ibaraki-ken, Honshu	Japan	05.14.1986	8			IBNM	GBIF [22.10.2018]
	Iwasemachi, Nishiibaraki-gun	36°17'N; 140°25'E	Ibaraki-ken, Honshu	Japan	05.28.1995	2			IBNM	GBIF [22.10.2018]
	Ishioka-shi	36°13.13'N; 140°12.95'E	Ibaraki-ken, Honshu	Japan	07.05.1987	2			IBNM	GBIF [22.10.2018]
	Chiba	35°36'N; 140°6'E	Chibai-ken, Honshu	Japan	05.13.1988	4			CMIC	GBIF [22.10.2018]
	Chiba	35°36'N; 140°6'E	Chibai-ken, Honshu	Japan	06.10.1988	2			CMIC	GBIF [22.10.2018]
	Chiba	35°36'N; 140°6'E	Chibai-ken, Honshu	Japan	05.20.1987	4			CMIC	GBIF [22.10.2018]
	Harbin (Charbin)	45°45'N; 126°39'E	Heilongjiang (Amur-Province)	China	07.02.1950	1	W. Alin	det. H. Goecke 1952 vid. E. Geiser 2017	SDEI	Specimen examined
	Harbin (Charbin)	45°45'N; 126°39'E	Heilongjiang (Amur-Province)	China	26.–29.08.1953	2	Kardakoff	det. H. Goecke 1952 vid. E. Geiser 2018	NHMW	Specimen examined
	Harbin (Charbin)	45°45'N; 126°39'E	Heilongjiang (Amur-Province)	China	26.–29.08.1953	2	Kardakoff	det. A. Schneider 1956 vid. E. Geiser 2018	ZSMC	Specimen examined
	Harbin (Charbin)	45°45'N; 126°39'E	Heilongjiang (Amur-Province)	China	26.–29.08.1953	36	Kardakoff	det. H. Goecke 1956 vid. E. Geiser 2018	NHMB	Specimen examined
	Harbin (Charbin)	45°45'N; 126°39'E	Heilongjiang (Amur-Province)	China	06.06.1954	6		det. S. Cong & P. Yu	ASIZ	Cong and Yu 1997

Species	Location	Lat.–Long.	Province	Country	Date	Qty	Legit	Determinavit	Coll.	Source
D. clavareaui	Harbin (Charbin)	45°45'N; 126°39'E	Heilongjiang (Amur-Province)	China	06.06.1954	4		det. I. Askevold	ISAC	Cong and Yu 1997
	Imianpo, Harbin (Charbin)	45°45'N; 126°39'E	Heilongjiang (Amur-Province)	China	July 1938	1	Weymarn	det. S. Cong	CASC	Cong and Yu 1997
	Guanhsien	30°08'N; 102°56'E	Szechuan (2000 – 3000 ft)	China	1930	1	D.C. Graham	vid. Cong&Yu	USNM	Cong and Yu 1997
	Nulno-ri, Papyeong-myeon, Paju-shi	37°55.23'N; 126°51.96'E	Gyeonggi-do	South Korea	06.18.2015	6	S.L. An	det. S.L. An	NSMK	An 2018
D. fukiensis	Kuatun	27°24.00'N; 117°24.00'E	Fujian (2300 m a.s.l.)	China	04.07.1938	2	J. Klapperich	det. E. Geiser 2018	NHMB	Specimen examined
	Kuatun	27°24.00'N; 117°24.00'E	Fujian (2300 m a.s.l.)	China	04.12.1938	1	J. Klapperich	det. E. Geiser 2018	NHMB	Specimen examined
	Kuatun	27°24.00'N; 117°24.00'E	Fujian (2300 m a.s.l.)	China	04.25.1938	2	J. Klapperich	det. E. Geiser 2018	NHMB	Specimen examined
	Kuatun	27°24.00'N; 117°24.00'E	Fujian (2300 m a.s.l.)	China	04.27.1938	3	J. Klapperich	(det. Goecke 1944) det E. Geiser 2018	NHMB	Paralectotypes examined
	Kuatun	27°24.00'N; 117°24.00'E	Fujian (2300 m a.s.l.)	China	05.07.1938	4	J. Klapperich	(det. Goecke 1944) det E. Geiser 2018	NHMB	Lectotype and paralectotypes examined
	Kuatun	27°24.00'N; 117°24.00'E	Fujian (2300 m a.s.l.)	China	05.11.1938	1	J. Klapperich	det. E. Geiser 2018	NHMB	Specimen examined
	Kuatun	27°24.00'N; 117°24.00'E	Fujian (2300 m a.s.l.)	China	05.24.1938	1	J. Klapperich	det. E. Geiser 2018	NHMB	Specimen examined
	Kuatun	27°24.00'N; 117°24.00'E	Fujian (2300 m a.s.l.)	China	05.07.1938	1	J. Klapperich	det. Goecke 1952 vid. E. Geiser 2017	SDEI	Specimen examined
	Huangkeng, Jiangyang	27°20'N; 118°7'E	Fujian	China	28.03.1960, 05.–12.04.1960	7	F. Pu	det. P. Yu	ASIZ	Cong and Yu 1997
	Jiangyang	27°20'N; 118°7'E	Fujian	China	–	1	F. Pu	det. I. Askevold	ISAC	Cong and Yu 1997
D. kweilina	Kweilin	25°16.92'N; 110°17.18'E	Guangxi	China	April-May 1952	47	–	det. S. Cong&Yu	ASIZ	Cong and Yu 1997
	Kweilin	25°16.92'N; 110°17.18'E	Guangxi	China	April-May 1952	2	–	det. I. Askevold	ISAC	Chen 1966, Cong and Yu 1997
D. mediohirsuta	Shishong-Baana (Xishuangbanna)	22°1.88'N, 100°50.29'E	Yunnan (1200 m a.s.l.)	China	05.15.1958	1	–	det. S. Chen; vid. Cong&Yu	ASIZ	Chen 1966, Cong and Yu 1997

Figures 1–4. **1** *Donacia fukiensis* Goecke, 1944, lectotype, male, China, Fujian, Kuatun (NHMB) **2** *D. fukiensis*, labels of lectotype **3** *D. fukiensis*, female, same data as lectotype **4** *Donacia clavareaui* Jacobson, 1906, male, China, Heilongjiang, Harbin (ZSMC). Scale bar 2 mm.

The characters of the type specimens of *D. kweilina* and *D. mediohirsuta* are analysed by the detailed first description of Chen (1966) and by further character descriptions mentioned in Cong and Yu (1997), who had examined these type specimens.

Species record list

In Table 1 all records of these four *Donacia* species known to date are listed. The specimens indicated with "det. E. Geiser" or "vid. E. Geiser" were examined.

Results

Taxonomic history

Jacobson (1906) described the species *D. clavareaui* from Kjachta (Russia) in south-east Siberia. It could be easily distinguished from all other *Donacia* species known by its pubescent pronotum combined with glabrous elytra. In the subsequent decades several *Donacia* specimens from East Asia where identified as *Donacia clavareaui*.

In the 1940s Goecke, a world-renowned Donaciinae specialist, examined specimens of *D. clavareaui* in the collection of the Museum Alexander Koenig in Bonn (Germany). He recognized that the specimens from Fujian (south-east China) were different in some characters which are typical for species limitation in *Donacia*. In 1944 Goecke published the description of the new species *D. fukiensis* which he split from *D. clavareaui*.

The description of Jacobson (1906) as well as the description of Goecke (1944) are both very detailed. However, Goecke did not describe which were the critical different characters for the distinction of *D. fukiensis* from *D. clavareaui.* He also published no identification key. Both descriptions match with both species (see Appendix 1, 2). This resulted in many misidentifications of East Asian specimens.

In 1961 Gressitt and Kimoto published their comprehensive volume "The Chrysomelidae of China and Korea". Because there were so many Chinese specimens misidentified as *D. fukiensis* they assumed that *D. clavareaui* was restricted to Siberia. Therefore their identification key contains only *D. fukiensis*. The characters they mention in their key are applicable to both species. Their key became famous and widespread. Subsequently almost all specimens of *D. clavareaui* outside Siberia were identified as *D. fukiensis* from then on.

Chen (1966) recognized that within *D. fukiensis*, some specimens have different characters. He split two new species, *D. kweilina* and *D. mediohirsuta*, off from what was actually still a mixture of the two species *D. clavareaui* and *D. fukiensis*.

In the 1980s Askevold worked on his comprehensive revision of the genus *Donacia*. He investigated the type specimen of *D. clavareaui* which has been stored in the collection of the MNHN Paris. He also intended to investigate the type specimen of *D. fukiensis* stored in the collection Goecke which was then part of the private

Coleopterea Museum Frey in Tutzing, Bavaria. Due to the special situation of the Museum Frey (see next chapter) no research on type or other specimens was possible at that time. Therefore Askevold studied series of *D. fukiensis* from Japan and China, which in fact were *D. clavareaui*. He concluded that there are no differences to the type specimen of *D. clavareaui* (he was right!) and therefore erroneously synonymized *D. fukiensis* with *D. clavareaui*. In 1990 Askevold published his comprehensive revision of the genus *Donacia* which has been widely used as a reference since.

In the 1990s Cong and Yu worked on a list of the Donaciinae of China. They recognized some differences in the specimens labelled *D. clavareaui* from Fujian as compared with specimens from other parts of China (as Goecke did more than 50 years before). Therefore they intended to study the type specimens of *D. fukiensis* from Goecke in Museum Frey. At that time, once again no loan of specimens was possible, but for a short period during the quarrels about the Frey collection it was stored at the ZSMC (see next chapter). Martin Baehr, the curator of Coleoptera section in Munich was in charge; Cong and Yu wrote to Baehr and asked him to check some critical characters at the syntype specimens of *D. fukiensis*, and Baehr confirmed these characters. Cong and Yu (1997) therefore removed *D. fukiensis* from synonymy and published the first identification key to distinguish *D. clavareaui* and *D. fukiensis;* they also included *D. kweilina* Chen, 1966 and *D. mediohirsuta* Chen, 1966. They also published accurate distribution data of these four species as far as they were substantiated.

The third volume of Water Beetles of China was published by Jäch and Ji in 2003 with Konstantinov as the author of the chapter about aquatic Chrysomelidae (Konstantinov 2003). He refers to all four species mentioned above, but he compiled their distribution data from sources where *D. clavareaui* and *D. fukiensis* were confused, and so they are not reliable.

In 2010 two very important comprehensive studies on Chrysomelidae were published: the Identification Key of Palaearctic Chrysomelidae (Warchalowski 2010) and the sixth volume of the Catalogue of Palaearctic Coleoptera which contained the Chrysomelidae in which Silfverberg was the author of the chapter on the Donaciinae (Silfverberg 2010). Both books are very useful and are the results of enormous workloads of the authors. Warchalowski is a specialist for Alticini (Galerucinae, Chrysomelidae) and Silfverberg is a specialist for Criocerinae und Galerucinae. Both wrote the Donaciinae chapter as no Donaciinae specialist was available and they both referred to the last comprehensive work on Donaciinae (Askevold 1990); therefore *D. fukiensis* is treated as a synonym to *D. clavareaui* in both volumes.

In 2015 a global checklist on Donaciinae was published (Geiser 2015), based on Silfverberg (2010) for the Palaearctic species and *D. fukiensis* is treated as a synonym to *D. clavareaui* there, also.

In 2017 I visited the collection of the SDEI in Müncheberg, Germany, which contains specimens of *D. clavareaui* and *D. fukiensis*, both identified by Goecke in 1952. I saw immediately what Goecke and Cong and Yu had seen before: that these two specimens differ in characters which are typical for separate species of Donaciinae. Fortunately the type specimens are accessible now in the NHMB and it was possible to check the characters of the seven syntypes and to finally designate a lectotype.

The Museum Georg Frey and its unusual situation from 1976 to 1997

Georg Frey (1902–1976) was the owner of a clothes-producing company ("Lodenfrey"). He had an ardent interest in beetles, and attended and paid for field trips worldwide to collect beetles; he also bought collections from specialists. Near his house in Tutzing (south of Munich, Bavaria, Germany) he established a private museum and employed up to five scientists and assistants. When the Donaciinae specialist Hans Goecke died in 1963 Georg Frey bought his famous collection containing many type specimens (Anonymous 1963, Evers 1963).

In the decades after the WWII scientific institutions like natural history museums had insufficient and often only provisional storage facilities. At the Museum Frey the Goecke collection was well maintained as Frey employed the then-Chrysomelidae specialists, Jan Bechyne and Gerhard Scherer. When Georg Frey died in 1976, a quarrel began in the Frey family. The sons of Georg Frey intended to donate the whole collection to the ZSMC, because that had been the will of their father they argued; but the widow of Georg Frey began negotiations and finally sold the whole collection to the Natural History Museum of Basel, Switzerland. This started a conflict which involved the Frey family, the Munich State collection, several Switzerland institutions, and German Government institutions. The latter declared this beetle collection a national treasure which must not be transferred outside the borders of Germany. In 1992 the widow died and the collection was clandestinely transferred to the ZSMC before the Basel Museum received information on her death. The legal dispute continued and from 1995 onwards the collection was stored in boxes in Weil am Rhein, Germany, a city near Basel at the Swiss border (Furth 1996). In 1997 it was confirmed that the Museum Basel was the legitimate owner of this beetle collection and it was then transferred there (see further details from the Basel perspective in "Käfer für Basel" [https://kaeferfuerbasel.ch/die-sammlung-georg-frey/]). These incidents were the reason that between 1976 and 1998 it was impossible for long periods to borrow specimens and even to visit the collection to examine it in situ.

Character analysis of *Donacia clavareaui* and *Donacia fukiensis*

Jacobson (1906) described *D. clavareaui* in Latin and Goecke (1944) described *D. fukiensis* in German, both languages being widely used in science at the time. For traceability the original descriptions and their translations are shown in Appendix 1, 2.

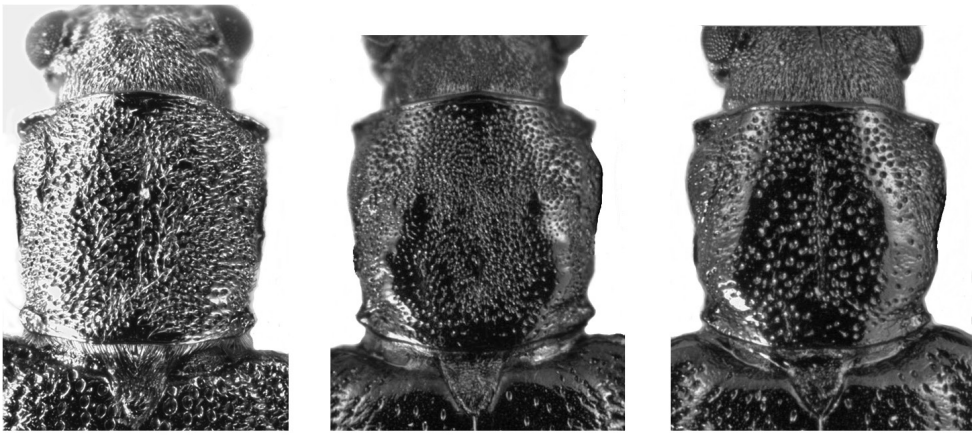
The head, antennae, legs, and pronota are very similar, but their elytra are strikingly different. The main character differences are

- Shape of the contour of the elytra
- Punctures of the elytra
- Elytral epipleura
- Elytral apex
- Female: last sternite
- Male: aedeagus

Table 2. Common and different characters of *Donacia clavareaui* and *Donacia fukiensis*. Each character was based on specimens indicated in Table 1.

	D. clavareaui	*D. fukiensis*
General	Medium sized, pitchy brown, dark bronze, shiny, antennae and legs partially reddish, hind femora don't reach the apex of the elytra, hind femora claviform with acute tooth, pronotal disc with very fine hairs, elytra glabrous	
Body		
Shape	Habitus like typical *Donacia* (Fig. 4)	Habitus resembles *Plateumaris* (Fig. 1)
Sex difference	Males in general more slender and shorter than the females	
Colour	Dark metallic-bronze, greenish-bronze, metallic-cupreous	Shiny bronze
Colour of antennae and legs	Antennae and legs partially yellow, reddish or brown, the extent of the colour is very variable within specimens	
Ventral	Ventral hairs as usual on *Donacia*, density variable, the colour of the hairs depends on the lighting	
Size	♂ 6.5- 8.0 mm (avg: 7.5), ♀ 8.0-9.0 mm (avg: 8.5)	
Head		
Antennae lenght	Filiform, slender, almost half as long as the length of the body, in some male specimens reaching farther than the middle of the elytra	
Antennomeres	A2+A3 ≈ A1 ≈ A4 ≈ A5; A2 < A3	
	The length relations of the single segments to each other are quite variable. The basal parts of the antennomeres are rufous or yellow, the apical parts are dark and sometimes metallic, the ratio between the two colour parts shows a great variation among the specimens	
Antennal tubercles	The antennal tubercles are flattened, with a narrow groove between them	
Head disc	Head disc straight at front with a deep middle groove	
Calli	Calli indistinct, some specimens without calli	
Frons and eyes	Eyes wide apart, the frons width is four times the measured value of the eye width, with no difference between male and female specimens	
Pronotum		
Surface	Pronotum pubescent, with very fine hairs, on some specimens very difficult to be seen	
Surface	Pronotum finely and densely punctured (Fig. 5)	Irregularly punctured, in between the punctures shiny. Often the punctures are more dense in the anterior and posterior part than in the middle part. Density of the punctures shows a great variation between individual specimens (Fig. 6, 7)
Shape	Almost quadratic, in some male specimens slightly longer than wide, in some female specimens wider than long. Anterior margin slightly convex, anterior angles well developed, anterior tubercles rather flat, only slightly protruding	
Scutellum	Scutellum with thin and short hairs	
Elytra		
Shape	Typically *Donacia*-shaped	Rather *Plateumaris*-shaped
General features	Approx. twice as long as wide, in most male specimens slightly longer than double width (ratio 2.1), in most female specimens slightly shorter (ratio 1.9) glabrous and shiny	
Impressions	Slightly visible only on some specimens	
Punctures and intervals	Punctures strong and deep, intervals distincly wrinkled (Fig. 8) interval ≈ 1x – 3x puncture diameter	Punctures very delicate, not deep, intervals only slightly wrinkled, very smooth (Fig. 9) interval ≈ 4x – 7x puncture diameter
Epipleura	Elytral epipleura approx. as wide or wider than 10th interval (Fig. 10) Epipleuron : Interval = 1 : (>) 1	Elytral epipleura narrower than 10th interval (Fig. 11) Epipleuron : Interval = 1 : (1.5 – 2)
Apex	Elytral apex truncated, the external angle slightly rounded (Fig. 12)	Elytral apex indistinctly truncated, evenly and widely rounded with very smooth outer and inner angles (Fig. 13)
Abdomen		
Pygidium	Distinctly arcuately emarginate	Truncated and slightly recessed in the middle
Male last sternite	Apex rectangularly truncated and triangularly impressed	Slightly impressed at the apical ridge
Female last sternite	Basic contour distinctive triangular (Fig. 14)	Basic contour convex without a distinctive peak and broadly rounded (Fig. 15)

	D. clavareaui	*D. fukiensis*
Legs		
General	Strong legs, all femora clavate, especially at the ♂, at the ♀ mostly more slender, hind femora short, even at the ♂ they don't reach the apex of the elytra by far. Posterior femora with a prominent tooth, which is often broader at the ♂, at the ♀ more slender and more acute. Legs partly reddish, some specimens with completely red anterior tibia, some specimens with rather dark legs	
Anterior Tibia	Anterior tibia shows a protruding tooth towards outward at the insertion of the tarsomere. *D. fukiensis*: Fig. 18	
	D. clavareaui: Fig. 4 and https://science.mnhn.fr/institution/mnhn/collection/ec/item/ec2130?listIndex=1&listCount=6 [26.11.2018]	
	It is clearly visible on most specimens, but on some indistinctly	
Tarsomeres	The 1st and 3rd tarsomere have approx. the same length, the 2nd one is by a third shorter	
Aedeagus		
Shape	Aedeagus very straight, outer contours in frontal view rather parallel. Median lobe distinctly protruding: Fig. 19, 20, 21	Aedeagus more curved, thickened, narrowed towards the apex. Median lobe slightly protruding: Fig. 22, 23, 24



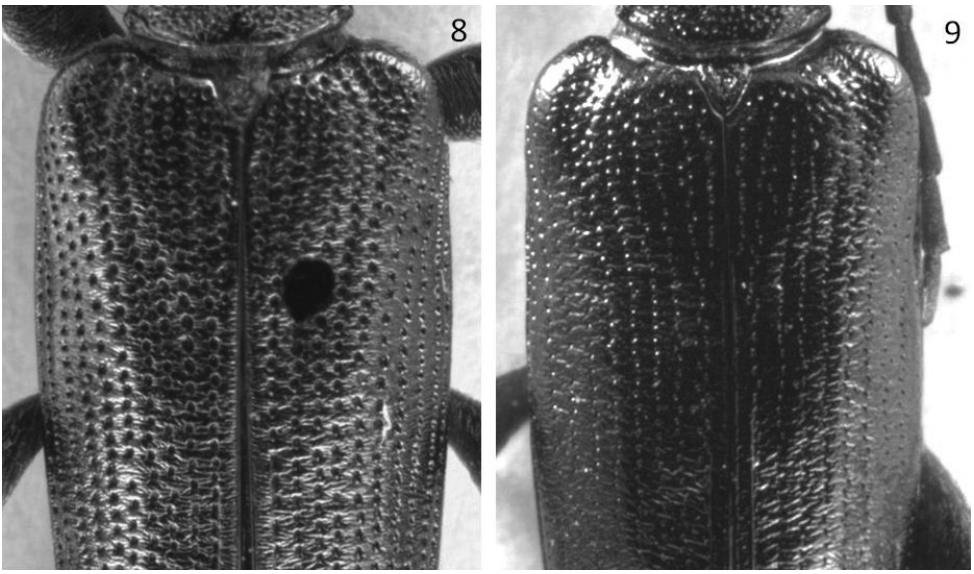
5 6 7

Figures 5–7. 5 *Donacia clavareaui*, Pronotum **6** *D. fukiensis*, Pronotum densely punctured **7** *D. fukiensis*, Pronotum irregularly punctured.

All these character differences are typical for species in the genus *Donacia*. There are some well-established species in *Donacia* which differ in much more subtle characters. Therefore it was correct that Cong and Yu (1997) re-established *D. fukiensis* as a valid species. Now that the type series of Goecke is available to scientists, I was able to designate a lectotype from the seven syntypes on which the description of Goecke had been based (Fig. 1).

Character analysis of *Donacia kweilina*

Chen (1966) described *D. kweilina* and *D. mediohirsuta* which he separated from the mixture of *D. fukiensis* and *D. clavareaui*. The common character of these four taxa is the pubescent pronotum combined with glabrous elytra. The first description is published



Figures 8, 9. Elytral punctures. **8** *Donacia clavareaui* **9** *D. fukiensis.*

in Chinese and in English. For practical considerations only the English text is shown in Appendix 3 (for *D. kweilina*) and Appendix 4 (for *D. mediohirsuta*). *Donacia kweilina* is known only from the type series (Cong and Yu 1997). No further records are known.

In Table 3 the characters of *D. kweilina* are listed according to the original description by Chen (1966) and provided by Cong and Yu (1997), who examined the type specimens. My comments result from the examination of specimens of *D. clavareaui*.

The characters which should distinguish *D. kweilina* from *D. clavareaui* are either the same or within the variations range of *D. clavareaui*. Therefore *D. kweilina* is a synonym of *D. clavareaui*.

Character analysis of *Donacia mediohirsuta*

Donacia mediohirsuta is known only by the type specimen, a single female specimen from Yunnan, Shishong-Baana (Cong and Yu 1997). No further records are known. In Table 4 the characters of *D. mediohirsuta* are listed according to the original description by Chen (1966) and supplemented by Cong and Yu (1997), who have examined the type specimen.

According to Cong and Yu (1997) this specimen resembles *D. kweilina* with only minor morphological differences. As shown in Table 4 the characters are identical or within the range of *D. clavareaui*. Therefore *D. mediohirsuta* is also a synonym of *D. clavareaui*.

Table 3. Characters of *Donacia kweilina*.

Characters of *D. kweilina*	Comments
Colour aeneo-cupreous (♂, ♀) sometimes sky-blue (♂)	*D. clavareaui* is also aeneo-cupreous, sometimes blue males occur in Donaciinae species
Antennae and legs entirely deep coloured, not partly rufous	This occurs also in other *Donacia* species where most of the specimens have partially rufous antennae and legs; colour also very variable in *D. clavareaui*
Antennae: third segment slightly longer than second and distinctly shorter than fourth	same proportions of antennomeres in *D. clavareaui*
Head with four weak tubercles, the median longitudinal furrow deep and complete. Pronotum more thickly pubescent, very closely punctured, and covered with silvery hairs, the antero-lateral tubercles distinct, the angles fairly strongly produced. Elytra rather smooth on inner disc, the punctures oblong, the interstices broad, approx. 2–3 times as broad as the cross diameter of the punctures. Apex truncate with the outer angles broadly rounded.	All these characters can be clearly seen at the holotype specimen of *D. clavareaui*
Elytral epipleuron narrow and divided from outermost interval by sharp ridge throughout the entire length of elytra	This character is also clearly shown at *D. clavareaui* (Fig. 10)
Last abdominal segment of ♀ much longer and somewhat triangular in shape (Fig. 16)	Same typical shape as *D. clavareaui* (Fig. 14)
Hind femora (♂, ♀) broadly toothed beneath, the femora of ♂ not distinctly thicker than those of ♀	Same as *D. clavareaui*, thickness of hind femora variable
Aedeagus: Apex of median lobe cordiform (Cong and Yu 1997)	Cong and Yu (1997) refer to the same figure which shows the aedeagus of *D. clavareaui* (Fig. 19)
Length: 8 mm	Length of *D. clavareaui*: 6.5–9.0 mm

Table 4. Characters of *Donacia mediohirsuta*.

Characters of *D. mediohirsuta*	Comments
General colour cupreous	Same colour as *D. clavareaui*
Antennae with the terminal segments rufo-piceous, 3–5 segments partly rufous and partly piceous	Same as *D. clavareaui*
Third antennae segment distinctly longer than the second one, but slightly shorter than the fourth one	Same as *D. clavareaui*
Pronotum more transversal	In *D. clavareaui* the pronotum is as long as wide or slightly longer than wide; female specimens of *Donacia* sp. sometimes have a slightly broader pronotum
Pronotum finely pubescent only on the median groove	Pronotum pubescence varies in *D. clavareaui*
The longitudinal furrow of interocular area much deeper, extending uninterrupted to between the supra-antennal tubercles	These characters are distinctly visible at the holotype specimen of *D. clavareaui*
Anterior tibiae scarcely produced at apex	Variable; the protruded angle of the anterior tibia is mostly distinct, but in some specimens difficult to recognize
Hind femora (♀) very weekly toothed beneath	Variable in *Donacia* sp., especially female specimens have weak teeth in comparison with male specimens
Last abdominal sternite (♀) more strongly angulate at apex (Fig. 17)	Same typical shape as *D. clavareaui* (Fig. 14)
Length ♀: 8 mm	Length of *D. clavareaui* ♀: 8.0-9.0 mm

Identification key

1 Pronotum with fine hairs on the disc (sometimes difficult to be seen, often more than 10 times magnification is necessary and lighting from different directions), elytra glabrous **2**

– Either pronotum and elytra are glabrous or both are pubescent .... **other *Donacia* spp.**

2 Specimen from Nearctic region ..... ***D. hirticollis* Kirby, 1837**

– Specimen from Palaearctic region **3**

3 Pronotum shape trapezoid, conical, anterior margin shorter than the posterior one, in male pronotum glabrous, here female only .... ***D. kraatzi* Weise, 1881**

– Pronotum shape rectangular, anterior margin wider than or as wide as the posterior one **4**

4 Pronotum as well as basal portion of elytra thickly covered with curved yellowish silver hairs, distal end of anterior tibia not produced laterally..... ..... ***D. hirtihumeralis* Komiya & Kubota, 1987**

– Pronotum covered with fine hairs, on elytra there are few hairs on the vertical surface anterior to humeral callus, distal end of anterior tibia produced laterally **5**

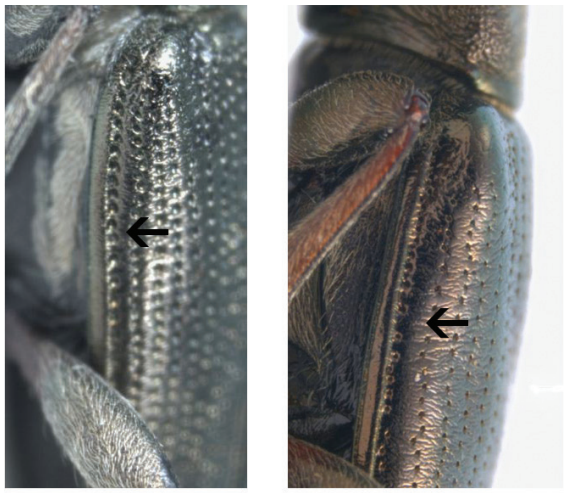
5 Punctures on elytra rather strong, intervals one to two (sometimes three) times as wide as the diameter of the punctures, elytral epipleuron approx. as wide or wider than 10th interval, elytral apex truncate (Fig. 12), the angles slightly rounded, female last sternite broadly triangular with posterior margin projected (Fig. 14), aedeagus rather straight and the median lobe cordiform with apex abruptly pointed (Figs 19, 20, 21) .... ***D. clavareaui* Jacobson, 1906**

– Punctures on elytra rather fine, intervals three to seven times as wide as the diameter of the punctures, elytral epipleuron less wide (ca. ½ or ¾ of width) than 10th interval, elytral apex rounded (Fig. 13), female last sternite broadly rounded (Fig. 15), aedeagus curved and the median lobe with slightly protruding apex (Figs 22, 23, 24) ..... ***D. fukiensis* Goecke, 1944**

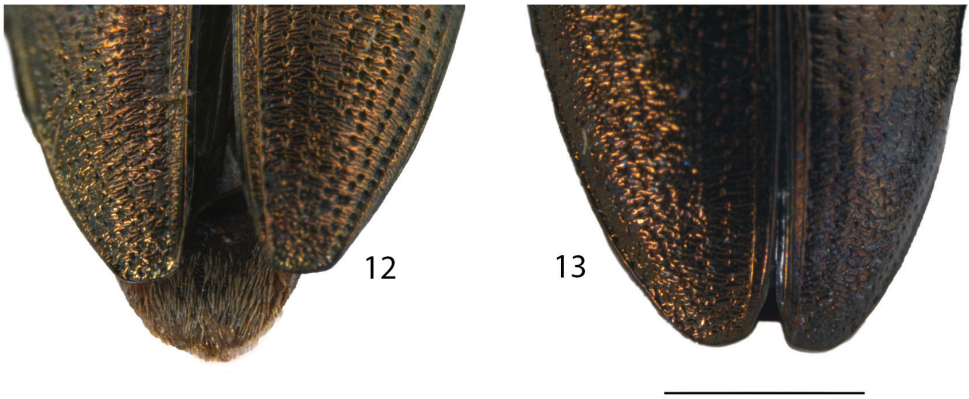
Distribution

Due to the taxonomic problems there are only few reliable records, listed in Table 1.

The known distribution of *D. clavareaui* is shown in Figure 25. Some dots represent more than one record and several nearby locations. The former *D. kweilina* and *D. mediohirsuta*, now synonymized with *D. clavareaui*, are shown by different coloured dots. The red dot represents the locations of *D. fukiensis*. No record of this species outside of Fujian is known. According to Fig. 25 *D. clavareaui* occurs south of 50° latitude



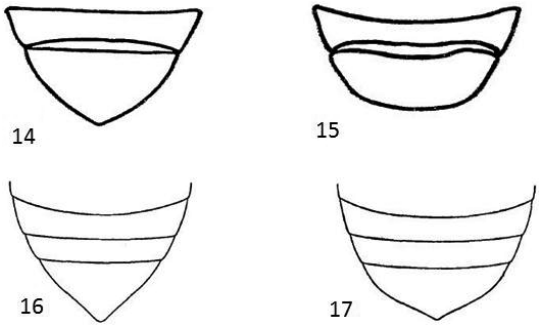
Figures 10, 11. Elytral epipleuron. **10** *Donacia clavareaui*, 10th interval narrower than epipleuron **11** *D. fukiensis*, 10th interval broader than epipleuron.



Figures 12, 13. Elytral Apex. **12** *Donacia clavareaui* **13** *D. fukiensis.* Scale bar: 1 mm.

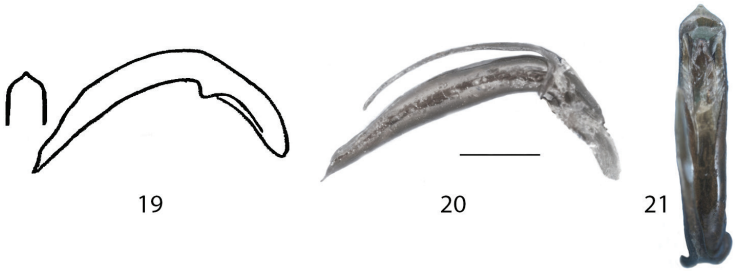
and east of 100° longitude. It is obvious that *D. clavareaui* must occur in many more locations than those shown in Fig. 25.

Donacia specimens are difficult to collect. The adults can be caught only during a period of a few weeks in late spring and early summer. This period shifts every year due to local weather conditions. Most rare species are found within groups of many specimens of other similar looking, more common *Donacia* species, and they are therefore often overlooked.



Figures 14–17. Female last sternite. **14** *Donacia clavareaui* **15** *D. fukiensis* **16** *Donacia kweilina* **17** *D. mediohirsuta* (Figs 14, 15 original drawings from Cong and Yu 1997, Figs 16, 17 original drawings from Chen 1966).

Figures 18. Anterior tibia: the protruding tooth towards outward at the insertion of the tarsomere is a common character of *Donacia clavareaui* and *D. fukiensis* (original drawing from Goecke 1944).



Figures 19–21. 19 *Donacia clavareaui* and *D. kweilina*, aedeagus (Original drawings from Cong and Yu 1997) **20** *D. clavareaui*, aedeagus, lateral **21** *D. clavareaui*, aedeagus, frontal. Scale bar: 0.5 mm.

Figures 22–24. 22 *Donacia fukiensis*, aedeagus (Original drawings from Cong and Yu 1997) **23** *D. fukiensis*, aedeagus, lateral **24** *D. fukiensis*, Aedeagus, frontal. Scale bar: 0.5 mm.

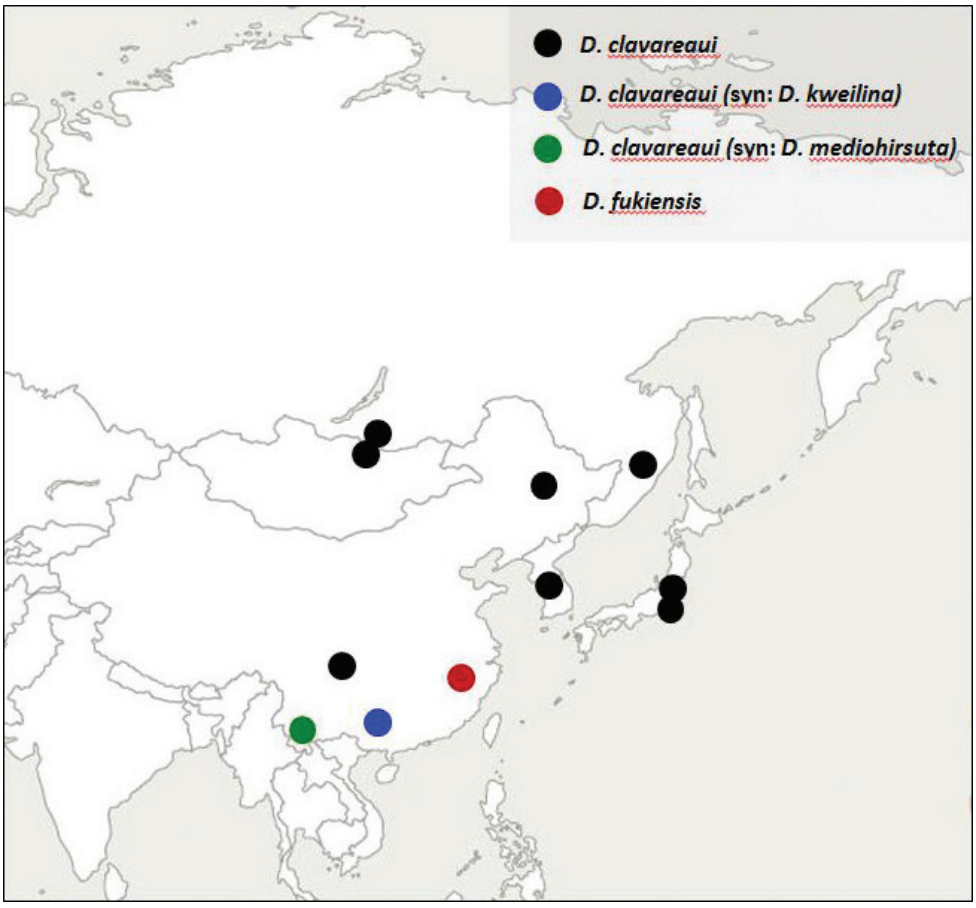


Figure 25. Distribution of records of the East Palaearctic species *Donacia clavareaui* and *D. fukiensis*.

Ecology

All Donaciinae species develop and feed on plants associated with water. As far as the food plants are known, *Donacia* species are monophagous or oligophagous. Some adults feed on pollen, mostly on Cyperaceae (Kleinschmidt and Kölsch 2011). The larvae live attached to the roots in the sediment. They breathe by piercing the aerenchyme of their food plant with two hollow abdominal stilettos, which are connected to their tracheal system.

The larva of *D. clavareaui* has been described by Narita (1991, 2003). The specimens were collected from roots of the Cyperaceae species *Scirpus fluviatilis* (Torr.) in Ibariki-ken in Honshu, Japan. According to Bienkowski (2014) *D. clavareaui* also feeds on *Isolepis fluitans* (L.) R.Br. (syn. *Scirpus fluitans*). An (2018) collected *D. clavareaui* in Korea on *Scirpus maritimus* L. The food plants of *D. fukiensis*, *D. kweilina*, and *D. mediohirsuta* are unknown.

Discussion

If specimens of *D. clavareaui* and *D. fukiensis* are compared directly, the differences are striking, especially of the elytra. Although the first descriptions of these species are comprehensive and detailed, they both described both species. Furthermore, it was not possible to create a reliable identification key without correctly identified specimens to hand. This created a vicious circle and caused decades of misidentifications, as well as the splitting of new species from a conglomerate of what was in fact two species. The situation was worsened by the inaccessibility of the type series of *D. fukiensis* in the Frey collection for a long period.

If specimens are identified incorrectly, all further studies on ecology and distribution are useless. In Figure 25 only reliable data of correctly identified specimens are used. In fact, it shows more the serendipity of the collectors than the reality of the distribution, but this is always the case within rare species. There are certainly more specimens stored in collections throughout the world, but they need to be examined and re-identified in light of the current classification as they may have been mistaken for other *Donacia* species. *Donacia fukiensis* may be also hidden within specimens of *Plateumaris*.

It is also very difficult to infer the distribution of *D. clavareaui* from its food plant. According to GBIF [https://www.gbif.org/species/2718286; 24.10.2018] *Scirpus fluviatilis* occurs outside of North America only in Japan and Korea and some spots on the east coast of Australia. The data provided by KewScience [https://wcsp.science.kew.org/namedetail.do?name_id=221898; 24.10.2018] indicate further records from New Zealand, but no records in Asia; GBIF shows only one record of *Isolepis fluitans* from Ceylon. *Scirpus maritimus* is widespread, but there is only one record from China and none from Russia. It is very likely that *D. clavareaui* feeds on *Scirpus* sp. sensu lato.

Although both species are rare, I hope this paper will trigger some interest to examine the fauna more carefully during field trips in this area. If recent sample sites are known, it would be possible to find the food plant and larvae of *D. fukiensis* and to analyse the DNA of both species, to include them in the phylogenetic tree published by Kölsch and Pedersen (2008). Because the development of a pubescent upper side occurred several times in the evolution of the genus *Donacia* it is likely that they are not closely related.

Acknowledgements

As this work shows the importance of accessible and well-maintained museum collections, I am happy to thank these colleagues for their support during my research in their collections: Matthias Borer, Eva Sprecher, Christoph Germann, and Isabelle Zürcher (NHMB), Thomas Schmitt and Konstantin Nadein (SDEI), Manfred Jäch, Helena Shaverdo, and Wolfgang Schönleithner (NHMW), Michael und Ditta Balke (ZSMC). Wolfgang Brunnbauer (NHMW) and Jan Bezdek (Mendel University Brno, Czech Republik) supported me during my literature research, and the latter provided

some good advice as a reviewer. Martin Baehr (ZSMC) and Michael Theo Schmitt (Ernst-Moritz-Arndt University Greifswald, Germany) provided useful information about the G Frey and J Klapperich collections. Furthermore, I would like to thank Michaela Brojer, Harald Bruckner (both NHMW), and Remigius Geiser jun. (Vienna, Austria) for their support with the photographs and image processing. Remigius Geiser sen. (Salzburg, Austria) translated the Latin text of Jacobson (1906) into German and helped to identify locations in China. I would like to thank him also for correcting the manuscript and helpful discussions. I also benefitted from the helpful advice of the reviewer Horst Kippenberg (Herzogenaurach, Germany).

References

An SL (2018) Two new records of the subfamily Donaciinae (Coleoptera, Chrysomelidae) from Korea. Journal of Asia-Pacific Biodiversity. https://doi.org/10.1016/j.japb.2018.11.005 [21.01.2019]

Anonymous (1963) Hans Goecke †. Entomologische Arbeiten Museum G. Frey 14: 695.

Askevold IS (1990) Reconstructed phylogeny and reclassification of the genera of Donaciinae (Coleoptera: Chrysomelidae). Quaestiones Entomologicae 26(4): 600–664.

Bienkowski AO (2014) Reed-Beetles (Coleoptera: Chrysomelidae: Donaciinae) [Russian]. Livny: Publishing Company Mukhametov GV, 380 pp.

Borowiec L (1984) Zoogeographical study on Donaciinae of the world (Coleoptera, Chrysomelidae). Polskie Pismo Entomologiczne 53: 433–518.

Chen SH (1966) Notes on Chinese Donaciinae. Acta Entomologica Sinica 15: 137–147.

Cong S, Yu P (1997) The identity and distribution of *Donacia fukiensis* Goecke with notes on three related species from China (Coleopterea: Chrysomelidae: Donaciinae). The Coleopterologist's Bulletin 51(3): 203–207.

Evers A (1963) Hans Goecke 1892 – 1963. Entomologische Blätter 59: 65–68. http://www.koleopterologie.de/arbeitsgemeinschaft/historie/biografien/gruender/goecke.html [09.10.2018]

Furth D (1996) Visits to the Bavarian State Collection (Munich) and Frey Collection (Weil am Rhein). Chrysomela Newletter 32. https://www.coleopsoc.org/chrys/chryso32/index.htm

GBIF (2018) Scirpus fluviatilis. https://www.gbif.org/species/2718286 [24.10.2018]

Geiser E (2015) World checklist of freshwater Coleoptera: Chrysomelidae – Donaciinae species. Freshwater Animal Diversity Assessment (FADA). World Wide Web electronic publication. http://fada.biodiversity.be/group/show/65

Goecke H (1944) Revision asiatischer Donaciinen (Col. Chrys.). III. Entomologische Blätter 40: 7–14.

Gressitt JL , Kimoto S (1961) The Chrysomelidae (Coleoptera) of China and Korea, Part 1. Pacific Insects Monograph 1A: 1–299.

Hayashi M, Shiyake S (2004) A Check-list of the Japanese Members of Donaciinae (Coleoptera: Chrysomelidae). Entomological Review of Japan 59(1): 113–125.

Jacobson G (1906) *Donacia clavareaui* spec. nova. Annales de la Société Entomologique de Belgique 50: 311–312.

Käfer für Basel (2018) Wie Basel zur Sammlung Frey kam. https://kaeferfuerbasel.ch/die-sammlung-georg-frey/ [04–09–2018]

Kleinschmidt B, Kölsch G (2011) Adopting Bacteria in Order to Adapt to Water – How Reed Beetles Colonized the Wetlands (Coleoptera, Chrysomelidae, Donaciinae). Insects 2: 540–554. https://doi.org/10.3390/insects2040540

Kölsch G, Pedersen BV (2008) Molecular phylogeny of reed beetles (Col., Chrysomelidae, Donaciinae); The signature of ecological specialization and geographical isolation. Molecular Phylogenetics and Evolution 48: 936–952. https://doi.org/10.1016/j.ympev.2008.05.035

Konstantinov AS (2003) Chrysomelidae. Aquatic leaf beetles of China (Coleoptera). In: Jäch, Ji (Eds) Water Beetles of China3: 563 – 572.

Narita Y (1991) Description of the Larva of *Donacia clavareaui* (Coleoptera, Chrysomelidae). Elytra, Tokyo 19(1): 21–23.

Narita Y (2003) Descriptions of Donaciine Larvae (Coleoptera, Chrysomelidae) from Japan. Elytra, Tokyo 31(1): 1–30.

Silfverberg H (2010) Donaciinae. In Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera, vol. 6. Apollo Books, Stenstrup, 354–368.

Warchalowski A (2010) The Palaearctic Chrysomelidae – Identification Keys. Natura Optima Dux Foundation, Warszawa, 1212 pp. https://doi.org/10.1649/072.065.0210

Appendix 1

Donacia clavareaui **Jacobson, 1906.** Original description in Latin and translation into English. The Latin text from Jacobson (1906) was translated in German by Remigius Geiser sen. The English translation results from this translated German text.

Character	Latin	English
General	Forma corporis coloreque superficiei supernae *D. bactrianam* Weise turcestanicam et *D. Koenigi* m. caucasiam admonet, in systemate generis autem solum prope *D. intermediam* m. collocanda (**1**);	Owing to shape and surface colour as to be seen on the upper side it looks like *D. bactriana* Weise from Turkestan and like my *D. Koenigi* from the Caucasus, but in the system of the genus has to be placed near my *D. intermedia* only (**1**);
	(**1**) Cf. Opusculum meum in Ann. Mus. Zool. St.-Pétersb., V, 1899, pp. 4 et 7. Quam speciem novam prope *D. cineream* Herbst, *tomentosam* Ahr., *Kraatzi* Weise et *microcephalam* J. Daniel non pono, quod hae species pilositatem superficiei supernae talemcunque habent, ac pilositatem superficiei infernae.	(**1**) Compare my article in Ann. Mus. Zool. St.-Pétersburg, V, 1899, pp 4 and 7. This new species I don't put near *D. cinerea* Herbst, *tomentosa* Ahr., *Kraatzi* Weise and *microcephala* J Daniel, because the surface of these species is as pubescent on the upper side as it is on the underside.
	nam ab omnibus speciebus, quae femora dentata habent, pronoto hirto tibiisque rufis unicoloribus facillime distinguenda;	because it can be easily distinguished from all other species with teeth on the femora by the pubescent pronotum and the uniformly coloured red tibiae;
	inter ceteras species pedibus antennisque rufovariegatis ornatas femoribus omnibus fortiter incrassatis posticisque dente sat valido atque acuto armatis agnoscitur. – ♂.	it is recognizable among the other species which are decorated with red patterned legs and antennae by the heavily thickened femora at each leg and the rather prominent and acute tooth on the hind femora. – ♂.
	Sat elongata, nitidula, subtus ut in *D. thalassina* Germ. dense flavaureo-pubescens [solum in prothoracis epipleuris pubescentia densa minus expansa, partem inferiorem occupante],	Quite longish, feebly shiny, underside with dense golden hairs as on *D. thalassina* Germ. [only at the epipleura of the prothorax the dense pubescence less spread and occupying the lower part],

Character	**Latin**	**English**
General	aeneo-cuprea, antennarum *articulis omnibus* (apicalibus majore parte) basi, palpis omnino, mandibularum apice, labri margine apicali, trochanteribus, femorum triente basali ipsoque apice, tibiis omnibus tarsisque fere omnibus [superne nonnihil infuscatis] rufis.	metallic-cupreous, rufous are the basal parts of *all* antennae *segments* ([and] the major part of the apical ones), the whole palpae, the apical part of the mandibles, the apical margin of the labrum, the trochanters, the basal third and the end part of the femora, all tibiae and almost all [on the upper part slightly brownish] tarsomeres.
Head	Caput oculis sat magnis valdeque prominentibus;	The head with quite large and very protruding eyes;
	temporibus dense scopariis;	the tempora with dense, brush-like hairs;
	canaliculo mediano profundo latoque;	*the middle groove deep and broad;*
	tuberculis frontalibus indistinctis.	*the frontal calli indistinct.*
Antennae	Antennae dimidiam corporis longitudinem attingentes, tenues, articulo 2° tertio in ¼ breviore, art. 4° quinto vix perspicue breviore.	The antennae half as long as the length of the body, slender, the 2nd segment by a quarter shorter than the third one, the 4th one almost unrecognizably shorter than the fifth one.
Pronotum	Pronotum sericeum, latitudine aequilongum, postrorsum distincte subrectilineatim angustatum, medio nonnihil constrictum, callis lateralibus vix discretis, angulis anticis nonnihil incrassatis, sed extrorsum parum eminentibus;	Pronotum silky, as long as broad, towards the rear part distinctly almost rectangularly constricted, in the middle part slightly narrowed, lateral tubercles indistinct, anterior angles slightly thickened, but protruding only a little bit;
	canaliculo mediano haud profundo, solum medio distincto, antice posticeque omnino evanescente;	middle groove non deep, distinct only in the middle part, towards the front and backwards dissolving;
	disco nec profonde [sic!], nec fortiter punctato, *punctis omnibus piliferis*, medio majoribus sparsisque, antice posticeque minutis confertisque;	the disc punctured neither deeply nor strongly, *all punctures with hairs*, in the middle part larger and scattered, at the front and backwards small and dense;
	pilis semierectis, pallidis;	the hairs *half-erect*, pale;
	interspatiis puncturum [sic!] dense inaequaliterque rugulosis;	intervals between the punctures densely and irregularly wrinkled;
	rugulis irregularibus; proëpipleuris densissime irregulariter rugulosis ac punctulatis, subopacis, sparsim pilosulis.	wrinkles irregular; the pro-epipleura very densely irregularly wrinkled and finely punctured, almost matt, with scattered small hairs.
Scutellum	Scutellum dense ruguloso punctulatum atque tenuiter breviterque pubescens.	Scutellum dense wrinkly finely punctured and with thin and short hairs.
Elytra	Elytra quadrante basali subparallela, dein ad apicem gradatim rotundato-angustata, apice rectissime truncata, angulo exteriore parum rotundato;	The elytra in the basal quarter almost parallel, then toward the apex gradually roundly narrowed, the apex exactly rectangularly truncated, external angle slightly rounded;
	impressionibus, punctura et sculptura interspatiorum eadem ut in *bactriana*, solum interstitio primo postice rugulis transversis minus copiosis, minus expressis minusque regularibus.	impressions, puncture and texture of the intervals the same as with *bactriana*, only the first interval apically with fewer, lesser distinct and lesser regular transverse wrinkles.
Meta-sternum	Metasternum medio late excavatum (♂).	Metasternum with a broad hollow in the middle (♂).
Abdomen	Abdomen segmento primo medio longitudinaliter late impresso, segmento ultimo apice recte truncato et triangulariter impresso (♂).	The first segment of the abdomen in the middle longwise broadly impressed, the apex of the last segment rectangularly truncated and triangularly impressed (♂).
Pygidium	Pygidium distincte arcuato-emarginatum.	Pygidium distinctly arcuately emarginate.
Legs	Pedes fortes, femoribus omnibus incrassatis, posticis dente sat valido acutoque armatis deinque nonnihil crenulatis;	Strong legs, all femora thickened, the hind ones armed with a quite prominent and acute tooth and afterwards slightly notched;
	elytrorum apicem non attingentibus;	not reaching the apex of the elytra;
	tibiis posticis flexuosis, trientis primi apice vix inflato, absque crenulis.	hind tibiae curved, scarcely broadened at the end of the first third, without notches.
Size	Long. 8 mill.; lat. 2,6 mill. Habitat Provinciae Transbaicalicae urbem Kjachta in Sibira orientali (coll. Clavareau).	Length 8 mm; width 2.6 mm. Inhabits the town of Kjachta in the province of Transbaicalia in eastern Siberia (coll. Clavareau).

Appendix 2

***Donacia fukiensis* Goecke, 1944.** Original description in German and translation into English.

Character	German	English
General	Mittelgroße einheitlich dunkelbronzefarbige glänzende Tiere mit äußerst fein behaartem Halsschild, die ♂♂ schlanker und kleiner als die ♀♀, deren Schenkel viel weniger keulig verdickt und deren 1. Hinterleibssegment nicht abgeplattet ist. Die Tiere sind im Habitus sehr einheitlich, in der Ausbildung der einzelnen Merkmale sehr variabel.	Medium sized uniform dark bronzy shiny animals with an extremelyfinely pubescent pronotum, the males more slender and shorter than the females, which have a much lesser clubbed thickened femur and their 1st abdominal segment is not flattened. The animals' habitus is very uniform, the formation of the single characters is very variable.
Head	**Oberkiefer** überragt die Oberlippe um etwas mehr als deren Länge, pechbraun, Kiefertaster gelb, bei einigen Stücken das letzte Glied an der Spitze braun.	**Mandibula** overlaps the labrum a bit more than its length, pitchy brown, maxillary palps yellow, at some specimens the last segment brown at the apex.
	Oberlippe etwa 2mal so breit wie lang, Vorderrand schwach konvex abgerundet, hinterer Rand mit langen Borsten, die bis über den Vorderrand ragen, Vorderrand mit kürzeren Borsten, dazwischen unbehaart.	**Labrum** ca. twice as broad as long, front margin slightly convexly rounded, basal margin with long setae, reaching beyond the front margin, front margin with shorter setae, in between without setae.
	Kopfschild vorn gerade, 2mal so breit wie die Seitenkante lang.	**Head plate** straight at front, twice as broad as the length of the side margin.
Anten-nae	Die **Fühler** sind fadenförmig, nicht sehr lang, ihr Ende überragt beim ♂ die Mitte der Flügeldecke, beim ♀ sind sie erheblich kürzer. 2. Glied am kürzesten, etwa halb so lang wie das 1., das 3. um 1/5 bis um die Hälfte länger als das 2., das 4. 1 ½ fach bis doppelt so lang als das zweite. Die einzelnen Glieder in ihrer Länge zueinander recht variabel. Fühlerglieder gelb bis dunkelbraun. 1. - 6. Glied mäßig dicht, 7. – 11. dichter behaart.	The **antennae** are filiform, not very long, in males reaching farer than the middle of the elytra, in females they are significantly shorter. 2nd segment the shortest, about half as long as the 1st one, the 3rd one about one fifth to one half longer than the 2nd one, the 4th one is one and a half times to double the length of the second one. The length relations of the single segments are quite variable to each other. Antennomeres yellow to dark brown. The 1st to 6th one with moderately dense hairs, the 7th to 11th one with more densely packed hairs.
	Die **Fühlerhöcker** sind abgeplattet, dazwischen befindet sich eine schmale Furche, die Abplattung ist mehr oder weniger glänzend, fast ohne Punkte oder mäßig dicht punktiert, dahinter befindet sich eine mehr oder weniger deutliche Vertiefung, die gegen die Fühlerhöcker durch eine querliegende Kante abgesetzt ist. Die Stirnhöcker sind ziemlich flach und breit. Äußere Gruben flacher oder tiefer, innere Gruben schwach entwickelt.	The **antennal tubercles** are flattened, with a narrow groove between them, the flattened part is more or less shiny, almost without punctures or moderately densely punctured, behind it there is a more or less distinct depression, which is separated against the antennal tubercles by a transverse ridge. The calli are quite flattened and broad. Outer grooves more flattened or deeper, inner grooves shallow.
	Stirn mäßig dicht punktiert und behaart, glänzend.	**Frons** moderately densely punctured and pubescent, shiny.
	Hals hinter den Augen kaum verengt, **Schläfen** schwach entwickelt.	**Neck** scarcely narrowed behind the eyes, temples indistinct.
	Augen klein, weit auseinanderstehend.	**Eyes** small, wide apart.
Pro-notum	**Halsschild** an den vorderen Seitenhöckern am breitesten und etwa so breit wie in der Mitte lang. Bei einem Exemplar war das Halsschild allerdings erheblich länger.	Broadest part of the **pronotum** at the anterolateral tubercles and approximately as broad as its length in the midst. However the pronotum of one specimen was considerably longer.
	Die **Vorderecken** sind gut entwickelt, sie ragen aber weder über den Vorderrand noch über die Seitenhöcker vor.	The **anterior angles** are well developed, but neither protruding beyond the anterior margin nor the lateral tubercles.
	Vorderrand leicht konvex, gegen die Scheibe nicht, oder durch eine feine, oft unregelmäßige Linie abgesetzt.	**Anterior margin** slightly convex, not distinctly separated against the disc, or by a subtle, often irregular line.
	Hinterecken mehr oder weniger gut entwickelt, wenig vorragend.	**Posterior angles** more or less well developed, scarcely protruding.
	Hinterrand stark konvex, gegen die Scheibe nicht, oder durch eine feine, oft unregelmäßige Linie abgesetzt.	**Posterior margin** distinctly convex, not distinctly separated against the disc, or by a subtle, often irregular line.
	Die **Scheibe** des Halsschildes ist sehr variabel, gleichmäßig flach gewölbt, fast ohne Andeutung einer Mittelfurche oder auch abgeplattet und mit kräftiger Längsfurche. Die Mittelfurche erreicht weder den Vorderrand noch den Hinterrand, sie geht vorne oder hinten höchstens in eine sehr schwache oder nur angedeutete Vertiefung über.	The **disc** of the pronotum is very variable, evenly shallowly domed, almost without a hint of a central groove or flattened and with a distinct longitudinal groove. The central groove neither reaches the anterior nor the posterior margin, at the most it peters out to a shallow or only indistinct impression ahead or rearmost.

Character	German	English
Pro-notum	Vordere **Seitenhöcker** deutlich, nach oben ein wenig oder kaum, gegen die Vorderecken kräftig, nach hinten schwach abgesetzt. Hintere Seitenhöcker schwach entwickelt. Wenig dicht, unregelmäßig punktiert, zwischen den Punkten glänzend. Oft ist die Punktierung vorne und hinten dichter als in der Mitte. Die Dichte der Punktierung ist aber bei den einzelnen Exemplaren sehr verschieden.	Anterior **lateral tubercles** distinct, against above slightly or scarcely, against the anterior angles distinctly, against backwards slightly separated. Posterior lateral tubercles poorly developed. Not densely, irregularly punctured, in between the punctures shiny. Often the punctures are more dense in the anterior and posterior part than in the middle part. But the density of the punctures is very different between single specimens.
	Der Halsschild ist behaart. Es befinden sich nämlich in den Punkten äußerst feine, kurze, sehr schwer sichtbare Borsten.	**The pronotum is pubescent**. For inside the punctures there are exceedingly delicate, short setae which are very difficult to be seen.
Prothorax	Die **Episternen** der Vorderbrust sind grob längs gerunzelt, der behaarte Fleck ist nur schwach behaart.	The **episterna** of prothorax are coarsely longitudinally wrinkled, the hairy patch is only feebly pubescent.
Elytra	**Flügeldecken** von vorn nach hinten schwach, zu den Seiten stärker gleichmäßig gewölbt, doppelt so lang wie zusammen breit. Die Seiten verlaufen parallel bis zum 2. Drittel und sind dann gleichmäßig zu den einzeln abgerundeten Enden gewölbt. Eine Abstutzung ist kaum angedeutet.	**Elytra** feebly domed from anterior to posterior, more distinctly and evenly towards the margins, twice as long as the breadth of both. Outer contour parallel from anterior to the second third, then evenly domed towards the singly rounded apices. Truncation indistinct.
	Die **Punktierung** ist sehr fein. Die Punkte sind länglich.	The **dotting** is very delicate. The punctures are longish.
	Die **Zwischenräume** sind flach und breit, glänzend mit flachen weit auseinander stehenden Querrunzeln und einer sehr feinen mehr oder weniger dichten Mikropunktur. Der 1. Zwischenraum ist fast glatt mit nur sehr schwacher Quer-, Längs- oder Schrägrunzelung und im hinteren Drittel auf beiden Seiten von einer linienförmigen Kante begrenzt.	The **intervals** are flattened and broad, shiny with flat, greatly separated transverse wrinkles and with very fine more or less dense micropuncture. The 1st interval is almost glabrous with only weak transversal, longitudinal or diagonal wrinkles and margined on both sides with a ridge like a solid line in the last third.
	Die **Schulter** ist schwach entwickelt, ziemlich glänzend, schwach punktiert und gerunzelt.	The **humeral callus** is indistinct, rather lustrous, weakly punctured, and wrinkled.
	Der erste **Nahteindruck** ist bei einigen Stücken deutlich vorhanden, bei anderen kaum noch sichtbar. Andere Eindrücke außer der schwach entwickelten Schulterfurche fehlen.	The first **impression at the suture** is distinct only at some specimens, almost invisible at others. Other impressions are lacking besides the weakly developed humeral groove.
Meta-thorax	Die Unterseite der **Hinterbrust** ist beim ♂ herzförmig abgeplattet, beim ♀ gewölbt mit tiefer liegender Mittelfurche.	The underpart of the **metathorax** at the ♂ is heart-shaped and flattened, at the ♀ it is domed with a more prominent middle groove.
Abdominal segments	Das 1. **Hinterleibssegment** ist beim ♂ etwas, beim ♀ um die Hälfte länger als das 2. - 5. zusammen, es ist beim ♂ abgeplattet und etwas eingedrückt, beim ♀ gewölbt.	The 1st **abdominal segment** is slightly longer at the ♂, at the ♀ longer by the half than the 2nd to 5th together, at the ♂ flattened and slightly impressed, at the ♀ domed.
	Das letzte Segment ist beim ♂ an der Hinterkante leicht eingedrückt, beim ♀ konvex vorgezogen ohne eigentliche Spitze.	The last segment is slightly impressed at the apical ridge at the ♂, at the ♀ convexly protruding without a distinctive peak.
	Die Unterseite des Hinterleibes ist glänzend, mäßig dicht punktiert und behaart.	The underpart of the abdomen is shiny, moderately densely punctured and pubescent.
	Das **Pygidium** ist abgestutzt und in der Mitte schwach ausgebuchtet.	The **pygidium** is truncated and slightly recessed in the middle.
Legs	Die **Vorderschiene** ist an der Ansatzstelle der Tarse zahnförmig nach außen gebogen (siehe Abb. 6).	The **anterior tibia** shows a protruding tooth towards outward at the insertion of the tarsomere.
	Die **Hinterschenkel** sind kurz, sie erreichen auch beim ♂ das Flügeldeckenende bei weitem nicht, Vorder-, Mittel – und Hinterschenkel besonders beim ♂ stark keulig verdickt, beim ♀ schlanker.	The **posterior femora** are short, even at the ♂ they don't reach the apex of the elytra by far, anterior, middle and posterior femora much thickened like clubs especially at the ♂, at the ♀ more slender.
	Hinterschenkel mit einem kräftigen Zahn, der beim ♂breiter, beim ♀ schmaler und spitzer ist (siehe Abb. 5).	Posterior femora with a prominent tooth, which is broader at the ♂, at the ♀ more slender and more acute.
	Das 1. und 3. Tarsenglied sind etwa gleich lang, das 2. um 1/3 kürzer.	The 1st and 3rd tarsomere have about the same length, the 2nd one is by a third shorter.
Colour	Die Tiere sind einheitlich dunkel bronzefarben, nur die Fühler gelb bis dunkelbraun, die Schienen und Tarsen und die Hinterschenkel von der Basis bis zur Mittel hellbraun.	The animals are uniformly dark bronze, only the antennae yellow to dark brown, the tibae and tarsi and the hind femora light brown from the basal part to the middle.
Size	Länge: ♂ 7–8 mm, ♀ 9 mm. Breite: ♂ 2,4–2,6 mm, ♀ 3,5 mm.	Length: ♂ 7–8 mm, ♀ 9 mm. Width: ♂ 2.4–2.6 mm, ♀ 3.5 mm.
Locus typicus	Mir liegen vor 7 Exemplare aus dem Reichsmuseum **Alexander König** in Bonn, gesammelt am 27.4. und 7.5.1938 von Herrn **J. Klapperich** in Kuatun (Fukien, China) 27.40 nördl. Breite, 117.40 östl. Länge, in 2300 m Höhe.	There are 7 specimens on hand for me from the Reichsmuseum **Alexander König** in Bonn, collected at 27th of April and 7th of May 1938 by Mister **J. Klapperich** in Kuatun (Fukien, China) 27.40 northern latitude, 117.40 eastern longitude, at 2300 m a.s.l.

Appendix 3

Donacia kweilina Chen, 1966

Original description in English. The following species was described by Chen (1966) in Chinese and English. Only the English text and the illustration are provided here. The type specimens are stored in the collections of ASIZ.

"Closely related to *D. fukiensis* Goecke, distinguished by the pronotum much more thickly pubescent, the femora of ♂ not distinctly thicker than those of ♀ and the last abdominal segment of ♀ much longer and somewhat triangular in shape (Fig. 16).

Also allied to *D. clavareaui* Jacobson, but the antennae end legs entirely deep coloured, not partly rufous and the elytra rather more finely punctured with the interstices much broader and more sparingly and finely wrinkled.

Aeneo-cupreous (♂, ♀), sometimes sky-blue (♂). Antennae long and slender, metallic, the terminal segments black; third segment slightly longer than second and distinctly shorter than fourth. Head with four weak tubercles, the median longitudinal furrow deep and complete. Pronotum very closely punctured and covered with silvery hairs, the antero-lateral tubercles distinct, the angles fairly strongly produced. Elytra rather smooth on the inner disc, the punctures oblong, the interstices broad, about 2–3 times as broad as the cross diametre[sic!] of the punctures; apex truncate with the outer angles broadly rounded. Hind femora (♂, ♀) broadly toothed beneath.

Length: 6.8–8 mm.

Holotype ♂, allotype ♀, paratypes 47 ♂♂, ♀♀ Kwangsi: Kweilin (April-May, 1952)."

Appendix 4

Donacia mediohirsuta Chen, 1966

Original description in English. The following species was described by Chen (1966) in Chinese and English. Only the English text and the illustration are shown here. The type specimen is stored in the collections of ASIZ.

"Very like *D. fukiensis* Goecke, but with the pronotum more transversal, finely pubescent only on the median longitudinal area; the longitudinal furrow of interocular area much deeper, extending uninterrupted to between the supra-antennal tubercles; the anterior tibiae scarcely produced at apex; the hind femora (♀) very weakly toothed beneath and the last abdominal sternite (♀) more strongly angulate at apex (Fig. 17). General colour aeneo-cupreous. Antennae with the terminal segments rufo-piceous, 3–5 segments partly rufous and partly piceous, third segment distinctly longer than second, but slightly shorter than fourth.

Length: 8 mm

Holotype ♀ Yunnan: Shishong-Baana (1200 m, 15, May, 1958)."

ZooKeys 856: 51–73 (2019)
doi: 10.3897/zookeys.856.33724
http://zookeys.pensoft.net

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Adaptation of flea beetles to Brassicaceae: host plant associations and geographic distribution of *Psylliodes* Latreille and *Phyllotreta* Chevrolat (Coleoptera, Chrysomelidae)*

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Academic editor: *M. Schmitt* | Received 11 February 2019 | Accepted 30 April 2019 | Published 17 June 2019

http://zoobank.org/A85D775A-0EFE-4F32-9948-B4779767D362

Citation: Gikonyo MW, Biondi M, Beran F (2019) Adaptation of flea beetles to Brassicaceae: host plant associations and geographic distribution of *Psylliodes* Latreille and *Phyllotreta* Chevrolat (Coleoptera, Chrysomelidae). In: Schmitt M, Chaboo CS, Biondi M (Eds) Research on Chrysomelidae 8. ZooKeys 856: 51–73. https://doi.org/10.3897/zookeys.856.33724

Abstract

The cosmopolitan flea beetle genera *Phyllotreta* and *Psylliodes* (Galerucinae, Alticini) are mainly associated with host plants in the family Brassicaceae and include economically important pests of crucifer crops. In this review, the host plant associations and geographical distributions of known species in these genera are summarised from the literature, and their proposed phylogenetic relationships to other Alticini analysed from published molecular phylogenetic studies of Galerucinae. Almost all *Phyllotreta* species are specialised on Brassicaceae and related plant families in the order Brassicales, whereas *Psylliodes* species are associated with host plants in approximately 24 different plant families, and 50% are specialised to feed on Brassicaceae. The current knowledge on how *Phyllotreta* and *Psylliodes* are adapted to the characteristic chemical defence in Brassicaceae is reviewed. Based on our findings we postulate that *Phyllotreta* and *Psylliodes* colonised Brassicaceae independently from each other.

Keywords

Alticini, chemical plant defence, detoxification, glucosinolates, plant-insect interaction, secondary plant metabolites, sequestration

* extended versions of a talk presented to the 3rd European Symposium on the Chrysomelidae, Naples, Italy, 5 July, 2018.

Introduction

Plant-feeding insects are often classified as specialists or generalists according to their food plant range. While generalist insect herbivores are able to feed on plants that belong to distantly related plant families, specialist insect herbivores feed selectively on one or a few closely related plant species (Schoonhoven et al. 2005). Many phytophagous insects, including numerous leaf beetle species, have a narrow food plant range (Jolivet and Hawkeswood 1995; Forister et al. 2015), which is at least partially determined by toxic and deterrent plant secondary metabolites. Plants produce more than 200,000 different secondary metabolites, and many of them are involved in defence against herbivores (Mithöfer and Boland 2012). The distribution of secondary metabolites in related plant species often correlates with the food plant range of specialised insect herbivores, which evolved strategies to avoid, tolerate, or detoxify these defence compounds (Heckel 2014). Such adaptations presumably played an important role in the species diversification of plant-feeding insects (Ehrlich and Raven 1964; Futuyma and Agrawal 2009), but the specific molecular mechanisms underlying host plant adaptation, and their role in insect ecology and speciation, are largely unknown.

Several genera in the family Chrysomelidae include species that are specialised to feed on plants in the family Brassicaceae (Table 1). In the subfamily Chrysomelinae, the genera *Colaphellus*, *Entomoscelis*, and *Microtheca* feed primarily on Brassicaceae (Jolivet and Petitpierre 1976b; Nielsen 1988), whereas the genus *Phaedon* is associated with several different plant families, e.g. Asteraceae, Brassicaceae, Scrophulariaceae, and Ranunculaceae (Table 1). In the subfamily Galerucinae, the flea beetle genera *Phyllotreta*, *Psylliodes*, *Leptophysa*, *Caeporis*, and *Hemiglyptus* utilise Brassicaceae as host plants (Furth 1979; Nielsen 1988; Jolivet 1991; Nadein 2010). In addition, many other polyphagous chrysomelid genera feed occasionally on this plant family. However, within Chrysomelidae, the genera *Psylliodes* and *Phyllotreta* comprise the highest number of crucifer specialists.

Glucosinolates are the characteristic secondary metabolites of Brassicaceae and other families in the order Brassicales (Agerbirk and Olsen 2012). Upon herbivory, glucosinolates are hydrolysed by β-thioglucosidase enzymes (myrosinases) to unstable aglucones, which can generate various hydrolysis products such as isothiocyanates, thiocyanates, and nitriles (Wittstock et al. 2016). Isothiocyanates, the most toxic glucosinolate hydrolysis products, are primarily reactive towards thiol- (-SH) and amino- ($-NH_2$) groups in peptides and proteins (Brown and Hampton 2011). Previous studies revealed that insects developed different strategies to overcome this plant defence (reviewed in Winde and Wittstock (2011) and Jeschke et al. (2016)). For example, *Plutella xylostella* larvae (Lepidoptera, Plutellidae) prevent glucosinolate breakdown by rapidly converting ingested glucosinolates to stable desulfo-glucosinolates (Ratzka et al. 2002), while *Pieris rapae* larvae (Lepidoptera, Pieridae) express a nitrile specifier protein (NSP) in their gut, which promotes the formation of less toxic nitriles instead of isothiocyanates (Wittstock et al. 2004). The evolution of NSP activity in Pierinae butterflies is regarded as an evolutionary key innovation that enabled a host shift from Fabales

Table 1. Overview of Chrysomelidae genera that are associated with Brassicaceae hosts plants.

Genus	Approx. no. of species	Major host plant families	Known species feeding on Brassicaceae	References
Subfamily Chrysomelinae				
Chrysolina Motschulsky, 1860	450	Lamiaceae	*C. cavigera*, *C. colasi*	Jolivet and Petitpierre 1976a, 1976b; Clark et al. 2004; Jurado-Rivera and Petitpierre 2015
Colaphellus Weise, 1916	15	Brassicaceae	*C. bowringi*, *C. hoeftii*, *C. sophiae*	Döberl 2010; Gavrilović et al. 2014; Bieńkowski and Orlova-Bienkowskaja 2015; Rheinheimer and Hassler 2018
Entomoscelis Chevrolat, 1836	14	Brassicaceae	*E. adonidis*, *E. americana*, *E. berytensis*, *E. nigriventris*, *E. orientalis*, *E. pilula*	Mohr 1966; Gerber 1994; Ge et al. 2009
Microtheca Dejean, 1835	15	Brassicaceae	*M. ochroloma*, *M. picea*, *M. punctigera*, *M. semilaevis*	Jolivet 1951; Balsbaugh 1978; Jolivet and Hawkeswood 1995; Ameen 1996; Clark et al. 2004; Menezes et al. 2005; Balusu et al. 2017
Phaedon Latreille, 1829	80	Brassicaceae, Ranunculaceae, Plantaginaceae, Asteraceae	*P. brassicae*, *P. cochleariae*, *P. laevigatus*, *P. prasinellus*, *P. viridis*	Ge et al. 2003, 2013, 2015; Clark et al. 2004; Lopatin 2005; Rheinheimer and Hassler 2018
Timarcha Latreille, 1829	316	Rubiaceae, Plantaginaceae	*T. intermedia*, *T. lugens*, *T. strangulata*	Jolivet and Petitpierre 1973; Gómez-Zurita et al. 2000a, 2000b; González-Megías and Gómez 2001
Subfamily Galerucinae, Alticini				
Caeporis Dejean, 1837	1	Brassicaceae	*C. stigmula*	Jolivet and Hawkeswood 1995; Cabrera and Rocca 2012; Nadein 2012
Hemiglyptus Horn, 1889	1	Brassicaceae, Hydrophyllaceae	*H. basalis*	Clark et al. 2004; Nadein 2012
Leptophysa Baly, 1877	15	Brassicaceae, Cleomaceae	*L. batesi*, *L. bordoni*, *L. littoralis*	Jolivet 1991; Jolivet and Hawkeswood 1995; Bechyné 1997; Flowers and Janzen 1997
Phyllotreta Chevrolat, 1836	242	Brassicaceae	see Suppl. material 3	This study; Heikertinger 1943; Furth 1979; Smith 1985; Clark et al. 2004
Psylliodes Latreille, 1829	207	Brassicaceae, Poaceae	see Suppl. material 1	This study; Furth 1983; Cox 1998; Clark et al. 2004; Nadein 2010; Baviera and Biondi 2015

plants to the glucosinolate-containing Brassicales. As predicted by the coevolutionary 'escape and radiate' hypothesis, speciation rates were higher in the clade that colonised Brassicales plants compared to their sister taxon (Wheat et al. 2007; Edger et al. 2015). In contrast, the host shift of Ceutorhynchini weevils from the plant family Lamiaceae to Brassicaeae was not associated with a speciation rate shift (Letsch et al. 2018).

Glucosinolates and their hydrolysis products are well known to affect the behavior of crucifer-feeding Chrysomelidae (reviewed in Mitchell (1988, 1994), and Nielsen (1988)). Volatile isothiocyanates, for example, attracted high numbers of *Phyllotreta* spp. and *Psylliodes chrysocephala* in field trapping experiments, indicating that isothiocyanates might play a role in host plant localisation (Görnitz 1956; Bartlet et al. 1992; Pivnick et al. 1992; Tóth et al. 2007). Glucosinolates, on the other hand, stimulated feeding of *Phyllotreta* spp., *Ps. chrysocephala*, *Phaedon cochleariae*, and *Entomoscelis americana* in laboratory experiments (Hicks 1974; Mitchell 1978; Nielsen 1978; Bartlet et al. 1994; Reifenrath and Müller 2008). Although these specialists are adapted to the glucosinolate-

myrosinase defence system, both glucosinolate levels and myrosinase activity affected herbivory by *Phyllotreta cruciferae* in the field. The highest flea beetle damage was observed on *Brassica rapa* plants with intermediate glucosinolate levels (Siemens and Mitchell-Olds 1996), and *B. rapa* lines selected for high myrosinase activity displayed significantly less feeding damage (ca. 10%) than those with low enzyme activity (Mitchell-Olds et al. 1996). In contrast, studies with *Ps. chrysocephala* did not reveal a correlation between glucosinolate levels and feeding damage (Bartlet et al. 1996; Bartlet et al. 1999).

Here, we provide an overview on the host plants, diet breadth, and geographic distribution of known *Phyllotreta* and *Psylliodes* species, as well as their proposed relationships to other genera of Alticini. Diet breadth was classified according to Biondi (1996). Species feeding on one or two closely related botanical genera are considered as monophagous, species feeding on more plant genera of one or two closely related families are defined as oligophagous, and species feeding on many distantly related plant species are considered as polyphagous. For species with limited information on food plants, we did not specify the diet breadth. Data on the geographical distribution of the Palearctic *Psylliodes* and *Phyllotreta* species was primarily obtained from Döberl (2010) and is described according to Löbl and Smetana (2010). The zoogeographical regions are abbreviated as follows: Afrotropical Region (AFR), Australian Region (AUR), Nearctic Region (NAR), Neotropical Region (NTR), Oriental Region (ORR), Palearctic Region (PAR). In the second part of this review, we summarise the knowledge on the adaptations of *Phyllotreta* and *Psylliodes* spp. to the glucosinolate-myrosinase defence system and other defences in their host plants.

Host plant associations of *Psylliodes* and *Phyllotreta* flea beetles

The genus *Psylliodes* Latreille, 1829 comprises over 200 species (Suppl. material 1). Adult *Psylliodes* beetles are distinguished from other flea beetle genera based on their 10-segmented antennae and tarsi inserted pre-apically on the metatibia of the hind legs. Most other Alticini genera have 11-segmented antennae except for *Psylliodes*, *Decaria*, and *Monotalla* with ten segments and *Nonarthra* with nine segments (Konstantinov and Vandenberg 1996; Nadein and Bezděk 2014). The genus comprises five subgenera: *Psylliodes* s. str. (194 species), *Semicnema* Weise (5 species), *Eupus* Wollaston (5 species), *Minicnema* Nadein (2 species) and *Psyllobactra* Lopatin (1 species) (Nadein 2007a, 2010). A subdivision of the subgenus *Psylliodes* s. str. based on morphological features was proposed by Leonardi (1970) and Nadein (2006, 2007a, 2007b) (Suppl. material 2).

According to the literature, host plants of 107 *Psylliodes* species have been reported, and these belong to 24 plant families (Suppl. material 1). Most *Psylliodes* species have a restricted host plant range (35% are monophagous and 51% are oligophagous), and only 14% are polyphagous. For instance, *Psylliodes toelgi* feeds only on *Biscutella laevigata* (Brassicaceae), whereas *Psylliodes luteola* has been recorded on Poaceae, Fagaceae, Salicaceae, Ulmaceae, and Solanaceae.

Of all *Psylliodes* species with known host plants, 50% are specialised on Brassicaceae, followed by 13% feeding on Poaceae, 10% on Solanaceae and 10% on Fagaceae (Fig. 1A). Previous surveys of host plant associations of *Psylliodes* spp. focused on specific countries or regions and thus included a much smaller total number of *Psylliodes* species (Furth 1983; Cox 1998; Döberl 2010; Baviera and Biondi 2015). Interestingly, host plant use often correlates with the proposed *Psylliodes* s. str. species groups, which indicates that presumably closely related *Psylliodes* species feed on closely related host plants (Suppl. material 2). For example, *Psylliodes* species in the *chrysocephala* and *pyritosa* groups are specialised to feed on Brassicaceae, while species in the *luteola* group are mainly associated with Fagaceae.

The genus *Phyllotreta* Chevrolat, 1836 comprises about 242 species and host plant information is available for 117 species (Suppl. material 3). Most *Phyllotreta* species are specialised on glucosinolate-containing plants in the order Brassicales (Fig. 1B). An analysis of the diet breadth of *Phyllotreta* species revealed that 31% are monophagous, 64% are oligophagous, and 5% are polyphagous. In *Phyllotreta*, 63% are specialised on Brassicaceae, whereas 18% feed on plants in more than one family in the order Brassicales (Fig. 1B).Very few *Phyllotreta* species feed on plant families, which do not contain glucosinolates, for instance, *Phyllotreta cruralis* is specialised on Amaranthaceae.

Several *Psylliodes* and *Phyllotreta* species are of economic importance. The cabbage stem flea beetle, *Ps. chrysocephala* is a serious pest of winter oilseed rape in Northern Europe (Zimmer et al. 2014), whereas *Phyllotreta striolata* and *Ph. cruciferae* are oilseed rape pests in Canada where their damage causes losses of tens of millions of US dollars annually (Lamb 1989; Hill 2008; Knodel 2017). On the other hand, the Palearctic species *Psylliodes chalcomera* (feeding on Asteraceae) was introduced to North America in 1997 as a control agent for the invasive weed *Carduus nutans* (musk thistle), but it likely did not establish in the Nearctic region (Antonini et al. 2008).

Geographic distribution of *Psylliodes* and *Phyllotreta* flea beetles

The genus *Psylliodes* has a worldwide distribution (Biondi and D'Alessandro 2018). The highest number of species occurs in the Palearctic region (160 species, 145 endemic species), followed by the Oriental region (27 species, 19 endemic species), the Nearctic region (13 species, 4 endemic species), the Afrotropical region (13 species, 9 endemic species), the Neotropical region (8 species, 4 endemic species), and the Australian region (8 species, 7 endemic species; Suppl. material 1). A graphical overview of the species distribution is shown in Figure 2A; the host plant associations of all species and endemic species in each zoogeographical region are shown in Figure 2B. Some species are wide-spread in more than one zoogeographical region such as *Ps. brettinghami* (feeding on Solanaceae), which is found in the Australian, Oriental, and Palearctic regions, while others are strictly endemic to very limited areas, e.g. *Ps. tarsata*, which is only found on Madeira (Portugal). *Psylliodes* species that are endemic to the Palearctic region account

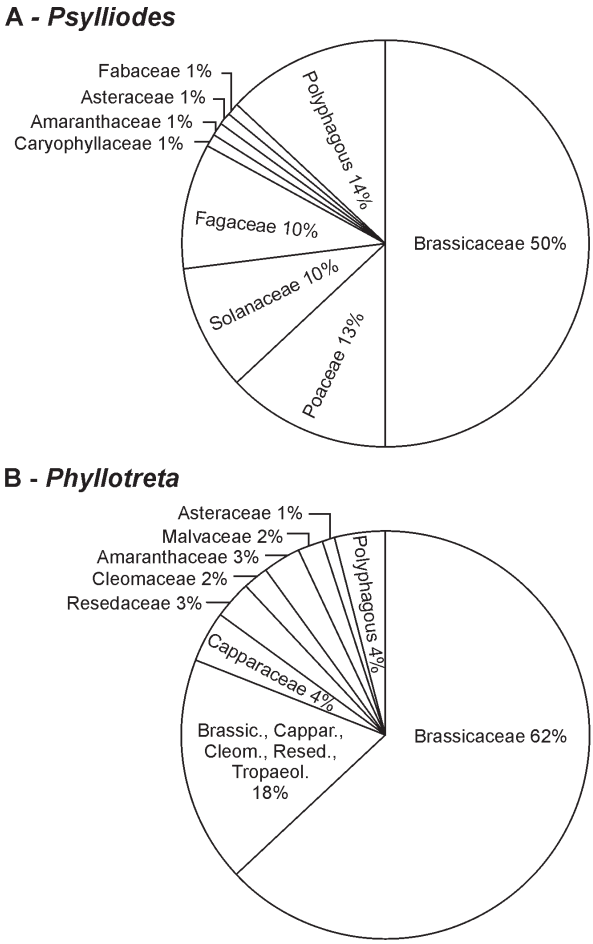

Figure 1. Host plant associations of the genera *Psylliodes* (**A**) and *Phyllotreta* (**B**). The host plants of 107 *Psylliodes* species and 117 *Phyllotreta* species have been reported in the literature. The numbers of species which feed on plants in one plant family (monophagous and oligophagous), and the number of polyphagous species are given as percentages. 18% of the *Phyllotreta* species feed on more than one family in the order Brassicales (Brassic., Brassicaceae; Cappar., Capparaceae; Cleom., Cleomaceae; Resed., Resedaceae; Tropaeol., Tropaeolaceae). For detailed information, refer to Suppl. material 1 (*Psylliodes*) and 3 (*Phyllotreta*).

for 83% of those associated with Brassicaceae. All other Brassicaceae-feeding species are found in other zoogeographical regions except for Australia (Fig. 2B).

The geographic distribution of the genus *Phyllotreta* shows the highest number of species in the Palearctic region (137 species, 118 endemic species) followed by the Afrotropical region (49 species, 39 endemic species), the Nearctic region (49 species, 40 endemic species), the Oriental region (25 species, 18 endemic species), the Neotropical Region (5 species, 3 endemic species), and the Australian Region (4 species,

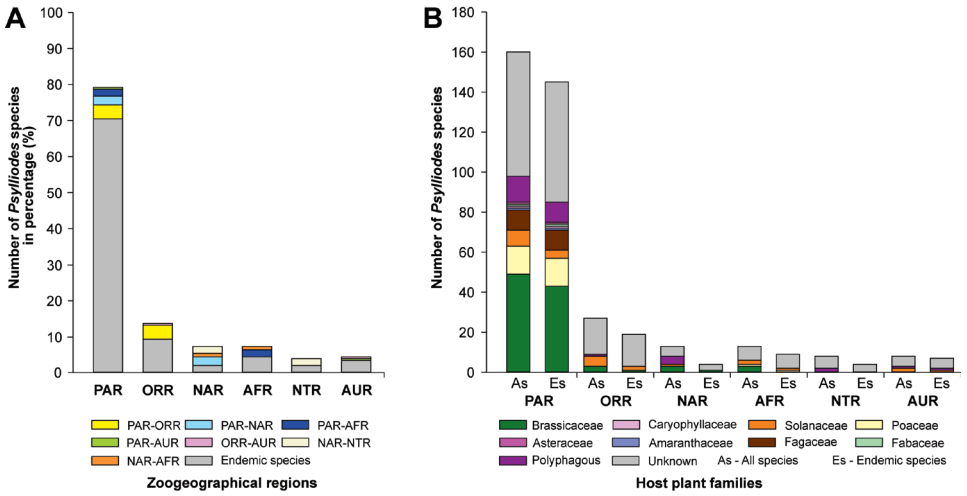

Figure 2. Distribution of 207 *Psylliodes* species in the different zoogeographical regions (**A**), and host plant associations of all species (As) and endemic species (Es) for each zoogeographical region (**B**). For detailed information, refer to Suppl. material 1.

3 endemic species; Suppl. material 3). The species distribution is shown in Figure 3A, and the host plant associations of all species and endemic species in each zoogeographical region are shown in Figure 3B. In general, a high percentage of endemic *Phyllotreta* species is found in all geographical regions (≥ 60%) with highest values in the Palearctic, Afrotropical, and Nearctic regions (≥ 80%). In some areas, especially in the Nearctic region, several species of *Phyllotreta* are not native and have been introduced from other regions (Milliron 1953; Smith 1985). Most species feeding on Brassicaceae are found in the Palearctic and Nearctic regions. The host plants of a large proportion of the species endemic to the Afrotropical, Australian, and Neotropical regions are unknown (Fig. 3B; Suppl. material 3).

Phylogenetic relationships of *Psylliodes* and *Phyllotreta* to other Alticini

The most comprehensive phylogenetic analyses of the subfamily Galerucinae *sensu lato* are those of Ge et al. (2011, 2012) and Nie et al. (2018), which included about 80 and 70 genera of Alticini (including problematic genera), respectively. Ge et al. (2011, 2012) used two mitochondrial (16S rRNA and cytochrome oxidase (cox) 1) and two nuclear genes (18S and 28S rRNA) to infer phylogenetic relationships, while Nie et al. (2018) used the mitochondrial genome and nuclear rRNA genes. In these analyses, *Psylliodes* and *Phyllotreta* were never retrieved as sister genera, but instead clustered in distinct clades with other Alticini as summarised in Table 2. All three studies suggest a close phylogenetic relationship of *Psylliodes* to *Chaetocnema* and *Crepidodera* (see Table 2 for Bayesian posterior probability values and/or Maximum Likelihood bootstrap support values). Surprisingly, two different *Crepidodera* species included in

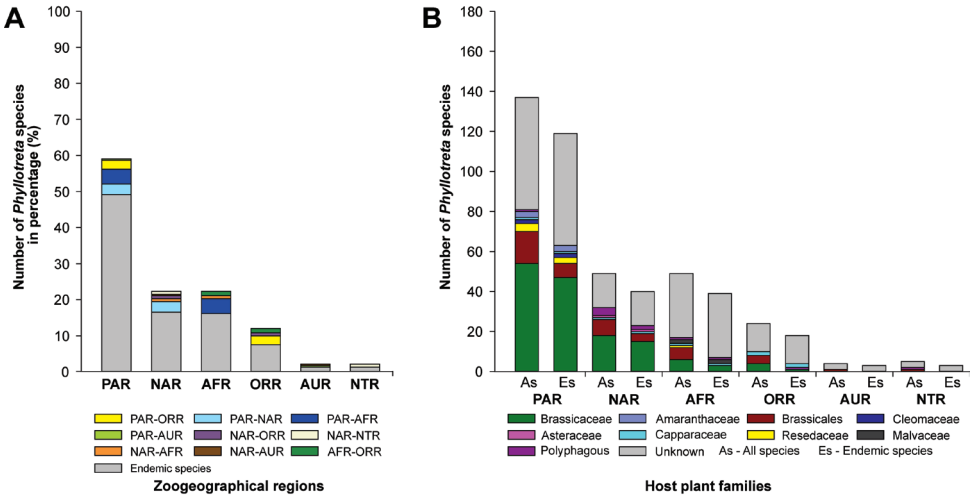

Figure 3. Distribution of 242 *Phyllotreta* species in the different zoogeographical regions (**A**), and host plant associations of all species (As) and endemic species (Es) for each zoogeographical region (**B**). For detailed information, refer to Suppl. material 3.

the analysis of Nie et al. (2018) were not monophyletic. *Crepidodera pluta* clustered in the *Chaetocnema* group with *Psylliodes*, while the second *Crepidodera* sp. clustered together with two *Phyllotreta* species in a distant clade. However, the proposed relationships of *Phyllotreta* to other Alticini differ among the studies, and are usually less supported than those suggested for *Psylliodes*. None of the genera with proposed close phylogenetic relationships to *Phyllotreta* and *Psylliodes* are associated with Brassicaceae plants (Table 2).

Adaptations of crucifer-feeding flea beetles to chemical plant defences

An unexpected observation revealed that *Ph. striolata* adults emit low amounts of toxic isothiocyanates, which are derived from glucosinolates that are stored at high concentrations of up to 50 µmol/g fresh weight (ca. 2% of the body weight) in adults (Beran 2011; Beran et al. 2014). When adults were transferred to different crucifer species, they selectively accumulated mainly aliphatic glucosinolates from their food plants, e.g. allyl glucosinolate from *Brassica juncea*, and 4-methylsulfinylbutyl (4MSOB) glucosinolate from *Arabidopsis thaliana*. In contrast, adults sequestered only low amounts of the benzenic 4-hydroxybenzyl glucosinolate from *Sinapis alba*. The glucosinolate accumulation pattern depended both on glucosinolate structure and on the host plant background, suggesting that the plants' glucosinolate composition affects sequestration in *Ph. striolata*. The ability to accumulate high glucosinolate amounts demonstrates that *Ph. striolata* can at least partially prevent activation of ingested glucosinolates.

Table 2. Phylogenetic relationships of *Psylliodes* and *Phyllotreta* to other Alticini genera.

Study	*Psylliodes*	*Phyllotreta*
Ge et al. (2011)	Sister genus: *Chaetocnema* (Poaceae)[1] Phylogenetic support (B/ML): 0.84/67 Clade: *Crepidodera* (Salicaceae), *Epitrix* (Solanaceae) Phylogenetic support (B/ML): 0.52/<50 Taxonomic group: Unspecified	Sister genus: *Batophila* (Rosaceae) Phylogenetic support (B/ML): 0.79/<50 Clade: *Lipromela* (unknown), *Syphrea* (Euphorbiaceae), *Altica* (Onagraceae, Lythraceae), *Macrohaltica* (Gunneraceae) Phylogenetic support (B/ML): 0.98/<50
Ge et al. (2012)	**Bayesian and Maximum-Likelihood phylogenies** Sister genus: *Chaetocnema* (Poaceae) Phylogenetic support (B/ML): 0.95/67 Clade: *Crepidodera* (Salicaceae), *Epitrix* (Solanaceae), *Syphrea* (Euphorbiaceae), *Altica* (Onagraceae, Lythraceae), *Macrohaltica* (Gunneraceae) Phylogenetic support (B/ML): 0.89/<50 Taxonomic group: *Chaetocnema*	**Bayesian phylogeny** Sister genus: *Epitrix* (Solanaceae) Phylogenetic support (B): 0.95 Clade: *Diphaltica* (Aquifoliaceae), *Agasicles* (Amaranthaceae), *Disonycha* (Amaranthaceae) Phylogenetic support (B): 0.81 **Maximum-Likelihood phylogeny** Clade: *Lanka* (Piperaceae), *Longitarsus* (Boraginaceae), *Tegyrius* (Piperaceae) Phylogenetic support (ML): <50
Nie et al. (2018)	Sister genus: *Chaetocnema* (Poaceae), *Epitrix* (Solanaceae) Phylogenetic support (B): 0.48 Clade: *Crepidodera* (Salicaceae), *Xuthea* (Urticaceae) Phylogenetic support (B): 0.89 Taxonomic group: *Chaetocnema*	Sister genus and clade: *Crepidodera* (Salicaceae) Phylogenetic support (B): 0.83

[1]The major host-plant family for each genus according to Jolivet and Hawkeswood (1995) is given in parentheses.
ML – Maximum Likelihood bootstrap value; B – Bayesian posterior probability

However, quantitative feeding studies, for instance with radiolabeled glucosinolates, are needed to determine to which degree ingested glucosinolates are sequestered intact.

To activate sequestered glucosinolates, *Ph. striolata* possesses an insect myrosinase with high activity towards aliphatic glucosinolates, which evolved from insect β-*O*-glucosidases (Figure 4; Beran et al. 2014). To investigate how *Ph. striolata* activate sequestered glucosinolates and prevent autointoxication, dissected tissues from adults were analysed for the presence of glucosinolates and myrosinase activity, respectively. Interestingly, both glucosinolates and myrosinase were mainly localised in the hemolymph and elytra (Beran and Ahn, unpublished), but whether both components are stored separately in hemoplasma and hemocytes as previously reported for cyanogenic glycosides and the cyanogenic β-glucosidase in *Zygaena filipendulae* larvae (Lepidoptera, Zygaenidae; Pentzold et al. 2017), is not yet known.

In the genus *Psylliodes*, the cabbage stem flea beetle, *Ps. chrysocephala*, selectively sequesters glucosinolates as well, but compared to *Ph. striolata*, glucosinolate concentrations are much lower (ca. 4 μmol/g fresh weight; Beran et al. 2018). Although glucosinolates are present in all life stages of *Ps. chrysocephala*, a defensive function is unlikely, as neither larvae nor adults possess endogenous myrosinase activity (Beran et al. 2018). An analysis of the metabolic fate of ingested 4MSOB glucosinolate in *Ps. chrysocephala* adults revealed that adults utilise at least three strategies to prevent isothiocyanate formation and toxicity. *Ps. chrysocephala* sequester intact glucosinolates, detoxify glucosinolates by desulfation, and detoxify dietary isothiocyanates by conjugation to glutathione. The isothiocyanate-glutathione conjugate is metabolised via the conserved mercapturic acid pathway to three different cyclic cysteine conjugates, which are excreted. These three strategies accounted for the metabolic fate of 18.5%, 8%, and 17% of the total ingested glucosinolates, respectively. The amounts of other glucosinolate breakdown products (4MSOB-isothiocyanate, -cyanide, -amine, and –acetamide) corresponded to 17.5% of the total ingested glucosinolate (Figure 4; for details, refer to Beran et al. 2018). However, the metabolic fate of about 39% of the total ingested glucosinolate remained unknown in this study.

The detoxification of isothiocyanates in *Ps. chrysocephala* comes at the expense of the amino acid cysteine. Therefore, interference with protein digestion, for instance by plant proteinase inhibitors or other digestibility reducers, might affect the detoxification capacity for isothiocyanates by limiting the availability of cysteine for glutathione biosynthesis. Interestingly, there is evidence that *Ps. chrysocephala* can compensate for the ingestion of plant proteinase inhibitors. *Ps. chrysocephala* larvae reared on a transgenic *Brassica napus* line that overexpressed the cysteine proteinase inhibitor oryzacystatin I showed doubled proteolytic activity and were heavier than those reared on the corresponding *B. napus* wild type (Girard et al. 1998). This unexpected result shows that *Ps. chrysocephala* is not only adapted to glucosinolates but also to plant proteinase inhibitors.

Specialist chrysomelids are well known for discriminating between crucifer species (Feeny et al. 1970; Nielsen 1977; Bartlet and Williams 1991; Pachagounder and Lamb 1998; Pachagounder et al. 1998), but the factors that determine host suitability and preference are often not understood. Although leaf beetles recognise and differentially respond to individual glucosinolates when offered in isolation, there is little evidence that host plant preference relies on specific glucosinolate profiles (Nielsen 1988). Instead, the presence of other toxic secondary metabolites such as cucurbitacins and cardenolides was shown to affect host suitability for *Phyllotreta* spp. and *Phaedon cochleariae* (abbreviated *Phaedon*) (Nielsen 1978). Toxic cucurbitacins B, E, and I present in *Iberis* spp. deterred feeding of *Phyllotreta nemorum* but not of *Phaedon*, an effect that correlated with their feeding behavior towards *Iberis* plants. On the other hand, *Phaedon*, *Phyllotreta undulata*, and *Phyllotreta tetrastigma* did not feed on cardenolide-containing *Cheiranthus* and *Erysimum* spp., which are accepted as food plants by *Ph. nemorum* (Nielsen 1978).

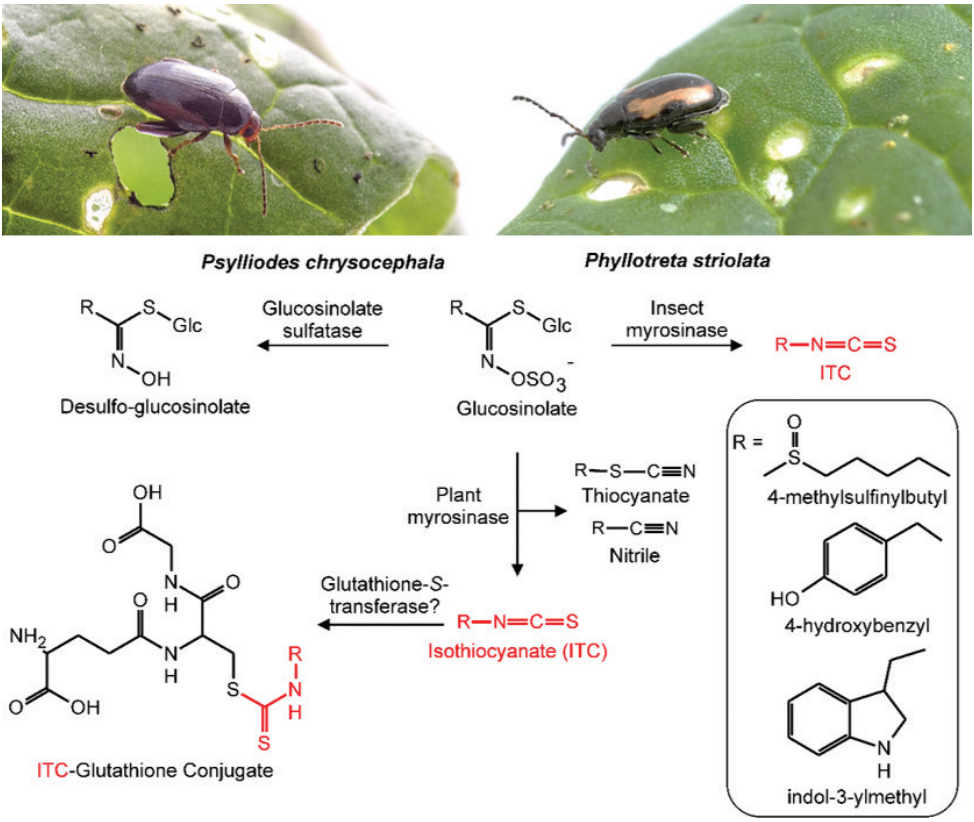

Figure 4. Metabolism of glucosinolates in *Psylliodes chrysocephala* and *Phyllotreta striolata*. Upon herbivory, glucosinolates are usually hydrolysed by the plant enzyme myrosinase to an unstable aglucone, which spontaneously rearranges to a toxic isothiocyanate. In the presence of plant specifier proteins, other hydrolysis products such as thiocyanates and nitriles are formed. Both flea beetle species sequester glucosinolates in their bodies, suggesting that not all glucosinolates are hydrolysed in feeding-damaged plant tissue. Sequestered glucosinolates may be activated for defensive purposes by an insect myrosinase in *Ph. striolata*, but not in *Ps. chrysocephala*. In addition, *Ps. chrysocephala* partially detoxifies glucosinolates by desulfation, whereas no glucosinolate sulfatase activity was found in *Ph. striolata*. According to a quantitative feeding study performed with *Ps. chrysocephala*, most ingested glucosinolates are activated, and isothiocyanates are detoxified by conjugation to glutathione. The isothiocyanate-glutathione conjugate is metabolized via the mercapturic acid pathway to several cyclic metabolites in *Ps. chrysocephala* adults (Beran et al. 2018). Examples of three structurally different glucosinolate side-chains are shown in the box. Beetle photos: Anna Schroll.

The oligophagous species *Ph. nemorum* is used as a model to study the genetic basis of host plant adaptation. The common wild crucifer, *Barbarea vulgaris* ssp. *arcuata* (abbreviated *B. vulgaris*), is an atypical host plant for *Ph. nemorum*. However, the discovery of two different flea beetle populations using *B. vulgaris* as natural host plant suggests that *Ph. nemorum* is extending its host plant range to include *B. vulgaris* in Denmark (Nielsen 1996; de Jong et al. 2000). There are two distinct types of *B.*

vulgaris. The so-called P-type with pubescent leaves is susceptible to all *Ph. nemorum* genotypes, whereas the G-type with glabrous leaves is resistant to most *Ph. nemorum* genotypes (Nielsen 1997b). The flea beetle-resistant G-type represents the common *B. vulgaris* genotype in Western Europe, while the P-type is rare (Hauser et al. 2012; Christensen et al. 2014).

The two *B. vulgaris* types differ not only morphologically but also regarding their chemical defences, i.e. glucosinolates and saponins. Feeding assays showed that susceptible *Ph. nemorum* larvae started to mine into the leaves of the G-type, but then either left and refused to feed or died in the mine, showing that the G-type is toxic for them (Nielsen 1997a, 1997b). Resistance of the G-type to *Ph. nemorum* is linked to the presence of the triterpenoid saponins hederagenin cellobioside, oleanolic acid cellobioside, gypsogenin cellobioside, and 4-epihederagenin cellobioside, and not to distinct glucosinolate profiles (Agerbirk et al. 2001; Kuzina et al. 2009; Nielsen et al. 2010). The toxicity of saponins is at least partially due to their interactions with cell membranes, which can cause cell death (Augustin et al. 2011). The activity of isolated hederagenin cellobioside and oleanolic acid cellobioside was tested separately in no-choice feeding assays with *Ph. nemorum* adults from five different near-isogenic lines (Nielsen et al. 2010). In these experiments, hederagenin cellobioside had a much stronger negative effect on adult feeding than oleanolic acid cellobioside, whereas the corresponding aglycones of both saponins were not active. An even stronger negative effect on some *Ph. nemorum* lines was observed for α-hederin, a saponin which is not present in *B. vulgaris*, and only differs from hederagenin cellobioside in its glycosylation pattern (Nielsen et al. 2010). These results show that aglycone structure as well as glycosylation pattern affect the biological activity of saponins towards *Ph. nemorum*.

Although the saponin-based defence of *B. vulgaris* is a dead-end for most *Ph. nemorum* genotypes, resistant individuals that performed well on the G-type were found at varying frequencies in all sampled populations (Nielsen and de Jong 2005; Nielsen 2012; Vermeer et al. 2012). The ability to use the G-type as a host plant clearly shows that resistant individuals can tolerate or detoxify saponins by an unknown mechanism. In genetic analyses, Nielsen and de Jong identified the presence of dominant resistance-conferring genes (R-genes) in all resistant individuals, but divergent modes of inheritance of these R-genes (autosomal and sex-linked) between populations (Nielsen 1997a; de Jong et al. 2000; de Jong and Nielsen 2002; Nielsen 2012). For example, in the resistant population from Ejby (Denmark), two major R-genes were linked to the sex chromosomes with additional autosomal R-genes. In a resistant population from Kværkeby (Denmark), most individuals were homozygous for a single autosomal R-gene (Nielsen 1997a; de Jong et al. 2000). In crossing experiments with resistant males from a Swiss population, an autosomal R-gene was inherited only to female offspring due to non-random segregation. The most likely explanation for this non-random segregation of the autosomal R-gene together with the X chromosome is the fusion of an autosome carrying the susceptible allele to the Y-chromosome in Swiss males (Nielsen 2012). When this R-gene was introduced into the genetic background

of the susceptible *Ph. nemorum* line, it showed a normal Mendelian inheritance pattern (Nielsen 2012). These results strongly suggest that the genetic architecture of *Ph. nemorum* males differs among flea beetle populations, and that this polymorphism affects the inheritance of R-genes that enable the offspring to use the otherwise toxic *B. vulgaris* G-type as a host plant. Interestingly, attempts to generate *Ph. nemorum* lines that are homozygous for an autosomal R-gene resulted in very low survival rated of the homozygous larvae (de Jong and Nielsen 2000; Breuker et al. 2007). This observation was surprising as the homozygous resistant genotype was common at least in the *B. vulgaris*-feeding population from Kværkeby, which suggests that co-adapted genes present in the field population counteract the fitness cost of R-genes (de Jong et al. 2000; de Jong and Nielsen 2002). The genetic diversity and population structure of *Ph. nemorum* makes this species an ideal model to study the genetic basis of host range expansion in an oligophagous herbivore.

Conclusions and future directions

The flea beetle genera *Psylliodes* and *Phyllotreta* are closely associated with glucosinolate-containing plants mainly in the family Brassicaceae. Nevertheless, they differ remarkably in their overall host plant use and their adaptations to glucosinolates, the characteristic defence metabolites in Brassicaceae. While *Ph. striolata* can utilise sequestered glucosinolates for its defence against predators, *Ps. chrysocephala* apparently does not possess endogenous myrosinase activity and accumulates much lower amounts of glucosinolates compared to *Ph. striolata*. In addition, both species differ regarding their ability to detoxify glucosinolates by desulfation (Beran et al. 2014, 2018).

Despite this progress, our knowledge on the adaptations of *Phyllotreta* and *Psylliodes* to the glucosinolate-myrosinase defence is far from complete. It is unknown, for instance, whether *Phyllotreta* rapidly sequester glucosinolates to prevent their breakdown to toxic isothiocyanates, and whether *Phyllotreta* gain protection from natural enemies by activating sequestered glucosinolates using their own myrosinase. In *Ps. chrysocephala*, the importance of the various detoxification strategies and their evolution needs to be investigated. To this end, a robust phylogenetic tree of the genus and comparative studies on how other *Psylliodes* species are processing dietary glucosinolates are necessary.

A future goal is to place adaptations of *Phyllotreta* and *Psylliodes* to their glucosinolate-containing host plants into a broader evolutionary context. While recent phylogenetic studies support the hypothesis that both genera adapted independently to Brassicaceae, their relationships to other genera of Alticini remain largely unresolved (Ge et al. 2011; Ge et al. 2012; Nie et al. 2018). At this background, a comprehensive and well-resolved phylogenetic tree of the tribe Alticini will enable studies on interactions with plants in general and adaptations to plant chemical defences, and how they contributed to the evolutionary success of this megadiverse lineage.

Acknowledgements

MWG and FB are grateful for the financial support by the Max Planck Society and the International Max Planck Research School. The authors also thank Susanne Dobler (Hamburg), Theo Schmitt (Greifswald), Rolf Beutel (Jena), and Frank Fritzlar (Jena) for their comments, which improved the manuscript.

References

Agerbirk N, Olsen CE (2012) Glucosinolate structures in evolution. Phytochemistry 77: 16–45. https://doi.org/10.1016/j.phytochem.2012.02.005

Agerbirk N, Olsen CE, Nielsen JK (2001) Seasonal variation in leaf glucosinolates and insect resistance in two types of *Barbarea vulgaris* ssp *arcuata*. Phytochemistry 58: 91–100. https://doi.org/10.1016/S0031-9422(01)00151-0

Ameen AO (1996) The biology and ecology of the yellow-margined leaf beetle, *Microtheca ochroloma* Stål, (Coleoptera: Chrysomelidae) on crucifers. LSU Historical Dissertations and Theses. 6173: https://digitalcommons.lsu.edu/gradschool_disstheses/6173

Antonini G, Audisio P, Biase AD, Mancini E, Rector BG, Cristofaro M, Biondi M, Korotyaev BA, Bon MC, Konstantinov A, Smith L (2008) The importance of molecular tools in classical biological control of weeds: two case studies with yellow starthistle candidate biocontrol agents. In: Julien MH, Sforza R, Bon MC, Evans HC, Hatcher PE, Hinz HL, Rector BG (Eds) Proceedings of the XII International Symposium on Biological Control of Weeds, La Grande Motte, France, 22–27 April 2007. C.A.B. International, Wallingford, Oxfordshire, UK, 263–269.

Augustin JM, Kuzina V, Andersen SB, Bak S (2011) Molecular activities, biosynthesis and evolution of triterpenoid saponins. Phytochemistry 72: 435–457. https://doi.org/10.1016/j.phytochem.2011.01.015

Balsbaugh EU (1978) A second species of *Microtheca* Stål (Coleoptera: Chrysomelidae found in North America. The Coleopterist Bulletin 32: 219–222.

Balusu RR, Rhodes EM, Majumdar A, Cave RD, Liburd OE, Fadamiro HY (2017) Biology, ecology, and management of *Microtheca ochroloma* (Coleoptera: Chrysomelidae) in organic crucifer production. Journal of Integrated Pest Management 8: 1–10. https://doi.org/10.1093/jipm/pmx007

Bartlet E, Kiddle G, Williams I, Wallsgrove R (1999) Wound-induced increases in the glucosinolate content of oilseed rape and their effect on subsequent herbivory by a crucifer specialist. Entomologia Experimentalis et Applicata 91: 163–167. https://doi.org/10.1046/j.1570-7458.1999.00479.x

Bartlet E, Mithen R, Clark SJ (1996) Feeding of the cabbage stem flea beetle *Psylliodes chrysocephala* on high and low glucosinolate cultivars of oilseed rape. Entomologia Experimentalis et Applicata 80: 87–89. https://doi.org/10.1111/j.1570-7458.1996.tb00892.x

Bartlet E, Parsons D, Williams IH, Clark SJ (1994) The influence of glucosinolates and sugars on feeding by the cabbage stem flea beetle, *Psylliodes chrysocephala*. Entomologia Experimentalis et Applicata 73: 77–83. https://doi.org/10.1111/j.1570-7458.1994.tb01841.x

Bartlet E, Williams IH (1991) Factors restricting the feeding of the cabbage stem flea beetle (*Psylliodes chrysocephala*). Entomologia Experimentalis et Applicata 60: 233–238. https://doi.org/10.1111/j.1570-7458.1991.tb01543.x

Bartlet E, Williams IH, Blight MM, Hick AJ (1992) Responses of the oilseed rape pests, *Ceutorhynchus assimilis* and *Psylliodes chrysocephala*, to a mixture of isothiocyanates. In: Menken SBJ, Visser JH, Harrewijn P (Eds) Proceedings of the 8th International Symposium on Insect-Plant Relationships. Kluwer Academic Publishers, Dordrecht, 103–104. https://doi.org/10.1007/978-94-011-1654-1_29

Baviera C, Biondi M (2015) The Alticini (Coleoptera: Chrysomelidae, Galerucinae) of Sicily: Recent records and updated checklist. Atti della Accademia Peloritana dei Pericolanti, Classe di Scienze Fisiche, Matematiche e Naturali 93: A2-A50. https://doi.org/10.1478/AAPP.932A2

Bechyné J (1997) Evaluación de los datos sobre los Phytophaga dañinos en Venezuela (Coleoptera). Parte II. In: Savini V (Ed.) Boletín de Entomología Venezolana. Serie Monografias No 1. Aragua, Venezuela, 459 pp.

Beran F (2011) Host preference and aggregation behavior of the striped flea beetle, *Phyllotreta striolata*. Berliner ökophysiologische und phytomedizinische Schriften. Der Andere Verlag, Uelvesbüll, 143 pp.

Beran F, Pauchet Y, Kunert G, Reichelt M, Wielsch N, Vogel H, Reinecke A, Svatos A, Mewis I, Schmid D, Ramasamy S, Ulrichs C, Hansson BS, Gershenzon J, Heckel DG (2014) *Phyllotreta striolata* flea beetles use host plant defense compounds to create their own glucosinolate-myrosinase system. Proceedings of the National Academy of Sciences of the United States of America 111: 7349–7354. https://doi.org/10.1073/pnas.1321781111

Beran F, Sporer T, Paetz C, Ahn SJ, Betzin F, Kunert G, Shekhov A, Vassao DG, Bartram S, Lorenz S, Reichelt M (2018) One pathway is not enough: The cabbage stem flea beetle *Psylliodes chrysocephala* uses multiple strategies to overcome the glucosinolate-myrosinase defense in its host plants. Frontiers in Plant Science 9. https://doi.org/10.3389/fpls.2018.01754

Bieńkowski AO, Orlova-Bienkowskaja MJ (2015) Trophic specialization of leaf beetles (Coleoptera, Chrysomelidae) in the Volga Upland. Biology Bulletin 42: 863–869. https://doi.org/10.1134/S1062359015100015

Biondi M (1996) Proposal for an ecological and zoogeographical categorization of the Mediterranean species of the flea beetle genus *Longitarsus* Berthold. In: Jolivet PHA, Cox ML (Eds) Chrysomelidae Biology Volume 3: General Studies. SPB Academic Publishing bv, Amsterdam, 13–35.

Biondi M, D'Alessandro P (2018) Two new species of the flea beetle genus *Psylliodes* Latreille of the *montana* species-group from Eastern Africa (Coleoptera: Chrysomelidae). Fragmenta Entomologica 50: 87–93. doi:doi.org/10.4081/fe.2018.305

Breuker CJ, de Jong PW, Victoir K, Vrieling K, Brakefield PM (2007) Pleiotropic effects associated with an allele enabling the flea beetle *Phyllotreta nemorum* to use *Barbarea vulgaris* as a host plant. Evolutionary Ecology 21: 13–26. https://doi.org/10.1007/s10682-006-9121-0

Brown KK, Hampton MB (2011) Biological targets of isothiocyanates. Biochimica Et Biophysica Acta-General Subjects 1810: 888–894. https://doi.org/10.1016/j.bbagen.2011.06.004

Cabrera N, Rocca M (2012) First records of Chrysomelidae (Insecta, Coleoptera) on blueberries in Argentina: new associations between native chrysomelids and an exotic crop. Revista de la Sociedad Entomológica Argentina 71: 45–55.

Christensen S, Heimes C, Agerbirk N, Kuzina V, Olsen CE, Hauser TP (2014) Different geographical distributions of two chemotypes of *Barbarea vulgaris* that differ in resistance to insects and a pathogen. Journal of Chemical Ecology 40: 491–501. https://doi.org/10.1007/s10886-014-0430-4

Clark SM, LeDoux DG, Seeno TN, Riley EG, Gilbert AJ, Sullivan JM (2004) Host plants of leaf beetle species occurring in the United States and Canada (Coleoptera: Orsodacnidae, Megalopodidae, Chrysomelidae exclusive of Bruchinae). Coleopterist Society, Special Publication no. 2, 476 pp. https://doi.org/10.1603/0013-8746(2005)098[0243:HPOLBS]2.0.CO;2

Cox ML (1998) The genus *Psylliodes* Latreille (Chrysomelidae: Alticinae) in the U.K.: with keys to the adults of all species and to the larvae of those species feeding on Brassicaceae. The Coleopterist 7: 33–65.

de Jong PW, Frandsen HO, Rasmussen L, Nielsen JK (2000) Genetics of resistance against defences of the host plant *Barbarea vulgaris* in a Danish flea beetle population. Proceedings of the Royal Society B-Biological Sciences 267: 1663–1670. https://doi.org/10.1098/rspb.2000.1193

de Jong PW, Nielsen JK (2000) Reduction in fitness of flea beetles which are homozygous for an autosomal gene conferring resistance to defences in *Barbarea vulgaris*. Heredity 84: 20–28. https://doi.org/10.1046/j.1365-2540.2000.00613.x

de Jong PW, Nielsen JK (2002) Host plant use of *Phyllotreta nemorum*: do coadapted gene complexes play a role? Entomologia Experimentalis et Applicata 104: 207–215. https://doi.org/10.1046/j.1570-7458.2002.01008.x

Döberl M (2010) Subfamily Alticinae. In: Löbl I, Smetana A (Eds) Catalogue of Palearctic Coleoptera. Apollo Books, Stenstrup, Denmark, 491–563.

Edger PP, Heidel-Fischer HM, Bekaert M, Rota J, Gloeckner G, Platts AE, Heckel DG, Der JP, Wafula EK, Tang M, Hofberger JA, Smithson A, Hall JC, Blanchette M, Bureau TE, Wright SI, dePamphilis CW, Schranz ME, Barker MS, Conant GC, Wahlberg N, Vogel H, Pires JC, Wheat CW (2015) The butterfly plant arms-race escalated by gene and genome duplications. Proceedings of the National Academy of Sciences of the United States of America 112: 8362–8366. https://doi.org/10.1073/pnas.1503926112

Ehrlich PR, Raven PH (1964) Butterflies and plants - a study in coevolution. Evolution 18: 586–608. https://doi.org/10.2307/2406212

Feeny P, Paauwe KL, Demong NJ (1970) Flea beetles and mustard oils - host plant specificity of *Phyllotreta cruciferae* and *P. striolata* adults (Coleoptera: Chrysomelidae). Annals of the Entomological Society of America 63: 832–841. https://doi.org/10.1093/aesa/63.3.832

Flowers RW, Janzen DH (1997) Feeding records of Costa Rican leaf beetles (Coleoptera: Chrysomelidae). Florida Entomologist 80: 319–324. https://doi.org/10.2307/3495765

Forister ML, Novotny V, Panorska AK, Baje L, Basset Y, Butterill PT, Cizek L, Coley PD, Dem F, Diniz IR, Drozd P, Fox M, Glassmire AE, Hazen R, Hrcek J, Jahner JP, Kaman O, Kozubowski TJ, Kursar TA, Lewis OT, Lill J, Marquis RJ, Miller SE, Morais HC,

Murakami M, Nickel H, Pardikes NA, Ricklefs RE, Singer MS, Smilanich AM, Stireman JO, Villamarin-Cortez S, Vodka S, Volf M, Wagner DL, Walla T, Weiblen GD, Dyer LA (2015) The global distribution of diet breadth in insect herbivores. Proceedings of the National Academy of Sciences of the United States of America 112: 442–447. https://doi.org/10.1073/pnas.142304211

Furth DG (1979) Zoogeography and host plant ecology of the alticinae of Israel, especially *Phyllotreta*; with descriptions of three new species (Coleoptera: Chrysomelidae). Israel Journal of Entomology 28: 1–37.

Furth DG (1983) Alticinae of Israel: *Psylliodes* (Coleoptera: Chrysomelidae). Israel Journal of Entomology 17: 37–58.

Futuyma DJ, Agrawal AA (2009) Macroevolution and the biological diversity of plants and herbivores. Proceedings of the National Academy of Sciences of the United States of America 106: 18054–18061. https://doi.org/10.1073/pnas.0904106106

Gavrilović B, Gavrilović B, Ćurčić S, Stojanović D, Savić D (2014) Leaf beetles (coleoptera: Chrysomelidae) of Mt. Fruška Gora (Vojvodina Province, Northern Serbia), with an overview of host plants. Šumarski list 138: 29–41.

Ge D, Chesters D, Gómez-Zurita J, Zhang L, Yang X, Vogler AP (2011) Anti-predator defence drives parallel morphological evolution in flea beetles. Proceedings of The Royal Society B – Biological sciences 278: 2133–2141. https://doi.org/10.1098/rspb.2010.1500

Ge D, Gómez-Zurita J, Chesters D, Yang X, Vogler AP (2012) Suprageneric systematics of flea beetles (Chrysomelidae: Alticinae) inferred from multilocus sequence data. Molecular Phylogenetics and Evolution 62: 793–805. https://doi.org/10.1016/j.ympev.2011.11.028

Ge S-Q, Daccordi M, Ren J, Li W-Z, Yang X-K (2013) *Odontoedon*, a new genus from China with descriptions of nine new species (Coleoptera: Chrysomelidae: Chrysomelinae). Stuttgarter Beiträge zur Naturkunde A Neue Serie 6: 199–222.

Ge S-Q, Daccordi M, Ren J, Yang X-K (2015) Revision of *Phaedon* Latreille from China (Coleoptera: Chrysomelidae). Zoological Systematics 40: 1–30. https://doi.org/10.11865/zs.20150101

Ge S-Q, Daccordi M, Wang S-Y, Yang X-K (2009) Study of the Genus *Entomoscelis* Chevrolat (Coleoptera: Chrysomelidae: Chrysomelinae) from China. Proceedings of the Entomological Society of Washington 111: 410–425. https://doi.org/10.4289/0013-8797-111.2.410

Ge S-Q, Yang XK, Cui JZ (2003) A key to the genus *Phaedon* (Coleoptera: Chrysomelidae: Chrysomelinae) from China and the description of a new species. Entomological News 114: 75–80.

Gerber GH (1994) Biology of *Entomoscelis* Chevrolat. In: Jolivet PH, Cox ML, Petitpierre E (Eds) Novel aspects of the biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, 549–553. https://doi.org/10.1007/978-94-011-1781-4_42

Girard C, Le Metayer M, Zaccomer B, Bartlet E, Williams I, Bonade-Bottino M, Pham-Delegue MH, Jouanin L (1998) Growth stimulation of beetle larvae reared on a transgenic oilseed rape expressing a cysteine proteinase inhibitor. Journal of Insect Physiology 44: 263–270. https://doi.org/10.1016/S0022-1910(97)00142-X

Gómez-Zurita J, Juan C, Petitpierre E (2000a) The evolutionary history of the genus *Timarcha* (Coleoptera, Chrysomelidae) inferred from mitochondrial COII gene and partial

16S rDNA sequences. Molecular Phylogenetics and Evolution 14: 304–317. https://doi.org/10.1006/mpev.1999.0712

Gómez-Zurita J, Juan C, Petitpierre E (2000b) Sequence, secondary structure and phylogenetic analyses of the ribosomal internal transcribed spacer 2 (ITS2) in the *Timarcha* leaf beetles (Coleoptera: Chrysomelidae). Insect Molecular Biology 9: 591–604. https://doi.org/10.1046/j.1365-2583.2000.00223.x

González-Megías A, Gómez JM (2001) Adult and larval plant range and preference in *Timarcha lugens* (Coleoptera: Chrysomelidae): strict monophagy on an atypical host. Annals of the Entomological Society of America 94: 110–115. https://doi.org/10.1603/0013-8746(2001)094[0110:AALPRA]2.0.CO;2

Görnitz K (1956) Weitere Untersuchungen über Insekten-Attraktivstoffe aus Cruciferen. Nachrichtenblatt Deutscher Pflanzenschutzdienst 10: 137–147

Hauser TP, Toneatto F, Nielsen JK (2012) Genetic and geographic structure of an insect resistant and a susceptible type of *Barbarea vulgaris* in western Europe. Evolutionary Ecology 26: 611–624. https://doi.org/10.1007/s10682-011-9515-5

Heckel DG (2014) Insect detoxification and sequestration strategies. In: Voelckel C, Jander G (Eds) Annual Plant Reviews; Insect-Plant Interactions. Wiley-Blackwell, Chichester, 77–114. https://doi.org/10.1002/9781118472507.Ch3

Heikertinger F (1943) Die *Phyllotreta*-Arten des äthiopischen Faunengebietes. Arbeiten über morphologische und taxonomische Entomologie aus Berlin-Dahlem 10: 33–56.

Hicks KL (1974) Mustard oil glucosides: feeding stimulants for adult cabbage flea beetles, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). Annals of the Entomological Society of America 67: 261–264. https://doi.org/10.1093/aesa/67.2.261

Hill DS (2008) Pests of crops in warmer climates and their control. Springer, Netherlands, 708 pp. https://doi.org/10.1017/CBO9781107415324.004

Jeschke V, Gershenzon J, Vassão DG (2016) Insect detoxification of glucosinolates and their hydrolysis products. In: Kopriva S (Ed.) Advances in Botanical Research - Glucosinolates. Elsevier, Amsterdam, 199–245. https://doi.org/10.1016/bs.abr.2016.06.003

Jolivet P (1951) Contribution a l'etude des *Microtheca* Stål (Coleoptera Chrysomelidae) (2eme Note). Institut royal des sciences naturelles de Belgique 27: 1–7.

Jolivet P (1991) Sélection trophique chez les *Alticinae* (Coleoptera Chrysomelidae). Bulletin mensuel de la Société Linnéenne de Lyon 60: 26–40. https://doi.org/10.3406/linly.1991.10916

Jolivet P, Hawkeswood T (1995) Host-plants of Chrysomelidae of the world: an Essay about the relationships between the leaf-beetles and their Food-plants. Backhuys Publishers, Leiden, Netherlands, 281 pp.

Jolivet P, Petitpierre E (1973) Plantes-hôtes connues des *Timarcha* Latreille. Bulletin de la Société entomologique de France 78: 9–25.

Jolivet P, Petitpierre E (1976a) Les plantes-hotes connues des *Chrysolina* (Col. Chrysomelidae) Essai sur les types de selection trophique. Annales de la Société Entomologique de France 12: 123–149.

Jolivet P, Petitpierre E (1976b) Selection trophique et evolution chromosomique chez les Chrysomelinae (Col. Chrysomelidae). Acta zoologica et pathologica antverpiensia 66: 59–90.

Jurado-Rivera JA, Petitpierre E (2015) New contributions to the molecular systematics and the evolution of host-plant associations in the genus *Chrysolina* (Coleoptera, Chrysomelidae, Chrysomelinae). In: Jolivet P; Santiago-Blay, J; Schmitt, M (Eds) Research on Chrysomelidae 5 - ZooKeys 547: 165–192. https://doi.org/10.3897/zookeys.547.6018

Knodel JJ (2017) Flea Beetles (*Phyllotreta* spp.) and Their Management. In: Reddy GVP (Ed.) Integrated Management of Insect Pests on Canola and Other Brassica Oilseed Crops. CAB International, Oxfordshire, 1–12. https://doi.org/10.1079/9781780648200.0001

Konstantinov AS, Vandenberg NJ (1996) Handbook of Palearctic flea beetles (Coleoptera: Chrysomelidae: Alticinae). In: Gupta VK (Ed.) Contributions on Entomology, International. Associated Publishers, Gainesville, FL, 237–437.

Kuzina V, Ekstrøm CT, Andersen SB, Nielsen JK, Olsen CE, Bak S (2009) Identification of defense compounds in *Barbarea vulgaris* against the herbivore *Phyllotreta nemorum* by an ecometabolomic approach. Plant Physiology 151: 1977–1990. https://doi.org/10.1104/pp.109.136952

Lamb RJ (1989) Entomology of oilseed *Brassica* crops. Annual Review of Entomology 34: 211–229. https://doi.org/10.1146/annurev.en.34.010189.001235

Leonardi C (1970) Materiali per uno studio filogenetico del genere *Psylliodes* Coleoptera Chrysomelidae). Atti della Società italiana di scienze naturali e del Museo civico di storia naturale di Milano 110: 201–223.

Letsch H, Gottsberger B, Metzl C, Astrin J, Friedman ALL, McKenna DD, Fiedler K (2018) Climate and host-plant associations shaped the evolution of ceutorhynch weevils throughout the Cenozoic. Evolution 72: 1815–1828. https://doi.org/10.1111/evo.13520

Löbl I, Smetana A (2010) Catalogue of Palaearctic Coleoptera, Volume 6. Chrysomeloidea. Apollo Books, Stenstrup, Denmark, 924 pp.

Lopatin IK (2005) New species of leaf-beetles (Coleoptera, Chrysomelidae) from China: V. Entomological Review 85: 934–939.

Menezes AO, Mikami AY, Ide AK, Ventura MU (2005) Feeding preferences of *Microtheca punctigera* (Achard) (Coleoptera: Chrysomelidae) for some Brassicaceae plants in multiple-choice assays. Scientia Agricola 62: 72–75. https://doi.org/10.1590/S0103-90162005000100014

Milliron HE (1953) A European flea beetle injuring crucifers in North America. Journal of Economic Entomology 46: 179–179. https://doi.org/10.1093/jee/46.1.179

Mitchell-Olds T, Siemens D, Pedersen D (1996) Physiology and costs of resistance to herbivory and disease in *Brassica*. Entomologia Experimentalis et Applicata 80: 231–237. https://doi.org/10.1111/j.1570-7458.1996.tb00925.x

Mitchell BK (1978) Some aspects of gustation in the larval red turnip beetle, *Entomoscelis americana*, related to feeding and host plant selection. Entomologia Experimentalis et Applicata 24: 540–549. https://doi.org/10.1111/j.1570-7458.1978.tb02815.x

Mitchell BK (1988) Adult leaf beetles as models for exploring the chemical basis of host-plant recognition. Journal of Insect Physiology 34: 213–225. https://doi.org/10.1016/0022-1910(88)90052-2

Mitchell BK (1994) The chemosensory basis of host-plant recognition in Chrysomelidae. In: Jolivet PH, Cox ML, Petitpierre E (Eds) Novel aspects of the biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, 141–151. https://doi.org/10.1007/978-94-011-1781-4_7

Mithöfer A, Boland W (2012) Plant defense against herbivores: chemical aspects. Annual Review of Plant Biology 63: 431–450. https://doi.org/10.1146/annurev-arplant-042110-103854

Mohr KH (1966) Chrysomelidae. In: Freude H, Harde KW, Lohse GA (Eds) Die Käfer Mitteleuropas. Goecke & Evers Verlag, Krefeld, 95–280.

Nadein KS (2006) A significance of the tegmen structure for classification of the genus *Psylliodes* Latreille, 1829 (Coleoptera: Chrysomelidae: Psylliodina). Proceedings of the Russian Entomological Society St. Petersburg 77: 250–254.

Nadein KS (2007a) On the taxonomy and classification of the genus *Psylliodes* Latreille, 1825 (Coleoptera, Chrysomelidae, Galerucinae). Entomologica Basiliensia et Collectionis Frey 29: 307–332.

Nadein KS (2007b) A review of the leaf-beetle genus *Psylliodes* Latreille (Coleoptera, Chrysomelidae) from Russia and neighboring countries: I. A key to subgenera, species-groups, and species. Entomological Review 87: 330–360. https://doi.org/10.1134/S0013873807030086

Nadein KS (2010) A review of the genus *Psylliodes* Latreille (Coleoptera, Chrysomelidae) from Russia and neighboring countries: II. An annotated list of species. Entomological Review 90: 1035–1074. https://doi.org/10.1134/S0013873810080099

Nadein KS (2012) Catalogue of Alticini genera of the World (Coleoptera: Chrysomelidae). Beetles and Coleopterists website, Zoological Institute, Saint-Petersburg. http://www.zin.ru/Animalia/Coleoptera/eng/alticinw.htm [accessed 02.01.2019]

Nadein KS, Bezděk J (2014) Galerucinae Latreille, 1802. In: Leschen, RAB, Beutel RG (Eds) Handbook of Zoology. Coleoptera, beetles. Morphology and Systematics. Volume 3. Walter De Gruyter, Berlin/Boston, 251–259.

Nie RE, Breeschoten T, Timmermans MJTN, Nadein K, Xue HJ, Bai M, Huang Y, Yang XK, Vogler AP (2018) The phylogeny of Galerucinae (Coleoptera: Chrysomelidae) and the performance of mitochondrial genomes in phylogenetic inference compared to nuclear rRNA genes. Cladistics 34: 113–130. https://doi.org/10.1111/cla.12196

Nielsen JK (1977) Host plant relationships of *Phyllotreta nemorum* L (Coleoptera: Chrysomelidae). 1. Field Studies. Journal of Applied Entomology 84: 396–407. https://doi.org/10.1111/j.1439-0418.1977.tb04301.x

Nielsen JK (1978) Host plant discrimination within cruciferae: feeding responses of four leaf beetles (Coleoptera: Chrysomelidae) to glucosinolates, cucurbitacins and cardenolides. Entomologia Experimentalis et Applicata 24: 41–54. https://doi.org/10.1111/j.1570-7458.1978.tb02755.x

Nielsen JK (1988) Crucifer-feeding Chrysomelidae: mechanisms of host plant finding and acceptance. In: Jolivet PH, Petitpierre, E, Hsiao TH (Eds) Biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, 25–40. https://doi.org/10.1007/978-94-009-3105-3_2

Nielsen JK (1996) Intraspecific variability in adult flea beetle behaviour and larval performance on an atypical host plant. Entomologia Experimentalis et Applicata 80: 160–162. https://doi.org/10.1111/j.1570-7458.1996.tb00909.x

Nielsen JK (1997a) Genetics of the ability of *Phyllotreta nemorum* larvae to survive in an atypical host plant, *Barbarea vulgaris* ssp *arcuata*. Entomologia Experimentalis et Applicata 82: 37–44. https://doi.org/10.1046/j.1570-7458.1997.00111.x

Nielsen JK (1997b) Variation in defences of the plant *Barbarea vulgaris* and in counteradaptations by the flea beetle *Phyllotreta nemorum*. Entomologia Experimentalis et Applicata 82: 25–35. https://doi.org/10.1046/j.1570-7458.1997.00110.x

Nielsen JK (2012) Non-random segregation of an autosomal gene in males of the flea beetle, *Phyllotreta nemorum*: implications for colonization of a novel host plant. Entomologia Experimentalis et Applicata 143: 301–312. https://doi.org/10.1111/j.1570-7458.2012.01262.x

Nielsen JK, de Jong PW (2005) Temporal and host-related variation in frequencies of genes that enable *Phyllotreta nemorum* to utilize a novel host plant, *Barbarea vulgaris*. Entomologia Experimentalis et Applicata 115: 265–270. https://doi.org/10.1111/j.1570-7458.2005.00293.x

Nielsen JK, Nagao T, Okabe H, Shinoda T (2010) Resistance in the plant, *Barbarea vulgaris*, and counter-adaptations in flea beetles mediated by saponins. Journal of Chemical Ecology 36: 277–285. https://doi.org/10.1007/s10886-010-9758-6

Pachagounder P, Lamb RJ (1998) Feeding preferences of a flea beetle, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae), among wild crucifers. The Canadian Entomologist 130: 241–242. https://doi.org/10.4039/Ent130241-2

Pachagounder P, Lamb RJ, Bodnaryk RP (1998) Resistance to the flea beetle *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae) in false flax, *Camelina sativa* (Brassicaceae). The Canadian Entomologist 130: 235–240. https://doi.org/10.4039/Ent130235-2

Pentzold S, Jensen MK, Matthes A, Olsen CE, Petersen BL, Clausen H, Moller BL, Bak S, Zagrobelny M (2017) Spatial separation of the cyanogenic β-glucosidase ZfBGD2 and cyanogenic glucosides in the haemolymph of *Zygaena* larvae facilitates cyanide release. Royal Society Open Science 4: 170262. https://doi.org/10.1098/rsos.170262

Pivnick KA, Lamb RJ, Reed D (1992) Response of flea beetles, *Phyllotreta* spp, to mustard oils and nitriles in field trapping experiments. Journal of Chemical Ecology 18: 863–873. https://doi.org/10.1007/BF00988327

Ratzka A, Vogel H, Kliebenstein DJ, Mitchell-Olds T, Kroymann J (2002) Disarming the mustard oil bomb. Proceedings of the National Academy of Sciences, USA 99: 11223–11228. https://doi.org/10.1073/pnas.172112899

Reifenrath K, Müller C (2008) Multiple feeding stimulants in *Sinapis alba* for the oligophagous leaf beetle *Phaedon cochleariae*. Chemoecology 18: 19–27. https://doi.org/10.1007/s00049-007-0389-5

Rheinheimer J, Hassler M (2018) Die Blattkäfer Baden-Württembergs. Kleinsteuber Books, Karlsruhe, 928 pp.

Schoonhoven LM, Van Loon JJA, Dicke M (2005) Insect-Plant Biology. Oxford University Press, Oxford, 421 pp.

Siemens DH, Mitchell-Olds T (1996) Glucosinolates and herbivory by specialists (Coleoptera: Chrysomelidae, Lepidoptera: Plutellidae): Consequences of concentration and induced resistance. Environmental Entomology 25: 1344–1353. https://doi.org/10.1093/ee/25.6.1344

Smith EH (1985) Revision of the genus *Phyllotreta* Chevrolat of America North of Mexico. Part I. The maculate species (Coleoptera: Chrysomelidae: Alticinae). Fieldiana Zoology, 168 pp. https://doi.org/10.5962/bhl.title.3408

Tóth M, Csonka É, Bakcsa F, Benedek P, Szarukán I, Gomboc S, Toshova T, Subchev M, Ujváry I (2007) Species spectrum of flea beetles (*Phyllotreta* spp., Coleoptera, Chrysomelidae) attracted to allyl isothiocyanate-baited traps. Zeitschrift für Naturforschung 62c: 772–778. https://doi.org/10.1515/znc-2007-9-1022

Vermeer KMCA, Verbaarschot P, de Jong PW (2012) Changes in frequencies of genes that enable *Phyllotreta nemorum* to utilize its host plant, *Barbarea vulgaris*, vary in magnitude and direction, as much within as between seasons. Entomologia Experimentalis et Applicata 144: 37–44. https://doi.org/10.1111/j.1570-7458.2012.01241.x

Vig K (1996) Host plant selection by *Phyllotreta vittula* (Redtenbacher, 1849). Proceedings of the Fourth International Symposium on the Chrysomelidae, Proceedings of XX ICE, Firenze. Museo Regionale di Scienze Naturali, Torino, 233–251.

Wheat CW, Vogel H, Wittstock U, Braby MF, Underwood D, Mitchell-Olds T (2007) The genetic basis of a plant-insect coevolutionary key innovation. Proceedings of the National Academy of Sciences of the United States of America 104: 20427–20431.

Winde I, Wittstock U (2011) Insect herbivore counteradaptations to the plant glucosinolate-myrosinase system. Phytochemistry 72: 1566–1575. https://doi.org/10.1016/j.phytochem.2011.01.016

Wittstock U, Agerbirk N, Stauber EJ, Olsen CE, Hippler M, Mitchell-Olds T, Gershenson J, Vogel H (2004) Successful herbivore attack due to metabolic diversion of a plant chemical defense. Proceedings of the National Academy of Sciences, USA 101: 4859–4864. https://doi.org/10.1073/pnas.0308007101

Wittstock U, Kurzbach E, Herfurh A-M, Stauber EJ (2016) Glucosinolate breakdown. In: Kopriva S (Ed.) Advances in Botanical Research – Glucosinolates. Elsevier, Amsterdam, 125–169. https://doi.org/10.1016/bs.abr.2016.06.006

Zimmer CT, Müller A, Heimbach U, Nauen R (2014) Target-site resistance to pyrethroid insecticides in German populations of the cabbage stem flea beetle, *Psylliodes chrysocephala* L. (Coleoptera: Chrysomelidae). Pesticide Biochemistry and Physiology 108: 1–7. https://doi.org/10.1016/j.pestbp.2013.11.005

Supplementary material 1

Table S1

Authors: Matilda W. Gikonyo, Maurizio Biondi, Franziska Beran

Data type: (Species, host plants, diet breadth, geographic distribution)

Explanation note: List of *Psylliodes* species according to their subgenera, including their food plants, diet breadth and geographical distribution.

Link: https://doi.org/10.3897/zookeys.856.33724.suppl1

Supplementary material 2

Table S2

Authors: Matilda W. Gikonyo, Maurizio Biondi, Franziska Beran

Data type: (Species, host plant families)

Explanation note: Species groups of *Psylliodes* s. str. and their associated host plant families.

Link: https://doi.org/10.3897/zookeys.856.33724.suppl2

Supplementary material 3

Table S3

Authors: Matilda W. Gikonyo, Maurizio Biondi, Franziska Beran

Data type: (Species, host plants, diet breadth, geographic distribution)

Explanation note: List of *Phyllotreta* species including their food plants, diet breadth and geographical distribution.

Link: https://doi.org/10.3897/zookeys.856.33724.suppl3

ZooKeys 856: 75–100 (2018)
doi: 10.3897/zookeys.856.30838
http://zookeys.pensoft.net

RESEARCH ARTICLE

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The genus *Lochmaea* Weise, 1883 in Taiwan: results of taxonomic expeditions by citizen scientists (Coleoptera, Chrysomelidae, Galerucinae)

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Academic editor: *M. Schmitt* | Received 25 October 2018 | Accepted 12 December 2018 | Published 17 June 2019

http://zoobank.org/7AC126FD-DF70-43C2-93E2-15359F160D90

Citation: Lee C-F (2019) The genus *Lochmaea* Weise, 1883 in Taiwan: results of taxonomic expeditions by citizen scientists (Coleoptera, Chrysomelidae, Galerucinae). In: Schmitt M, Chaboo CS, Biondi M (Eds) Research on Chrysomelidae 8. ZooKeys 856: 75–100. https://doi.org/10.3897/zookeys.856.30838

Abstract

More than 520 specimens of the chrysomelid genus *Lochmaea* were available for study as the result of collecting efforts by citizen scientists. Taiwanese species of *Lochmaea* can be separated into two species groups based on presence or absence of hind wings. The *Lochmaea lesagei* group (winged) contains *L. lesagei* Kimoto, 1996 and *L. tsoui* **sp. n.** The *L. smetanai* group (wingless) contains *L. smetanai* Kimoto, 1996, *L. cheni* **sp. n.**, and *L. jungchani* **sp. n.** Members of the *L. smetanai* group inhabit alpine microhabitats and are the only wingless galerucines in Taiwan that occur in harsh environments, as is the case with most brachelytrous Chrysomelidae.

Keywords

Alpine, Ericaceae, host plants, leaf beetles, taxonomic revision

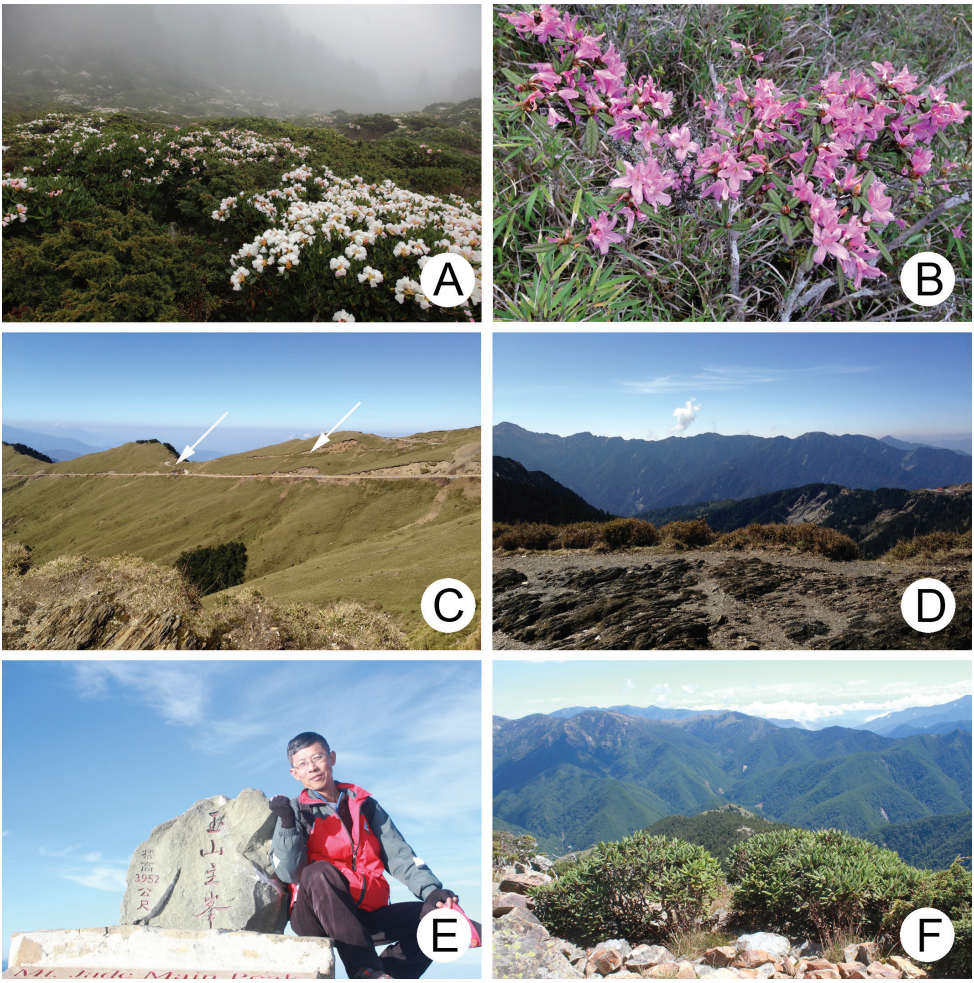
Introduction

The genus *Lochmaea* Weise belongs to the Galerucini (Beenen 2010) based on antennal insertions that are close or equal to the anterior margins of the eyes. This genus is easily distinguished from similar genera such as *Galerucella* Crotch, 1873, *Mimastracella*

Jacoby, 1903, and *Pyrrhalta* Joannis, 1865 by the absence of hairs on the dorsum with exception of *Lochmaea limbata* by having erect hairs on the dorsal surface and presence of a longitudinal convexity along the lateral margin of each elytron. Five species have been recorded from Europe and East Asia by Wilcox (1971), including *L. caprea* (Linnaeus, 1758), *L. crataegi* (Forster, 1771), *L. joliveti* Cobos, 1955, *L. limbata* Pic, 1898, and *L. suturalis* (Thomson, 1866). *Lochmaea setulosa* (Sahlberg, 1913) was transferred from *Galerucella* by Silfverberg (1974). Kimoto (1979) described a new species, *L. maculata* Kimoto, 1979 from India. *Lochmaea singalilaensis* Takizawa (1990) was also described from India. Two additional species, *L. lesagei* and *L. smetanai*, were described from Taiwan by Kimoto (1996). Beenen (1996) regarded *L. joliveti* Cobos, 1955 as a junior synonym of *L. scutellata* (Chevrolat, 1840). *Lochmaea huanggangana* Yang and Wang was described from Fujian, China (Yang et al. 1998). Bezděk (2004) removed *L. machulkai* Roubal, 1926 from synonymy with *L. crataegi* (Forster, 1771). One more species, *L. nepalica*, was described from Nepal by Medvedev (2005). Gök et al. (2006) regarded *L. setulosa* (Sahlberg, 1913) as a junior synonym of *L. limbata* Pic, 1898. In total, twelve species are, at present, recognized as valid.

Members of *Lochmaea* utilize members of Betulaceae, Salicaceae, Rosaceae, Fagaceae, Ericaceae, and Cucurbitaceae as host plants (Jolivet and Hawkeswood 1995). *Lochmaea suturalis* is well-known and referred to as "heather beetles" due to its monophagous feeding habits on heather foliage, *Calluna vulgaris* (L.) Hull (Ericaceae) ((Stephens, 1831), Cameron et al. 1944). But Waloff (1987) noted that *Erica cinerea* L., *E. tetralix* L., and various cultivated species of *Erica* may also be suitable hosts. *Crataegus monogyna* Jacq. (Rosaceae) was determined to be the host plant of *L. limbata* (Gök et al. 2006) in Turkey.

No species of this genus was described from Taiwan until recently, when *L. lesagei* (winged) and *L. smetanai* (wingless) were described by Kimoto (1996) based on three specimens lacking biological information. The distribution and biology of Taiwanese species of Chrysomelidae have been investigated by members of the Taiwan Chrysomelid Research Team (TCRT) since 2005. As a result of their activities, larvae and adults of *Lochmaea* were found feeding on various species of *Rhododendron* (Ericaceae) at different localities. For example, populations have been discovered feeding on *R. formosanum* in Lupi (魯壁, 1450 m), *R. indicum* (Fig. 4E), and *R. hyperythrum* (Fig. 4C, D) in Lengshuikeng (冷水坑, 750 m), *R. pseudochrysanthum* in various localities above 2000 m (Fig. 4A, F). Moreover, wingless populations of *Lochmaea* were found only in alpine habitats above 3000 m. *Rhododendron pseudochrysanthum* are dominant plants in alpine regions and are the preferred hosts for wingless *Lochmaea* species. Members of this genus bloom and sprout during late spring (May and June) (Fig. 1A, B). In Taiwan, more than 250 mountains exceed 3000 m elevation, but only a few are easily accessable by hiking. Hehuanshan Moutain's Main Peak (合歡山主峰, 3400 m) (Fig. 1C) and surrounding mountains (Eastern Peak, 3420 m; Western Peak 3145 m) can be accessed by walking only an hour since they are near the Central Cross-Island Highway (中横



Figures 1. Field photographs. **A** *Rhododendron pseudochrysanthum* blooming in June, Hsuehshan **B** *R. rubropilosum* Hayata var. *taiwanalpinum* blooming in June, Hehuanshan **C** Central Cross-Island Highway, arrows indicate road to top of Hehuanshan Main Peak **D** Wuling (武嶺), 3275 m, the highest spot at the Central Cross-Island Highway **E** Jung-Chan Chen, a member of the Taiwan Chrysomelid Research Team, at the top of Yushan Main Peak, 3952 m **F** *R. pseudochrysanthum* , common at the top of Yushan East Peak.

公路) (Fig. 1D). Other mountains require days of climbing. Mr Jung-Chan Chen (陳榮章) (Fig. 1E), one member of TCRT, is capable of such hikes. For example, he took two days to reach the top of Yushan Main Peak (玉山主峰, 3952 m), but collecting was unproductive due to presence of only small host plants. He subsequently hiked for three days to reach the tops of Yushan East Peak (玉山東峰, 3869 m) (Fig. 1F), Yushan West Peak (玉山西峰, 3518 m), and Yushan North Peak (玉山北峰, 3833 m) and collected more than 30 specimens. These are in addition to

material collected from various mountains by him during several years. As a result, species richness and distributions for each species of this genus can be accurately delimited based on robust sampling.

Beenen and Jolivet (2008) stated that most of brachelytrous chrysomelids (correlated with reduction of hind wings) occur in harsh environments including deserts, islands, and alpine regions. The proposed adaptive explanation for this condition is that in harsh environments energy has to be invested as efficiently as possible and investing in flight is maladaptive. *Lochmaea* is a unique genus in that it contains both winged species (*L. lesagei*) and wingless species (*L. smetanai*) in Taiwan. Thus, it is a good example to test whether the two species groups fit assumptions based on distributions in harsh habitats and correlated wing reduction.

Materials and methods

Prior to the current study, a small number of specimens were collected using sweep nets and deposited at the Taiwan Agricultural Research Institute (**TARI**). Additional specimens collected using Malaise traps are deposited at the National Museum of Natural Science, Taichung (**NMNS**). Although adults are nocturnal, they stay on hosts during daytime where they can be collecting using sweep nets. They are active and walking during night time. Malaise traps can be effective, but beating host plants at night is the most effective way to collect adults, especially on plants with obvious feeding damage. In total, more than 520 specimens were available for this study using these collecting methods.

For rearing studies, larvae were placed in plastic containers (diameter 90 mm × height 57 mm) with cuttings from their host plants. When mature larvae began searching for pupation sites, they were transferred to other plastic containers of the same size but filled with moist soil (about 80% of container volume).

For taxonomic study, the abdomens of adults were separated from the forebody and boiled in 10% KOH solution, followed by washing in distilled water to prepare genitalia for illustrations. The genitalia were then dissected from the abdomen, mounted on slides in glycerin, and studied and drawn using a Leica M165 stereomicroscope. For detailed examinations a Nikon ECLIPSE 50i microscope was used.

At least two pairs from each species were examined to delimit variability of diagnostic characters. For species collected from more than one locality, at least one pair from each locality was examined. Length was measured from the anterior margin of the eye to the elytral apex, and width at the greatest width of the elytra.

Exact label data are cited for all type specimens of described species; a double slash (//) divides the data on different labels and a single slash (/) divides the data in different rows. Other comments and remarks are in square brackets: [p] – preceding data are printed, [h] – preceding data are handwritten, [w] – white label, [y] – yellow label, [g] – green label, [b] – blue label, and [r] – red label.

Key to Taiwanese species of *Lochmaea*

1 Elytral humerus and hind wing well developed (Fig. 2).....**2 (*L. lesagei* group)**
– Elytral humerus and hind wing reduced (Figs 8, 11)..... **3 (*L. smetanai* group)**
2 Median lobe symmetrical, with apex rounded (Fig. 3C); southern Taiwan.... ..... ***L. lesagei* Kimoto**
– Median lobe asymmetrical, with apex tapering (Fig. 6C); northern Taiwan... .....***L. tsoui* sp. n.**
3 Elytra green, with yellowish brown suture and lateral margins (Fig. 11A–C); median lobe parallel-sided (Fig. 12C); apical margin of abdominal ventrite V in females with median notch narrow and shallow (Fig. 12I) .....***L. cheni* sp. n.**
– Elytra entirely reddish brown or yellowish brown (Figs 8, 11D–F); median lobe apically tapering (Figs 9C, 13C); apical margin of ventrite V in female with median notch angular (Fig. 9I) or margined with longitudinal ridges (Fig. 13I) **4**
4 Median lobe relatively broader, 5.7× longer than wide, elongate endophallic sclerite relatively longer, 0.7× as long as median lobe (Fig. 9C, D); apical margin of abdominal ventrite V in females with median notch angular (Fig. 9I).... .....***L. smetanai* Kimoto**
– Median lobe relatively more narrow, 6.8× longer than wide, elongate endophallic sclerite relatively shorter, 0.5× as long as median lobe (Fig. 13C, D); apical margin of abdominal ventrite V in females with median notch narrow and margined with longitudinal ridges (Fig. 13I).....***L. jungchani* sp. n.**

Lochmaea lesagei species group

Members of this species group have well-developed elytral humeri and hind wings. Two species are recognized in Taiwan: *L. lesagei* Kimoto in South Taiwan and *L. tsoui* sp. n. in North Taiwan.

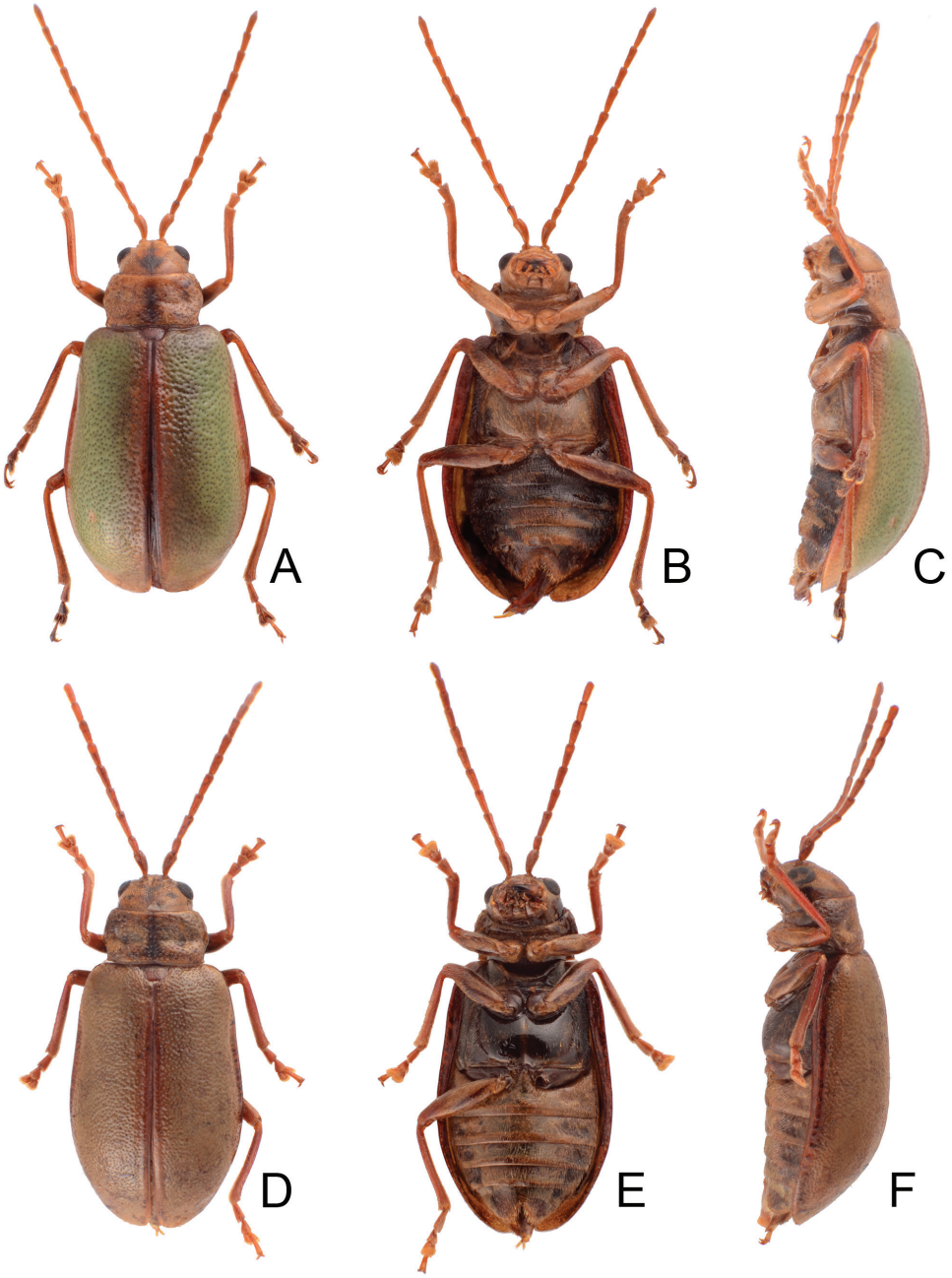
Lochmaea lesagei Kimoto, 1996

Figs 2A–C, 3, 4A, B

Lochmaea lesagei Kimoto, 1996: 32.

Type material. Holotype ♂ (NMNS), labeled: "TAIWAN: Yushan / Nat. Park Mun-li / Cliff. 27.IV.90 / L. LeSage 2700 m [p, w] // Lochmaea / lesagei / Kimoto, n. sp. [h] / Det. S. Kimoto, 19 [p, w] // HOLOTYPE [p, r] // 2279-4 [p, w]".

Other material examined (n = 109). Chiayi: 2♂♂, 2♀♀ (TARI), Alishan (阿里山), 2400 m, 5–9.VIII.1981, leg. L.-Y. Chou & S.-C. Lin; **Hualien**: 1♂ (TARI), Tay-



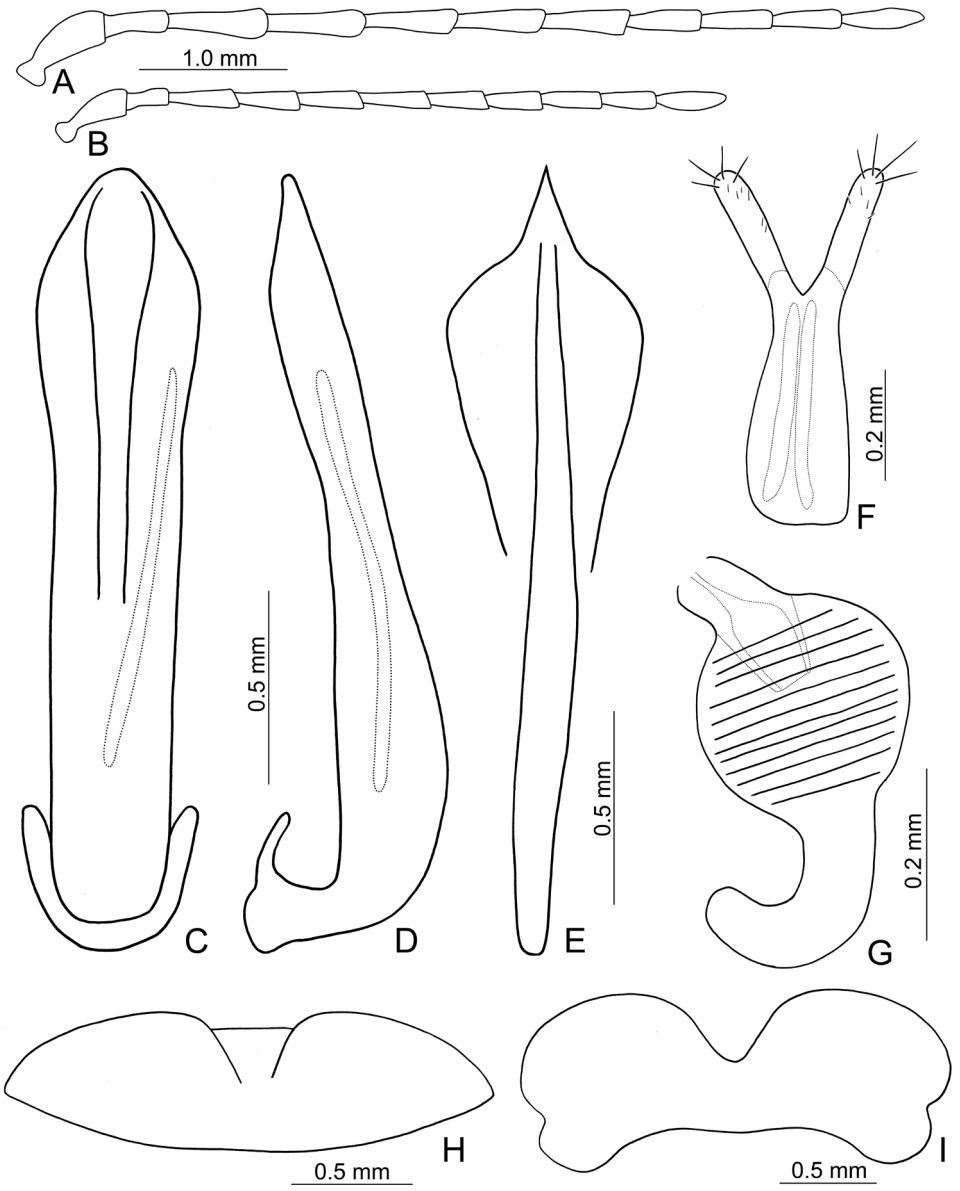
Figures 2. Habitus of *Lochmaea* species. **A** *L. lesagei* Kimoto, female, dorsal view **B** Ditto, ventral view **C** Ditto, lateral view **D** *L. tsoui* Lee, sp. n., female, dorsal view **E** Ditto, ventral view **F** Ditto, lateral view.

uling (大禹嶺), 2550 m, 12–15.IX.1980, leg. K.-S. Lin & C.-H. Wang; 1♀ (TARI), same locality, 3.VIII.2015, leg. Uika; **Nantou**: 1♂ (TARI), Chilai South Peak (奇萊南峰), 3350 m, 23.VII.2017, leg. J.-C. Chen; 1♀ (TARI), Hehuanshan (合歡山), 3400

m, 6.IX.2017, leg. Y.-F. Hsu; 3♂♂ (TARI), Hsiaochilai (小奇萊), 3150 m, 23.IX.2016, leg. J.-C. Chen; 2♀♀ (TARI), Huakang (華崗), 2550 m, 12.IX.2010, leg. C.-F. Lee; 9♂♂, 9♀♀ (TARI), Kunyang (昆陽), 3050 m, reared from larvae, 23.VI.2009, leg. C.-F. Lee; 2♂♂, 2♀♀ (TARI), Tatachia (塔塔加), 2600 m, 20–21.VII.2009, leg. H. Lee; 2♂♂, 2♀♀ (TARI), same locality, 20.VII.2009, leg. C.-F. Lee; 1♂ (TARI), same locality, 21.IX.2009, leg. C.-F. Lee; 19♂♂, 19♀♀ (TARI), same locality, 9.IX.2015, leg. C.-F. Lee; 2♂♂, 1♀ (TARI), Tsuifeng (翠峰), 2300 m, 1–3.VIII.1981, leg. T. Lin & W.-S. Tang; 2♀♀ (TARI), same locality, 1–3.IX.1982, leg. L.-Y. Chou & K.-C. Chou; 1♂, 2♀♀ (TARI), same locality, 12–14.IX.1984, leg. K.-S. Lin & S.-C. Lin; 1♂, 1♀ (NMNS), Wushe (霧社), 1150 m, 15.X.2002, leg. C.-S. Lin; 1♀ (NMNS), Yuanfeng (鳶峰), 2750 m, 13.VI.-18.VII.2001, leg. C.-S Lin & W. T. Yang; 1♂ (NMNS), same but with "7.VIII.-11.IX.2001"; 1♂ (NMNS), same but with "9.IV.-7.V.2002"; 1♂ (NMNS), same but with "9.VII.-13.VIII.2002"; 1♂, 1♀ (NMNS), same but with "13.VIII.-10.IX.2002"; 1♀ (NMNS), same but with "10.IX.-15.X.2002"; 1♀ (NMNS), same but with "15.X.-12.XI.2002"; 1♀ (NMNS), same but with "7.V.-11.VI.2003"; 1♂ (NMNS), same but with "8.VII.-5.VIII.2003"; 1♂ (NMNS), same but with "7.X.-4.XI.2003"; 1♂ (NMNS), same but with "5.X.-16.XI.2004"; 1♂ (NMNS), same but with "4.X.-8.XI.2005"; 1♀ (NMNS), same but with "21.IX.-17.X.2006"; **Pingtung**: 1♂ (TARI), Peitawushan (北大武山), 3050 m, 15.VIII.2016, leg. Y.-M. Weng; **Taichung**: 1♀ (TARI), Nanhutashan (南湖大山), 3700 m, 23.VII.2016, leg. J.-C. Chen; **Taitung**: 1♂, 5♀♀ (TARI), Hsiangyangshan (向陽山), 3600 m, 20.VI.2014, leg. J.-C. Chen; 1♂ (TARI), same but with "19.IX.2014".

Diagnosis. *Lochmaea lesagei* Kimoto cannot be distinguished from *L. tsoui* sp. n. based on external morphology but it differs by the rounded apex of the symmetrical median lobe (Fig. 3C) (tapering apex of asymmetrical median lobe (Fig. 6C) in *L. tsoui* sp. n.), the acute apex of abdominal ventrite VIII in females (Fig. 3E) (rounded apex (Fig. 6E) in *L. tsoui* sp. n.), and northern Taiwan distribution (southern Taiwan in *L. tsoui* sp. n.).

Redescription. Length 6.6–7.4 mm, width 3.3–2.9 mm. General color (Fig. 2A, C) yellowish brown to reddish brown; vertex and pronotum with median longitudinal dark band; each elytron green but with wide yellowish brown band along suture and lateral margin. Antennae filiform in males (Fig. 3A), length ratios of antennomeres I–XI 1.0 : 0.6 : 1.0 : 1.0 : 1.0 : 0.9 : 0.9 : 0.7 : 0.7 : 0.7 : 0.9, length to width ratios of antennomeres I–XI 2.7 : 3.0 : 3.3 : 3.4 : 3.6 : 3.6 : 3.6 : 3.5 : 3.7 : 3.6 : 4.0; much shorter in females (Fig. 3B), length ratios of antennomeres I–XI 1.0 : 0.5 : 0.9 : 0.8 : 0.9 : 0.9 : 0.7 : 0.7 : 0.7 : 0.7 : 0.9, length to width ratios of antennomeres I–XI 2.7 : 2.2 : 3.7 : 3.3 : 3.8 : 3.6 : 3.0 : 3.1 : 3.3 : 3.1 : 3.6. Pronotum transverse, 1.8× wider than long, disc with dense, extremely coarse punctures, and one pair of lateral depressions; lateral margins strongly narrowed basally; margins concave basally and apically. Elytra elongate and parallel-sided, 1.4× longer than wide; disc with random, dense, coarse punctures. Apical margin of abdominal ventrite V in males with median notch bearing short, longitudinal ridges along margin, concave between ridges (Fig. 3H). Ventrite V in females with deep, wide, median, rounded notch (Fig. 3I). Median lobe symmetrical, (Fig. 3C, D) slender, 6.4× longer than wide, parallel-sided from base to



Figures 3. Diagnostic characters of *Lochmaea lesagei* Kimoto. **A** Antenna, male **B** Antenna, female **C** Median lobe, dorsal view **D** Median lobe, lateral view **E** Abdominal ventrite VIII **F** Gonocoxae **G** Spermatheca **H** Abdominal ventrite V, male **I** Abdominal ventrite V, female.

apical 1/3, broader towards 1/7, widest at apical 1/7, apex rounded; opening elongate, apically broader; in lateral view almost straight, strongly curved near base, apically narrowed from apical 1/7; internal sac with one elongate sclerite, 0.6× as long as median lobe. Gonocoxae (Fig. 3F) elongate, membranous except apical parts, with one pair of

weakly sclerotized, elongate sclerites at base; apical parts elongate, bearing tiny, scattered setae and four long setae at apices. Ventrite VIII (Fig. 3E) longitudinal and well sclerotized; apex acute; abruptly broader at apical 1/5, spiculum long and wide. Receptacle of spermatheca (Fig. 3G) strongly swollen; pump slender and strongly curved; proximal spermathecal duct deeply inserted into receptacle, broad but short.

Host plants. Ericaceae: *Rhododendron pseudochrysanthum* Hayata (Fig. 4A, B) and *R. rubropilosum* Hayata var. *taiwanalpinum* (Ohwi).

Biology. Larvae appear when host plants begin sprouting. A number of young larvae (first-instar) were collected from *Rhododendron pseudochrysanthum* in Kunyang (昆陽) (3050 m), May 18, 2009 and transferred to the laboratory for rearing. Mature larvae burrowed into the soil and built underground chambers for pupation after seven days (May 25). Adults emerged from soil after 24 days (June 28). Twenty larvae emerged successfully as adults. From this sample, eighteen adults were identified as *L. lesagei* (winged) and the other two as *L. smetanai* (wingless). Adults appeared in the field from late June to October.

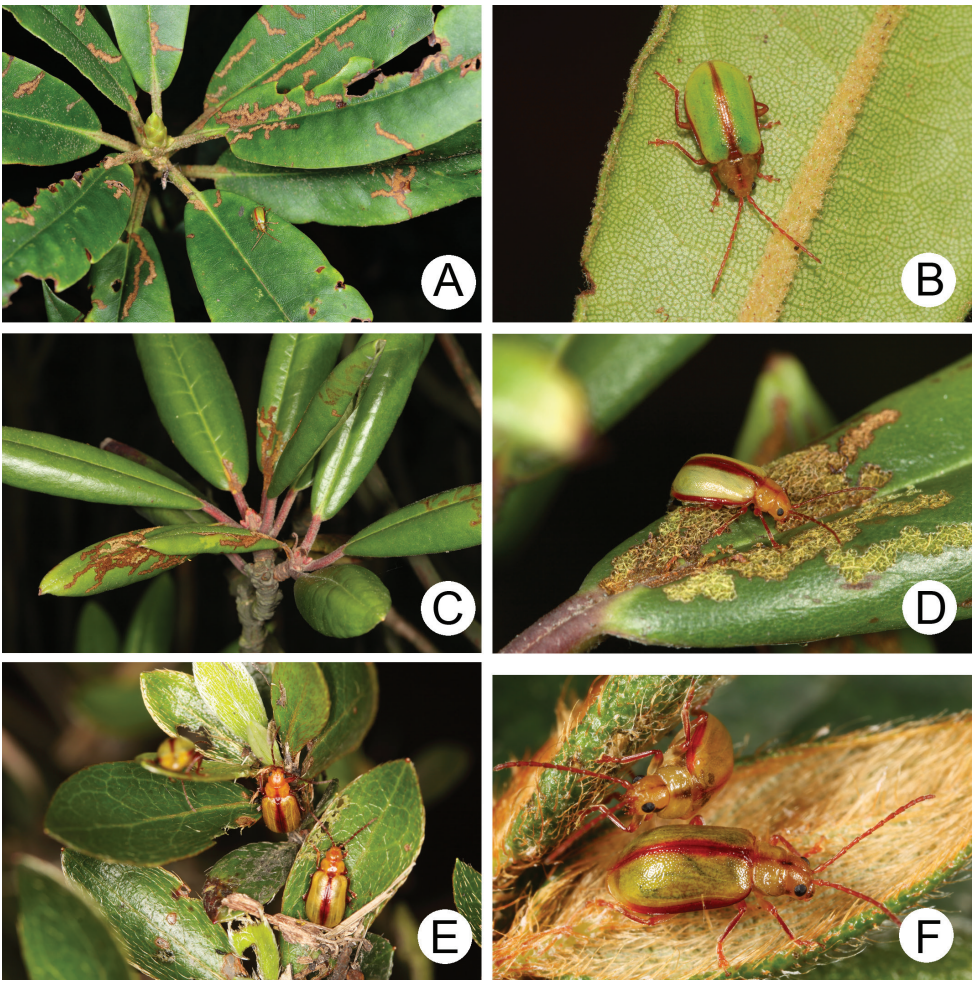
Distribution. Southern Taiwan, including Nantou, Hualien, Chiayi, Pingtung, Taitung, and Taichung (only found in Nanhutashan (南湖大山)) Counties (Fig. 5A).

***Lochmaea tsoui* sp. n.**
http://zoobank.org/570DA489-1D13-4208-80D8-0D253EA53573
Figs 2A–2C, 4C–4F, 6, 7

Type material (n = 84). Holotype ♂ (TARI). **Hsinchu**: Lupi (魯壁), 1450 m, 26.VII.2008, leg. M.-H. Tsou. Paratypes. 5♂♂, 4♀♀ (TARI), same data as holotype; 4♂♂, 4♀♀ (TARI), same but with "20.VII.2008"; 1♀ (TARI), Kuanwu (觀霧), 2200 m, 6.XI.2009, leg. H. Lee; **Ilan**: 1♂, 1♀ (TARI), Tsuifenghu (翠峰湖), 1900 m, 3.VII.2010, leg. M.-H. Tsou; **Taichung**: 1♂ (TARI), Cika Lodge (七卡山莊), 2450 m, 30.IV.2012, leg. T.-H. Lee; 3♂♂, 1♀ (TARI), same locality, 3.IX.2014, leg. T.-H. Lee; 1♂ (TARI), Hsuehshan (雪山), 3850 m, 7.X.2011, leg. W.-B. Yeh; 1♂ (TARI), same but with "26.VI.2017"; 1♂ (TARI), same but with "15.VIII.2017"; 3♂♂, 3♀♀ (TARI), Kupo (哭坡), 2950 m, 2.IX.2014, leg. J.-C. Chen; 1♂ (TARI), Tahsuchshan (大雪山), 2550 m, 23.VII.2011, leg. J.-C. Chen; **Taipei**: 2♂♂, 7♀♀ (TARI), Lengshuikeng (冷水坑), 750 m, 26.V.2009, leg. J.-C. Chen; 9♂♂, 22♀♀ (TARI), same locality, 28.V.2009, leg. M.-H. Tsou; 3♂♂, 4♀♀ (TARI), same locality, 13.VI.2009, leg. H. Lee; **Taoyuan**: 1♂ (TARI), Lalashan (拉拉山), 1600 m, 30.X.2008, leg. S.-F. Yu.

Diagnosis. *Lochmaea tsoui* sp. n. cannot be distinguished from *L. lesagei* Kimoto based on external morphology but differs by the tapering apex of the asymmetrical median lobe (Fig. 6C) (rounded apex of symmetrical median lobe (Fig. 3C) in *L. lesagei*), the rounded apex of abdominal ventrite VIII in females (Fig. 6E) (acute apex (Fig. 3E) in *L. lesagei*), and northern Taiwan distribution (southern Taiwan in *L. lesagei*)

Description. Length 5.3–6.8 mm, width 2.7–3.3 mm. General color (Fig. 2D–F) yellowish brown to reddish brown; each elytron green but with wide yellowish brown



Figures 4. Field photographs. **A** Adult of *Lochmaea lesagei* on the leaves of *Rhododendron pseudochrysanthum* at Tatachia **B** Same species also on *R. pseudochrysanthum* at Hsiangyangshan **C** Feeding marks on *R. hyperythrum* by *L. tsoui* sp. n. **D** Adult of *Lochmaea tsoui* sp. n. feeding leaves of *R. hyperythrum* at Lengshuikeng **E** Many adults of *L. tsoui* sp. n. were found on leaves of *R. indicum* at Lengshuikeng **F** Adults of *L. tsoui* sp. n. on the leaves of *R. pseudochrysanthum* at Hsuehshan.

band along suture and lateral margin. Antennae filiform in males (Fig. 6A), length ratios of antennomeres I–XI 1.0 : 0.7 : 1.1 : 1.0 : 0.9 : 0.9 : 0.9 : 0.8 : 0.8 : 0.7 : 0.9, length to width ratios of antennomeres I–XI 2.6 : 2.4 : 3.7 : 3.1 : 2.9 : 2.9 : 2.9 : 2.5 : 2.6 : 2.4 : 3.2; similar in females (Fig. 6B), length ratios of antennomeres I–XI 1.0 : 0.5 : 0.8 : 0.8 : 0.7 : 0.7 : 0.7 : 0.6 : 0.6 : 0.6 : 0.7, length to width ratios of antennomeres I–XI 2.4 : 2.1 : 3.2 : 3.0 : 2.6 : 2.7 : 2.7 : 2.8 : 2.9 : 2.9 : 3.2. Pronotum transverse, 1.8× wider than long, disc with dense, extremely coarse punctures, and one pair of lateral depressions; lateral margins strongly narrowed basally; margins concave basally and apically. Elytra elongate and parallel-sided, 1.4× longer than wide; disc with random, dense, coarse

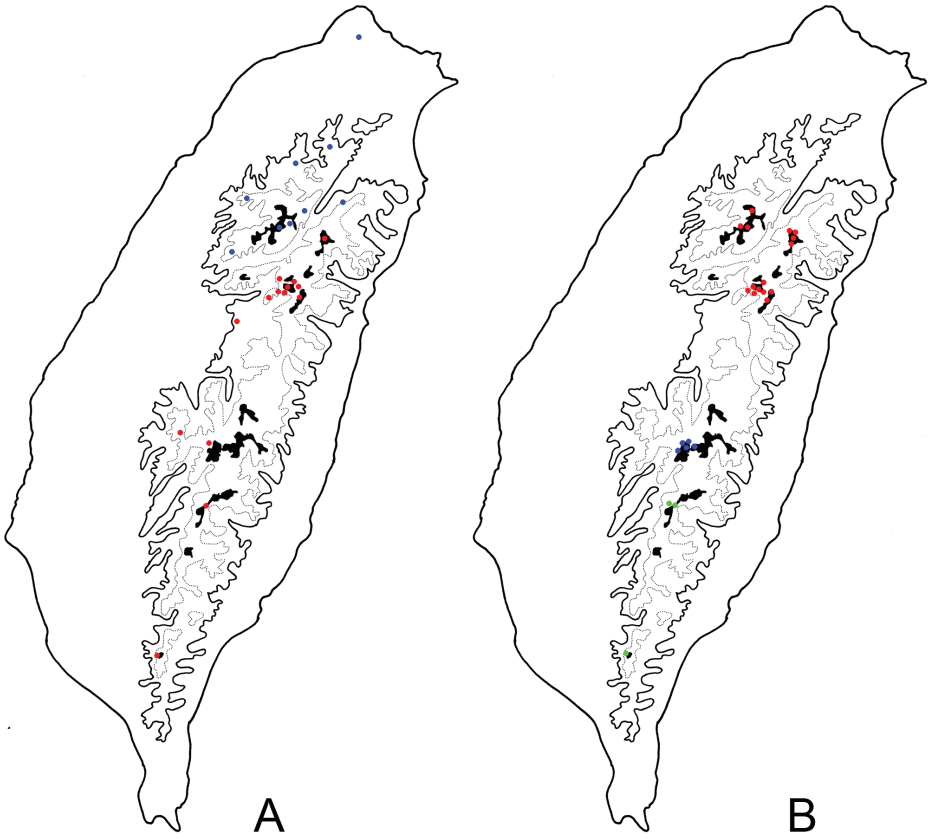
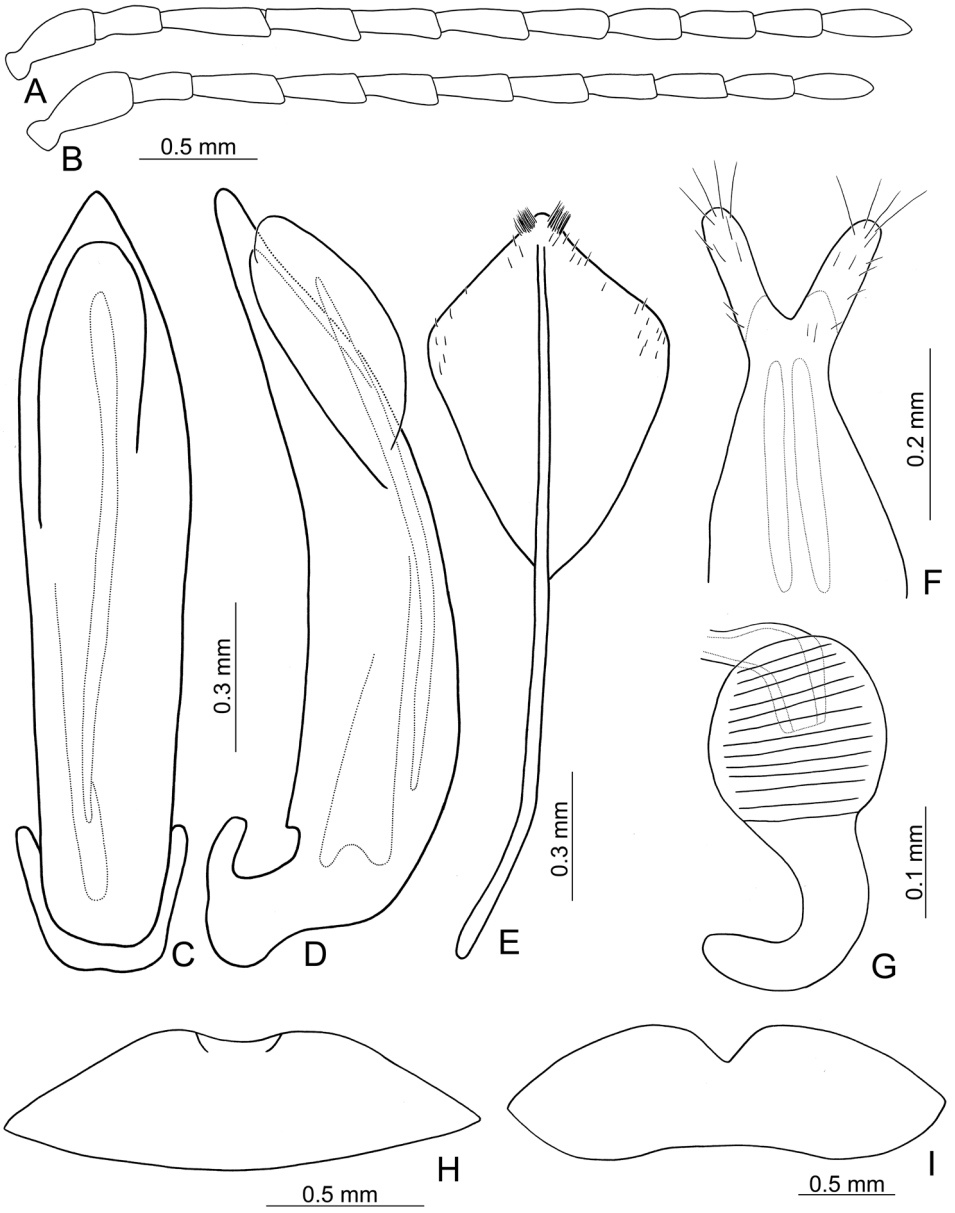


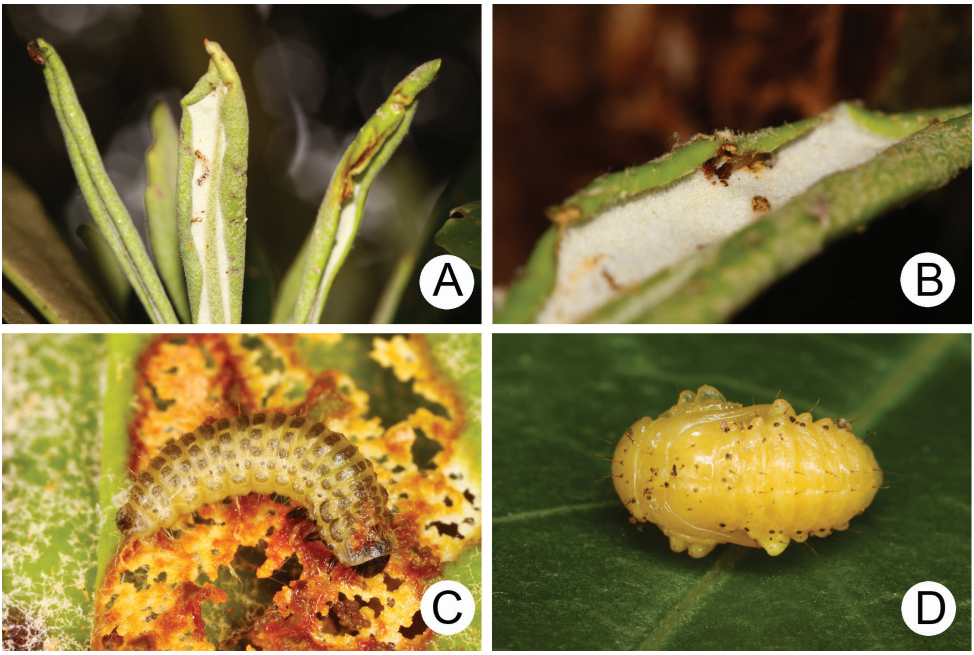
Figure 5. Distribution map of *Lochmaea* species, solid line: 1000 m, broken line: 2000 m, black areas: 3000 m. **A** *L. lesagei* group. Key: Red Dots *L. lesagei* Kimoto Blue Dots *L. tsoui* sp. n. **B** *L. smetanai* group. Red Dots *L. smetanai* Kimoto Blue Dots *L. jungchani* sp. n Green Dots *L. cheni* sp. n.

punctures. Apical margin of abdominal ventrite V in males with median notch, bearing short, longitudinal ridges along margin, shallow concave between ridges (Fig. 6H). Ventrite V in females with shallow, wide, median, angular notch (Fig. 6I). Median lobe (Fig. 6C, D) broad, 4.8× longer than wide, asymmetrical, left lateral margin straight, right lateral margin widest at apical 1/5, apically tapering; opening broad, located on right, starting from apical 1/12; in lateral view strongly curved, distinctly oblique; internal sac with one elongate sclerite, 0.8× as long as median lobe, one additional sclerite located near base of elongate sclerites, base wide and bifurcate, apically membranous. Gonocoxae (Fig. 6F) elongate, membranous except apical parts, with one pair of weakly sclerotized, elongate sclerites at base; apical parts elongate, bearing tiny, scattered setae and four long setae at apices. Ventrite VIII (Fig. 6E) longitudinal and well sclerotized; apex rounded; abruptly broader at apical 1/5, with paired cluster of long setae near middle, disc bearing tiny, scattered setae along apical margin; spiculum long and narrow. Receptacle of spermatheca (Fig. 6G) strongly swollen; pump slender and strongly curved; proximal spermathecal duct deeply inserted into receptacle, broad but short.



Figures 6. Diagnostic characters of *Lochmaea tsoui* Lee sp. n. **A** Antenna, male **B** Antenna, female **C** Penis, dorsal view **D** Penis, lateral view **E** Abdominal ventrite VIII **F** Gonocoxae **G** Spermatheca **H** Abdominal ventrite V, male **I** Abdominal ventrite V, female.

Host plants. Ericaceae: *Rhododendron formosanum* Hemsl., *R. indicum* (L.) Sweet (introduced species) (Fig. 4E), and *R. hyperythrum* Hayata (Fig. 4C, D), and *R. pseudochrysanthum* Hayata (Fig. 4F).



Figures 7. Ecological photography of *Lochmaea tsoui* Lee sp. n. **A** Feeding marks made by mining first-instar larvae **B** First-instar larva concealed inside coiled leaf **C** Third-instar larva **D** Pupa.

Biology. Different species of *Rhododendron* are available as food plants at different localities. A population feeds on *R. formosanum* in Lupi (魯壁, 1450 m), *R. indicum,* and *R. hyperythrum* in Lengshuikeng (冷水坑, 750 m), and *R. pseudochrysanthum* in various localities above 2000 m. First-instar larvae were collected in Lupi (魯壁, 1450 m) and transferred to the laboratory for rearing in April 4, 2009. They mined leaves (Fig. 7A), and some concealed themselves inside coiled leaves (Fig. 7B). Mature larvae (Fig. 7C) burrowed in soil and built underground chambers for pupation (Fig. 7D) after 15 days (April 19). Adults emerged from soil after 23 days. Adults appeared in the field from June to November.

Etymology. This new species is named after Mr. Mei-Hua Tsou, a member of the TCRT and the first to collect this new species.

Distribution. Northern Taiwan (Fig. 5A), including Taipei, Ilan, Taoyuan, Hsinchu, and Taichung Counties.

Lochmaea smetanai species group

Members of this species group have reduced elytral humeri and hind wings. Three species are recognized in Taiwan: *L. smetanai* Kimoto in northern Taiwan, *L. cheni* sp. n. in central Taiwan, and *L. jungchani* sp. n. in southern Taiwan.

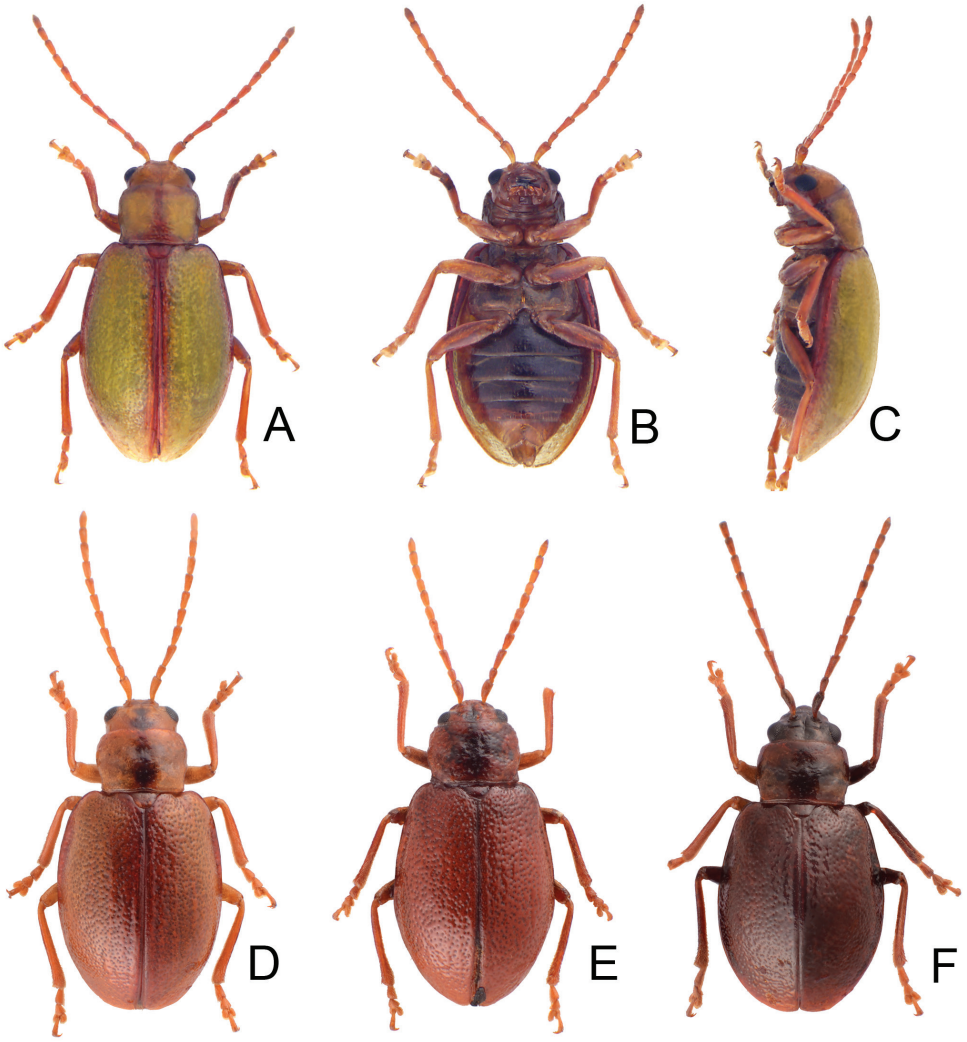
***Lochmaea smetanai* Kimoto, 1996**
Figs 8, 9, 10A–10C

Lochmaea smetanai Kimoto, 1996: 30.

Type material. Holotype ♂ (NMNS), labeled: "TAIWAN Taichung Hsien / Hsuehshan, Hsuehshan / Main Peak 3650 m / 9.V.91 A. Smetana [T73] // Lochmaea / smetanai / Kimoto, n. sp. [h] / Det. S. Kimoto, 19 [p, w] // HOLOTYPE [p, r] // 2279-3 [p, w]".

Other material examined (n = 233). Hualien: 3♂♂, 4♀♀ (TARI), Chilai North Peak (奇萊北峰), 3600 m, 21.X.2017, leg. J.-C. Chen; **Miaoli**: 4♂♂, 10♀♀ (TARI), Chungpaping (中霸坪), 3300 m, 23.VI.2018, leg. J.-C. Chen; 4♂♂, 4♀♀ (TARI), Tsuichih Lodge (翠池山莊), 3550 m, 2.IX.2014, leg. J.-C. Chen; 19♂♂, 19♀♀ (TARI), same but with "leg. T.-H. Lee"; **Nantou**: 2♂♂, 3♀♀ (TARI), Chilai South Peak (奇萊南峰), 3350 m, 2.IX.2017, leg. J.-C. Chen; 6♂♂, 6♀♀ (TARI), Hehuanshan (合歡山), 3400 m, 26.VII.2014, leg. J.-C. Chen; 1♂, 4♀♀ (TARI), same locality, 30.VII.2014, leg. T.-H. Lee; 21♂♂, 13♀♀ (TARI), same but with "leg. C.-F. Lee"; 5♀♀ (TARI), same locality, 9.VIII.2014, leg. M.-H. Tsou; 3♂♂, 2♀♀ (TARI), Hehuan Eastern Peak (合歡東峰), 3420 m, 23.VII.2015, leg. J.-C. Chen; 2♂♂, 5♀♀ (TARI), same but with "22.VI.2016"; 7♂♂, 5♀♀ (TARI), Hehuan Western Peak (合歡西峰), 3145 m, 23.VI.2016, leg. J.-C. Chen; 5♂♂, 2♀♀ (TARI), Hsiaochilai (小奇萊), 3150 m, 23.IX.2016, leg. J.-C. Chen; 4♂♂, 3♀♀ (TARI), same but with "22.X.2016"; 1♂, 1♀ (TARI), Kunyang (昆陽), 3050 m, reared from larvae, 23.VI.2009, leg. C.-F. Lee; 1♂, 1♀ (NMNS), Yuanfeng (鳶峰), 2750 m, 7.VIII.-11.IX.2001, leg. C.-S. Lin & W.-T. Yang; 2♂♂, 1♀ (NMNS), same but with "16.X.-14.XI.2001"; 1♂ (NMNS), same but with "12.III.-9.IV.2002"; 1♀ (NMNS), same but with "9.VII.-13.VIII.2002"; 1♂ (NMNS), same but with "13.VIII.-10.IX.2002"; 1♂, 1♀ (NMNS), same but with "17.IV.-7.V.2003"; 2♂♂ (NMNS), same but with "11.VI.-8.VII.2003"; 1♂ (NMNS), same but with "4.XI.-15.XII.2003"; 1♂ (NMNS), same but with "5.X.-16.XI.2004"; 1♂ (NMNS), same but with "8.XI.-8.XII.2005"; 1♀ (NMNS), same but with "2–30.X.2007"; 1♀ (TARI), same locality, 29.VII.2014, leg. C.-F. Lee; 1♀ (TARI), same locality, 9.IX.2014, leg. C.-F. Lee; 3♂♂, 2♀♀ (TARI), same locality, 9.VIII.2014, leg. M.-H. Tsou; **Taichung**: 3♀♀ (TARI), Chungyangchienshan (中央尖山), 3705 m, 29.VII.2018, leg. J.-C. Chen; 1♂ (TARI), Hsuehshan (雪山), 3850 m, 1.IV.2010, leg. W.-B. Yeh; 1♂ (TARI), same but with "18.VI.2010"; 1♂, 1♀ (TARI), same but with "10.VI.2011"; 3♂♂, 1♀ (TARI), same locality, 3.IX.2014, leg. J.-C. Chen; 1♂, 2♀♀ (TARI), Nanhupeishan (南湖北山), 3536 m, 26.VII.2018; 7♂♂, 4♀♀ (TARI), Nanhutashan (南湖大山), 3700 m, 23.VII.2016, leg. J.-C. Chen; 3♂♂, 5♀♀ (TARI), Shengmacheng (審馬陣), 3200 m, 26.V.2018, leg. J.-C. Chen; 1♂ (TARI), same but with "26.VII.2018".

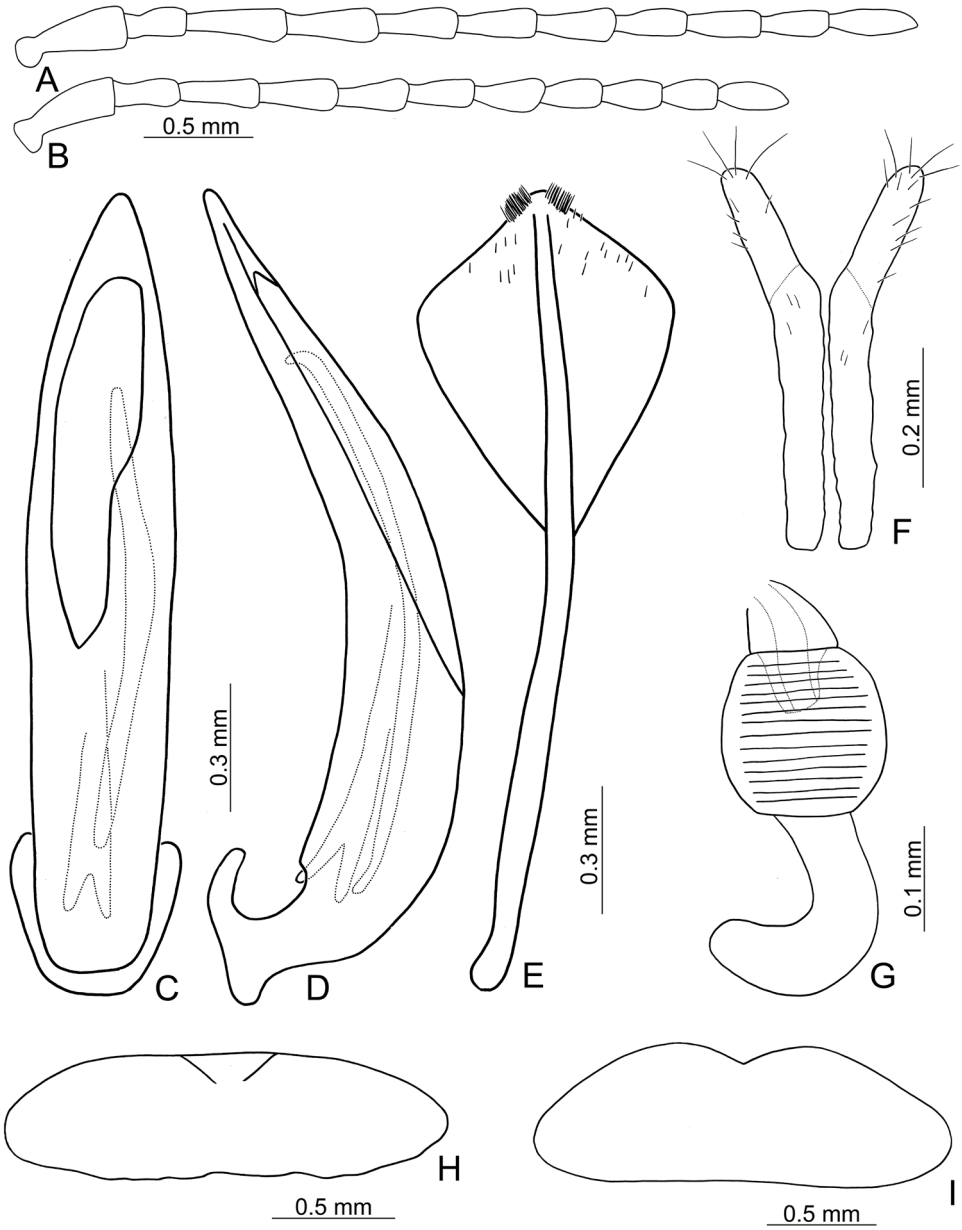
Diagnosis. *Lochmaea smetanai* Kimoto cannot be distinguished from *L. jungchani* sp. n. based on external morphology but differs in the relatively broader median lobe, 5.7× longer than wide (Fig. 9C) (more slender median lobe in *L. jungchani* sp. n., 6.8×



Figures 8. Habitus of *Lochmaea smetanai* Kimoto. **A** Female, from Hehuan East Peak, dorsal view **B** Ditto, ventral view **C** Ditto, lateral view **D** Color variation, from Huhua Main Peak, dorsal view **E** Color variation, from Tsuichih, dorsal view **F** Color variation, from Hsiaochilai, lateral view.

longer than wide (Fig. 13C)); longer elongate endophallic sclerite, 0.7× as long as median lobe (Fig. 9C) (shorter elongate endophallic sclerite in *L. jungchani* sp. n., 0.5× as long as median lobe (Fig. 13C)); apical margin of abdominal ventrite V in females with a median angular notch (Fig. 9I) (narrow notch margined with longitudinal ridges (Fig. 13I) in *L. jungchani* sp. n.).

Redescription. Length 5.7–6.4 mm, width 2.9–3.5 mm. General color (Fig. 8A–C) reddish brown, but vertex and pronotum greenish brown, with median longitudinal dark band on pronotum, each elytron greenish brown except suture and lateral



Figures 9. Diagnostic characters of *Lochmaea smetanai* Kimoto. **A** Antenna, male **B** Antenna, female **C** Median lobe, dorsal view **D** Median lobe, lateral view **E** Abdominal ventrite VIII **F** Gonocoxae **G** Spermatheca **H** Abdominal ventrite V, male **I** Abdominal ventrite V, female.

margins. Antennae filiform in males (Fig. 9A), length ratios of antennomeres I–XI 1.0 : 0.5 : 0.9 : 0.8 : 0.7 : 0.7 : 0.7 : 0.6 : 0.6 : 0.6 : 0.8, length to width ratios of antennomeres I–XI 2.6 : 2.0 : 3.1 : 2.8 : 2.7 : 2.6 : 2.6 : 2.5 : 2.6 : 2.5 : 3.3; a little smaller

in females (Fig. 9B), length ratios of antennomeres I–XI 1.0 : 0.6 : 0.7 : 0.7 : 0.7 : 0.6 : 0.6 : 0.6 : 0.5 : 0.5 : 0.7, length to width ratios of antennomeres I–XI 2.7 : 2.4 : 2.6 : 2.5 : 2.2 : 2.3 : 2.3 : 2.1 : 2.0 : 2.0 : 2.5. Pronotum transverse, 1.5× wider than long, disc with dense, extremely coarse punctures, and one pair of lateral depressions; lateral margins strongly narrowed basally; margins concave basally and apically. Elytra longitudinal and broadly rounded, 1.4× longer than wide; disc with random, dense, and extremely coarse punctures. Apical margin of abdominal ventrite V in males straight, with median notch bearing short, oblique ridges at margin (Fig. 9H). Ventrite V in females with shallow, wide, median, angular notch (Fig. 9I). Median lobe (Fig. 9C, D) slender, 5.7× longer than wide, apically tapering from apical 1/3, parallel-sided from base to apical 1/3; opening elongate, located on right, starting from apical 1/7; in lateral view strongly curved, slightly oblique; internal sac with one elongate sclerite, 0.7× as long as median lobe, one additional sclerite located near base of elongate sclerites, base wide and bifurcate, apically membranous. Gonocoxae (Fig. 9F) elongate, separated, weakly sclerotized except apical parts; apical parts elongate, bearing small, scattered setae and four long setae at apices. Ventrite VIII (Fig. 9E) longitudinal and well sclerotized; apex rounded; abruptly broader at apical 1/5, with paired cluster of long setae near middle, disc bearing scattered, tiny setae along apical margin; spiculum long and narrow. Receptacle of spermatheca (Fig. 9G) strongly swollen; pump slender and strongly curved; proximal spermathecal duct deeply inserted into receptacle, broad but short.

Variability. Some specimens have reduced punctation on the pronotum. Different individuals have different color patterns from brown to dark reddish brown (Fig. 8D–F).

Host plants. Ericaceae: *Rhododendron pseudochrysanthum* Hayata (Fig. 10A–C).

Biology. Some populations *Lochmaea smetanai* Kimoto are sympatric with *L. lesagei* Kimoto or *L. tsoui* sp. n. when microhabitats are stable at high altitudes (at or above 3000 m). For example, larvae of this species were collected in Kunyang (昆陽) (3050 m) with those of *L. tsoui* sp. n. (see biology to *L. tsoui* sp. n. for details). Adults might be long-lived, based on their occurrence in the field from April to December.

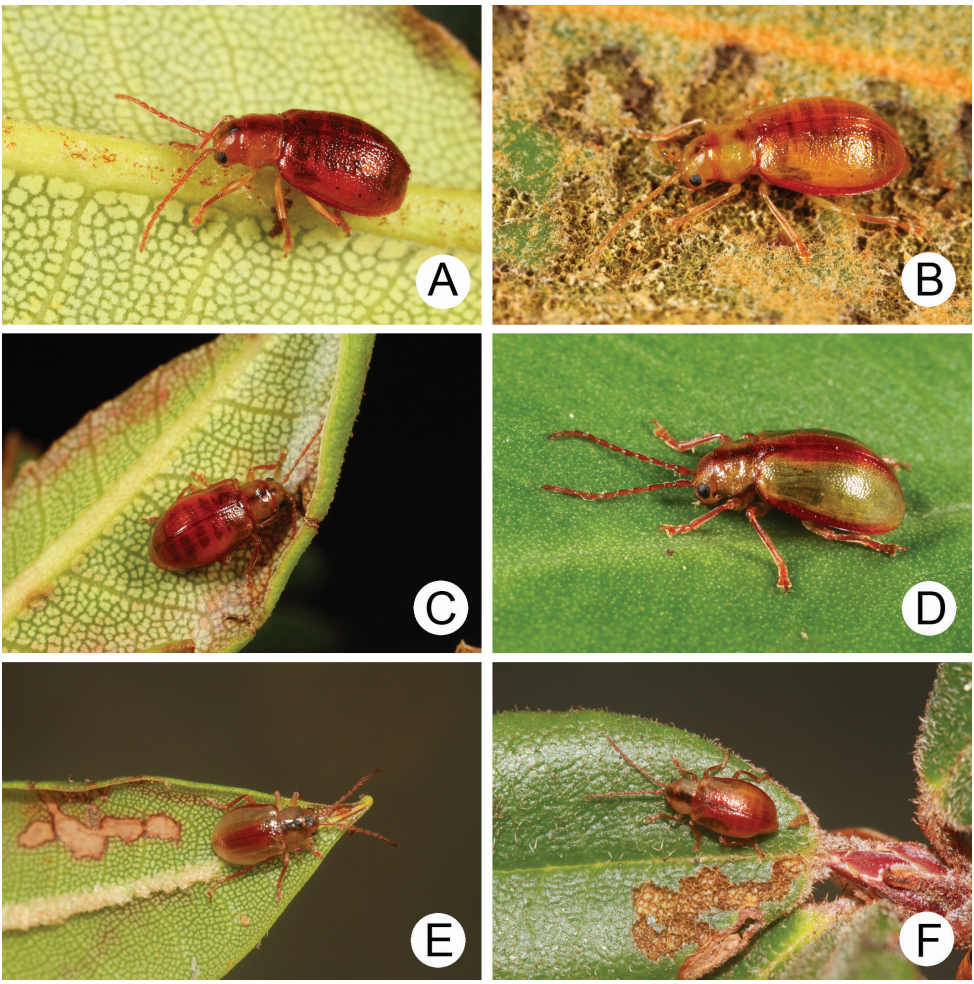
Distribution. Central Taiwan, including Miaoli, Taichung, Nantou, and Hualien Counties (Fig. 5B).

***Lochmaea cheni* sp. n.**

http://zoobank.org/7C059985-0473-4858-BC5F-06346B3A9E5F

Figs 10D, 11A–11C, 12

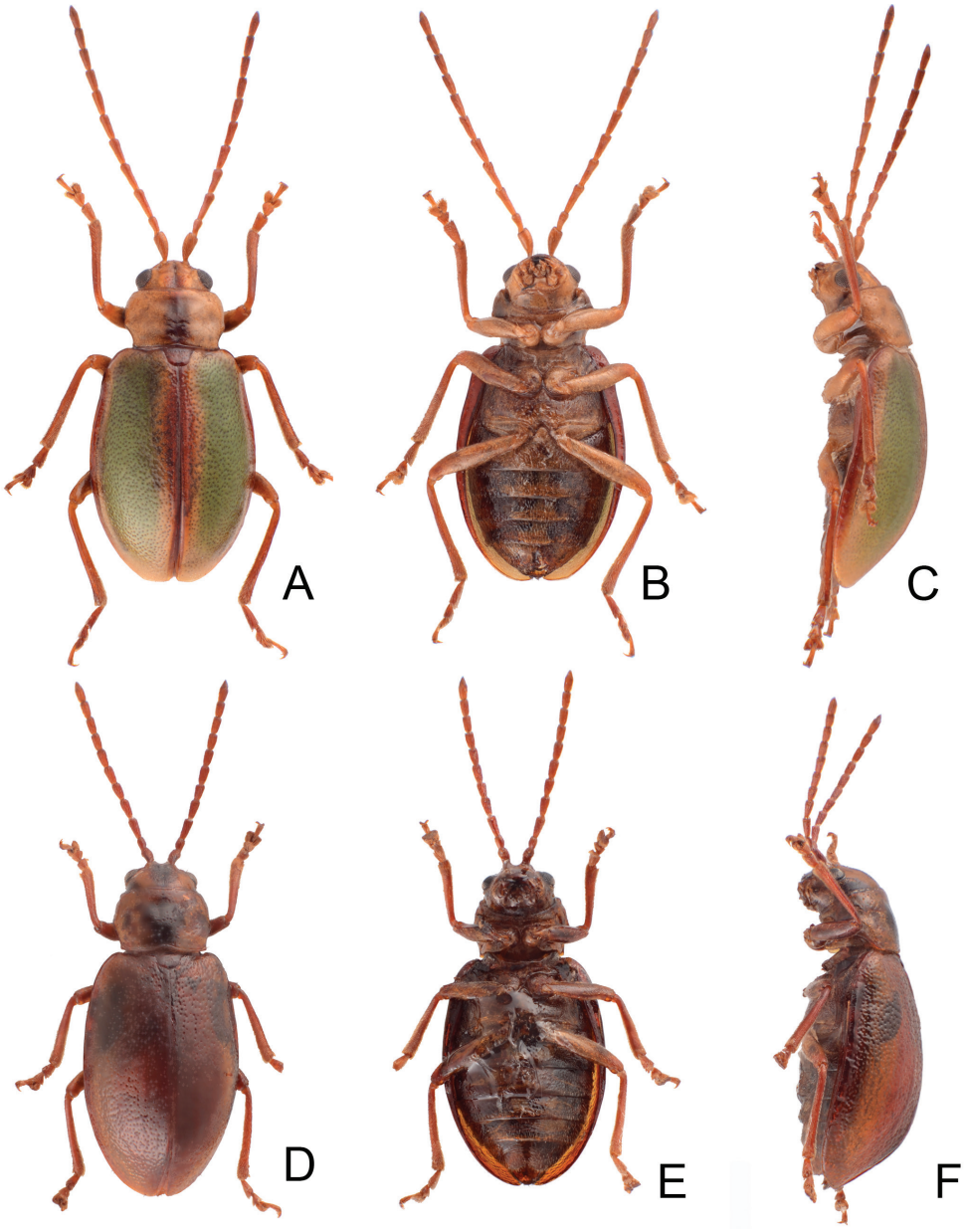
Type material (n = 64). Holotype ♂. **Kaoshiung**: Kuanshan Wind Gap (關山啞口), 2700 m, 30.VII.2015, leg. C.-F. Lee. Paratypes. 39♂♂, 18♀♀, same data as holotype; **Pingtung**: 1♀ (TARI), Peitawushan (北大武山), 3050 m, 13.X.2018, leg. J.-C. Chen; **Taitung**: 3♂♂, 2♀♀ (TARI), Hsiangyangshan (向陽山), 3600 m, 19.IX.2014, leg. J.-C. Chen; 1♂ (TARI), same but with "6.VIII.2015.



Figures 10. Ecological photography of *Lochmaea* species. **A** *L. smetanai* Kimoto, from Hsuehshan **B** Same species, from Nanhutashan **C** Same species, from Hehuashan **D** *L. cheni* Lee, sp. n., from Kuanshan Wind Gap **E** *L. jungchani* Lee, sp. n., from Yushan West Peak **F** Same species, from Yushan East Peak.

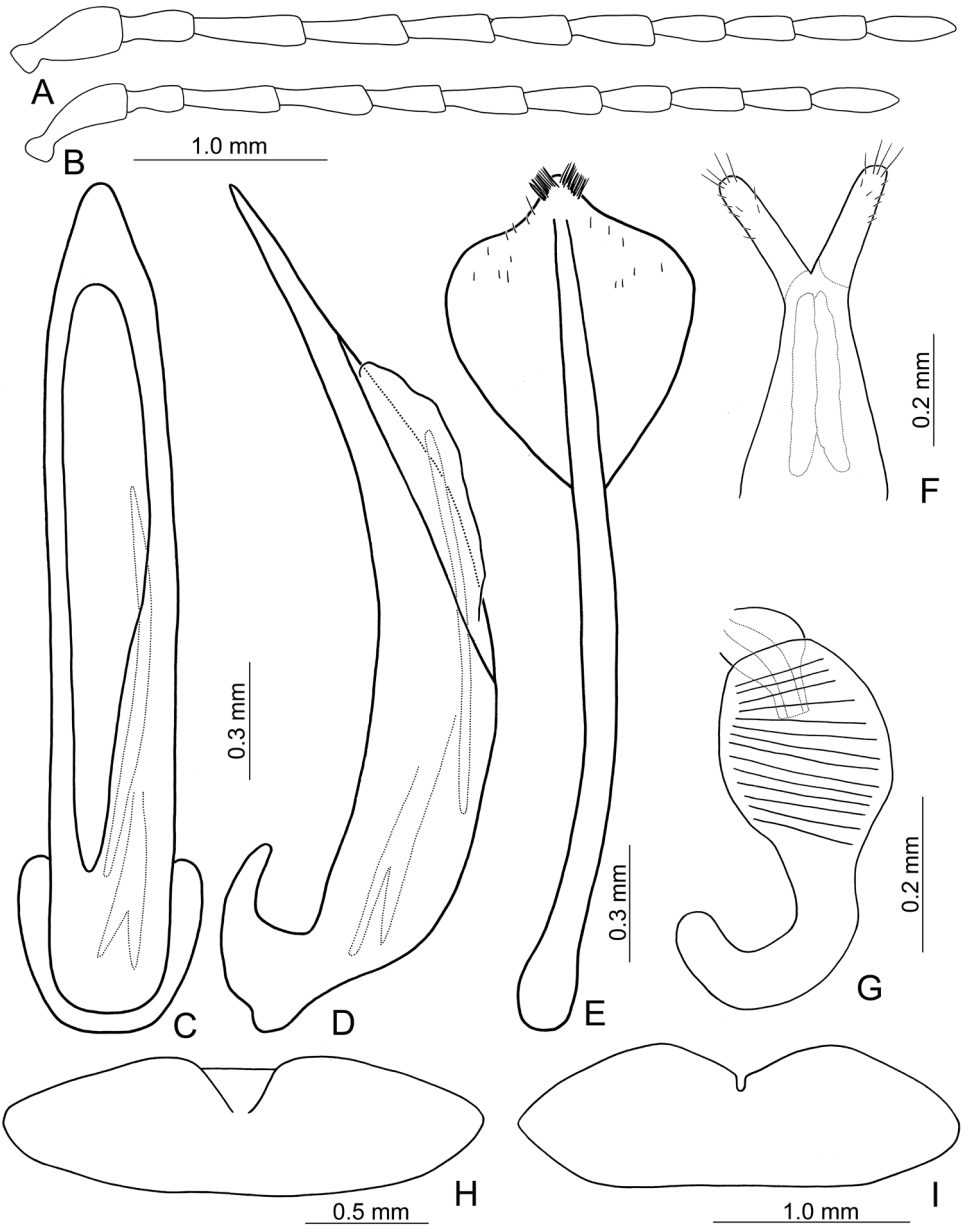
Diagnosis. *Lochmaea cheni* sp. n. is easily distinguished from other members of the species group by the green elytra (Fig. 11A–C) (entirely reddish brown or yellowish brown elytra in others (Figs 8, 11D–F)), parallel-sided median lobe (Fig. 12C) (tapering median lobe (Figs 9C, 13C) in others) and opening located more posteriorly, and apical margin of abdominal ventrite V in females bearing a narrow, shallow notch (Fig. 12I) (angular notch (Fig. 9I) in *L. smetanai*; narrower notch margined with longitudinal ridges (Fig. 13I) in *L. jungchani* sp. n.).

Description. Length 6.2–7.2 mm, width 3.3–3.9 mm. General color (Fig. 11A–C) yellowish brown to reddish brown; vertex and pronotum with median longitudinal dark band; each elytron green but with wide yellowish brown band along suture and



Figures 11. Habitus of *Lochmaea* species. **A** *L. cheni* Lee, sp. n., male, dorsal view **B** Ditto, ventral view **C** Ditto, lateral view **D** *L. jungchani* Lee, sp. n., female, dorsal view **E** Ditto, ventral view **F** Ditto, lateral view.

lateral margin. Antennae filiform in males (Fig. 12A), length ratios of antennomeres I–XI 1.0 : 0.6 : 1.0 : 0.9 : 0.8 : 0.7 : 0.7 : 0.6 : 0.6 : 0.6 : 0.8, length to width ratios of antennomeres I–XI 2.4 : 2.2 : 3.7 : 3.5 : 3.1 : 2.6 : 2.7 : 2.6 : 2.7 : 3.0 : 3.6; similar in



Figures 12. Diagnostic characters of *Lochmaea cheni* Lee, sp. n. **A** Antenna, male **B** Antenna, female **C** Median lobe, dorsal view **D** Median lobe, lateral view **E** Abdominal ventrite VIII **F** Gonocoxae **G** Spermatheca **H** Abdominal ventrite V, male **I** Abdominal ventrite V, female.

females (Fig. 12B), length ratios of antennomeres I–XI 1.0 : 0.5 : 0.8 : 0.8 : 0.7 : 0.7 : 0.7 : 0.6 : 0.6 : 0.6 : 0.8, length to width ratios of antennomeres I–XI 3.0 : 2.1 : 3.4 : 3.4 : 2.7 : 2.8 : 2.6 : 2.8 : 3.0 : 3.0 : 3.7. Pronotum transverse, 1.6× wider than long,

disc with sparse, extremely coarse punctures, and one pair of lateral depressions; lateral margins strongly narrowed basally; margins concave basally and apically. Elytra longitudinal with lateral margins broadly rounded, 1.3–1.4× longer than wide; disc bearing random, dense, coarse punctures. Apical margin of abdominal ventrite V in males with median notch, bearing short, oblique ridges at margin, weakly concave between ridges. Ventrite V in females medially depressed, with narrow, shallow notch at middle. Median lobe (Fig. 12C, D) slender, 6.8× longer than wide, apically tapering from apical 1/7, parallel-sided from base to apical 1/7; opening elongate, starting from apical 1/5 located on right; in lateral view strongly curved, slightly oblique; internal sac with one elongate sclerite, 0.5× as long as median lobe, one additional sclerite located near base of elongate sclerites, base wide and bifurcate, apically membranous. Gonocoxae (Fig. 12F) elongate, membranous except apical parts, with one pair of weakly sclerotized, elongate sclerites at base; apical parts elongate, bearing tiny, scattered setae and four long setae at apices. Ventrite VIII (Fig. 12E) longitudinal and well sclerotized; apex rounded; abruptly broader at apical 1/5, with paired cluster of long setae near middle, disc bearing scattered, tiny setae along apical margin; spiculum long and narrow. Receptacle of spermatheca (Fig. 12G) strongly swollen; pump slender and strongly curved; proximal spermathecal duct deeply inserted into receptacle, broad but short.

Variability. Some specimens have reduced punctures on the pronotum. Few specimens have yellowish brown elytra but suture and lateral margin reddish brown.

Host plants. Ericaceae: *Rhododendron pseudochrysanthum* Hayata (Fig. 10D).

Biology. Unknown. Adults are active from July to September.

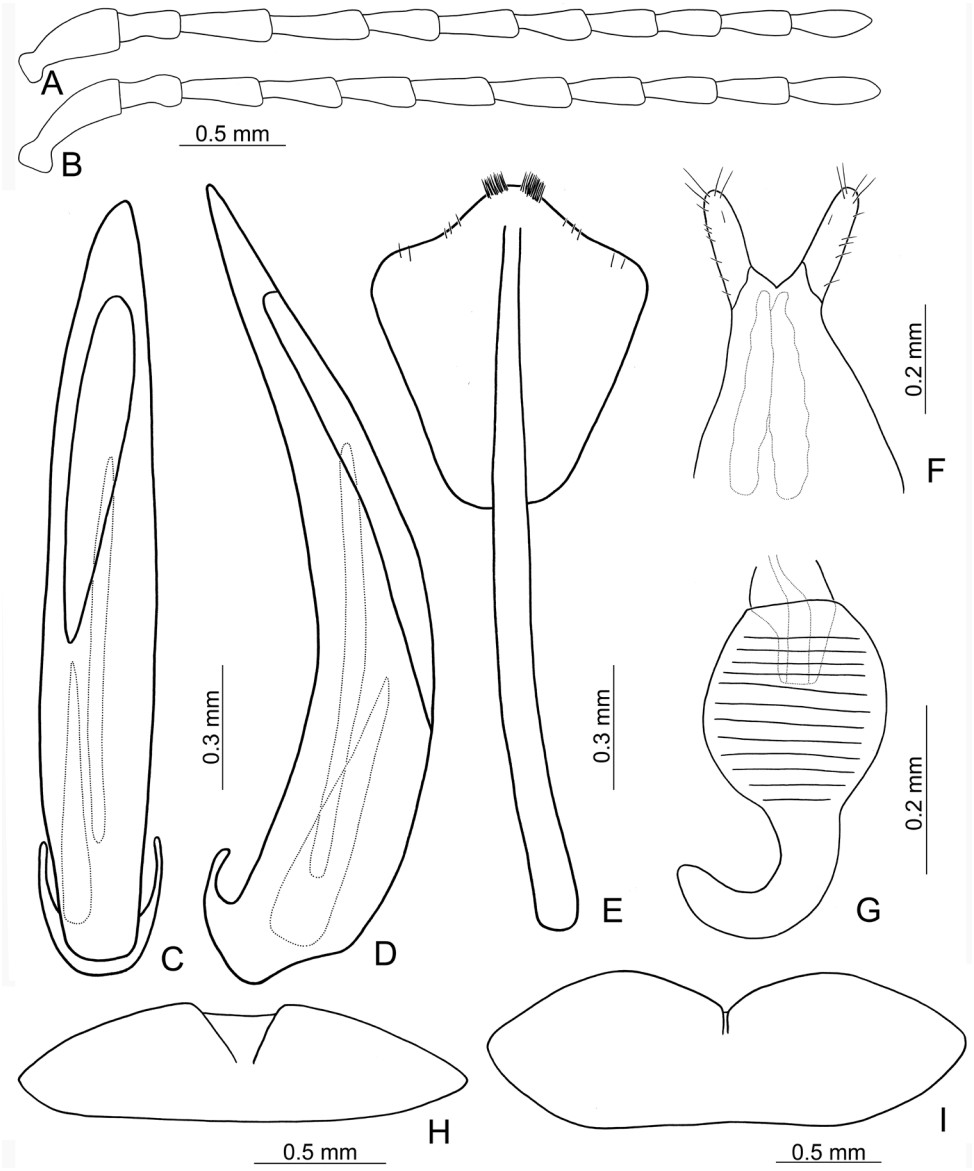
Etymology. This new species is named after Mr Jung-Chan Chen, a member of the TCRT and the first to collect this new species.

Distribution. High mountains along South Cross-Island Highway (Kaoshiung and Taitung Counties).

***Lochmaea jungchani* sp. n.**
http://zoobank.org/80392637-C8B1-4DE4-B3BE-080509E7E975
Figs 10E, F, 11D–F, 13

Type material (n = 33). Holotype ♂ (TARI): **Chiayi**: Yushan East Peak (玉山東峰), 3869 m, 20.IX.2018, leg. J.-C. Chen. Paratypes. 7♂♂, 8♀♀ (TARI), same data holotype; 6♂♂, 5♀♀ (TARI), Yushan North Peak (玉山北峰), 3858 m, 20.IX.2018, leg. J.-C. Chen; 2♂♂ (TARI), Yushan West Peak (玉山西峰), 3518 m, 19.IX.2018, leg. J.-C. Chen; 3♀♀ (TARI), Yushan Main Peak (玉山主峰), 3950 m, 17.VIII.2017, leg. J.-C. Chen; 1♂ (TARI), Paiyun Lodge (排雲山莊), 3400 m, 24.X.2017, leg. J.-C. Chen.

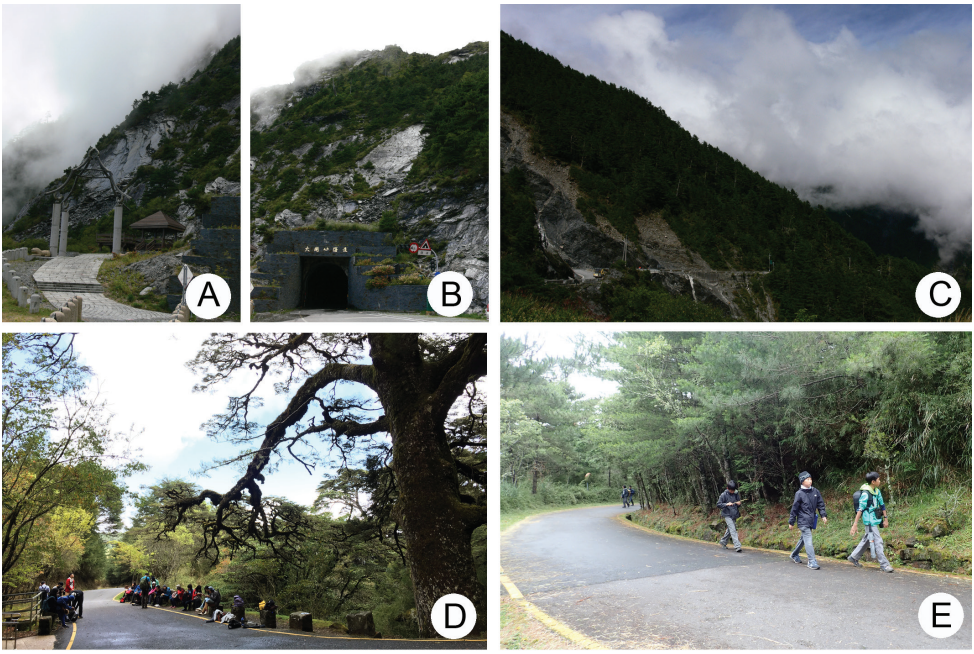
Diagnosis. *Lochmaea jungchani* sp. n. cannot be distinguished from *L. smetanai* Kimoto based on external morphology but differs with the relatively slender median lobe, 6.8× longer than wide (Fig. 13C) (broader median lobe in *L. semtanai*, 5.7× longer than wide (Fig. 9C)); shorter elongate endophallic sclerite, 0.5× as long as median lobe



Figures 13. Diagnostic characters of *Lochmaea jungchani* Lee, sp. n. **A** Antenna, male **B** Antenna, female **C** Median lobe, dorsal view **D** Median lobe, lateral view **E** Abdominal ventrite VIII **F** Gonocoxae **G** Spermatheca **H** Abdominal ventrite V, male **I** Abdominal ventrite V, female.

(Fig. 13C) (longer elongate endophallic sclerite in *L. smetanai*, 0.7× as long as median lobe (Fig. 9C)); apical margin of abdominal ventrite V in females with narrow notch margined with longitudinal ridges (Fig. 13I) (angular notch in *L. smetanai* (Fig. 9I)).

Description. Length 5.5–6.5 mm, width 2.8–3.3 mm. General color (Fig. 11D–F) yellowish brown to reddish brown; vertex and pronotum with median longitudinal



Figures 14. Microhabitats. **A** Kuanshan Wind Gap **B** Same locality, different angle **C** Same locality, different angle **D** Tatachia **E** Same locality, different angle.

dark stripe. Antennae filiform in males (Fig. 13A), length ratios of antennomeres I–XI 1.0 : 0.6 : 0.9 : 0.9 : 0.7 : 0.7 : 0.7 : 0.7 : 0.6 : 0.7 : 0.8, length to width ratios of antennomeres I–XI 2.1 : 2.1 : 2.9 : 3.2 : 2.5 : 2.6 : 2.5 : 2.6 : 2.5 : 2.8 : 3.1; similar in females (Fig. 13B), length ratios of antennomeres I–XI 1.0 : 0.5 : 0.7 : 0.7 : 0.6 : 0.7 : 0.6 : 0.6 : 0.6 : 0.6 : 0.8, length to width ratios of antennomeres I–XI 3.3 : 2.0 : 2.7 : 2.7 : 2.5 : 2.7 : 2.6 : 2.7 : 2.8 : 2.8 : 3.3. Pronotum transverse, 1.6× wider than long, disc with sparse, extremely coarse punctures, and one pair of lateral depressions; lateral margins strongly narrowed basally; margins concave basally and apically. Elytra longitudinal and broadly rounded, 1.4× longer than wide; disc with random, dense, and extremely coarse punctures. Apical margin of abdominal ventrite V in males rounded, with median notch bearing short, oblique ridges at margin, weakly depressed between ridges. Ventrite V in females medially depressed, with narrow notch margined with longitudinal ridges at middle. Median lobe (Fig. 13C, D) extremely slender, 6.8× longer than wide, apically tapering from middle, parallel-sided from base to middle; opening elongate, located on right, starting from apical 1/6; in lateral view strongly curved, slightly oblique; internal sac with one elongate sclerite, 0.5× as long as median lobe, one additional sclerite located near base of elongate sclerites, base wide, apically tapering. Gonocoxae (Fig. 13F) elongate, membranous except apical parts, with one pair of weakly sclerotized, elongate sclerites at base; apical parts elongate, bearing tiny, scattered setae and four long setae at apices. Ventrite VIII (Fig. 13E) longitudinal and well sclerotized; apex rounded;

abruptly broader at apical 1/5, with paired cluster of long setae near middle, disc bearing scattered, tiny setae along apical margin; spiculum long and narrow. Receptacle of spermatheca (Fig. 13G) strongly swollen; pump slender and strongly curved; proximal spermathecal duct deeply inserted into receptacle, broad but short.

Host plant. Ericaceae: *Rhododendron pseudochrysanthum* Hayata (Fig. 10E, F).

Biology. Unknown. Adults are active in the field from August to October.

Etymology. This new species is named after Mr. Jung-Chan Chen, a member of the TCRT and the first to collect this new species.

Distribution. Yushan and surrounding areas (Chiayi County).

Discussion

Taiwanese species of *Lochmaea* are characterized by the uniform first tarsomere of the metatarsus (enlarged first tarsomere of male metatarsus in others), last abdominal ventrite in males, and median lobes (both characters are very complex and diagnostic for others). Species richness of the wingless *Lochmaea smetanai* group is less than that of any other wingless galerucines in Taiwan, including ten species in *Paraplotes* Laboissière (Lee 2015), five species in *Sikkimia* Duvivier (Lee and Bezděk 2016), and six species in *Shairella* Chûjô (Lee and Beenen 2017). Moreover, the aedeagi of congeners are more similar to each other than in other genera. Both features imply that reduction of hind wings is a recent evolutionary event. Although male genitalic characters are less diagnostic, some female genitalic characters are useful in species delimitation, including the shapes of abdominal ventrites V and VIII. Abdominal ventrites VIII in females are characteristic in that they are well sclerotized, subapically expanding, and with sides curving inwards. They appear to replace the base of the gonocoxae functionally.

Members of the winged *Lochmaea lesagei* group usually inhabit mountains above 2000 m, but some populations occur at less than 1500 m in northern Taiwan. They seem to occur in alpine environments only when microhabitats are stable. For example, most larvae collected from Kunyang (昆陽, 3050 m) belong to *L. lesagei*. By contrast, adults and larvae of *L. smetanai* group (wingless) are restricted to alpine habitats above 3000 m. One exception is Kuanshan Wind Gap (關山啞口, 2700 m) (Fig. 14A–C) where it is so windy that it takes on "alpine" characteristics although the altitude is below 3000 m. This microhabitat is suitable for a wingless population (*L. cheni* sp. n.) where more than 50 specimens of *L. cheni* sp. n. were collected from three plants by beating. For comparison, Tatachia (塔塔加, 2600 m) is almost as high as Kuanshan Wind Gap, but the microhabitats are stable (Fig. 14D, F). Although adults of *Lochmaea* were common there, all were winged (*L. lesagei*). Other wingless galerucines in Taiwan inhabit stable, mid-altitude habitats. These include members of *Sikkimia* Duvivier (Lee and Bezděk 2016) and *Sharella* Chûjô (Lee and Beenen 2017). These observations suggest that distributions of winged and wingless species of *Lochmaea* are the only chrysomelids in Taiwan that fit expectations of preferred habitats in brachyelytrous species (Beenen and Jolivet 2008).

Acknowledgements

I thank the Taiwan Chrysomelid Research Team for taking photographs of specimens and live individuals in the field, including Jung-Chan Chen, Hsueh Lee, Ta-Hsiang Lee, Mei-Hua Tsou, and Su-Fang Yu. I especially thank Jung-Chan Chen for collecting specimens from various alpine localities by climbing up to them. I thank Ta-Hsiang Lee, Chi-Lung Lee, Cheng-Lung Tsai, Mei-Hua Tsou, and Hsueh Lee, Cheng-Lung Tsai, and Weiting Liu for taking photographs, and Chih-Kai Yang for identifying host plants. I thank Chris Carlton for reading the draft and editing for American English style. This study was supported by the Ministry of Science and Technology MOST 107-2313-B-055-002. Finally, I am grateful for Ron Beenen and Tomas Wagner for reviewing the manuscript.

References

Beenen R (1996) The forgotten *Adimonia scutellata* Chevrolat (Coleoptera: Chrysomelidae). Entomologische Blätter 92: 85–89.

Beenen R (2010) Galerucinae. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera, vol 6. Apollo Books, Stenstrup, 443–491.

Beenen R, Jolivet P (2008) Classification and habitat of brachelytrous Chrysomelidae (Coleoptera). In: Jolivet P, Santiago-Blay J, Schmitt M (Eds) Research on Chrysomelidae (Vol. 1). Brill, Leiden and Boston, 161–173.

Bezděk J (2004) A review of the *Lochmaea crataegi* (Forster, 1771) species group from Asia Minor, Near East and Caucasus (Coleoptera: Chrysomelidae: Galerucinae). Annales Zoologici 54: 1–6.

Cameron AE, McHardy JW, Benneth AH (1944) The heather beetle (*Lochmaea suturalis*). Petworth, Sussex, British Field Sports Society, 69 pp.

Chevrolat A (1840) Description de quelques Coléoptères de la Galice et du Portugal provenant d'envois de M. Deyrolles fils. Revue Zoologique 1840: 8–18.

Cobos A (1955) Dos nuevas formas de coleópteros Phytophagoidea de Andalucía y notas complementarias. Archivos del Instituto de Aclimatación (Almería) 4: 59–62.

Forster JR (1771) Novae species Insectorum. Centuria I. T. Davies et B. White, Londini, 100 pp. https://doi.org/10.5962/bhl.title.152194

Gök A, Aslan EG, Şen I, Ayvaz Y (2006) Redescription of *Lochmaea limbata* Pic, 1898 with a new synonym (Coleoptera: Chrysomelidae: Galerucinae). Annales Zoologici 56: 610–604.

Jolivet P, Hawkeswood TJ (1995) Host-plants of Chrysomelidae of the Wrold: An Essay about the Relationships between the Leaf-beetles and their Food-plants. Backhuys Publishers, Leiden, 281 pp.

Kimoto S (1979) The Galerucinae (Coleoptera: Chrysomelidae) of Nepal, Bhutan and northern territories of India, in the Natural History Museum in Basel, I. Entomologica Basiliensia 4: 463–478.

Kimoto S (1996) Notes on the Chrysomelidae from Taiwan, China, XIII. Entomological Review of Japan 51: 27–51.

Lee C-F (2015) The genus *Paraplotes* Laboissière, 1933, a speciose group with brachelytrous females (Coleoptera: Chrysomelidae: Galerucinae). Zootaxa 3904: 223–248. https://doi.org/10.11646/zootaxa.3904.2.3

Lee C-F, Beenen R (2017) Revision of the genus *Shairella* Chûjô, 1962 (Coleoptera: Chrysomelidae: Galerucinae) from Taiwan, with descriptions of five new species. Zootaxa 4268: 489–507. https://doi.org/10.11646/zootaxa.4268.4.2

Lee C-F, Bezděk J (2016) Revision of the wingless *Sikkimia* Duvivier (Coleoptera, Chrysomelidae, Galeruciane) from Taiwan, including a new generic synonymy and four new species descriptions. ZooKeys 553: 79–106. https://doi.org/10.3897/zookeys.553.6576

Linnaeus C (1758) Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymies, locis. Tomus I. Editio decima, reformata. Impensis Direct. Laurentii Salvii, Holmiae, 824 pp.

Medvedev LN (2005) New and poorly-known genera and species of Oriental Chrysomelidae (Coleoptera). Entomologica Basiliensia et Collectionis Frey 27: 279–295.

Pic M (1898) Descriptions de Coleopteres d'Anatolie et de Syrie. Revue Scientifique du Bourbonnais et du Centre de la France 11: 91–94.

Roubal J (1926) Sieben neue Coleopteren aus der paläarktischen Region. Coleopterologisches Centralblatt 1: 244–249.

Sahlberg J (1913) Coleoptera mediterranea et rosso-asiatica. Öfversigt af Finska Vetenskaps-societetens Förhanslingar 55: 1–88.

Silfverberg H (1974) The West Palaearctic species of *Galerucella* Crotch and related genera (Coleoptera, Chrysomelidae). Natulae Entomologicae 54: 1–11.

Stephens JF (1831) Illustrations of British entomology; or, a synopsis of indigenous insects: containing their generic and specific distinctions; with an account of their metamorphoses, times of appearance, localities, food, and economy, as far as practicable. Mandibulata, vol IV. Baldwin & Cradock, London, 413 pp.

Takizawa H (1990) Chrysoemlid beetles of Nepal, northern India, and western Sikkim collected by the Himalaya Expeditions of the National Science Museum, Tokyo (Part 2). Japanese Journal of Entomology 58: 275–291.

Thomson J (1866) Systema Cerambycidarium ou exposé de tous les genres compris dans la famille des cérambycides et familles limitrophes. Mémoires de la Société Royale des Sciences de Liège 19: 1–538.

Waloff N (1987) Observations on the heather beetle *Lochmaea suturalis* (Thomson) (Coleoptera: Chrysomelidae) and its parasitoiods. Journal of Natural History 21: 545–556. https://doi.org/10.1080/00222938700770321

Weise J (1883) Ueber die mit *Galeruca* Geoffr. verwandten Gattungen. Deutsche Entomologische Zeitschrift 27: 315–216.

Wilcox JA (1971) Chrysomelidae: Galerucinae (Oidini, Galerucini, Metacyclini, Sermylini). In: Wilcox JA (Ed.) Coleopterorum Catalogus Supplementa. Pars 78 (1), 2nd ed. W Junk, 's-Gravenhage, 1–220.

Yang X-K, Wang JS, Wu YY (1998) Three new species of Galerucinae (Coleoptera: Chrysomelidae) from Wuyi Mountain. Entomtaxonomia 20: 261–263.

ZooKeys 856: 101–114 (2019)
doi: 10.3897/zookeys.856.32430
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Host plant associations in Western Palaearctic *Longitarsus* flea beetles (Chrysomelidae, Galerucinae, Alticini): a preliminary phylogenetic assessment

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Academic editor: *Caroline S. Chaboo* | Received 14 December 2018 | Accepted 15 April 2019 | Published 17 June 2019

http://zoobank.org/3198EFC5-DC91-4AFB-B394-654AE769858C

Citation: Salvi D, D'Alessandro P, Biondi M (2019) Host plant associations in Western Palaearctic *Longitarsus* flea beetles (Chrysomelidae, Galerucinae, Alticini): a preliminary phylogenetic assessment. In: Schmitt M, Chaboo CS, Biondi M (Eds) Research on Chrysomelidae 8. ZooKeys 856: 101–114. https://doi.org/10.3897/zookeys.856.32430

Abstract

Longitarsus Latreille (Chrysomelidae, Galerucinae, Alticini) is a very large genus of phytophagous insects, with more than 700 species distributed in all zoogeographical regions. Patterns of host use have been a central topic in phytophagous insect research. In this study a first assessment is provided to test the hypothesis that host-plant association is phylogenetically conserved in Western Palaearctic *Longitarsus* species. Maximum Likelihood and Bayesian Inference methods were used to infer a phylogeny based on DNA sequence data from two mitochondrial genes from 52 *Longitarsus* species from the Western Palaearctic. In agreement with the host phylogenetic conservatism hypothesis, a strict association between most of the recovered clades and specific plant families was found, except for species associated with Boraginaceae. Low phylogenetic resolution at deep nodes limited the evaluation of whether closely related *Longitarsus* clades are associated with the same plant family or to closely related plant families.

Keywords
Longitarsus, molecular phylogeny, Palaearctic region, phylogenetic conservatism in host use, phytophagous insects

Introduction

Longitarsus Latreille, 1829 is a mega-diverse genus of phytophagous insects and the most speciose among flea beetles (Chrysomelidae, Galerucinae, Alticini) with more than 700 known species. It is widespread through all zoogeographical regions (Furth 2007, Biondi and D'Alessandro 2010, 2012, Döberl 2010, Prathapan and Viraktamath 2011, Reid 2017, unpublished data). *Longitarsus* is also ecologically diversified with specialized feeders, monophagous or oligophagous (Schoonhoven et al. 2005), on different angiosperm families. Larvae feed mostly on roots, and adults target leaves of their host plants (Dobler et al. 2000, Furth 1980). The monophyly of *Longitarsus* is accepted based on molecular evidence (Gómez-Rodríguez et al. 2015, Nie et al. 2018). Members of the genus are recognized mainly by the length of first metatarsomere, exceeding half-length of hind tibia, along with confuse elytral punctuation and absence of dorsal pubescence (Biondi and D'Alessandro 2012).

Relationships among Chrysomelidae and their host plants has been investigated from a biochemical, behavioural, and phylogenetic point of view, and at various taxonomic levels, often with the aim of understanding the biology of actual or potential pests (Jolivet and Hawkeswood 1995, Becerra and Vernable 1999, Dobler et al. 2000, Clark et al. 2004, Fernandez and Hilker 2007, Kergoat et al. 2007, Reid 2017). Understanding the mechanisms which drive observed host-use patterns has been a central topic in phytophagous insect research. Among the non-mutually exclusive hypotheses proposed (Gripenberg et al. 2010, Balagawi et al. 2013, Charlery de la Masselière et al. 2017, Kergoat et al. 2017, Lima Bergamini et al. 2017, Jones et al. 2019), the phylogenetic conservatism states that the phylogeny of host plants strongly constrains host affiliations. The phylogenetic conservatism hypothesis is widely demonstrated, even though it can be masked to varying degrees of convergent evolution in both plant and herbivore traits, and/or by phenotypic plasticity of both plants and herbivores; in addition, evolutionary processes that have generated phylogenetic conservatism patterns often remain unclear (Fernandez and Hilker 2007, Kergoat et al. 2017, Lima Bergamini et al. 2017). A comprehensive phylogenetic assessment of the insect-host plant relationship in the genus *Longitarsus* is still lacking, as well as comprehensive systematic studies on the genus.

In this paper, we conduct a molecular phylogenetic analysis on 52 Western Palaearctic *Longitarsus* species to map host plant data in order to assess whether the pattern observed is consistent with the phylogenetic conservatism hypothesis. If it is consistent, we would expect to find a) closely related *Longitarsus* species (single clades) to be associated with a specific plant family; b) *Longitarsus* clades associated with a specific plant family to form a single lineage.

Methods

Dataset, DNA extraction, amplification, and sequencing

We analysed 52 *Longitarsus* species (Table 1) from the Western Palaearctic, i.e., with distribution ranges centred on the Western Palaearctic area up to Urals, Caucasus, Anatolia, Iran, Near East, North Africa, and Macaronesia. Data on species distribution were mainly from Döberl (2010), and Gruev and Döberl (1997, 2005).

To assess the association between phylogeny and patterns of host use, we used information on host plants for each species of *Longitarsus* from field observations over many years, and from a critical analysis of information reported in the literature (Furth 1980, Doguet 1994, Biondi 1995a, b, 1996, Bienkovski 2004, Konstantinov 2005, Aslan and Gok 2006, Gruev and Tomov 2007). We ignored isolated observations or reports of one or a few individual herbivores seen only one time on a host, as well as cases of post-season host refugium (Furth 1980). According to Biondi (1996), species feeding on one or two phylogenetically very closely related plant genera were considered as monophagous (**MON**); species feeding on one or two phylogenetically very closely related plant families were considered as oligophagous (**OLI**); species feeding on more plant species not phylogenetically closely related were considered as polyphagous (**POL**).

Phylogenetic relationships among plant families were discussed according to The Angiosperm Phylogeny Group 2016 (hereafter The APG 2016). Molecular analyses included DNA sequences from the mitochondrial genes cytochrome oxidase subunit I (cox1) and 16S rDNA (16S). These sequences were obtained from 20 alcohol-preserved specimens, each representing a distinct species, and retrieved from GenBank for 32 species (see Table 1 for information on specimens). We selected these two genes because they are the most represented in GenBank for *Longitarsus* species and because their phylogenetic utility at the genus level have been demonstrated by Nie et al. (2018). Details on sample data, along with GenBank accession numbers are provided in Table 1.

Total genomic DNA was extracted from preserved specimens using either a standard high-salt protocol (Sambrook et al. 1989) or the DNeasy Blood & Tissue extraction kit (Qiagen, Hilden, Germany), following the manufacturer's protocol. Polymerase chain reaction (PCR) amplification were performed using the universal primers LCO1490 and HC02198 (Folmer et al. 1994) and the primers specifically designed in this study for *Longitarsus* LonLCO-F (5'-CTC AGC CAT TTT ACC GAA TAA ATG-3') and LonHCO-R (5'-GGA TTT GGI ATA ATT TCY CATA TTG-3') targeting the barcoding fragment of the cox1 gene, and the primers 16sar-L (5-CGCCTGTTTATCAAAAACAT-3) and 16sbr-H (5'-CCG GTC TGA ACT CAG ATC AC-3') slightly modified in Bologna et al. (2005) after Palumbi et al. (1991) targeting the fragment encompassing the domains IV and V of the16S rDNA. Amplification was carried out in a total volume of 25µl, with 3µl of PCR buffer, 2–2.5 µl of $MgCl_2$ (50 mM), 0.5 µl of each primer (10mM), 0.5 µl of BSA, 1 U of BIOTAQ DNA polymerase (Bioline Ltd, London, UK) and 0.5–1 µL DNA template. PCR cycling conditions for cox1 followed Salvi et al. (2018), for 16S were 3 min at 94 °C, 35 cycles of 60 s at 94 °C, 90 s at 49.5 °C, 90 s at 72 °C, 10 min at 72 °C for final extension. Purification and sequencing of PCR products were carried out by an external service (Genewitz, UK).

Table 1. Information on host plants, collection, and GenBank accession numbers for the 52 species of *Longitarsus* and *Batophila aerata* (outgroup) used in this study.

Species	Host plant family	Trophic Range	Source for molecular analysis	Permits	Deposits	GenBank accession number	
						cox1	16S
Batophila aerata (Marsham)	Rosaceae	OLI	Italy, Abruzzo (AQ), Roio Piano, 42°20'00.85"N 13°20'06.28"E, 930 m a.s.l., 13.v.2017, adult on *Rubus* sp. (Rosaceae) [det. M. Biondi, voucher db37]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus aeneicollis (Faldermann)	Asteraceae, Boraginaceae, Lamiaceae	POL	Italy, Abruzzo (TE), Prati di Tivo, 42°30'26.40"N 13°33'14.46"E; 1344 m a.s.l., 11.vii.2018, adult on Boraginaceae [det. M. Biondi, voucher db46]	Gran Sasso e Monti della Laga National Park. Prot. n. 0007403/18	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus aeneus Kutschera	Boraginaceae	OLI	Italy, Abruzzo (TE), Guazzano, 42°44'03.6"N 13°38'49.8"E, 563 m a.s.l., 24.iv.2017, adult on *Borago officinalis* (Boraginaceae) [det. M. Biondi, voucher db15]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	KX943357	requested
Longitarsus anchusae (Paykull)	Boraginaceae	OLI	Italy, Abruzzo (AQ), Aprati, 42°32'10.9"N 13°27'14.9"E, 862 m a.s.l., 19.v.2017, adult on *Anchusa italica* (Boraginaceae) [det. M. Biondi, voucher db19]	Gran Sasso e Monti della Laga National Park. Prot. n. 0007804/17	Collection M. Biondi, University of L'Aquila (Italy)	KM448991	requested
Longitarsus atricillus (Linnaeus)	Asteraceae, Ranunculaceae, Fabaceae, Scrophulariaceae	POL	GenBank			KX943363	KP763161
Longitarsus ballotae (Marsham)	Lamiaceae	OLI	GenBank			KM446857	KC186008
Longitarsus bedelii Uhagon	?	?	GenBank			–	KP763150
Longitarsus brisouti Heikertinger	Asteraceae	OLI	GenBank			KM439696	–
Longitarsus brunneus (Duftschmid)	Ranunculaceae	MON	GenBank			KM452511	–
Longitarsus celticus Leonardi	Lamiaceae	OLI	GenBank			KU908777	–
Longitarsus cerinthes (Schrank)	Boraginaceae	OLI	GenBank			KX943478	KX943478
Longitarsus curtus (Allard)	Boraginaceae	OLI	GenBank			KX943501	KX943501
Longitarsus dorsalis (Fabricius)	Asteraceae	MON	GenBank			KX943359	KX943359
Longitarsus echii (Koch)	Boraginaceae	OLI	GenBank			KM439361	–
Longitarsus exsoletus (Linnaeus)	Boraginaceae	OLI	GenBank			KX943418	KX943418
Longitarsus fallax Weise	Boraginaceae	OLI	Italy, Abruzzo (TE), Piancarani, 42°44'30.6"N 13°43'58.2"E, 191 m a.s.l., 24.iv.2017, adult on *Borago officinalis* (Boraginaceae) [det. M. Biondi, voucher db14]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus foudrasi Weise	Scrophulariaceae	OLI	Italy, Abruzzo (AQ), Casaline, 42°25'01.4"N 13°11'58.2"E, 1126 m a.s.l., 8.vii.2018, adult on *Scrophularia* sp. (Scrophulariaceae) [det. M. Biondi, voucher db43]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus helvolus Kutschera	Lamiaceae	OLI	GenBank			KU916133	–

Species	Host plant family	Trophic Range	Source for molecular analysis	Permits	Deposits	GenBank accession number	
						cox1	16S
Longitarsus holsaticus (Linnaeus)	Plantaginaceae	OLI	GenBank			KJ965710	–
Longitarsus isoplexidis Wollaston	Boraginaceae	MON	Portugal, Madeira Island, Encumeada, 32°44'24.2"N 17°02'55.0"W, 1316 m a.s.l., 1.iii.2017, adult on *Echium candicans* (Boraginaceae) [det. M. Biondi, voucher db7]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus languidus Kutschera	Asteraceae	MON	GenBank			KU906343	–
Longitarsus lateripunctatus (Rosenhauer)	Boraginaceae	OLI	Italy, Lazio (RM), Rome, 41°52'45.62"N 12°27'31.96"E, 50 m a.s.l., 7.v.2017, adult on *Echium vulgare* (Boraginaceae) [det. M. Biondi, voucher db16]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus lewisii (Baly)	Plantaginaceae	OLI	GenBank			KJ964861	–
Longitarsus lindbergi Madar & Madar	Asteraceae	OLI	Portugal, Madeira Island, Encumeada, 32°44'24.2"N 17°02'55.0"W, 1316 m a.s.l., 1.iii.2017, adult on *Pericallis aurita* (Asteraceae) [det. M. Biondi, voucher db23]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus linnaei (Duftschmid)	Boraginaceae	OLI	Italy, Abruzzo (AQ), Onna, 42°19'22"N 13°28'24"E; 650 m a.s.l., 14.iv.2017, adult on *Symphytum tuberosum* (Boraginaceae) [det. M. Biondi, voucher db12]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus lycopi (Foudras)	Lamiaceae	OLI	Italy, Abruzzo (TE), Prato Selva, 42°31'46.74"N 13°30'19.08"E, 1178 m a.s.l., 11.vii.2018, adult on *Mentha* sp. (Lamiaceae) [det. M. Biondi, voucher db50]	Gran Sasso e Monti della Laga National Park. Prot. n. 0007403/18	Collection M. Biondi, University of L'Aquila (Italy)	KX943332	requested
Longitarsus melanocephalus (De Geer)	Plantaginaceae	MON	GenBank			KX943469	KX943469
Longitarsus membranaceus (Foudras)	Lamiaceae	OLI	GenBank			KX943473	KX943473
Longitarsus minusculus (Foudras)	Lamiaceae	OLI	GenBank			KM442213	KP763142
Longitarsus nasturtii (Fabricius)	Boraginaceae	OLI	Italy, Lazio (RM), Rome, 41°54'50.58"N 12°22'57.12"E, 65 m a.s.l., 14.v.2017 [det. M. Biondi, voucher db34]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	KM442304	requested
Longitarsus niger (Koch)	Plantaginaceae	OLI	GenBank			KX943504	KX943504
Longitarsus nigrocillus (Motschulsky)	Convolvulaceae	OLI	GenBank			KX943464	KX943464
Longitarsus nigrofasciatus (Goeze)	Scrophulariaceae	OLI	GenBank			KX943438	KX943438
Longitarsus obliteratus (Rosenhauer)	Lamiaceae	OLI	Italy, Abruzzo (AQ), Roio Piano, 42°19'29.91"N 13°20'24.87"E, 1011 m a.s.l., 15.vii.2018, adult on *Thymus* sp. (Lamiaceae) [det. M. Biondi, voucher db57]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	KM447410	requested
Longitarsus ochroleucus (Marsham)	Asteraceae	OLI	GenBank			KM448633	KP763117

Species	Host plant family	Trophic Range	Source for molecular analysis	Permits	Deposits	GenBank accession number	
						cox1	16S
Longitarsus ordinatus (Foudras)	Lamiaceae	OLI	GenBank			KX943383	KP763143
Longitarsus pellucidus (Foudras)	Convolvulaceae	OLI	GenBank			KR480207	–
Longitarsus pinguis Weise	Boraginaceae	OLI	Italy, Abruzzo (AQ), Campo Imperatore, 42°26'17.8"N 13°35'41.2"E, 1760 m a.s.l., 21.vi.2017, adult on *Cynoglossum magellense* (Boraginaceae) [det. M. Biondi, voucher db21]	Gran Sasso e Monti della Laga National Park. Prot. n. 0007804/17	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus plantagomarittimus Dollman	Plantaginaceae	MON	GenBank			–	EF421523
Longitarsus pratensis (Panzer)	Plantaginaceae	OLI	GenBank			KX943360	KX943360
Longitarsus pulmonariae Weise	Boraginaceae	OLI	GenBank			KU907407	–
Longitarsus quadriguttatus Pontoppidan	Boraginaceae	OLI	GenBank			KM446524	–
Longitarsus rectilineatus (Foudras)	Lamiaceae	OLI	Italy, Lazio (RI), Val di Fua, 42°10'30"N 13°19'19"E; 1300–1500 m a.s.l.,13.ix.2017, adult on *Daphne laureo*la (Thymelaeaceae; refuge plant) [det. M. Biondi, voucher db35]	Sirente Velino Natural Park Prot. n. 1441 22/06/2017	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus reichei (Allard)	Plantaginaceae	OLI	GenBank			KU907319	–
Longitarsus rutilus (Illiger)	Scrophulariaceae	MON	GenBank			KX943491	KX943491
Longitarsus salviae Gruev	Lamiaceae	MON	Italy, Abruzzo (AQ), Ortolano, 42°29'51.3"N 13°23'12.5"E, 1133 m a.s.l., 27.vii.2017, adult on *Thymus* sp. (Lamiaceae) [det. M. Biondi, voucher db31]	Gran Sasso e Monti della Laga National Park. Prot. n. 0007804/17	Collection M. Biondi, University of L'Aquila (Italy)	KU907298	requested
Longitarsus saulicus Gruev & Doeberl	Boraginaceae	OLI	Israel, Har Bracha, Amasa Spring, 32°11'35.93"N 35°15'54.21"E, 864 m a.s.l., 27.iii.2017, adult on *Anchusa* sp. (Boraginaceae) [det. M. Biondi, voucher db11]	not needed	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus scutellaris (Mulsant & Rey)	Plantaginaceae	MON	GenBank			KR484199	–
Longitarsus springeri Leonardi	Asteraceae	MON	Italy, Abruzzo (AQ), Campo Imperatore, 42°26'55"N 13°32'24"E, 2140 m a.s.l., 23.viii.2018, adult on *Senecio rupestris* (Asteraceae) [det. M. Biondi, voucher db24]	Gran Sasso e Monti della Laga National Park. Prot. n. 0007403/18	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested
Longitarsus succineus (Foudras)	Asteraceae	OLI	Italy, Abruzzo (AQ), Valico delle Capannelle, 42°27'33.96"N 13°21'7.56"E, 1312 m a.s.l., 15.v.2017 [det. M. Biondi, voucher db53]	Gran Sasso e Monti della Laga National Park. Prot. n. 0007804/17	Collection M. Biondi, University of L'Aquila (Italy)	KJ962137	requested
Longitarsus suturellus (Duftschmid)	Asteraceae	OLI	GenBank			KU915636	–
Longitarsus tabidus (Fabricius)	Scrophulariaceae	OLI	GenBank			KX943424	KX943424
Longitarsus zangherii Warchalowski	Asteraceae	MON	Italy, Abruzzo (TE), Prati di Tivo, 42°30'26.40"N 13°33'14.46"E, 1344 m a.s.l., 11.vii.2018, adult on *Petasites* sp. (Asteraceae) [det. M. Biondi, voucher db47]	Gran Sasso e Monti della Laga National Park. Prot. n. 0007403/18	Collection M. Biondi, University of L'Aquila (Italy)	requested	requested

Phylogenetic analyses

Multiple sequence alignment was performed with MAFFT v.7 (Katoh and Standley 2013) using the E-INS-i iterative refinement algorithm. Phylogenetic analyses were conducted using Maximum Likelihood (ML) and Bayesian Inference (BI) approaches on the concatenated alignment of cox1 and 16S sequences, using as outgroup *Batophila aerata* (Marsham, 1802). This outgroup belongs to *Altica* group, and has been demonstrated as a closely related lineage to *Longitarsus* group based on molecular evidence by Nie et al. (2018). Maximum Likelihood analyses were performed in raxmlGUI 1.5b2 (Silvestro and Michalak 2012), a graphical front-end for RAxML 8.2.1 (Stamatakis 2014), with 10,000 rapid bootstrap replicates and 2000 independent ML searches (20% of the number of bootstrap replicates; command "*-f a*"; Stamatakis et al. 2008), applying the general time-reversible model with a gamma model of rate heterogeneity (GTRGAMMA), with individual gene partitions.

Bayesian Inference analyses were performed in MrBayes 3.2.6 (Ronquist et al. 2012) using the best models of nucleotide substitution selected by JModelTest 2.1.1 (Darriba et al. 2012) under the corrected Bayesian Information Criterion (cox1: HKY+G; 16S: GTR+I+G). Two independent Markov chain Monte Carlo (MCMC) analyses with 6 chains each were run in parallel for 50 million generations, sampling every 5000 generations. The first 25% were discarded as burn-in. MCMC chains convergence was verified by average standard deviation of split frequencies values below 0.0035 and confirmed in Tracer 1.7 (Rambaut et al. 2018). A majority rule consensus tree with posterior probability of each node was calculated with the *sumt* command in MrBayes.

Phylogenetic results were summarised using the ML tree and reporting for each node both BS and BPP from the Bayesian analysis. Nodes with bootstrap values (BS) between 70 and 90% and Bayesian posterior probability (BPP) between 0.95 and 0.98 were considered as supported, and those with BS greater than 90% and BPP greater than 0.98 as highly supported.

Results and discussion

Host plants information is available for 165 out of 197 *Longitarsus* species known for the Western Palaearctic region. More than 96% of the species for which hosts are known, are specialized, either oligophagous or monophagous. The remaining species are generally considered as polyphagous (Fig. 1). Specialized feeders are distributed on plant families as follows (Fig. 1): Boraginaceae (51 species, 32.1%), Lamiaceae (39, 24.5%), Asteraceae (23, 14.5%), Plantaginaceae (18, 11.3%), Scrophulariaceae (12, 7.5%), Convolvulaceae (6, 3.8%), Thymeleaceae (4, 32.5%), Ranunculaceae (3, 1.9%), Caprifoliaceae (2, 1.3%), Lentibulariaceae (1, 0.6%).

Among the 52 *Longitarsus* species used in our molecular phylogenetic analyses (Table 1), 49 are monophagous or oligophagous; *L. atricillus* and *L. aeneicollis* are polyphagous, while no information is available about host plants of *L. bedelii*. Such a

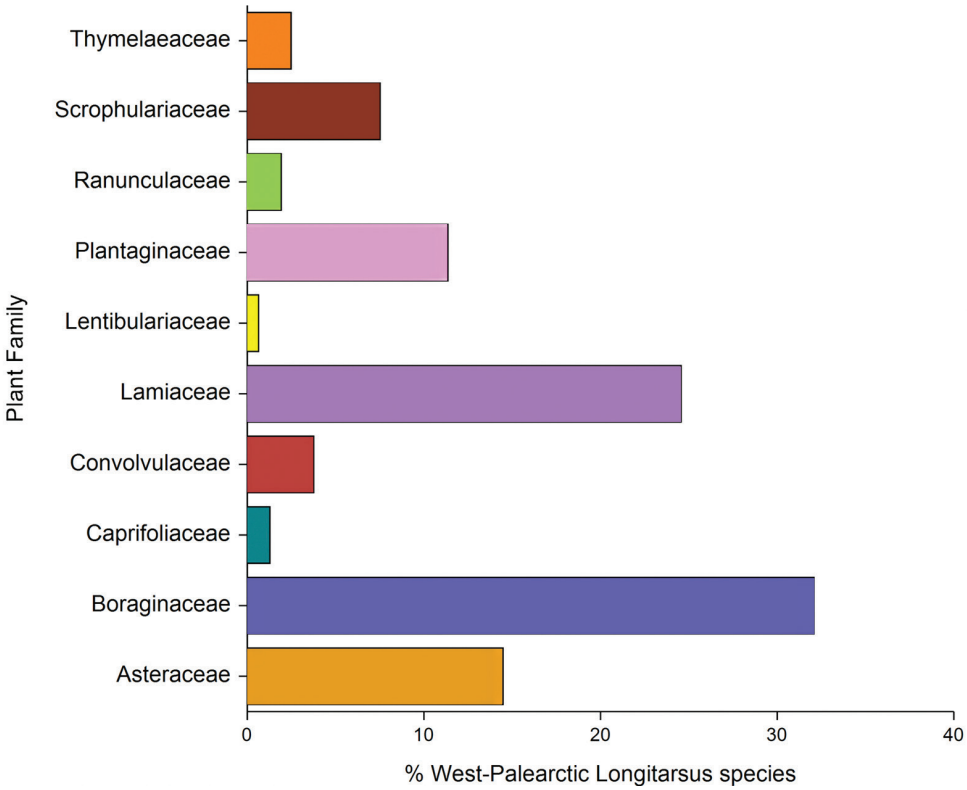

Figure 1. Percent distribution of oligophagous and monophagous Western Palaearctic species of *Longitarsus* on host plant families.

high number of specialized species allows a straightforward assessment of phylogenetic conservatism in host plant use, given a phylogenetic tree of the *Longitarsus* species and the relationships among host plant families.

Phylogenetic analyses based on ML and BI methods gave consistent results and identified the same supported clades (Fig. 2). Most of these clades have been previously recognized as distinct species-groups based on morphology (external morphology, aedeagus and/or spermatheca): (1) clade H includes species of the *tabidus* group sensu Leonardi (1972); (2) species of the *pratensis* group sensu Leonardi and Doguet (1990) are clustered in the clade B2; (3) *L. pulmonariae*, *L. exsoletus*, and *L. cerinthes* (clade O) were already known to be closely related (Leonardi 1972); (4) *L. anchusae* and *L. saulicus* (within clade D) belong to the *anchusae* group sensu Biondi (1995a).

In agreement with the host phylogenetic conservatism hypothesis, we recovered a strict association between most of the recovered *Longitarsus* clades and specific plant families, except for species associated with Boraginaceae (Fig. 2). *Longitarsus* species associated with Plantaginaceae form two closely related and supported clades (clades B1 and B2) and those associated with Scrophulariaceae form a distinct, well supported

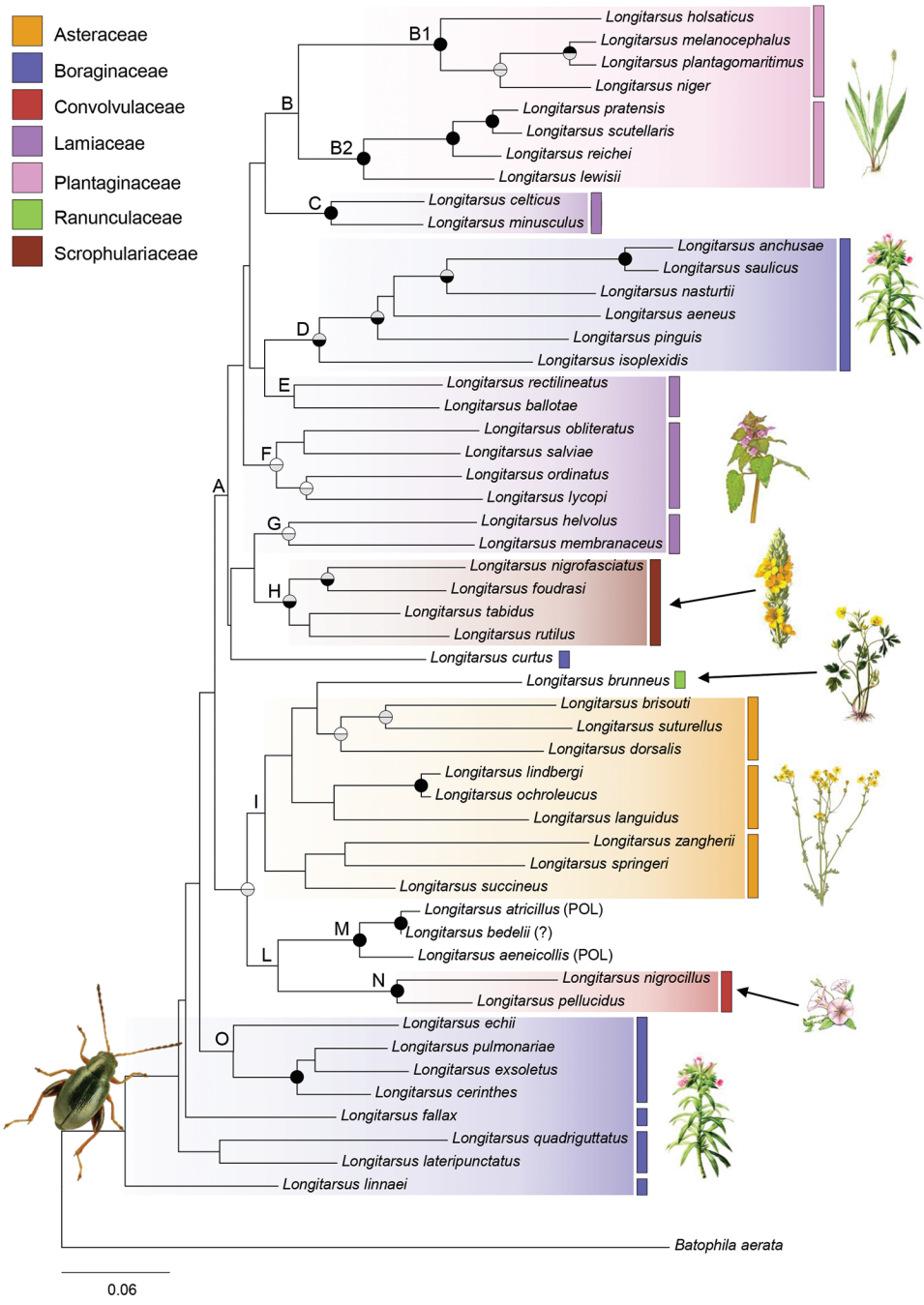

Figure 2. Maximum Likelihood phylogenetic tree of 52 species of *Longitarsus* based on concatenated cox1 and 16S DNA sequences. Circles in correspondence of nodes represent bootstrap support (BS, upper half) and posterior probability (BPP, bottom half) from Bayesian analysis: black for BS > 90 and BPP > 0.98; grey for BS of 70–90% and BPP of 0.95–0.98; white for BS of 50–70% only for nodes supported by Bayesian analysis. Abbreviations: POL = polyphagous; ? = host plants unknown.

clade (clade H). Species associated with Lamiaceae are included in four clades (C, E, F, G) within a major lineage of Western Palaearctic *Longitarsus* (clade A). Relationships between clades within this lineage are poorly resolved; additional molecular data will be required to clarify relationships within clade A and to assess whether clades associated with Lamiaceae are truly polyphyletic or instead if increased phylogenetic resolution will allow recovering them as a monophyletic assemblage. All nine species associated with Asteraceae are grouped in the clade I; this clade also includes *L. brunneus* feeding on Ranunculaceae, and might represent an instance of host-shift towards an unrelated plant family (The APG 2016).

The two species associated with Convolvulaceae, *L. nigrocillus*, and *L. pellucidus*, cluster together with high support in clade N. The polyphagous species, *L. atricillus* and *L. aeneicollis*, plus *L. bedelii*, for which no host plants are known, form the highly supported clade M. On the other hand, clades grouping species associated with Boraginaceae are distant in the phylogenetic tree: clade D with six species and the isolated branch of *L. curtus* are included in clade A, whereas clade O with four species occupies a basal position of the phylogenetic tree together with other four species with poorly resolved phylogenetic position (*L. fallax*, *L. quadriguttatus*, *L. lateripunctatus*, *L. linnaei*).

Overall the phylogenetic tree of Western Palaearctic *Longitarsus* shows a decrease of statistical support from the tips to the root, with highly supported terminal clades and weakly supported basal relationships (Fig. 2). Therefore, the inference of phylogenetic conservatism in host-plant association is only robust at the lower hierarchical level. While the strong association between closely related *Longitarsus* species to the same plant family is clear, it is difficult to identify an association between closely related *Longitarsus* clades and closely related plant families. Most of the clades of *Longitarsus* (clades B-H) belonging to the same main lineage (clade A) are associated with plant families (Plantaginaceae, Scrophulariaceae, and Lamiaceae) that belong to the same order Lamiales (The APG 2016).

Ideally, for a conclusive assessment of phylogenetic conservatisms in host-plant association between closely related *Longitarsus* clades and closely related plant families we would require well-resolved phylogenies for both insects and plants at all taxonomic levels. While limited uncertainty exists for interrelationships between plant families (e.g., over the exact placement of Boraginaceae family (The APG 2016)), our molecular phylogenetic analysis only provides a first appraisal of relationships between Western Palaearctic *Longitarsus*. To assess whether the pattern of basal polytomy we observed (Fig. 2) is a solid polytomy or is due to a lack of data (see Mendes et al. 2016) further studies based on increased taxon and marker sampling are required. Improving field research is also crucial because the ecology and feeding biology of several species are still unknown. True host affiliation can be difficult to detect, due to the different interaction that phytophagous insects can have with plant species (Furth 1980, Schoonhoven et al. 2005), even though the use of molecular techniques, such as DNA barcoding of gut contents, can help to detect real trophic interactions (Jurado-Rivera et al. 2009).

Conclusions

In this study, we provided first evidence that host-use patterns are phylogenetically constrained in Western Palaearctic *Longitarsus*. Despite the limited set of species analysed, we found a clear association between closely related *Longitarsus* species and specific plant families (Plantaginaceae, Asteraceae, Scrophulariaceae, and Convolvulaceae). However, relationships between clades of species were poorly resolved thus preventing the assessment of whether all *Longitarsus* clades associated with a specific plant family, or to related plant families, represent a single lineage. Such a relationship is unlikely for those *Longitarsus* species feeding on Boraginaceae which were resolved in unrelated clades. A better understanding of the phylogenetic relationships between *Longitarsus* species associated with Boraginaceae is of great interest also from a biogeographical point of view. In fact, two groups of species feeding on Boraginaceae and sharing a number of striking morphological features show a disjunct Mediterranean-South African distribution (Biondi 1995a, Biondi and D'Alessandro 2008, 2017). Molecular studies with additional markers are in progress on an extended set of species to further our understanding of hostplant relationships in *Longitarsus*.

Acknowledgements

We are grateful to Caroline S. Chaboo, Anthony Deczynski, and Chris Reid for their suggestions, that have improved the early version of the manuscript. We thank Gran Sasso e Monti della Laga National Park and Sirente Velino Natural Park that allowed the collection of specimens used in this work. DS is supported by the program 'Rita Levi Montalcini' (MIUR, Ministero dell'Istruzione, dell'Università e della Ricerca) for the recruitment of young researchers at the University of L'Aquila.

References

Aslan EG, Gok A (2006) Host-plant relationships of 65 flea beetle species from Turkey, with new associations (Coleoptera: Chrysomelidae: Alticinae). Entomological News 117(3): 297–308. https://doi.org/10.3157/0013-872X(2006)117[297:HROFBS]2.0.CO;2

Balagawi S, Drew RAI, Clarke AR (2013) Simultaneous tests of the preference-performance and phylogenetic conservatism hypotheses: is either theory useful? Arthropod-Plant Interactions 7: 299–313. https://doi.org/10.1007/s11829-012-9244-x

Becerra JX, Vernable DL (1999) Macroevolution of insect–plant associations: The relevance of host biogeography to host affiliation. PNAS 96(22): 12626–12631. https://doi.org/10.1073/pnas.96.22.12626

Bieńkowski AO (2004) Leaf-beetles (Coleoptera: Chrysomelidae) of the eastern Europe. New key to subfamilies, genera, and species. Mikron-print, Moscow, 278 pp.

Biondi M (1995a) The *Longitarsus anchusae* complex in Near East and description of a new species (Coleoptera, Alticinae). Nouvelle Revue d'Entomologie (n.s.) 12: 259–271.

Biondi M (1995b) Gli Alticini delle Isole Canarie (Coleoptera, Chrysomelidae). Fragmenta Entomologica 26 (supplemento): 1–133.

Biondi M (1996) Proposal for an ecological and zoogeographical categorization of the Mediterranean species of the flea beetle genus *Longitarsus* Berthold. In: Jolivet PHA, Cox ML (Eds) Chrysomelidae biology 3 General Studies. SPV Academic Publishing bv, Amsterdam, 13–35.

Biondi M, D'Alessandro P (2008) Taxonomical revision of the *Longitarsus capensis* species-group: An example of Mediterranean-southern African disjunct distributions (Coleoptera: Chrysomelidae). European Journal of Entomology 105: 719–736. https://doi.org/10.14411/eje.2008.099

Biondi M, D'Alessandro P (2010) Genus-group names of Afrotropical flea beetles (Coleoptera: Chrysomelidae: Alticinae): Annotated catalogue and biogeographical notes. European Journal of Entomology 107: 401–424. https://doi.org/10.14411/eje.2010.049

Biondi M, D'Alessandro P (2012) Afrotropical flea beetle genera: A key to their identification, updated catalogue and biogeographical analysis (Coleoptera, Chrysomelidae, Galerucinae, Alticini). Zookeys 253: 1–158. https://doi.org/10.3897/zookeys.253.3414

Biondi M, D'Alessandro P (2017) *Longitarsus doeberli*, a wingless new species from Socotra Island (Coleoptera: Chrysomelidae). Acta Entomologica Musei Nationalis Pragae 57: 165–172. https://doi.org/10.1515/aemnp-2017-0116

Bologna MA, D'Inzillo B, Cervelli M, Oliverio M, Mariottini P (2005) Molecular phylogenetics of the Mylabrini blister beetles (Coleoptera, Meloidae). Molecular Phylogenetics and Evolution 37: 306–311. https://doi.org/10.1016/j.ympev.2005.03.034

Charlery de la Masselière M, Facon B, Hafsi A, Duyck P-F (2017) Diet breadth modulates preference–performance relationships in a phytophagous insect community. Scientific Reports 7: 16934. https://doi.org/10.1038/s41598-017-17231-2

Clark SM, LeDoux DG, Seeno TN, Riley EG, Gilbert AJ, Sullivan JM (2004) Host plants of leaf beetle species occurring in the United States and Canada (Coleoptera: Orsodacnidae, Megalopodidae, Chrysomelidae exclusive of Bruchinae). Coleopterist Society, Special Publication 2: 1–476. https://doi.org/10.1603/0013-8746(2005)098[0243:HPOLBS]2.0.CO;2

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. Nature Methods 9: 772. https://doi.org/10.1038/nmeth.2109

Döberl M (2010) Alticinae. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera. Volume 6. Chrysomeloidea. Apollo Books, Stenstrup, 491–563.

Dobler S, Haberer W, Witte L, Hartmann T (2000) Selective sequestration of pyrrolizidine alkaloids from diverse host plants by *Longitarsus* flea beetles. Journal of Chemical Ecology 26(5): 1281–1298. https://doi.org/10.1023/A:1005444313447

Doguet S (1994) Coléoptères Chrysomelidae. Vol. 2 Alticinae. Faune de France 80, 687 pp.

Fernandez P, Hilker M (2007) Host plant location by Chrysomelidae. Basic and Applied Ecology 8: 97–116. https://doi.org/10.1016/j.baae.2006.05.001

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.

Furth DG (1980) Wing polymorphism, host plant ecology, and biogeography of *Longitarsus* in Israel (Coleoptera: Chrysomelidae). Israel Journal of Entomology 13: 125–148.

Furth DG (2007) *Longitarsus warchalowskianus*, a new species from Chihuahua, Mexico (Coleoptera: Chrysomelidae: Alticinae). Genus 18(4): 623–630.

Gómez-Rodríguez C, Crampton-Platt A, Timmermans MJTN, Baselga A, Vogler AP (2015) Validating the power of mitochondrial metagenomics for community ecology and phylogenetics of complex assemblages. Methods in Ecology and Evolution 6: 883–894. https://doi.org/10.1111/2041-210X.12376

Gruev B, Döberl M (1997) General distribution of the flea-beetles in the Palaearctic Subregion (Coleoptera, Chrysomelidae: Alticinae). Scopolia 37: 1–496.

Gruev B, Döberl M (2005) General distribution of the flea-beetles in the Palaearctic Subregion (Coleoptera, Chrysomelidae: Alticinae). Supplement. Pensoft Publishers, Sofia-Moscow, 6–239.

Gruev B, Tomov V (2007) Distributional Atlas and Catalogue of the Leaf Beetles of Bulgaria (Coleoptera: Chrysomelidae). Zoocartographia Balcanica 3. Pensoft, Sofia-Moscow, 350 pp.

Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference–performance relationships in phytophagous insects. Ecology Letters 13: 383–393. https://doi.org/10.1093/molbev/mst010

Jolivet P, Hawkeswood T (1995) Host-plants of Chrysomelidae of the world. Backhuys Publishers, Leiden, 281 pp.

Jones LC, Rafter MA, Walter GH (2019) Insects allocate eggs adaptively across their native host plants. Arthropod-Plant Interactions. https://doi.org/10.1007/s11829-019-09688-x

Jurado-Rivera JA, Vogler AP, Reid CAM, Petitpierre E, Gómez-Zurita J (2009) DNA barcoding insect-host plant associations. Proceeding of the Royal Society B 276: 639–648. https://doi.org/10.1098/rspb.2008.1264

Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. Molecular biology and evolution 30: 772–780.

Kergoat GJ, Silvain J-F, Delobel A, Tuda M, Klaus-Werner A (2007) Defining the limits of taxonomic conservatism in host–plant use for phytophagous insects: Molecular systematics and evolution of host–plant associations in the seed-beetle genus *Bruchus* Linnaeus (Coleoptera: Chrysomelidae: Bruchinae). Molecular Phylogenetics and Evolution 43: 251–269. https://doi.org/10.1016/j.ympev.2006.11.026

Kergoat GJ, Meseguer AS, Jousselin E (2017) Evolution of Plant–Insect Interactions: Insights from Macroevolutionary Approaches in Plants and Herbivorous Insects. Advances in Botanical Research 81: 25–53. https://doi.org/10.1016/bs.abr.2016.09.005

Konstantinov AS (2005) New species of Middle Asian *Longitarsus* Latreille with discussion of their subgeneric placement (Coleoptera: Chrysomelidae). Zootaxa 1056: 19–42. https://doi.org/10.11646/zootaxa.1056.1.2

Latreille PA (1829) Suite e fin des insectes. In: Cuvier G (Ed.) Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Nouvelle édition, revue et augmentée. Tome V. Paris, Déterville, 556 pp.

Leonardi C (1972) La spermateca nella sistematica del genere *Longitarsus* (Coleoptera Chrysomelidae). Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano 113(1): 5–27.

Leonardi C, Doguet S (1990) Studio critico sui *Longitarsus* del gruppo *pratensis* (Panzer) (Coleoptera Chrysomelidae). Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano 131(2): 13–74.

Lima Bergamini L, Lewinsohn TM, Jorge LR, Almeida-Neto M (2017) Manifold influences of phylogenetic structure on a plant-herbivore network. Oikos 126: 703–712.https://doi.org/10.1111/oik.03567

Marsham T (1802) Entomologia Britannica, sistens insecta britanniae indigena, secundum methodum linnaeanam disposita. Tomus I. Coleoptera. Wilks & Taylor, Londini, 547 pp. https://doi.org/10.5962/bhl.title.65388

Mendes J, Harris DJ, Carranza S, Salvi D (2016) Evaluating the phylogenetic signal limit from mitogenomes, slow evolving nuclear genes, and the concatenation approach. New insights into the Lacertini radiation using fast evolving nuclear genes and species trees. Molecular Phylogenetics and Evolution 100: 254–267. https://doi.org/10.1016/j.ympev.2016.04.016

Nie R-E, Breeschoten T, Timmermans MJTN, Nadein K, Xue H-J, Bai M, Huang Y, Yang X-K, Vogler AP (2018) The phylogeny of Galerucinae (Coleoptera: Chrysomelidae) and the performance of mitochondrial genomes in phylogenetic inference compared to nuclear rRNA genes. Cladistics 34: 113–130. https://doi.org/10.1111/cla.12196

Palumbi SR, Martin A, Romano S, McMillan WO, Stice L, Grabowski G (1991) The Simple Fool's Guide to PCR. University of Hawaii Press, Honolulu, 45 pp.

Prathapan KD, Viraktamath CA (2011) A new species of *Longitarsus* Latreille, 1829 (Coleoptera, Chrysomelidae, Galerucinae) pupating inside stem aerenchyma of the hydrophyte host from the Oriental Region. ZooKeys 87: 1–10. https://doi.org/10.3897/zookeys.87.1294

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67(5): 901–904. https://doi.org/10.1093/sysbio/syy032

Reid CAM (2017) Australopapuan leaf beetle diversity: the contributions of hosts plants and geography. Austral Entomology 56: 123–137. https://doi.org/10.1111/aen.12251

Ronquist F, Teslenko M, Van der Mark P, Ayres DL, Darling A, Höhna S, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Salvi D, Maura M, Pan Z, Bologna MA (2018) Phylogenetic systematics of *Mylabris* blister beetles (Coleoptera, Meloidae): a molecular assessment using species trees and total evidence. Cladistics, in press. https://doi.org/10.1111/cla.12354

Sambrook J, Fritsch EF, Maniatis T (1989) Molecular Cloning: A Laboratory Manual. Cold Spring Harbor Laboratory Press, Cold Spring Harbor.

Schoohoven LM, van Loon, JJA, Dicke M (2005) Insect-Plant Biology (2nd edn). Oxford University Press, New York, 421 pp.

Silvestro D, Michalak I (2012) raxmlGUI: A graphical front-end for RAxML. Organisms Diversity & Evolution 12: 335–337. https://doi.org/10.1007/s13127-011-0056-0

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. Systematic Biology 57: 758–771. https://doi.org/10.1080/10635150802429642

The Angiosperm Phylogeny Group (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1–20. https://doi.org/10.1111/boj.12385

ZooKeys 856: 115–135 (2019)
doi: 10.3897/zookeys.856.32564
http://zookeys.pensoft.net

RESEARCH ARTICLE

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Leaf beetle decline in Central Europe (Coleoptera: Chrysomelidae s.l.)?*

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Academic editor: *M. Biondi* | Received 19 December 2018 | Accepted 13 February 2019 | Published 17 June 2019

http://zoobank.org/13713C89-7CC9-42BB-AA23-CD2FFE5D8E40

Citation: Wendorff A, Schmitt M (2019) Leaf beetle decline in Central Europe (Coleoptera: Chrysomelidae s.l.)? In: Schmitt M, Chaboo CS, Biondi M (Eds) Research on Chrysomelidae 8. ZooKeys 856: 115–135. https://doi.org/10.3897/zookeys.856.32564

Abstract

Based on 168,674 records in the database ChryFaun changes in distribution and abundance of leaf beetles (Chrysomelidae s.l.) in Central Europe were analysed from 1900 through 2009. From the first decade (1900–1909) to the last (2000–2009) the number of records per decade increased by factor 26, from 1513 to 41,269. The number of species increased from 395 in decade 1 to 606 in decade 10, but only 532 were reported in decade 11. The number of species with fewer records increased from 1990 although the total number of records increased continuously. Decrease and increase is found likewise in mono-, oligo-, and polyphagous species. Twenty-two species (3.0%) have not been reported since 1990, and 42 (5.8%) since 2000. 71% of all taxa reported between 2000 and 2009 had fewer records than in the immediately previous decade. These indications of decline correspond with numerous published studies on decline in other groups of arthropods. Analysis shows that data from private and public collections are useful for the retrospective analysis of numbers and distributions of leaf beetles (and other organisms).

Keywords

abundance, collection data, geographical distribution, insect decline

* extended versions of a talk presented to the 3rd European Symposium on the Chrysomelidae, Naples, Italy, 5 July, 2018.

Introduction

The alarming news that the biomass of flying insects decreased by 75% in the course of the past 30 years (Hallmann et al. 2017) raised a remarkable public awareness of the general decline of biodiversity in Europe and elsewhere. Earlier studies (e.g., Thomas et al. 2004; Conrad et al. 2006; Kosior et al. 2007) had pointed in the same direction but were hardly noticed by the media and decision makers. Biesmeijer et al. (2006) had even demonstrated a parallel decline of pollinators and insect-pollinated plants in The Netherlands.

There is an ongoing controversy as to the causation of this process. Change in land use and intensified agriculture, loss or fragmentation of habitats, and the global climate change are considered as possible causes (see Conrad et al. 2006; Potts et al. 2010; Hallmann et al. 2017). The average temperature in Europe increased between 2006 and 2015 by 1.45–1.59 °C as compared to pre-industrial times (Kurnik 2017). Habitat fragmentation prevents individuals from natural dispersal so that local extinction events occur. As a consequence, smaller population sizes and a reduced ability to disperse of, e.g., *Cryptocephalus nitidulus* Fabricius, 1787 (Chrysomelidae: Cryptocephalinae) were observed in Britain (Piper and Compton 2010).

Changes in land use, habitats and climate certainly not only cause a decline of insects (and other organisms) but will also further range shifts and colonisation of new habitats as animals will track their preferred conditions if ever possible. In literature, we find numerous reports of an expansion or shift of ranges in beetles, butterflies, dragonflies, and grasshoppers to the north or to higher elevations (Parmesan 1996; Parmesan et al. 1999; Konvicka et al. 2003; Hickling et al. 2006), as well as spiders (Krehenwinkel and Tautz 2013) and birds (Thomas and Lennon 1999). Also leaf beetles seem to respond to increasing temperature by changing their distributional area, as shown for *Oulema melanopus* (Linnaeus, 1758) in Canada (Olfert and Weiss 2006) and for *Leptinotarsa decemlineata* (Say, 1824) and *O. melanopus* in Europe (Svobodova et al. 2014).

We checked if decline and distributional change also occur in leaf beetles (Chrysomelidae s.l.) in Central Europe. To accomplish this we analysed the records in the database ChryFaun for the period from 1900 to 2009 or 2017. This database was compiled by the members of the working group "Faunistics of Central European leaf and seed beetles – ChryFaun", founded in 1987 (Schmitt et al. 2014). We expected to find a number of species that extended or shifted their range northwards, and that the number of records for some species had decreased towards the end of our study period.

Materials and methods

The database

The database ChryFaun contains records from the end of the 19th century to present, taken from museum and private collections, provided by institutions, individual amateur collectors, and regional entomological clubs (for details see Schmitt et al. 2014). Up to now (06.12.2018), 175,632 records for 726 species and 50 subspecies of Chrysomel-

idae sensu lato (i.e., including Megalopodidae, Orsodacnidae, and Bruchinae/Bruchidae) have been entered. We follow the nomenclature in Löbl and Smetana (2010).

Operationally, "Central Europe" is defined as the rectangle between 2° and 25° eastern longitude and between 45° and 55° northern latitude. This area comprises The Netherlands, Belgium, Luxembourg, Germany, Switzerland, Liechtenstein, Austria, The Czech Republic, Slovakia, Poland, Hungary, Slovenia, and parts of France, Italy, Croatia, Serbia, Romania, Ukraine, Belarus, Russia, and Lithuania (see Fig. 1).

Data analysis

Changes in distribution

We selected 246 species or subspecies out of the 776 taxa in ChryFaun. These are (1) species for which Schmitt and Rönn (2011) gave a northern, montane, southern, southeastern or southwestern distribution; (2) species for which we found an indication of distributional change in the literature; and (3) all additional species of the genera *Gonioctena*, *Orsodacne*, *Phyllotreta*, *Timarcha* and *Zeugophora*, as we suspected that they may be prone to behave ecologically similar to their congeneric species with ranges of the types listed under (1).

We divided the study period (1900 through 2017) into four quartiles, quartile 1: 1900–1929, quartile 2: 1930–1959, quartile 3: 1960–1989, and quartile 4: 1990–2017. We generated frequency maps of the distribution of all species studied for each quartile using the distribution mapping software DMAP (Alan Morton, Penrhyncoch, Aberystwyth, Ceredigion, UK – http://www.dmap.co.uk/, Version 7.4, 32-bit). Species with fewer than 24 records for the period from 1900 through 2017 were omitted.

We compared the four maps and recorded a change in distribution if the species extended or shifted its range from at least one quartile to the next for more than one degree latitude or/and longitude. We defined nine categories of change according to the direction of extension or shift: to the north, east, south, west, northeast, northwest, southeast, southwest, and "shrinking". Since a species could extend or shift its range in more than one direction, we sorted some species to more than one category. We categorized a species distribution as "shrinking" when its range diminished, or when the species disappeared.

Increase or decrease of the number of records

Here, we considered the time period from 1900 through 2009 because we have too few entries for the last eight years and for the period prior to 1900. In the ChryFaun database are 165,506 records for the time period under study (as of January, 2019). The figures for each of the 11 decades were ascertained, and increase or decrease from each decade to the following was coded qualitatively and quantitatively. The proportion of species with de- and increased records per decade were calculated, their deviation from the mean was tested with Pearson's Chi-squared test. We also tested the figures for mono-, oligo-, and polyphagous species separately. We performed χ^2- and Fisher's exact tests using 'R' v. 3.4.3 (R Core Team 2017).

Results

Changes of distribution

We could not detect a change in 84 of the selected 246 taxa. The remaining 162 taxa fall in one or more than one of the described categories (Tab. 1).

Increase and decrease of reported records

The 175,632 records in ChryFaun from the time period end of 19th century through 2017 are distributed unevenly over the area of Central Europe (Fig. 1). Approximately 114,500 records lie within Germany, with highest densities around Hamburg, in Thuringia, Saxony-Anhalt, in the Rhineland, and in the Alsace. Similarly high densities of records can be seen in eastern Austria around Lake Neusiedl, and also in the north and in the south of Poland. From some regions (white areas) we do not have records. Austria, Switzerland, Slovenia, and the major part of Germany are well covered.

We divided the study period into four quartiles, 1900–1929, 1930–1959, 1960–1989, 1990–2017, and identified the number of records for each quartile. The 173,981 records are distributed in a highly uneven manner, over time (Fig. 2) and in space (Fig. 3).

We have 7,412, 20,473, 57,251, and 88,845 records from quartile 1, 2, 3, and 4, respectively. The geographical distribution of the records (Fig. 3a–d) shows a similar pattern for each quartile in their overall distribution (Fig. 1).

We tested the figures of the four quartiles separately for species reported as monophagous, oligophagous, or polyphagous, respectively by Koch (1992). There were no significant differences in the proportions of species with de- or increased numbers of records from one quartile to the following.

For more detailed analysis we listed the records per decade from 1900 through 2000. The time period was truncated at 2009 in order to compare full decades and because collectors often hand in their contributions with a delay. From decade 1(1900–1909) to decade 11 (2000–2009) the number of records in ChryFaun increased from 1513 to 40,269, i.e., by factor 26.6. This increase (± 0.5) is, however, caused by records that pertain to only three species: *Lochmaea crataegi* (Forster, 1771), *Sclerophaedon orbicularis* (Suffrian, 1851), and *Chrysolina staphylaea* (Linnaeus, 1758). In 229 taxa (species and subspecies) the increase is lower than by factor 26, and 19 taxa show an absolute decrease in records. The factor of increase is higher than 26 in only 123 taxa. For 402 of the 776 taxa we did not calculate such factors as either the numbers of their records were constant over the eleven decades or records were missing for decade 1 or decade 11. The number of reported taxa increased from 399 in decade 1 to 657 in decade 10, but only 616 were reported in decade 11 (Fig. 4, orange line).

The number of species with increase or decrease from one decade to the following is not constant over time. There are significant deviations from equal distribution (increase: $\chi^2 = 195.18$, df = 9, p-value < 2.2e-16, decrease: $\chi^2 = 323.05$, df = 9, p-value < 2.2e-16, Pearson's Chi-squared test, Fig. 5).

Table 1. Change of distribution of 162 out of the 246 selected species of Chrysomelidae s.l. in central Europe (58 species are sorted into more than one category).

Change of distribution towards	Number of species
North	25
East	107
South	12
West	17
North-East	18
North-West	10
South-East	19
South-West	5
Shrinking	25

The complete list of species and their assignments are given in Appendix 1.

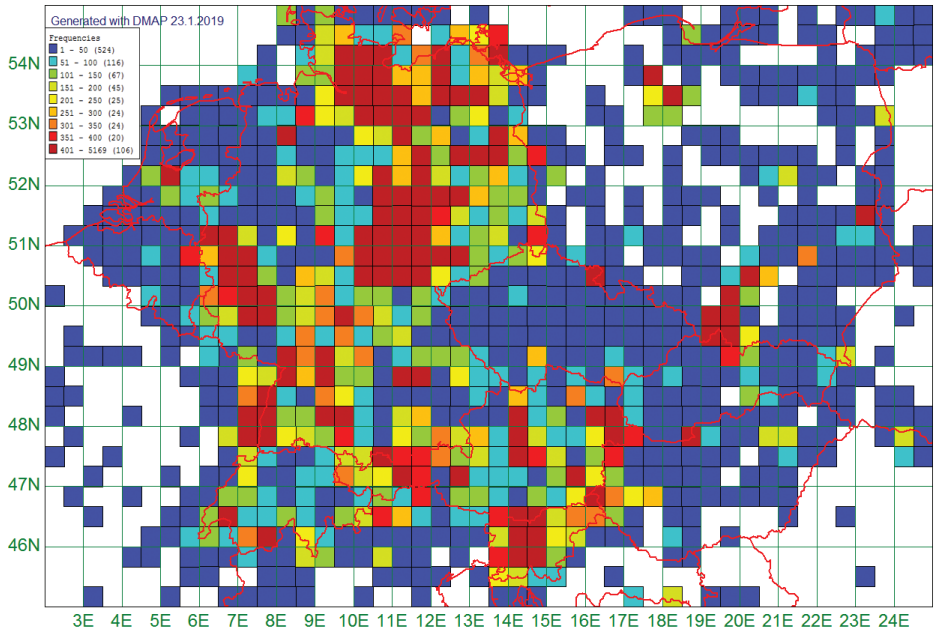

Figure 1. Distribution of the 175,632 records from 951 grid fields of 20 × 30 geographical minutes in Central Europe.

From decade 1 through decade 9 the number of those taxa with an increase in records (orange columns in Fig. 5) increases. At the same time, the number of taxa with a decrease of records (blue columns in Fig. 5) remains relatively constant, with the exception of the changes from decade 3 to 4 and from 4 to 5. Beginning with decade 9 (1990), our data show obvious changes. There are fewer taxa with an increase of records whereas there are considerably more taxa with a decrease of records. From decade 10 to 11 more taxa showed a decrease than an increase of records (Fig. 5).

In decade 10 (1990–1999) 22 species were no longer reported that were present in the previous decades. In decade 11 this figure increased to 42 species (see Appendix 2).

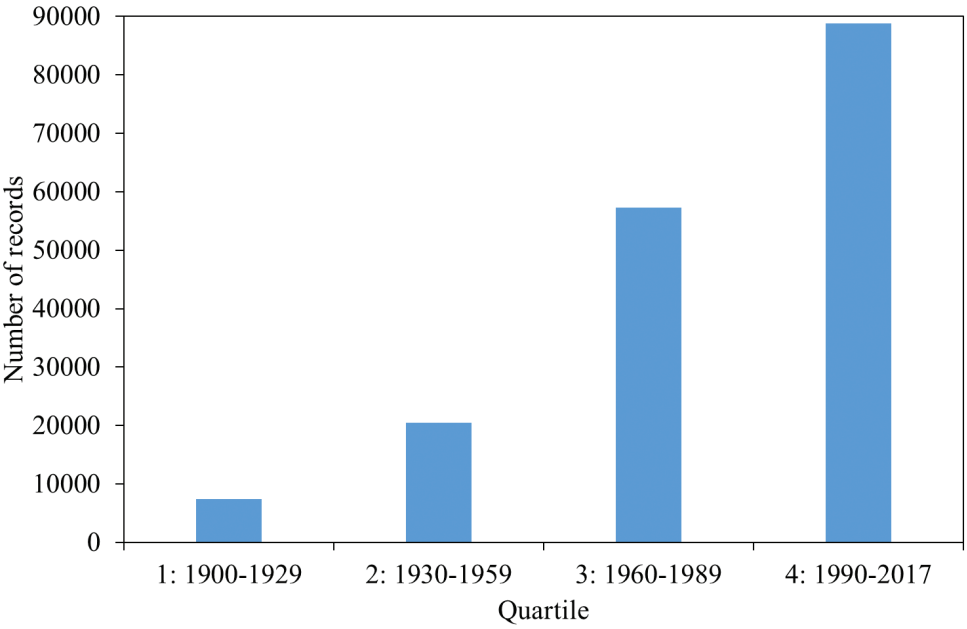

Figure 2. Numbers of records of Chrysomelidae s.l. in ChryFaun per quartile.

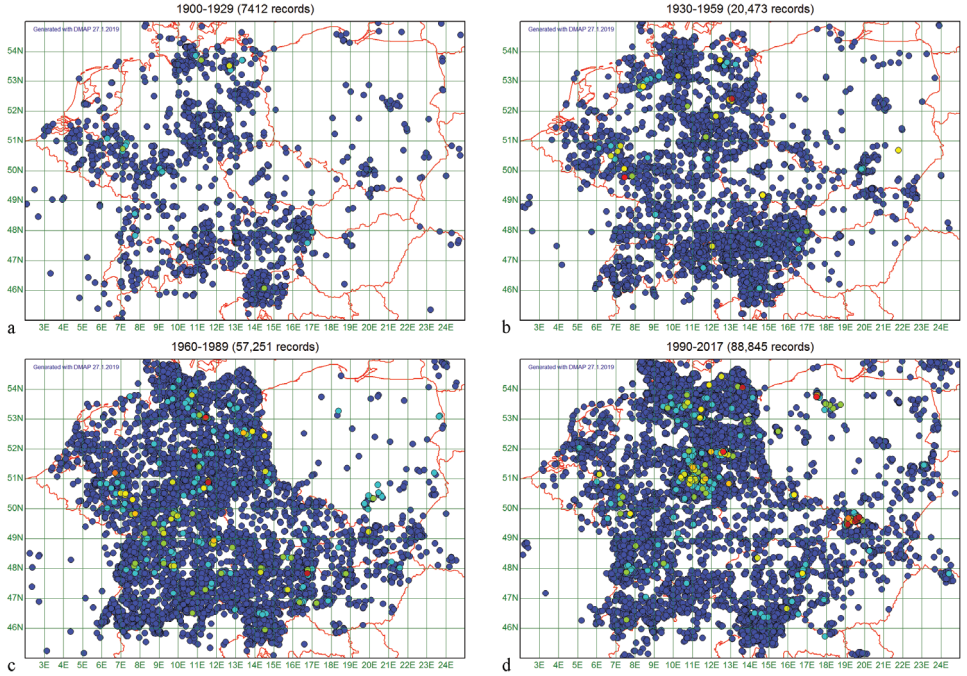

Figure 3. Geographical distribution of the records in ChryFaun for the four temporal quartiles shown as circles of 12.5 × 20 geographical minutes diameter. **a** 1900–1929 **b** 1930–1959 **c** 1960–1989 **d** 1990–2017.

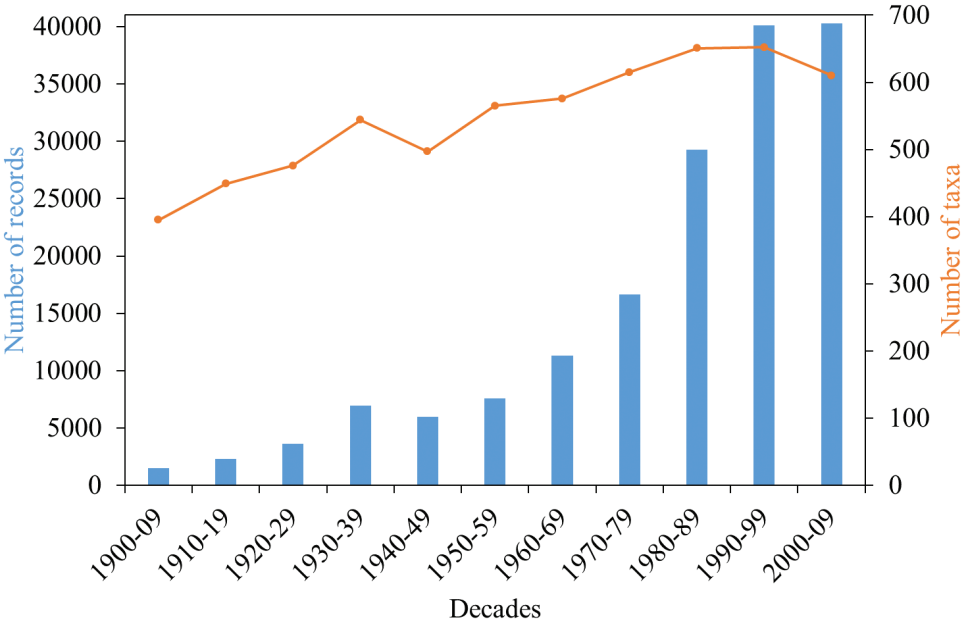

Figure 4. Number of records (blue columns) and number of reported taxa (species and subspecies -orange line) per decade between 1900 and 2009.

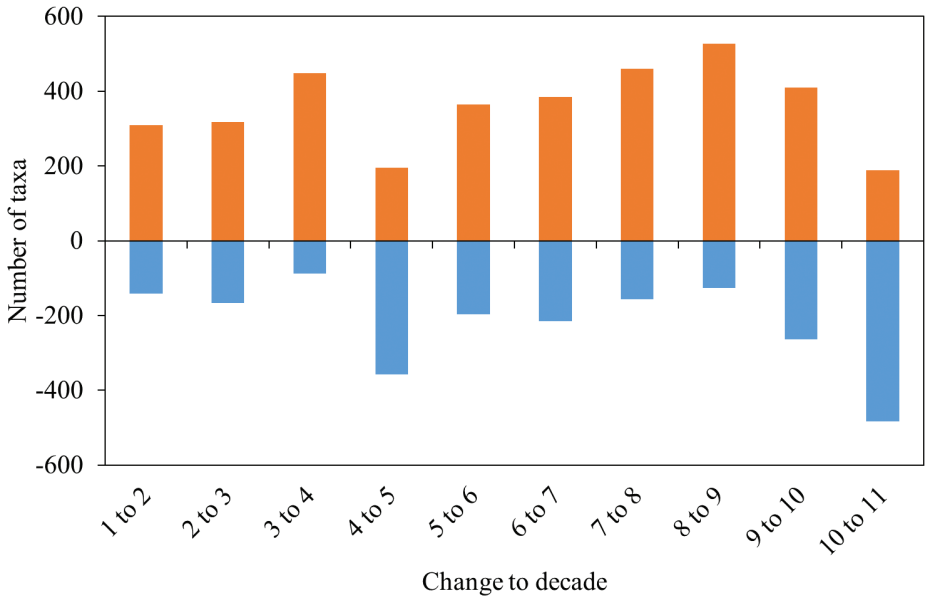

Figure 5. Number of taxa with an increase (orange) or a decrease (blue) of records from one decade to the following. The figures for increase and for decrease differ significantly from equal distribution (Pearson's Chi-squared test: $\chi^2 = 195.18$, df = 9, p-value < 2.2e-16 for the increase values, $\chi^2 = 323.05$, df = 9, p-value < 2.2e-16 for the decrease values).

Species that "disappeared" from Germany are e.g., *Ochrosis ventralis* (Illiger, 1807) and *Psylliodes luteola* (Müller, 1776). However, records from other areas, e.g., the Czech Republic exist for both species (Čižek 2006). The most recent record of *Entomoscelis adonidis* (Pallas, 1771) in whole Central Europe, e.g., is of 1982. From decade 10 to decade 11 only 192 taxa were reported with increased record numbers. Of these taxa, only eight species with more than 250 records each contributed 3,509 records to the total number. In decade 11, we had records of 687 taxa in total. Of these, 486 (71%) were reported with fewer records than in decade 10.

Discussion

Our database shows that the number of reported species decreased in the last decade although the total number of records increased (Fig. 4). This total increase of records is caused by only few highly abundant species. Our assessment suggests a decline in seed and leaf beetles in Central Europe since 1990. However, there are serious caveats: the continuous increase of records from 1900 to 2009 or 1900 to 2017, respectively (Figs 4, 2), reflects the activity of the collectors whose specimens are stored in the public collections we could exploit, and the motivation of those amateur collectors who reported their data to us or who published their findings. The activity of the amateur and professional collectors who contributed data varied over time and space. There are regions in Central Europe where entomological clubs are active whereas in others there are no such associations. Additionally, amateurs tend to collect in areas highly attractive to tourists, and where they expect a high diversity and abundance of the species in which they are interested. A major consequence is the inhomogeneous coverage of records over our study area (Fig. 1). Also, numerous collectors focus on certain subtaxa, sometimes even single genera, and ignore the remaining seed and leaf beetle species (see also Rheinheimer and Hassler 2018: 52). However, data on widespread and common species can also yield useful information on a possible biodiversity crisis (Conrad et al. 2006) but are probably underrepresented in our database. The collected specimens were identified to species or subspecies by taxonomists of different levels of expertise. Thus, our database likely contains some taxonomically incorrect records. During the past 20 years, a considerable number of leaf beetle taxonomists died, and only few younger taxonomists specialised on Chrysomelidae (E Geiser, Salzburg, pers. comm 2018, J Bezděk, Brno, pers. comm. 2019). As a consequence, the proportion of erroneous records probably increased because individuals of rare species were overlooked or incorrectly identified. This could in part explain the list of species with missing entries in ChryFaun since 1990 or 2000.

In the course of the last 100 years, the number of collected and reported seed and leaf beetles increased (Fig. 4). The number of reported species or subspecies increased more or less continuously from 1900 to 1999 but decreased markedly in the decade from 2000 to 2009. We conclude that there are fewer species of Chrysomelidae s.l. in Central Europe today than in 1990. Moreover, we consider the significant increase of the number of the species with decreased records during the last two decades of

our study period as an indication of a serious threat to leaf beetle diversity. Quite a remarkable number of species has not been reported since 1990, and even more since 2000 (see Appendix 2). Even if we take into account that many of these "disappeared" species were or are rare and/or occur in areas from where we have only a limited number of records at all, we argue that the missing records are an alarming indication of a disappearance or even extinction in nature. Winkelman and Beenen (2010) found that a similar number of leaf beetle species had disappeared from the fauna of The Netherlands since 2000. Even some introduced stored-product pest species (marked with an * in Appendix 2) were no longer reported after 2000. We decided not to omit them from our list as this decrease of records might be indicative of factors that also influence the data on non-pest species.

Several authors, e.g., Thomas and Lennon (1999), Hickling et al. (2006), and Mason et al. (2015) discuss a general latitudinal expansion or shift of ranges of numerous invertebrate and vertebrate species as a consequence of global warming, as was found for the spider *Argiope bruennichi* (Scopoli, 1772) (Krehenwinkel and Tautz 2013). As to leaf beetles, only a surprisingly low number of species, 25 of the 246 analysed ones, meet our expectations. Our finding that 107 species now have a more eastern distribution as compared to the time period prior to 1980, and 18 more to north-east and 19 to south-east, must be seen with great reservations since the data coverage of the eastern part of Central Europe is low, so this effect is most likely due to a strong general increase in number of records for the east. Nevertheless, even here there may be a real natural process underlying our data.

Generally, oscillations of abundances within certain limits are natural and might vary from year to year. Temperature, precipitation, plant growth, food availability, but also diseases, parasites, and predators influence the number of individuals in a given area (Rheinheimer and Hassler 2018: 52). Above all, climate change, loss or fragmentation of habitats or their degradation are discussed in literature as possible causes of species declines and/or changes of range (Thomas et al. 2004; Köhler 2010; Kosior et al. 2007; Piper and Compton 2010; Hallmann et al. 2017). According to the European Environment Agency (Kurnik 2017), the average temperature in Europe increased between 2006 and 2015 by 1.45 to 1.59 °C as compared to the pre-industrial era. As the development and growth of ectothermic organisms like leaf beetles is strongly influenced by the ambient temperature, an increase in the number of records could reflect global warming. However, the observation that only 25 species extended their range towards north and 18 to north-east might suggest that global warming is probably not a major, or at least not a crucial, driver of range extensions of leaf beetles in Central Europe. The critical finding is that the number of species in our database decreased although the total number of records increased.

Loss and fragmentation of habitats are known to be responsible for the decline or even complete disappearance of species. Increasing mobility and economic activity, urbanisation, and expansion and change of agriculture are the drivers of changing landscapes (Opdam and Wascher 2004). Between 2000 and 2006 an area of 6256 km² was turned from green land into settlements and traffic zones in Germany (UBA1 2018).

At the same time the German Environment Agency (Umweltbundesamt, UBA) reports a loss of 5278 km² of agricultural areas (fields and grassland, 1212 km² of forests and semi-natural areas, and 434 km² of wetlands (UBA1 2018). Additionally, the agriculture was intensified on the remaining areas (Gömann and Weingarten in press, Opdam and Wascher 2004). Hallmann et al. (2017) explained the decline of the biomass of flying insects in nature reserves by 75% over the past 27 years by these changes in agriculture. According to Kosior et al. (2007), the intensification of agriculture is responsible for the threat of 80% of the bumblebees and cuckoo bees in Western and Central Europe. The intensified forestry and agriculture is also a likely cause of the decline of butterflies (Warren et al. 2001) and moths (Conrad et al. 2006) in Great Britain.

Potts et al. (2010) state that the increased use of agrochemicals results in degradation of habitat quality. According to Biesmeijer et al. 2006, the application of agrochemicals caused a parallel decline of pollinating insects and insect-pollinated plants in The Netherlands and in Great Britain. We could not find data on the amount of pesticides applied in Europe. The German Environment Agency published only the national sales figures of the different types of pesticide products. These figures increased only minimally from 1995 to 2016 in pesticides for field crops (UBA2 2018).

In discussions on the possible causes of decline of species and biotope types, the authors of Red Lists agree that loss and fragmentation of habitats and changes in agriculture are the main driving factors (e.g., Korneck et al. 1998, Fritzlar 2011). Detailed analyses such as Heinig and Schoeller (2017) list manmade causes as the major factors of threat to leaf beetle diversity, e.g., increasing rarity of suitable habitats, lowering the groundwater table, and eutrophication of water bodies. Our observations point to the same direction: fewer than expected species extended their range towards the north, mono-, oligo- and polyphagous species are affected to similar degrees, and a remarkable increase of species with fewer records began with decade 8, i.e., from 1980. The above-mentioned suspected causes of insect decline have been known for a long time, as emphatically stated by Klausnitzer and Segerer (2018).

The usable habitats are fragmented like islands on which populations are trapped (Opdam and Wascher 2004). Species can react differently to fragmentation, with specialists suffering particularly (Kotze and O'Hara 2003; Biesmeijer et al. 2006; Nilsson et al. 2008). In contrast, our data do not show significant differences in de- and increase of record numbers from one quartile to the following in the species of the three trophic types. This could mean that specialists and generalists are affected in the same way and to similar degree by the factors causing insect decline.

Insects with low dispersal ability are less prone to escape from unfavourable habitat fragments in a landscape heavily modified by human activities (Warren et al. 2001; CD Thomas et al. 2004). The leaf beetle *Cryptocephalus nitidulus* Fabricius, 1787 is such a case (Piper and Compton 2010).

Loss and change of habitats are major factors influencing distribution and abundance of organisms (Hughes 2000) and have certainly also an impact in Chrysomelidae s.l. Our results are in concordance with numerous studies on insect decline over the past 30 years (e.g., Biesmeijer et al. 2006; Conrad et al. 2006; Hallmann et al.

2017; Kosior et al. 2007; Kotze and O'Hara 2003; Nilsson et al. 2008; Warren et al. 2001). However, such a parallelism is surprising because distribution and abundance of leaf beetles depend crucially on the availability of their food plants. Regrettably, data on changes of general plant distributions in Central Europe are not available.

The alarming news about the decline of insects of many different orders underpins the need for a continuous monitoring of their numbers and distribution. However, monitoring will only yield data from now on. For an analysis of past developments we do not have data meeting the standards of the monitoring (screening defined areas with identical sampling methods at regular intervals). Nevertheless, the fact that our results gained from the database ChryFaun (complete loss of ca. 6% of all species, decrease of records for 71% of all species since 2000) correspond to many other studies shows that data from private and museum collections can contribute to the analysis of insect decline. Such data are stored in numerous museum collections and even more in collections of amateurs, whose taxonomic expertise often excels that of museum curators (see Köhler 1997). It would be desirable to make collection data available for analyses of processes and possible causes of insect decline. Nevertheless, even taking all mentioned drawbacks into account, we are confident that the trends our results suggest are not mere artefacts but can be considered reliable proxies for real processes in nature.

Acknowledgements

We thank the members of the ChryFaun working group, the entomological associations of Hamburg, Thuringia, and Saxony-Anhalt, the natural history museums of Bern (Switzerland), Bonn, Braunschweig, Greifswald, and Waren/Müritz, the databases GBIF and ZOBODAT and the private collectors Manfred Döberl (**†, Abensberg), Horst Kippenberg (Herzogenaurach), and Klaus Renner (Bielefeld) for making their data available. We are grateful to Pierick Mouginot (Greifswald) for statistical advice, and to Gabriele Uhl (Greifswald), Jan Bezděk (Brno), and Matthias Schöller (Berlin) for valuable feedback on our manuscript, and to the Zoologisches Forschungsmuseum Alexander Koenig (Bonn), the department of General and Systematic Zoology at the University of Greifswald (Prof Dr Gabriele Uhl), and the Bayer AG – Crop Science Division, Bee Care (Monheim am Rhein) for financial support.

References

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313: 351–354. https://doi.org/10.1126/science.1127863

** Manfred Döberl passed away on 12 May 2016.

Čižek P (2006) Dřepčíci (Coleoptera: Chrysomelidae: Alticinae) Česka a Slovenska. Mětské muszeum, Nové Město nad Metují, 76 pp.

Conrad KF, Warren MS, Fox R, Parsons MS, Woiwod IP (2006) Rapid declines of common, widespread British moths provide evidence of an insect biodiversity crisis. Biological Conservation 132: 279–291. https://doi.org/10.1016/j.biocon.2006.04.020

Fritzlar F (2011) Rote Liste der Blattkäfer (Insecta: Coleoptera: Chrysomelidae) Thüringens. Naturschutz Report Thüringen 26: 250–260.

Gömann H, Weingarten P (in press) Landnutzungswandel. In: Handwörterbuch der Stadt- und Raumentwicklung. Akademie für Raumforschung und Landesplanung, Hannover, 14. Available from: https://literatur.thuenen.de/digbib_extern/dn059218.pdf [March 31, 2018]

Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H, Stenmans W, Müller A, Sumser H, Hörren T, Goulson D, de Kroon H (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PloS One 12: e0185809. https://doi.org/10.1371/journal.pone.0185809

Heinig U, Schöller M (2017) Rote Liste und Gesamtartenliste der Blattkäfer (Chrysomelidae und Megalopodidae) von Berlin. Der Landesbeauftragte für Naturschutz und Landschaftspflege/Senatsverwaltung für Umwelt, Verkehr und Umweltschutz, Berlin, 38 pp.

Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of taxonomic groups are expanding polewards. Global Change Biology 12: 450–455. https://doi.org/10.1111/j.1365-2486.2006.01116.x

Hughes L (2000) Biological consequences of global warming: is the signal already. Trends in Ecology & Evolution 15: 56–61. https://doi.org/10.1016/S0169-5347(99)01764-4

Klausnitzer B, Segerer AH (2018) Stellungnahme zum Insektensterben. DGaaE-Nachrichten 32(2): 72–80.

Koch K (1992) Die Käfer Mitteleuropas. Band 3. Ökologie. Goecke & Evers Verlag, Krefeld, 389 pp.

Köhler F (1997) Amateurwissenschaft, Entwicklung, Beschreibung und wissenschaftssoziologische Analyse am Beispiel der Koleopterologie. Decheniana Beiheft 36: 351–420.

Köhler F (2010) Die klimabedingte Veränderung der Totholzkäferfauna (Coleoptera) des nördlichen Rheinlandes. Wald und Holz NRW, Münster, 198 pp.

Konvicka M, Maradova M, Benes J, Fric Z, Kepka P (2003) Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. Global Ecology and Biogeography 12: 403–410. https://doi.org/10.1046/j.1466-822X.2003.00053.x

Korneck D, Schnittler M, Klingenstein F, Ludwig G, Takla M, Bohn U, May R (1998) Warum verarmt unsere Flora? Auswertung der Roten Liste der Farn- und Blütenpflanzen Deutschlands. Schriftenreihe für Vegetationskunde 29: 299–444.

Kosior A, Celary W, Olejniczak P, Fijal J, Król W, Solarz W, Plonka P (2007) The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. Oryx 41: 79. https://doi.org/10.1017/S0030605307001597

Kotze DJ, O'Hara RB (2003) Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. Oecologia 135: 138–148. https://doi.org/10.1007/s00442-002-1174-3

Krehenwinkel H, Tautz D (2013) Northern range expansion of European populations of the wasp spider *Argiope bruennichi* is associated with global warming-correlated genetic admixture and population-specific temperature adaptations. Molecular Ecology 22: 2232–2248. https://doi.org/10.1111/mec.12223

Kurnik B (2017) 3.2 Atmosphere. In: Climate change, impacts and vulnerability in Europe 2016: an indicator-based report. European Environment Agency, Copenhagen, 69–89. https://publications.europa.eu/en/publication-detail/-/publication/794dcba3-e922-11e6-ad7c-01aa75ed71a1 [January 10, 2018]

Löbl I, Smetana A (2010) Catalogue of Palaearctic Coleoptera vol. 6 Chrysomeloidea. Apollo Books, Stenstrup, 924 pp.

Mason SC, Palmer G, Fox R, Gillings S, Hill JK, Thomas CD, Oliver TH (2015) Geographical range margins of many taxonomic groups continue to shift polewards. Biological Journal of the Linnean Society 115: 586–597. https://doi.org/10.1111/bij.12574

Nilsson SG, Franzén M, Jönsson E (2008) Long-term land-use changes and extinction of specialised butterflies. Insect Conservation and Diversity 1: 197–207. https://doi.org/10.1111/j.1752-4598.2008.00027.x

Olfert O, Weiss RM (2006) Impact of climate change on potential distributions and relative abundances of *Oulema melanopus*, *Meligethes viridescens* and *Ceutorhynchus obstrictus* in Canada. Agriculture, Ecosystems & Environment 113: 295–301. https://doi.org/10.1016/j.agee.2005.10.017

Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117: 285–297. https://doi.org/10.1016/j.biocon.2003.12.008

Parmesan C (1996) Climate and species´ range. Nature 382: 765–766. https://doi.org/10.1038/382765a0

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399: 579–583. https://doi.org/10.1038/21181

Piper RW, Compton SG (2010) Population size and dispersal ability of *Cryptocephalus nitidulus* (Linnaeus, 1758) (Col.: Chrysomelidae). Entomologist's Record and Journal of Variation 122: 257.

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25: 345–353. https://doi.org/10.1016/j.tree.2010.01.007

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Rheinheimer J, Hassler M (2018) Die Blattkäfer Baden-Württembergs. Kleinsteuber Books, Karlsruhe, 928 pp.

Schmitt M, Rönn, T (2011) Types of geographical distribution of leaf beetles (Chrysomelidae) in Central Europe. ZooKeys 157 (Research on Chrysomelidae 3): 131–158. https://doi.org/10.3897/zookeys.157.1798

Schmitt M, Bäse W, Beenen R, Drovenik B, Fritzlar F, Geiser E, Jäckel R, Langer M, Mauser J, Ringel H, Schöller M, Siede D (2014) Das Projekt ChryFaun – Faunistik der mitteleuropäischen Blatt- und Samenkäfer (Chrysomelidae s.l.). Entomologische Blätter und Coleoptera 110: 33–38.

Svobodová E, Trnka M, Dubrovský M, Semerádová D, Eitzinger J, Štěpánek P, Žalud Z (2014) Determination of areas with the most significant shift in persistence of pests in Europe under climate change. Pest Management Science 70: 708–715. https://doi.org/10.1002/ps.3622

Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. Nature 399: 213. https://doi.org/10.1038/20335

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BF, De Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427: 145–148. https://doi.org/10.1038/nature02121

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JD, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative Losses of British Butterflies, Birds, and Plants and the Global Extinction Crisis. Science 303: 1879–1881. https://doi.org/10.1126/science.1095046

UBA1 (2018) UBA1 https://www.umweltbundesamt.de/daten/flaeche-boden-land-oekosysteme/boden/landbedeckung-landnutzung#textpart-1 [last access 23.10.2018]

UBA2 (2018) UBA2 https://www.umweltbundesamt.de/daten/land-forstwirtschaft/pflanzenschutzmittelverwendung-in-der#textpart-1 [last access 23.10.2018]

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414: 65–69. https://doi.org/10.1038/35102054

Winkelman JK, Beenen R (2010) Chrysomelidae – haantjes (excl. Bruchinae). In: Nederlandse Entomologische Vereniging (Ed.) Catalogus van de Nederlands kevers (Coleoptera). Monografieën van de Nederlandse Entomologische Vereniging 11: 149–158, 183–186.

Appendix 1

Table 2. List of species and their change in distribution (N - north, E - east, S - south, W - west, NE - north-east, NW - north-west, SE - south-east, SW - south-west, Sh - shrinking, / - no change).

Types of geographical distributio (Schmitt and Rönn 2011)	Name of species	Change in distribution
Not specified	*Diabrotica virgifera* LeConte, 1858	/
	Gonioctena arctica Mannerheim, 1853	Sh
	Gonioctena nivosa (Suffrian, 1851)	/
	Oulema septentrionis (Weise, 1880)	/
	Phyllotreta balcanica Heikertinger, 1909	/
	Phyllotreta consobrina (Curtis, 1837)	/
Fewer than 10 records	*Gonioctena flavicornis* (Suffrian, 1851)	/
	Gonioctena kaufmanni (Miller, 1880)	/
	Gonioctena variabilis (Olivier, 1790)	/
	Phyllotreta acutecarinata Heikertinger, 1941	/
	Phyllotreta hochetlingeri Fleischer, 1917	/
	Phyllotreta variipennis (Boieldieu, 1859)	/
	Phyllotreta ziegleri Lohse, 1980	/
	Timarcha gibba (Hagenbach, 1825)	/
	Timarcha rugulosa Herrich-Schaeffer, 1838	/
	Zeugophora turneri Power, 1863	/
Alpine	*Gonioctena holdhausi* (Leeder, 1950)	/
Fragmented	*Phyllotreta atra* (Fabricius, 1775)	N, SE
	Phyllotreta cruciferae (Goeze, 1777)	E, SE
	Phyllotreta striolata (Fabricius, 1803)	E, SE
Montane	*Aphthona ovata* Foudras, 1860	NW
	Calomicrus gularis (Gredler, 1857)	/
	Chaetocnema angustula (Rosenhauer, 1847)	/
	Chrysolina aurichalcea (Mannerheim, 1825)	/
	Cryptocephalus nitidulus Fabricius, 1787	E
	Longitarsus helvolus Kutschera, 1863	/
	Luperus viridipennis Germar, 1824	/
	Luperus xanthopoda (Schrank, 1781)	N, SE
	Oreina alpestris (Schummel, 1843)	E
	Oreina bifrons (Fabricius, 1792)	NE
	Oreina cacaliae (Schrank, 1785)	NE, SW
	Oreina intricata (Germar, 1824)	E
	Oreina speciosa (Linnaeus, 1767)	NE, Sh
	Oreina speciosissima (Scopoli, 1763)	NE
	Psylliodes glabra (Duftschmid, 1825)	N
	Psylliodes toelgi Heikertinger, 1914	/
	Psylliodes vindobonensis Heikertinger, 1914	/
	Sclerophaedon carniolicus (Germar, 1824)	Sh
Northern	*Galerucella grisescens* (Joannis, 1865)	E, S
	Longitarsus plantagomaritimus Dollman, 1912	E, W
	Mantura chrysanthemi (Koch, 1803)	E, NW
	Phaedon concinnus Stephens, 1831	S
	Phyllotreta armoraciae (Koch, 1803)	N, E
	Prasocuris hannoverana (Fabricius, 1775)	W
	Psylliodes crambicola Lohse, 1954	/
	Psylliodes marcida (Illiger, 1807)	E, W

Types of geographical distributio (Schmitt and Rönn 2011)	Name of species	Change in distribution
Eastern	*Colaphellus sophiae* (Schaller, 1783)	E, Sh
	Phyllotreta scheuchi Heikertinger, 1941	/
Southern	*Altica helianthemi* (Allard, 1859)	S, Sh
	Altica tamaricis Schrank, 1785	/
	Aphthona abdominalis (Duftschmid, 1825)	/
	Aphthona atrovirens (Förster, 1849)	W
	Aphthona cyparissiae (Koch, 1803)	/
	Aphthona herbigrada (Curtis, 1837)	W
	Aphthona pallida (Bach, 1856)	N
	Aphthona pygmaea (Kutschera, 1861)	E
	Aphthona venustula (Kutschera, 1861)	/
	Apteropeda orbiculata (Marsham, 1802)	/
	Derocrepis rufipes (Linnaeus, 1758)	/
	Hermaeophaga mercurialis (Fabricius, 1792)	NE, SE
	Lachnaia sexpunctata (Scopoli, 1763)	/
	Neocrepidodera femorata (Gyllenhal, 1813)	N, E
	Ochrosis ventralis (Illiger, 1807)	W, Sh
	Phratora tibialis (Suffrian, 1851)	N, E
	Phratora vulgatissima (Linnaeus, 1758)	E, S
	Phyllotreta nigripes (Fabricius, 1775)	E, SE
	Plagiodera versicolora (Laicharting, 1781)	E
	Sphaeroderma rubidum (Graëlls, 1858)	E, NE
	Calomicrus circumfusus (Marsham, 1802)	E
	Calomicrus pinicola (Duftschmid, 1825)	N, W
	Cassida panzeri Weise, 1907	E, Sh
	Chaetocnema arida Foudras, 1860	E
	Chaetocnema obesa (Boieldieu, 1859)	N, E
	Chaetocnema semicoerulea (Koch, 1803)	E, Sh
	Chrysolina cuprina (Duftschmid, 1825)	/
	Chrysolina hemisphaerica (Germar, 1817)	N
	Chrysolina herbacea (Duftschmid, 1825)	E, NE, SW
	Chrysolina hyperici (Forster, 1771)	E
	Chrysolina marginata (Linnaeus, 1858)	E
	Chrysolina rufa (Duftschmid, 1825)	NE, Sh
	Chrysomela cuprea Fabricius, 1775	E, NE
	Chrysomela saliceti (Weise, 1884)	E, Sh
	Chrysomela vigintipunctata (Scopoli, 1763)	E, NE
	Coptocephala rubicunda (Laicharting, 1781)	E
	Crepidodera aurea (Geoffroy, 1785)	E
	Crepidodera lamina (Bedel, 1901)	/
	Crepidodera nitidula (Linnaeus, 1758)	E
	Cryptocephalus biguttatus (Scopoli, 1763)	E
	Cryptocephalus frontalis Marsham, 1802	/
	Cryptocephalus laetus Fabricius, 1792	/
	Cryptocephalus primarius Harold, 1872	/
	Cryptocephalus pygmaeus Fabricius, 1792	/
	Cryptocephalus querceti Suffrian, 1848	E
	Cryptocephalus quinquepunctatus (Scopoli, 1763)	E, Sh
	Cryptocephalus saliceti Zebe, 1855	N, E
	Cryptocephalus schaefferi Schrank, 1789	SE

Types of geographical distributio (Schmitt and Rönn 2011)	Name of species	Change in distribution
Southern	*Cryptocephalus sexpunctatus* (Linnaeus, 1758)	E
	Cryptocephalus signatifrons Suffrian, 1847	N
	Cryptocephalus variegatus Fabricius, 1781	/
	Cryptocephalus vittatus Fabricius, 1775	E
	Dibolia foersteri Bach, 1859	NW, SW, Sh
	Donacia springeri Müller, 1916	/
	Epitrix atropae Foudras, 1860	E
	Epitrix intermedia Foudras, 1860	/
	Galeruca laticollis (Sahlberg, 1837)	E
	Galerucella tenella (Linnaeus, 1760)	E
	Gonioctena intermedia (Helliesen, 1913)	E, NW
	Gonioctena linnaeana (Schrank, 1781)	SE, Sh
	Gonioctena pallida (Linnaeus, 1758)	NE
	Gonioctena viminalis (Linnaeus, 1758)	E
	Hispa atra Linnaeus, 1767	E, NE
	Labidostomis humeralis (Schneider, 1792)	S
	Labidostomis lucida (Germar, 1823)	N
	Labidostomis pallidipennis (Gebler, 1839)	/
	Labidostomis tridentata (Linnaeus, 1758)	E
	Lilioceris merdigera (Linnaeus, 1758)	/
	Longitarsus absynthii Kutschera, 1862	/
	Longitarsus echii (Koch, 1803)	N, W
	Longitarsus lateripunctatus (Rosenhauer, 1856)	NW
	Longitarsus longiseta Weise, 1889	/
	Longitarsus membranaceus (Foudras, 1860)	/
	Longitarsus minusculus (Foudras, 1860)	/
	Longitarsus nanus (Foudras, 1860)	SW
	Longitarsus pellucidus (Foudras, 1860)	E
	Longitarsus pulmonariae Weise, 1893	N, E
	Longitarsus scutellaris (Rey, 1873)	Sh
	Luperus flaviceps Apfelbeck, 1912	E
	Mantura mathewsi (Curtis, 1833)	/
	Oomorphus concolor (Sturm, 1807)	N, E
	Orsodacne cerasi (Linnaeus, 1758)	N, E
	Pachnephorus pilosus (Rossi, 1790)	/
	Pachybrachis hieroglyphicus (Laicharting, 1781)	E
	Pachybrachis hippophaes Suffrian, 1848	/
	Pachybrachis picus Weise, 1882	Sh
	Pachybrachis sinuatus Mulsant, 1859	E
	Pachybrachis tessellatus (Olivier, 1791)	E, SE
	Phaedon laevigatus (Duftschmid, 1825)	NW
	Phyllotreta christinae Heikertinger, 1941	E, NW
	Phyllotreta ochripes (Curtis, 1837)	N, E
	Phyllotreta procera (Redtenbacher, 1849)	S, SE
	Phyllotreta punctulata (Marsham, 1802)	/
	Prasocuris glabra (Herbst, 1783)	E
	Psylliodes chalcomera (Illiger, 1807)	E, W
	Psylliodes instabilis Foudras, 1860	/
	Psylliodes isatidis Heikertinger, 1913	E, S
	Psylliodes thlaspis Foudras, 1860	/

Types of geographical distributio (Schmitt and Rönn 2011)	Name of species	Change in distribution
Southern	*Smaragdina affinis* (Illiger, 1794)	SE, Sh
	Smaragdina flavicollis (Charpentier, 1825)	NE
	Timarcha goettingensis (Linnaeus, 1758)	E, Sh
	Timarcha metallica (Laicharting, 1781)	Sh
	Timarcha pratensis (Duftschmid, 1825)	/
	Zeugophora frontalis Suffrian, 1840	/
South-Eastern	*Bruchidius marginalis* (Fabricius, 1776)	/
	Bruchus atomarius (Linnaeus, 1761)	N, E
	Cassida ferruginea Goeze, 1777	/
	Cassida rufovirens Suffrian, 1844	N
	Cassida sanguinolenta Müller, 1776	E
	Cassida subferruginea (Schrank, 1776)	/
	Cassida subreticulata Suffrian, 1844	N, E
	Cassida vibex Linnaeus, 1767	E
	Chrysochus asclepiadeus (Pallas, 1773)	/
	Chrysolina geminata (Paykull, 1799)	/
	Chrysolina kuesteri (Helliesen, 1912)	E
	Chrysolina lichenis (Richter, 1820)	NE
	Chrysolina sturmi (Westhoff, 1882)	E
	Chrysolina varians (Schaller, 1783)	E
	Chrysomela populi Linnaeus, 1758	E
	Chrysomela tremula Fabricius, 1783	SE
	Clytra laeviuscula Ratzeburg, 1837	E, Sh
	Clytra quadripunctata (Linnaeus, 1758)	E
	Coptocephala unifasciata (Scopoli, 1763)	E
	Cryptocephalus aureolus Suffrian, 1847	E, NE
	Cryptocephalus bilineatus (Linnaeus, 1767)	E
	Cryptocephalus chrysopus Gmelin, 1788	E, W, Sh
	Cryptocephalus cordiger (Linnaeus, 1758)	SE
	Cryptocephalus elegantulus Gravenhorst, 1807	SE
	Cryptocephalus exiguus Schneider, 1792	S
	Cryptocephalus frenatus Laicharting, 1781	/
	Cryptocephalus hypochaeridis (Linnaeus, 1758)	E
	Cryptocephalus marginatus Fabricius, 1781	/
	Cryptocephalus moraei (Linnaeus, 1758)	E
	Cryptocephalus octopunctatus (Scopoli, 1763)	N, E
	Cryptocephalus violaceus Laicharting, 1781	SE
	Cryptocephalus vittula Suffrian, 1848	/
	Dibolia depressiuscula (Letzner, 1847)	/
	Dibolia femoralis Redtenbacher, 1849	W
	Dibolia rugulosa Redtenbacher, 1849	SE. Sh
	Galeruca tanaceti (Linnaeus, 1758)	E
	Gonioctena fornicata (Brüggemann, 1873)	W
	Gonioctena gobanzi (Reitter, 1902)	E
	Labidostomis cyanicornis (Germar, 1817)	Sh
	Labidostomis longimana (Linnaeus, 1761)	E
	Longitarsus apicalis (Beck, 1817)	/
	Longitarsus ballotae (Marsham, 1802)	E
	Longitarsus foudrasi Weise, 1893	N
	Longitarsus melanocephalus (De Geer, 1775)	E

Types of geographical distributio (Schmitt and Rönn 2011)	Name of species	Change in distribution
South-Eastern	*Longitarsus nigrofasciatus* (Goeze, 1777)	N, E
	Longitarsus obliteratus (Rosenhauer, 1847)	NE, NW
	Longitarsus salviae Gruev, 1975	/
	Mantura obtusata (Gyllenhal, 1813)	/
	Minota obesa (Waltl, 1839)	/
	Oulema obscura (Stephens, 1831)	E, W
	Phyllotreta diademata Foudras, 1860	E, Sh
	Phyllotreta nodicornis (Marsham, 1802)	/
	Podagrica fuscicornis (Linnaeus, 1767)	E, Sh
	Smaragdina aurita (Linnaeus, 1767)	E
	Smaragdina salicina (Scopoli, 1763)	E
South-East	*Phyllotreta ganglbaueri* Heikertinger, 1909	/
South-Western	*Apteropeda globosa* (Illiger, 1794)	N
	Apteropeda splendida Allard, 1860	/
	Bruchus occidentalis Lukjanovitsh & Ter-Minassian, 1957	/
	Cryptocephalus ocellatus Drapiez, 1819	E
	Dibolia cryptocephala (Koch, 1803)	E
	Donacia bicolora Zschach, 1788	/
	Donacia simplex Fabricius, 1775	/
	Longitarsus aeruginosus (Foudras, 1860)	E, S
	Longitarsus ganglbaueri Heikertinger, 1912	/
	Longitarsus rubiginosus (Foudras, 1860)	E, W
	Mniophila muscorum (Koch, 1803)	SW
	Timarcha tenebricosa (Fabricius, 1775)	/
Unusual	*Gonioctena decemnotata* (Marsham, 1802)	E, W
	Gonioctena interposita (Franz & Palmén, 1950)	E, NW, Sh
	Gonioctena olivacea (Forster, 1771)	E, S
	Orsodacne humeralis Latreille, 1804	E, W
	Oulema duftschmidi (Redtenbacher, 1874)	E, S
	Phyllotreta astrachanica Lopatin, 1977	NE
	Phyllotreta austriaca Heikertinger, 1909	/
	Prasocuris junci (Brahm, 1790)	E
Scattered	*Cryptocephalus quadripustulatus* Gyllenhal, 1813	E
	Oulema erichsonii (Suffrian, 1841)	/
	Phyllotreta dilatata Thomson, 1866	E, NW
	Phyllotreta flexuosa (Illiger, 1794)	E, W
Wide	*Chrysolina coerulans* (Scriba, 1791)	E
	Cryptocephalus coryli (Linnaeus, 1758)	/
	Gonioctena quinquepunctata (Fabricius, 1787)	E, NE
	Leptinotarsa decemlineata (Say, 1824)	E
	Lilioceris lilii (Scopoli, 1763)	/
	Oulema melanopus (Linnaeus, 1758)	E, S
	Phyllotreta nemorum (Linnaeus, 1758)	E, SE
	Phyllotreta exclamationis (Thunberg, 1784)	E
	Phyllotreta tetrastigma (Comolli, 1837)	/
	Phyllotreta undulata Kutschera, 1860	SE
	Phyllotreta vittula (Redtenbacher, 1849)	E, SE
	Zeugophora flavicollis (Marsham, 1802)	/
	Zeugophora scutellaris Suffrian, 1840	/
	Zeugophora subspinosa (Fabricius, 1781)	E

Appendix 2

Table 3. List of species and subspecies that were not reported after 1990 (decade 10) or after 2000 (decade 11). Species marked with an asterisk (*) are pests of stored products, species marked ** were reported informally, but we have no label data in ChryFaun.

Since	Name of species
1990	*Aphthona aeneomicans* Allard, 1875
	Argopus bicolor Fischer, 1824
	Cassida inquinata Brullé, 1832
	Chrysolina didymata (Scriba, 1791)
	Cryptocephalus bimaculatus Fabricius, 1781
	Cryptocephalus bohemius Drapiez, 1819
	Cryptocephalus cyanipes Suffrian, 1847
	Cryptocephalus gridellii Burlini, 1950**
	Cryptocephalus loreyi Solier, 1836
	Entomoscelis adonidis (Pallas, 1771)**
	Epitrix intermedia Foudras, 1860
	Gonioctena gobanzi (Reitter, 1902)
	Longitarsus cizeki Döberl, 2004
	Neocrepidodera basalis (K Daniel, 1900)
	Oreina peirolerii (Bassi, 1834)
	Orestia heikertingeri Leonardi, 1974
	Prasocuris (Hydrotassa) flavocincta (Brullé, 1832)
	Psylliodes gibbosa Allard, 1860
	Psylliodes kiesenwetteri Kutschera, 1864
	Psylliodes luteola (Müller, 1776)
	Stylosomus ilicicola Suffrian, 1848
	Timarcha nicaeensis (Villa & Villa, 1835)
2000	*Aphthona illigeri* Bedel, 1898
	Aphthona stussineri Weise, 1888
	Bruchidius dispar (Gyllenhal, 1833)
	Bruchidius lividimanus (Gyllenhal, 1833)
	Bruchidius martinezi (Allard, 1868) – probably incorrect identification
	Bruchus griseomaculatus Gyllenhal, 1833
	Bruchus sibiricus Germar, 1824 – probably incorrect identification
	Bruchus venustus Fahraeus, 1839
	Callosobruchus chinensis (Linnaeus, 1758)*
	Caryedon serratus (Olivier, 1790)*
	Chaetocnema chlorophana (Duftschmid, 1825)
	Chaetocnema major (Jacquelin-Duval, 1852)
	Chrysolina americana (Linnaeus, 1758)
	Chrysolina asclepiadis asclepiadis (Villa & Villa, 1833)
	Chrysolina fimbrialis (Kuester, 1845)
	Chrysolina globosa (Panzer, 1805)
	Chrysolina grossa (Fabricius, 1792)
	Chrysolina olivieri (Bedel, 1892)
	Chrysolina relucens (Rosenhauer, 1847)
	Chrysolina rufoaenea (Suffrian, 1851)
	Chrysolina schneideri (Weise, 1882)**
	Chrysolina carpathica (Fuss, 1856)**
	Coptocephala chalybaea (Germar, 1824)**
	Cryptocephalus laevicollis Gebler, 1830**

Since	Name of species
2000	*Cryptocephalus planifrons* Weise, 1882**
	Cryptocephalus quatuordecimmaculatus Schneider, 1792**
	Cryptocephalus transiens Franz, 1949**
	Cryptocephalus virens Suffrian, 1847**
	Derocrepis sodalis (Kutschera, 1860)
	Entomoscelis sacra (Linnaeus, 1758)**
	Galeruca jucunda (Faldermann, 1837)
	Gonioctena kaufmanni (Miller, 1880)**
	Gonioctena variabilis (Olivier, 1790) – probably incorrect identification
	Labidostomis pallidipennis (Gebler, 1839)
	Lachnaia italica (Weise, 1882)
	Longitarsus weisei Guillebeau, 1895
	Luperus nigripes Kiessenwetter, 1861**
	Minota alpina Biondi, 1986
	Minota impuncticollis (Allard, 1860)
	Neocrepidodera adelinae (Binaghi, 1947)
	Neocrepidodera cyanipennis (Kutschera, 1860)
	Neocrepidodera obirensis (Ganglbauer, 1897)
	Neocrepidodera simplicipes (Kutschera, 1860)
	Oreina liturata (Scopoli, 1763)
	Orestia electra Gredler, 1868
	Phyllobrotica adusta (Creutzer, 1799)
	Phyllotreta consobrina (Curtis, 1837)
	Phyllotreta ziegleri Lohse, 1980
	Psylliodes danieli Weise, 1900
	Psylliodes rambouseki forojulensis Heikertinger, 1926
	Psylliodes subaenea styriaca Heikertinger, 1921
	Smaragdina diversipes Letzner, 1839**
	Zabrotes subfasciatus (Boheman, 1833)*

ZooKeys 856: 137–196 (2019)
doi: 10.3897/zookeys.856.32017
http://zookeys.pensoft.net

RESEARCH ARTICLE

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An annotated checklist of the leaf beetles (Coleoptera, Chrysomelidae) from El Salvador, with additions from the Bechyné collection in the Royal Belgian Institute of Natural Sciences

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Academic editor: *C.S. Chaboo* | Received 29 November 2018 | Accepted 22 February 2019 | Published 17 June 2019

http://zoobank.org/43D66957-539E-4DC7-AB82-DA175560D5AC

Citation: Van Roie M, De Wint F, Güngor A, Huyghe C, Dekoninck W, Sekerka L (2019) An annotated checklist of the leaf beetles (Coleoptera, Chrysomelidae) from El Salvador, with additions from the Bechyné collection in the Royal Belgian Institute of Natural Sciences. In: Schmitt M, Chaboo CS, Biondi M (Eds) Research on Chrysomelidae 8. ZooKeys 856: 137–196. https://doi.org/10.3897/zookeys.856.32017

Abstract

A checklist of the species of leaf beetles (Coleoptera: Chrysomelidae) of El Salvador is presented based on data from literature and a digitization project of the Bechyné collection of the Royal Belgian Institute of Natural Sciences (RBINS). The RBINS collections contain a total of 2797 individual chrysomelid specimens from El Salvador, sorted into 89 species and 132 genera. In total, the current checklist contains 420 species, of which 33 are new records for El Slavador from the Bechyné collection. In these collections, there are also ten nomina nuda named by Bechyné, which need further study. The leaf beetle diversity in El Salvador, partly due to the country's unstable political history, remains poorly studied, and many (new) species await discovery. This checklist provides a baseline for further study in El Salvador and nearby region.

Keywords

Digitization, Central America, Neotropics, Museum

Introduction

The description and inventory of biodiversity is facing hard times due to budgetary problems and the decline of taxonomists (Drew 2011). This is also certainly the case for leaf beetles (Coleoptera: Chrysomelidae). Nonetheless, leaf beetles can be of economic significance (Livia 2006), often possess interesting life histories (e.g., the semi-aquatic lifestyle of most Donaciinae, Kleinschmidt and Kölsch (2011)), and can display complex behavior like eusociality (Windsor et al. 2013). Leaf beetles are a taxonomically complex group and, although some regions where the diversity of this group is relatively well known (like the Palearctic and Nearctic regions), other areas like the Neotropics are in desperate need of more study.

One of the most important early studies on Neotropical Chrysomelidae was done for the multipartite series of the Biologia Centrali Americana (Baly and Champion 1885–1894; Jacoby 1880–1892; 1888–1892). The series remains the most complete source of information today on insect fauna of Central America. This work collated information from previous taxonomists, e.g., Crotch, Illiger, Harold and Baly, who published many monographs and species descriptions within Alticini, Eumolpinae, Cryptocephalinae and other subfamilies. In approximately the same period (1850–1862), Boheman had published his 'Monographia Cassididarum' dealing with the subfamily Cassidinae (Boheman 1850–1862). These early works were followed by the 'Coleopterorum Catalogus', published in multiple volumes, which represented the first actual checklist (Clavareau 1913a, 1913b, 1914; Heikertinger and Csiki 1939, 1940; Pic 1913; Spaeth 1914; Weise 1911, 1916, 1924). Further checklists include Blackwelder (1946), but, as stated by Furth and Savini (1996), this list contained mainly information derived from the 'Coleopterorum Catalogus'. After the 1940's, the works on Neotropical Chrysomelidae done by Jan Bechyné and his wife Bohumila Bechyné produced an impressive list of 188 publications about the Chrysomelidae from the Neotropical, Afrotropical and Palearctic regions, with a main focus on the subfamilies Eumolpinae and Galerucinae including Alticini (Seeno et al. 1976). Jan and Bohumila Bechyné described many species, and therefore significantly contributed to the knowledge of Neotropical Chrysomelidae. Another significant work is Scherer (1962) with an identification key to the genera of Neotropical Alticini (Scherer 1962). One of the most prolific taxonomists working on Neotropical leaf-beetles was Francisco Monrós (1922–1958). The Bechnynés' works focused mainly on describing new taxa, and less on revising previous works and often ignored biological aspects of the taxa. Francisco Monrós focused his studies on detailed complex revisions of particular groups and include numerous ecological observations on host plants and behavior of the species. He published mainly on Criocerinae, Clytrini, Fulcidacini, and Lamprosomatinae. He was in the process of writing his opus magnum 'Los géneros de Chrysomelidae', but unfortunately due to his premature death only the first volume was published covering Sagrinae, Donaciinae, and Criocerinae (Monrós 1960).

Records from El Salvador are relatively rare (e.g., see Rodrigues and Mermudes 2016)). The country is undersampled for insects and this can be demonstrated by the fact that only two chrysomelid beetles are recorded from El Salvador in the 'Biologia Centrali Americana' series. The most intensive effort to construct a national list for the family dates back to 1960 with three main works by the Bechynés (Bechyné 1954; Bechyné and Bechyné 1960; 1963). Another list of Chrysomelidae from El Salvador is found in the two-part series 'Lista de Insectos Clasificados de El Salvador' (Berry and Salazar 1957, Berry 1959). However, these are inadequate because most Chrysomelidae species identifications include the statements "probably" and "proximately", lacking information on who identified the species and depository of the specimens. Moreover, there are many misspellings and misinterpretations in species and author names and some species listed in Berry and Salazar (1957) are not included in Berry (1959) without any explanation. The occurrence data of these listed species should be verified by examination of material. Part of the material collected by Berry is deposited in the National Museum of Natural History (UNSM), Washington DC, USA. The Berry lists were unknown to most of subsequent authors, who explicitdly recorded species mentioned in the lists as new to El Salvador. This is particularly obvious in Cassidinae, which represent one of the best known chrysomelid subfamilies of the world.

Much of the Bechyné material from El Salvador was unfortunately lost during their trip from Europe to Brazil (Furth 2018, in litteris), but a total of 32 boxes remains in the Royal Belgian Institute of Natural Sciences (RBINS), and they contain hundreds of specimens of the Bechyné collection. These include numerous paratypes of the subfamily Eumolpinae and tribe Alticini.

We carried out a literature search, seeking any records of leaf beetles for El Salvador, with the main goal of constructing an updated and annotated checklist. Additionally, we added species data from the Bechyné El Salvador collection from the RBINS. The results of this work are presented here.

Materials and methods

Literature search

During our literature study, we accessed multiple historical references from eminent contributors to chrysomelid taxonomy, such as Bechyné, Stål, Jacoby, Baly, Blake, Harold, Illiger, and others as mentioned in the introduction. We also scouted some existing checklists from neighboring countries for references of El Salvadorean Chrysomelidae (e.g., Furth (2006), Furth (2013), Maes and Staines (1991)) as well as subfamily checklists for Central America level (e.g., Furth and Savini (1996)). A complete list of references containing records for El Salvador are indicated in our Results section. Species in Berry and Salazar (1957) and Berry (1959) which used the statements "probably" and "proximately" were not added in the present checklist to avoid incorrectly identified species.

Specimen digitization

Eighteen full and 14 partially-filled insect drawers with material from El Salvador were digitized by volunteers (following the protocol described in Merckx et al. (2018)). For this, at least one specimen per species was photographed in dorsal, lateral and frontal views, using an Olympus TG4 digital camera with focus stacking functionality (see Mertens et al. (2017), where this method is discussed thoroughly). Pictures of these specimens were stacked using the Helicon Focus software (HeliconSoft Ltd, Kharkiv, Ukraine). A total of 42 specimens from El Salvador belonging to the genus *Calligrapha* Chevrolat that had already been digitized in a previous project were added to the database (Merckx et al. 2018). Furthermore, a high-resolution picture was taken of every insect drawer; such that all specimens have a clear dorsal picture, making intraspecific variation clear. The original labels of all specimens in the Bechyné El Salvador collection were also digitized, however for this manuscript the months of dates were changed to roman numerals to avoid confusion. The pictures and accompanying data are publicly available on-line at the RBINS online database (http://collections.naturalsciences.be/ssh-entomology).

Taxonomy

We followed the system of Bouchard et al. (2011) for division of subfamilies and tribes. Names found in literature were screened for any nomenclatural changes in their relevant literature and/or were checked by experts on the respective groups (see acknowledgements). If a species record in literature had an outdated nomenclature, the name under which it was recorded is given under remarks at the relevant species checklist.

Used abbreviations

We used the following abbreviations for institutes:

RBINS Royal Belgian Institute of Natural Sciences;
BMNH British Museum of Natural History;
DBET collection of Lech Borowiec, Wroclaw, Poland;
LSC collection of Lukáš Sekerka, Prague, Czech Republic;
USNM National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Results

A total of 2.797 individual chrysomelid specimens from El Salvador, sorted into 89 species and 132 genera in the RBINS collections were digitized. A full list of the speci-

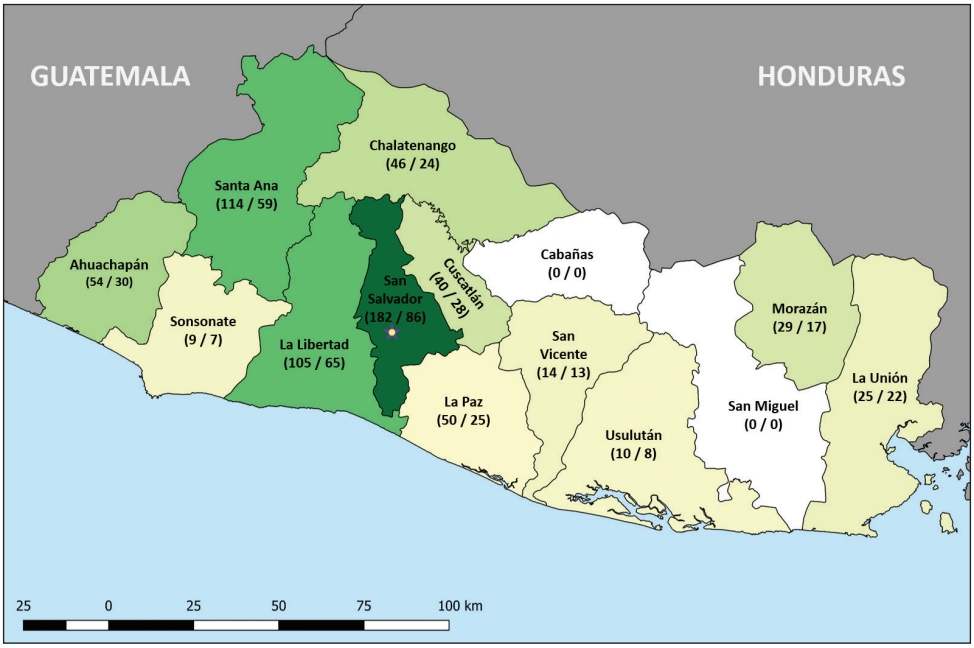

Figure 1. Heatmap of the species recorded per department of El Salvador. The darker the colour, the more species have been recorded. Numbers between brackets indicate number of species (first number) and number of genera (second number): (Species / Genera).

mens included in the RBINS can be found below. Included in the collection were ten *nomina nuda*, namely: *Antitypona* sp. (Manuscript species – Eumolpinae), *Brachypnoea* sp. *1* (Manuscript species – Eumolpinae), *Brachypnoea* sp. *2* (Manuscript species – Eumolpinae), *Hylax* sp. (Manuscript species – Eumolpinae), *Percolaspis* sp. *1* (Manuscript species – Eumolpinae), *Percolaspis* sp. *2* (Manuscript species – Eumolpinae), *Phanaeta* sp. (Manuscript species – Eumolpinae), *Chaetocnema* sp. (Manuscript species – Galerucinae, Alticini), *Phyllotreta* sp. (Manuscript species – Galerucinae, Alticini) and *Walterianella* sp. (Manuscript species – Galerucinae, Alticini). We chose to not give the names and photographs of these undescribed species here to avoid the cluttering of invalid names in the literature.

We noted a severe undersampling of Cryptocephalinae and Criocerinae. For example, Vencl et al. (2004) (Criocerinae) indicated the range of a species distribution (e.g., Mexico to Panama), but lacked specific records from El Salvador of which the authors are aware. Such unspecific records were left out of the present checklist. In total, the literature search led to a total of 385 chrysomelid species know to occur in El Salvador. Together with the Bechyné collection, this led to a combined total of 420 species (Figure 1 and Suppl. material 1: Table S1).

Suppl. material 1: Table S1 displays the number of species and genera per subfamily for each district. The departments with the highest species count to date are San Salvador (182 species), La Libertad (105 species), Santa Ana (114 species),

Ahuachapán (54 species), La Paz (50 species) and Chalatenango (46 species). No records from both San Miguel and Cabañas could be found, nor were there any specimens from these departments included in the RBINS collections. Below is the checklist of species from El Salvador taken from literature (the reference indicated between brackets after every record) and from the Bechyné collection in the RBINS. Additionally, some extra records of Cassidinae were added from other sources known to one of the authors. If the authors were aware of any nomenclatural changes, this is indicated under "remarks".

Checklist of chrysomelid species from EL Salvador

Subfamily Bruchinae

1. *Acanthoscelides argillaceus* (Sharp, 1885)

Remarks. Berry (1959) mentions *Acanthoscelides armitagei* Pic, 1931 as being present in El Salvador, but does not give specific records. This taxon was synonymized with *A. argillaceus* (Sharp, 1885) by Kingsolver (1969). Johnson (1990) also mentioned occurence in El Salvador without precise data.

2. *Acanthoscelides brevipes* (Sharp, 1885)

Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

3. *Acanthoscelides clitellarius* (Fahraeus, 1839)

Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

4. *Acanthoscelides desmoditus* Johnson, 1983

Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

5. *Acanthoscelides difficilis* (Sharp, 1885)

Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

6. *Acanthoscelides griseolus* (Fall, 1910)

Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

7. *Acanthoscelides guazumae* Johnson & Kingsolver, 1971

Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

8. *Acanthoscelides guerrero* Johnson, 1983

Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

9. *Acanthoscelides hectori* Kingsolver, 1980

Remarks. One specimen from El Salvador was intercepted at USDA Plant Quarantine, Washington DC (Kingsolver 1980).

10. ***Acanthoscelides macrophthalmus*** **(Schaeffer, 1907)**
Published records. LA LIBERTAD: San Andrés, 6/VI/1958 (Johnson 1979).

11. ***Acanthoscelides mankinsi*** **Johnson, 1983**
Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

12. ***Acanthoscelides megacornis*** **Kingsolver, 1980**
Published records. SANTA ANA: P. N. Montecristo, 7–9/V/1958 (Kingsolver 1980).

13. ***Acanthoscelides obvelatus*** **Bridwell, 1942**
Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

14. ***Acanthoscelides puelliopsis*** **Johnson, 1983**
Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

15. ***Acanthoscelides puellus*** **(Sharp, 1885)**
Remarks. Mancía and Cortéz (1975) and Johnson (1990) mention this species as being present in El Salvador, but do not give specific records.

16. ***Acanthoscelides pusillimus*** **(Sharp, 1885)**
Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

17. ***Acanthoscelides quadridentatus*** **(Schaeffer, 1907)**
Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

18. ***Acanthoscelides rufovittatus*** **(Schaeffer, 1907)**
Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

19. ***Acanthoscelides taboga*** **Johnson, 1983**
Remarks. Johnson (1990) mentions this species as being present in El Salvador, but does not give specific records.

20. ***Amblycerus mariae*** **Romero, Johnson & Kingsolver, 1996**
Published records. LA LIBERTAD: La Toma, 11/VI/1958 (Romero et al. 1996); SAN VICENTE: Santa Cruz Porrillo, 5/VI/1958.

21. ***Amblycerus multiflocculus*** **Kingsolver, 1980**
Published records. SAN SALVADOR: Tonocatepeque, 20/VI/1958 (Kingsolver 1980).

22. ***Amblycerus scutellaris*** **(Sharp, 1885)**
Remarks. Romero et al. (1996) mentions this species as being present in El Salvador, but does not give specific records.

23. ***Amblycerus spondiae*** **Kingsolver, 1980**
Published records. LA LIBERTAD: Santa Tecla, 5/VI/1958; LA UNIÓN: Volcan Conchagua, 27–29/V/1958 (Kingsolver 1980); SAN SALVADOR: 9/VI/1958.

24. ***Amblycerus vegai*** **Kingsolver, 1996**
Published records. LA UNIÓN: Volcan Conchagua, 27–29/V/1958 (Kingsolver 1980).

25. ***Callosobruchus maculatus*** **(Fabricius, 1775)**
Remarks. Mancía and Cortéz (1975) mention this species as being present in El Salvador, but do not give specific records. This species is native to the Oriental Region.

26. ***Callosobruchus chinensis*** **(Linnaeus, 1758)**
Remarks. Mancía and Cortéz (1975) mention this species as being present in El Salvador, but do not give specific records. This species is native to the Oriental Region.

27. ***Caryedes brasiliensis*** **(Thunberg, 1816)**
Published records. SAN SALVADOR: Tonacatepeque, VI/1931 (Kingsolver and Whitehead 1974a).

28. ***Caryedes clitoriae*** **(Gyllenhal, 1839)**
Published records. CHALATENANGO: Quetzaltepeque, 19/VI/1963 (Kingsolver and Whitehead 1974a, published under name *C. confinis* (Sharp, 1885)).

29. ***Caryedes longicollis*** **(Fahraeus, 1839)**
Published records. SANTA ANA: P. N. Montecristo, 23 km N of Metapan, 8–10/V/1971 (Kingsolver and Whitehead 1974a).

30. ***Caryedes quadridens*** **(Jekel, 1855)**
Published records. LA UNIÓN: Volcan Conchagua, 27–29/V/1958 (Kingsolver and Whitehead 1974a).

31. ***Caryobruchus curvipes*** **(Latreille, 1811)**
Published records. LA LIBERTAD: Santa Tecla (Berry and Salazar 1957). SAN SALVADOR (Bridwell 1929).

32. ***Ctenocolum crotonae*** **(Fahraeus, 1839)**
Published records. LA UNIÓN: Volcan Conchagua, 27–29/V/1958; SAN SALVADOR: 20/XII/1921–4/1/1922 (Kingsolver and Whitehead 1974b).

33. ***Gibbobruchus cristicollis*** **(Sharp, 1885)**
Published records. LA UNIÓN: Volcan Conchagua, 27–29/V/1958 (Kingsolver and Whitehead 1975b).

34. ***Gibbobruchus guanacaste*** **Kingsolver & Whitehead, 1975**
Published records. LA UNIÓN: Volcan Conchagua, 27–29/V/1958 (Kingsolver and Whitehead 1975b).

35. ***Megacerus*** **(*Pachybruchus*)** ***bifloccosus*** **(Motschulsky, 1874)**
Published records. LA UNIÓN: Volcan Conchagua, 27–29/V/1958 (Teran and Kingsolver 1977).

36. ***Megacerus*** **(*Serratibruchus*)** ***cubiciformis*** **(Sharp, 1885)**
Published records. LA UNIÓN: Volcan Conchagua, 27–29/V/1958 (Teran and Kingsolver 1977).

37. ***Megasennius muricatus*** **(Sharp, 1885)**
Published records. LA LIBERTAD: Quetzaltepeque, 19/VI/1958; SAN SALVADOR: 5/VI/1958 (Whitehead and Kingsolver 1975a).

38. ***Meibomeus apicicornis*** **(Pic, 1933)**
Published records. LA LIBERTAD: San Andrés (Kingsolver et al. 1976). LA UNIÓN: Volcan Conchagua (Kingsolver et al. 1976). SAN SALVADOR: San Salvador, Tonocatepeque (Kingsolver et al. 1976).

39. *Meibomeus campbelli* Kingsolver & Whitehead, 1976
Published records. LA LIBERTAD: Quezaltepeque (Kingsolver and Whitehead 1976).

40. *Meibomeus howdeni* Kingslover & Whitehead, 1976
Published records. SAN SALVADOR: San Salvador, Boquerón, 1800 m, nr. Santa Tecla, 2/V/1971, leg. F. Howden, (Kingsolver et al. 1976).

41. *Meibomeus surrubresus* (Pic, 1933)
Published records. El Salvador, without further data (Mancía and Cortéz 1975). LA LIBERTAD: La Libertad, Quezaltepeque, San Andrés; LA UNIÓN: Volcan Conchagua SAN SALVADOR: San Salvador; USULUTÁN: Santiago de Maria (Kingsolver et al. 1976).

42. *Merobruchus columbinus* (Sharp, 1885)
Published records. LA LIBERTAD, LA PAZ, SAN SALVADOR (Kingsolver 1988).

43. *Merobruchus cristoensis* Kingsolver, 1988
Published records. SANTA ANA: P. N. Montecristo, 23 km N of Metapan, 8–10/V/1971 (Kingsolver 1988).

44. *Merobruchus knulli* (White, 1941)
Published records. SAN VICENTE (Kingsolver 1988).

45. *Mimosestes humeralis* (Gyllenhal, 1833)
Published records. SANTA ANA: 8/I/1922 (Kingsolver and Johnson 1978).

46. *Mimosestes mimosae* (Fabricius, 1781)
Published records. SAN SALVADOR: San Salvador, 24/V/1958 and 14/VI/1958 (Kingsolver and Johnson 1978).

47. *Mimosestes nubigens* (Motschulsky, 1874)
Published records. CUSCATLÁN: 6 mi S of Candeleria, 20/VI/1968; El Carmen, 27/V/1958; LA UNIÓN: 14 mi SW of La Union, 23/VI/1968 (Kingsolver and Johnson 1978).

48. *Pygiopachymerus lineola* (Chevrolat, 1871)
Published records. LA UNIÓN: La Unión, (Berry and Salazar 1957). SAN SALVADOR: 1920 (Kingsolver, 1970).
Remarks. Berry and Salazar (1957) reported this species under the name *Phelomerus aberrans* (Shary).

49. *Sennius abbreviatus* (Say, 1824)
Published records. Mancía and Cortéz (1975) mention this species (under the name *S. bivulneratus* (Horn, 1873)) as being present in El Salvador, but do not give specific records.

50. *Sennius atripectus* Johnson & Kingsolver, 1973
Published records. SANTA ANA: Metapán, P. N. Montecristo, 7–9/V/1958, leg. O.L. Cartwright, (Johnson and Kingsolver 1973).

51. *Sennius discolor* (Horn, 1873)
Published records. Mancía and Cortéz (1975) mention this species as being present in El Salvador, but do not give specific records.

52. *Sennius fallax* (Boheman, 1839)
Published records. LA LIBERTAD: Santa Tecla (Berry and Salazar 1957).

Remarks. In Berry and Salazar (1957) this species is given under the name *S. probus* which was synonymized with *S. fallax* in (Johnson and Kingsolver 1973). This species record of Berry was not included in the publication of Johnson and Kingslover (1973).

53. *Sennius lebasi* (Fahraeus, 1839)

Remarks. Johnson and Kingsolver (1973) mention this species (under the name *S. celatus* (Sharp, 1885)) as being present in El Salvador, but do not give specific records.

54. *Sennius morosus* (Sharp, 1885)

Published records. Johnson and Kingsolver (1973) and Mancía and Cortéz (1975) mention this species as being present in El Salvador, but does not give specific records.

55. *Sennius obesulus* (Sharp, 1885)

Published records. LA UNIÓN: without further locality data (Johnson and Kingsolver 1973).

56. *Sennius rufomaculatus* (Motschulsky, 1874)

Published records. Johnson and Kingsolver (1973) mention this species as being present in El Salvador, but do not give specific records.

57. *Stator limbatus* (Horn, 1873)

Published records. LA LIBERTAD: San Andrés, V/1958 (Johnson and Kingsolver 1976). LA UNIÓN: 14 mi SW La Unión, 23/VI/1968, Leg. C. D. Johnson (Johnson 1976).

58. *Stator pruininus* (Horn, 1873)

Remarks. Johnson (1976) and Johnson and Kingsolver (1976) mention this species as being present in El Salvador, but do not give specific records.

59. *Stator sordidus* (Horn, 1873)

Remarks. Johnson (1976) and Johnson and Kingsolver (1976) mention this species as being present in El Salvador, but does not give specific records.

60. *Stator vachelliae* Bottimer, 1973

Remarks. Johnson and Kingsolver (1976) mention this species as being present in El Salvador, but do not give specific records.

61. *Zabrotes chavesi* Kingsolver, 1980

Published records. SAN SALVADOR: San Salvador, 14/VI/1958 (Kingsolver 1980).

62. *Zabrotes interstitialis* (Chevrolat, 1871)

Published records. SAN SALVADOR: San Salvador, 22–26/VI/1958 (Kingsolver 1970b).

63. *Zabrotes subfasciatus* (Boheman, 1833)

Published records. SAN SALVADOR: San Salvador (Berry 1957).

Remarks. Kingsolver (1990) mentioned cosmopolitan distribution for this species but did not name individual contries, where the species was confirmed.

Subfamily Cassidinae

1. *Anisostena funesta* (Baly, 1885)

Published records. SAN SALVADOR: San Salvador, 14/VI/1948, 9/VI/1958, 21/VI/1958, 25/VI/1958; SANTA ANA: Valiano (Staines 1994b).

Specimens examined. LA LIBERTAD: Santa Tecla, 28/IV/1960, 1 spec., J. Bechyné leg. (RBINS). MORAZÁN: Perguin, 22/VI/1959, 1 spec., J. Bechyné leg. (LSC).

2. *Anisostena perspicua* (Horn, 1883)

Published records. LA LIBERTAD: Quezaltepeque, 500 m a.s.l., 19/VI/1963, 7–8/VII/1963, 15/VII/1963, 4/VIII/1963 (Staines 1994b).

3. *Anisostena pilatei* (Baly, 1864)

Published records. LA LIBERTAD: Quezaltepeque, 500 m a.s.l., 19/VI/1963, 5/VII/1963, 15/VII/1963; Santa Tecla, 4/VI/1959 (Staines 1994a).

4. *Anisostena trilineata* (Baly, 1864)

Published records. SAN SALVADOR: San Salvador, 5/VI/1958, 21/VI/1958, 25/VI/1958 (Staines 1994a).

Specimens examined. SANTA ANA: Volcan San Diego, 22–24/VI/1959, 1 spec., J. Bechyné leg. (RBINS).

5. *Baliosus fraternus* (Baly, 1885) new record

Specimens examined. CUSCATLÁN: Hacienda Colima, 12/VII/1959, 9 spec., 22/VII/1959, 47 spec., J. Bechyné leg. (RBINS, 10 LSC); LA LIBERTAD: San Andrés, 15/VI/1959, 1 spec., J. Bechyné leg. (RBINS); SANTA ANA: Volcan San Diego, 22–24/VI/1959, 1 spec., J. Bechyné leg. (RBINS).

6. *Baliosus marmoratus* (Baly, 1885)

Published records. SAN VICENTE: Ichamichen, 150 m a.s.l., 5/IX/1958, 1 spec. (Uhmann 1961).

Specimens examined. LA UNIÓN: Cutuco, 2–3/VI/1959, 1 spec., J. Bechyné leg. (RBINS).

7. *Brachycoryna pumila* Guérin-Méneville, 1844

Published records. SAN SALVADOR: Toma de Aguilares (Berry and Salazar 1957).

Specimens examined. SAN SALVADOR: San Salvador, 14–30/VI/1959, 1 spec., J. Bechyné leg. (RBINS).

8. *Cephaloleia ruficollis* Baly, 1859

Published records. CUSCATLÁN: El Rosario (Berry and Salazar 1957). LA LIBERTAD: Los Chorros, 4 km S of Santa Tecla, 13/V/1971 (Staines 1996).

9. *Cephaloleia tenella* Baly, 1885

Published records. SAN SALVADOR: San Salvador, 14/VI/1958, 21/VI/1958, 1 spec. (Staines 1996).

10. *Chalepus acuticornis* (Chapuis, 1877)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. Species of *Chalepus* are rather difficult for identification and thus presence of this species El Salvador must be verified.

11. *Chalepus amabilis* Baly, 1885

Published records. CUSCATLÁN: El Rosario (Berry and Salazar 1957). LA LIBERTAD: Los Chorros, 500 m a.s.l., 12/X/1958, 3 spec. (Uhmann 1961).

12. *Chalepus bellulus* (Chapuis, 1877)

Published records. SAN VICENTE: Santa Cruz Porrillo (Berry and Salazar 1957). SONSONATE: Icalo [sic.!; = Izalco], 400 m a.s.l., 28/IX/1958, 1 spec. (Uhmann 1961).

Specimens examined. SANTA ANA: Volcan San Diego, 22–24/VI/1959, 2 spec., 25/VI/1959, 1 spec., J. Bechyné leg. (RBINS, 1 LSC).

13. *Chalepus pici* Descarpentries & Villiers, 1959

Specimens examined. LA LIBERTAD: Santa Tecla (Berry and Salazar 1957); LA PAZ: Volcan San Vicente, Finca La Paz, 1/VIII/1959, 1 spec., 5–6/VIII/1959, 1 spec., J. Bechyné leg. (RBINS, LSC).

Remarks. Berry and Salazar (1957) published this species as *Chalepus* cf. *quadricostatus reductus* Pic. The name is a homonym and was replaced by *C. pici*. Occurrence of this species in El Salvador confirmed.

14. *Chalepus similatus* Baly, 1885 new record (Fig. 2A)

Specimens examined. AHUACHAPÁN: Apaneca, 14–15/VII/1959, 5 spec., J. Bechyné leg. (RBINS, 2 LSC); LA UNIÓN: Cutuco, 2–3/VI/1959, 12 spec., J. Bechyné leg. (RBINS, 4 LSC); SANTA ANA: Volcan San Diego, 22–24/VI/1959, 3 spec., J. Bechyné leg. (RBINS, 1 LSC).

15. *Chalepus verticalis* (Chapuis, 1877) new record

Specimens examined. SAN SALVADOR: El Salvador, 12/VII/1959, 1 spec., J. Bechyné leg. (LSC). LA LIBERTAD: Santa Tecla, 28/IV/1960, 1 spec., J. Bechyné leg. (RBINS).

Remarks. Berry (1959) published a record of *Chalepus* sp. probably *verticalis* without stating precise collecting data.

16. *Charidotella* (s. str.) *bifossulata* (Boheman, 1855)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. Occurrence of this species in El Salvador is probable.

17. *Charidotella* (s. str.) *egregia* (Boheman, 1855)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. Occurrence of this species in El Salvador is probable.

18. *Charidotella* (s. str.) *sexpunctata* (Fabricius, 1781)

Published records. LA LIBERTAD: Santa Tecla; Zaragoza, 1 spec.; SAN SALVADOR: Guazapa, 11/V/1960, 2 spec., J. Bechyné leg. (Borowiec 1996). SAN VICENTE: Santa Cruz Porrillo (Berry and Salazar 1957). SANTA ANA: Cerro Verde, 14/V/1976, 1 spec., A. Muyshondt leg.; Montecristo, Metapán, 23/V/1976, 1 spec., A. Muyshondt leg. (Borowiec 2009).

Specimens examined. UNKNOWN PROVINCE: Cafetalera, 14/VIII/1956, 4 spec. (SMTD).

Remarks. Berry and Salazar (1957) and Berry (1959) published this species under the name *Metriona trisignata* (Boheman, 1855), which is considered a synonym of *C. sexpunctata*.

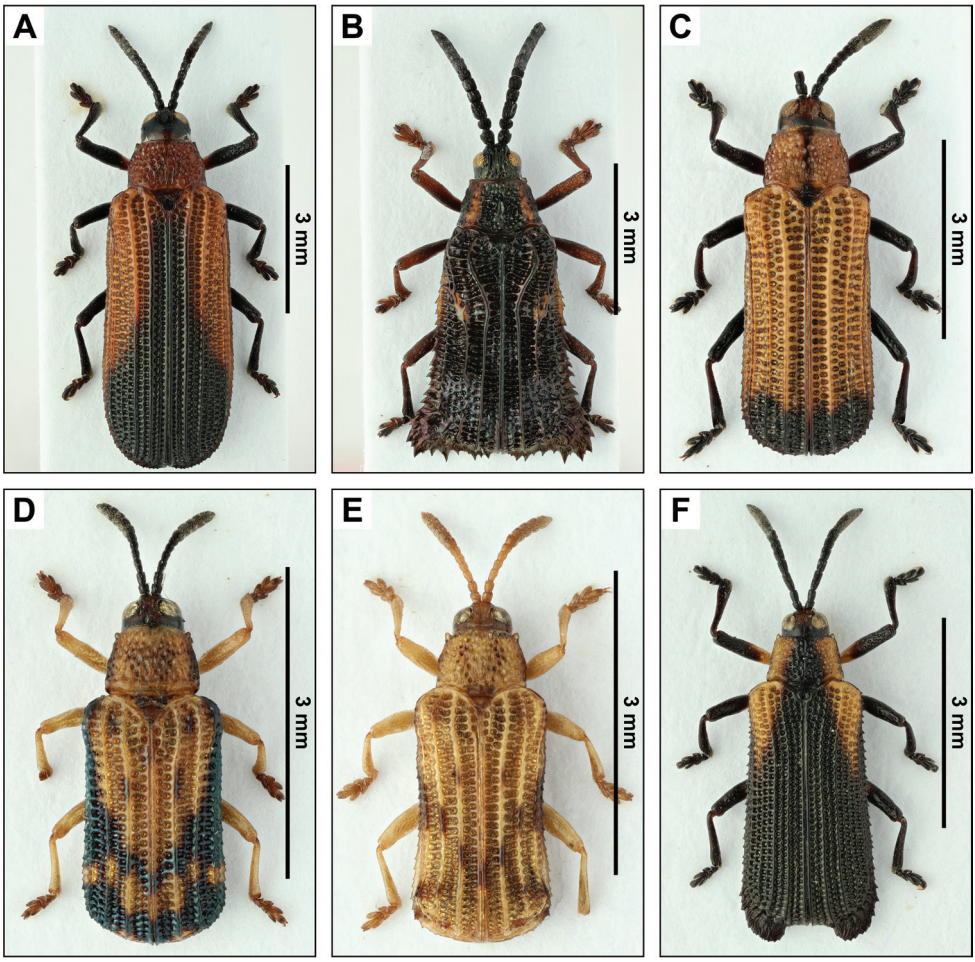

Figure 2. Dorsal pictures of some of the species of Cassidinae from El Salvador from the collections of the RBINS. **A** *Chalepus simulatus* **B** *Euprionota gebieni* **C** *Octhispa atroterminata* **D** *Sumitrosis distinctus* **E** *Sumitrosis fryi* **F** *Uroplata sculptilis*. High resolution images can be found at http://collections.naturalsciences.be/ssh-entomology.

19. *Charidotella* (s. str.) *succinea* (Boheman, 1855)

Published records. El Salvador, without further data (Berry 1959 as *Metriona* cf. *profligata* Boheman, 1862); SANTA ANA: Montecristo, Metapán, 23/V/1976, 1 spec., A. Muyshondt leg. (Borowiec 2009: 638).

20. *Charidotella* (s. str.) *tuberculata* (Fabricius, 1775)

Published records. LA LIBERTAD: Los Chorros, Santa Tecla; SAN SALVADOR: Guazapa, 10/IX/1959, 3 spec., J. Bechyné leg. (Borowiec 1996); SONSONATE: Sonsonate (Berry and Salazar 1957).

Remarks. Borowiec (1996) recorded the species as new to El Salvador.

21. ? *Charidotella* (s. str.) *tumida* (Champion, 1894)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. The species is known so far only from Costa Rica and Panama, and its occurrence in El Salvador is not very probable.

22. *Charidotella* (s. str.) *virgulata* (Boheman, 1855)

Specimens examined. SANTA ANA: Cerro Verde, 1500 m, 7.ix.1958, 1 spec., Steinhausen leg. (DBET); SAN SALVADOR: San Salvador env., 1500 m, 6.ix.1958, 1 spec., Steinhausen leg. (DBET).

Remarks. Borowiec (1989) mentions this species as being present in El Salvador, but does not give specific records. The record was based on the first of the above-mentioned specimens. The second specimen was originally identified as *C.* (*Xenocassis*) *irazuensis* (Champion, 1894), however, in fact belongs also to *C. virgulata* (L. Borowiec, pers. comm.). Therefore *C. irazuensis* does not occur in El Salvador.

23. *Charidotella* (*Chaerocassis*) *emarginata* (Boheman, 1855)

Published records. LA LIBERTAD: Santa Tecla (Berry and Salazar 1957).

Remarks. Occurrence of this species in El Salvador is probable.

24. ? *Charidotella* (*Xenocassis*) cf. *ambita* (Champion, 1894).

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not provide specific records. Certainly species of the subgenus *Xenocassis* Spaeth, 1936 must occur in El Salvador but so far formally none was recorded. The species are very similar to each to other and the identification is not easy without comparative material. *Charidotella* (*X.*) *ambita* is distributed in southern part of Central America (S Nicaragua to Panama), however, its occurrence in El Salvador cannot be excluded but is improbable.

25. *Charidotis vitreata* (Perty, 1830)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. Occurrence of this species in El Salvador is very probable.

26. *Chelymorpha comata* Boheman, 1854

Published records. El Salvador, without further data (Berry 1959 as *Chelymorpha* cf. *comata*). SAN SALVADOR: Guazapa, 10/IX/1959, 1 spec., J. Bechyné leg. (Borowiec 1996: 158); SANTA ANA: Volcan San Diego, 22.–24/VI/1959, 1 spec., J. Bechyné leg. (Borowiec 2009).

27. *Chelymorpha gressoria* Boheman, 1862

Published records. LA LIBERTAD: Comasagua, 1/VII/1959, 1 spec., J. Bechyné leg. (Borowiec 2009).

28. *Chelymorpha pubescens* Boheman, 1854

Published records. El Salvador, without further data (Berry 1959, as *Clelymorpha* [sic!] cf. *pubescens*). CUSCATLÁN: El Rosario (Berry and Salazar 1957).

Remarks. Occurrence of this species in El Salvador is probable.

29. *Coptocycla* (s. str.) *sordida* Boheman, 1855

Specimens examined. UNKNOWN PROVINCE: Alomeya, 17/VIII/1920, 1 spec. (BMNH).

30. *Coptocycla* (*Psalidonota*) *leprosa* Boheman, 1855

Published records. El Salvador, without further data (Berry 1959). LA LIBERTAD: Los Chorros (Berry and Salazar 1957). SAN SALVADOR: Guazapa, 11/V/1960, 1 spec., J. Bechyné leg. (Borowiec 1996).

31. *Deloyala fuliginosa* (Olivier, 1790)

Published records. LA LIBERTAD: Cerro Litoral, 6/VI/1976, 1 spec., A. Muyshondt leg.; Zaragosa, 1 spec. (Borowiec 2009). SAN SALVADOR: Guazapa, 10/IX/1959, 6 spec., J. Bechyné leg. (Borowiec 1996; as *D. guttata* (Olivier, 1790)). SAN VICENTE: Santa Cruz Porrillo (Berry and Salazar 1957).

Remarks. Berry and Salazar (1957), Berry (1959) and Borowiec (1996) published this species under the name *D. guttata* (Olivier, 1790). Althought we have not examined the respective specimens, these records must belong to *D. fuliginosa* as *D. guttata* does not occur south of USA.

32. ? *Deloyala lecontei* (Crotch, 1873)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. Occurrence of this species in El Salvador is dubious as it is distributed in southern part of United States and north and central Mexico.

33. *Deloyala zetterstedti* (Boheman, 1855)

Published records. El Salvador, without further data (Berry 1959). LA LIBERTAD: C. Litoral, 6/VI/1976, 1 spec., A. Muyshondt leg. (Borowiec 2009). SAN SALVADOR: Guazapa, 11/V/1960, 1 spec., J. Bechyné leg. (Borowiec 1996).

Remarks. Berry (1959) mentioned both colour forms, with and without posterolateral spots on explanate margin of elytra. The other form was named *Coptocycla sallei* Boheman, 1862.

34. *Euprionota atterima* Guérin-Méneville, 1844

Published records. LA LIBERTAD: Los Chorros, 500 m a.s.l., 12/X/1958, 1 spec. (Uhmann 1961).

35. *Euprionota gebieni* (Uhmann, 1930) (Fig. 2B)

Published records. SAN SALVADOR: San Salvador, 700 m a.s.l., 30/V/1956, 1 spec., E. Möhn leg. (Uhmann 1960).

Specimens examined. CHALATENANGO: La Paluma, 7–9/VII/1959, 1 spec., J. Bechyné leg. (RBINS); LA LIBERTAD: Hacienda Argentina, 4/IV/1960, 1 spec., J. Bechyné leg. (RBINS); Tamanique, 4/V/1960, 1 spec., J. Bechyné leg. (RBINS).

36. *Heterispa vinula* (Erichson, 1847) new record

Published records. El Salvador, without further data (Berry 1959) under the name *Uroplata* cf. *westwoodi* Baly, 1885.

Specimens examined. LA LIBERTAD: Los Chorros, 29/VI/1959, 2 spec., J. Bechyné leg. (RBINS, LSC). LA PAZ: Volcan San Vicente, Finca La Paz, 1/VIII/1959, 2 spec., J. Bechyné leg. (RBINS). USULUTÁN: Jucuaran, 10–11/XI/1959, 1 spec., J. Bechyné leg. (RBINS),

37. ? *Helocassis* cf. *clavata* (Fabricius, 1798)

Published records. SAN SALVADOR: San Salvador (Berry and Salazar 1957).

Remarks. Record by Berry and Salazar (1957) probably belongs to *H. testudinaria* as typical *H. clavata* does not occur in tropical America. Moreover, *H. clavata* is not repeated in his second list (Berry 1959).

38. *Helocassis crucipennis* (Boheman, 1855)

Published records. SONSONATE: San Julián (Berry and Salazar 1957).

Remarks. Occurrence of this species in El Salvador is very probable.

39. *Helocassis testudinaria* (Boheman, 1855)

Published records. El Salvador, without further data (Berry 1959). LA LIBERTAD: Los Chorros, 9/VI/1974, 1 spec., A. Muyshondt leg.; Zaragosa, 2 spec., A. Muyshondt leg. (Borowiec 2009).

40. *Ischnocodia annulus* (Fabricius, 1781)

Published records. El Salvador, without further data (Berry 1959). AHUACHAPÁN: Los Imposibles, 28/III/1976, 1 spec., A. Muyshondt leg. (Borowiec 2009).

41. *Metrionella bilimeki* Spaeth, 1932

Published records. SAN SALVADOR: Guazapa, 10/IX/1959, 1 spec., J. Bechyné leg. (Borowiec 1996).

42. *Metrionella erratica* (Boheman, 1855)

Published records. SAN SALVADOR: Guazapa, 10/IX/1959, 1 spec., J. Bechyné leg. (Borowiec 1996).

43. *Microctenochira ferranti* (Spaeth, 1926)

Published records. El Salvador, without further data (Berry 1959). SAN SALVADOR: Guazapa, 11/V/1960, 5 spec., J. Bechyné leg. (Borowiec 1996).

44. *Microctenochira hectica* (Boheman, 1855)

Published records. El Salvador, without further data (Berry 1959). CUSCATLÁN: El Rosario (Berry and Salazar 1957). SAN SALVADOR: Guazapa, 11/V/1960, 1 spec., J. Bechyné leg. (Borowiec 1996).

45. *Microctenochira* cf. *plebeja* (Boheman, 1855)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. Its occurrence in El Salvador is very probable.

46. *Microrhopala perforata* Baly, 1864

Published records. CUSCATLÁN: El Rosario (Berry and Salazar 1957). LA LIBERTAD: Los Chorros, 500 m a.s.l., 12/X/1958, 1 spec. (Uhmann 1961); Santa Tecla (Berry and Salazar 1957). SAN VICENTE: Ichamichen, 150 m a.s.l., 5/IX/1958, 1 spec.

Specimens examined. CUSCATLÁN: Hacienda Colima, 12/VII/1959, 1 spec., J. Bechyné leg. (LSC); LA LIBERTAD: El Boquerón, 26/V/1960, 1 spec., J. Bechyné leg. (RBINS). SANTA ANA: Volcan San Diego, 15/VI/1959, 1 spec., 22–24/VI/1959, 1 spec., J. Bechyné leg. (RBINS).

47. *Microrhopala pulchella* Baly, 1864

Published records. El Salvador, without further data (Berry 1959). SAN SALVADOR: San Salvador env., 17/VIII/1958, 1 spec. (Uhmann 1961).

48. *Octhispa atroterminata* Uhmann, 1943 new record (Fig. 2C)

Specimens examined. LA LIBERTAD: El Boquerón, 10/VI/1959, 1 spec., J. Bechyné leg. (LSC); Tamanique, 4/V/1960, 1 spec., J. Bechyné leg. (RBINS). USULUTÁN: Jucuaran, 10.–11/XI/1959, 1 spec., J. Bechyné leg. (RBINS).

Remarks. The three specimens from El Salvador have the black stripe on their pronotum rather thin and only apical 1/5 of elytra black while the holotype of *O. atroterminata* has a thick medial stripe on pronotum and apical 1/3 of elytra black and the dark colouration extending along suture forwards. However, Salvadorian specimens show variability in black colouration: one has the pronotal stripe only slightly indicated; two have the apical black colouration on elytra rather emarginate near suture anteriorly while the third specimen has a clearly projecting black stripe along suture. Therefore, we consider these as intraspecific variability as other characters (e.g. general shape, punctation of elytra and pronotum) are similar to the holotype.

49. *Octhispa centromaculata* (Chapuis 1877) new record

Specimens examined. LA LIBERTAD: Santa Tecla, 28/IV/1960, 1 spec., J. Bechyné leg. (RBINS).

50. *Octotoma championi* Baly, 1885

Published records. SAN VICENTE: Ichamichen, 150 m a.s.l., 17/V/1958, 17/VIII/1958, 5 spec. (Uhmann 1961).

Specimens examined. LA PAZ: Volcan San Vicente, Finca La Paz, 1/VIII/1959, 2 spec., J. Bechyné leg. (RBINS, LSC).

51. *Octotoma scabripennis* Guérin-Méneville, 1844

Published records. SAN SALVADOR: San Salvador, 1953, x.1965 (Staines 1989).

Specimens examined. LA PAZ: Volcan San Vicente, Finca La Paz, 1/VIII/1959, 1 spec., J. Bechyné leg. (LSC). SAN SALVADOR: El Salvador, 12/VII/1959, 1 spec., J. Bechyné leg. (RBINS); San Salvador, 14.–30/VI/1959, 2 spec., J. Bechyné leg. (RBINS).

52. *Oxychalepus alienus* (Baly, 1885)

Published records. MORAZÁN: Perguin, 22/VI/1959; SANTA ANA: Metapán, Hacienda Montecristo, 2300 m a.s.l., 12/III/1972 (Staines 2010).

53. *Oxychalepus anchora* (Chapuis, 1877)

Published records. LA LIBERTAD: La Libertad, 10 m a.s.l., 15/XII/1972; SAN SALVADOR: Santa Tecla, 9/IV/1957 (Staines 2010).

54. *Oxychalepus balyanus* (Weise, 1911)

Published records. SAN VICENTE: Ichamichen, 150 m a.s.l., 5/IX/1958, 2 spec. (Uhmann 1961: 20); SONSONATE: Ishuatan, 15/IX/1958 (Staines 2010).

Specimens examined. LA LIBERTAD: Comasagna, 3/VII/1959, 1 spec., J. Bechyné leg. (RBINS).

55. *Parorectis rugosa* (Boheman, 1854)

Published records. LA LIBERTAD: Los Chorros, 9/VI/1974, 1 spec., A. Muyshondt leg. (Borowiec 2009); SAN SALVADOR: Guazapa, 11/V/1960, 1 spec., J. Bechyné leg. (Borowiec 1996).

56. *Pentispa chevrolati* (Chapuis, 1877) new record

Specimens examined. AHUACHAPÁN: Apaneca, 14–15/VII/1959, 2 spec., J. Bechyné leg. (RBINS, 1 LSC); SANTA ANA: Cerro Verde, 16/V/1960, 7 spec., J. Bechyné leg. (RBINS, 1 LSC).

57. *Pentispa fairmairei* (Chapuis, 1877)

Published records. CUSCATLÁN: El Rosario (Berry and Salazar 1957). SAN SALVADOR: San Salvador env., 17/VIII/1958, 5 spec. (Uhmann 1961).

Specimens examined. CHALATENANGO: La Palma, 7–9/VII/1959, 1 spec., J. Bechyné leg. (RBINS). LA LIBERTAD: Comasagna, 3/VII/1959, 2 spec., J. Bechyné leg. (RBINS); El Boquerón, 10/VI/1959, 1 spec., 25/V/1960, 1 spec., J. Bechyné leg. (LSC); Santa Tecla, 28/IX/1959, 1 spec., J. Bechyné leg. (RBINS); Tamanique, 4/V/1960, 4 spec., J. Bechyné leg. (RBINS, 2 LSC). LA PAZ: Volcan San Vicente, Finca La Paz, 1/VIII/1959, 2 spec., J. Bechyné leg. (RBINS). USULUTÁN: Alegria, 22/II/1960, 1 spec., J. Bechyné leg. (RBINS).

Remarks. Berry and Salazar (1957) published this species as *Uroplata pairmairei* Chap., which is a wrong spelling.

58. *Pentispa melanura* (Chapuis, 1877)

Published records. LA LIBERTAD: Boqueron, 1700 m a.s.l., 11/X/1958, 2 spec. (Uhmann 1961).

59. *Physonota alutacea* Boheman, 1854

Published records. SONSONATE: San Julián, Sonsonate (Berry and Salazar 1957).

Specimens examined. LA LIBERTAD: La Toma, 16/V/1958, 1 spec., O. L. Cartwright leg. (USNM). LA PAZ: Olocuilta, 200 m a.s.l., 19/IX/1958, 1 spec., Steinh. leg. (DBET). LA UNION: La Union, 2/X/1924, 1 spec., K. A. Salman leg. (USNM), 10/V/1954, 10 spec., P. A. Berry leg. (USNM), 15/VI/1954, 1 spec., C. A. leg. (USNM). SAN SALVADOR: Lihuatan, 25/V/1960, 1 spec. (DBET); San Salvador, 1929, 2 spec., S. Calderon leg. (USNM). SAN VICENTE: Cuscutlán Bridge on Lempa River, 10/V/1954, 2 spec., P. A. Berry leg. (USNM). SONSONATE: Izalco, 1/IX/1905, 1 spec., F. Knab leg. (USNM); Sonsonate, 24/VIII/1905, 1 spec., F. Knab leg. (USNM). USULUTÁN: Volcan Conchagua, 27–29/V/1958, 1 spec., O. L. Cartwright leg. (USNM).

60. *Physonota attenuata* Boheman, 1854

Published records. SONSONATE: Sonsonate (Berry and Salazar 1957).

Remarks. Occurrence of this species in El Salvador should be verified as species of *Physonota* Boheman, 1854 are rather difficult for identification.

61. *Physonota citrina* Boheman, 1854

Published records. SANTA ANA: Montecristo, Metapán, 23/V/1976, 3 spec., A. Muyshondt leg. (Borowiec 2009).

62. ? *Physonota* cf. *eucalypta* Boheman, 1862

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. Occurrence of this species in El Salvador is possible. On the other hand identification of species of *Physonota* Boheman, 1854 is rather difficult and the record could belong to another species, e.g. *P. limoniata* Boheman, 1862.

63. *Physonota gigantea* Boheman, 1854
Published records. SONSONATE: Acajutla (Champion 1894), Sonsonate (Berry and Salazar 1957).
Specimens examined. SANTA ANA: Volcan San Diego, 22–24/VI/1959, 1 spec., J. Bechyné leg. (DBET).

64. *Physonota limoniata* Boheman, 1862
Published records. LA LIBERTAD: Jayaque, 1/VI/1975, 1 spec., A. Muyshondt leg. (Borowiec 2009).

65. *Platocthispa fulvescens* (Baly, 1886)
Published records. LA LIBERTAD: Sitio del Niño, 9/V/1956, 1 spec., E. Möhn leg. (Uhmann 1960).

66. ? *Stolas nigrolineata* (Champion, 1893)
Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records. The species is given under genus, *Championaspis* Spaeth, 1913. The species is so far known only from high mountains in Costa Rica and Panama, therefore its occurrence in El Salvador is very questionable. On the other hand it is very characteristic species, but there is *Hilarocassis exlamations* (Linnaeus, 1767) occuring in Central America, which has also thin black lines on elytra.

67. *Sumitrosis distinctus* (Baly, 1885) new record (Fig. 2D)
Specimens examined. LA UNIÓN: Cutuco, 2–3/VI/1959, 1 spec., J. Bechyné leg. (LSC). SANTA ANA: Volcan San Diego, 25/VI/1959, 1 spec., J. Bechyné leg. (RBINS).
Remarks. Berry (1959) mentioned *Anoptilis* sp. probabl. *distincta* Baly as being present in El Salvador, but does not give specific records. Occurrence of *S. distinctus* in El Salvador confirmed.

68. *Sumitrosis fryi* (Baly, 1885) new record (Fig. 2E)
Specimens examined. AHUACHAPÁN: Los Ausoles, 26/I/1960, 1 spec., J. Bechyné leg. (RBINS). LA LIBERTAD: El Boquerón, 10/VI/1959, 1 spec., J. Bechyné leg. (LSC).

69. *Uroplata fusca* Chapuis, 1877
Published records. SONSONATE: Izalco, 400 m a.s.l., 28/IX/1958, 1 spec. (Uhmann 1961).

70. *Tapinaspis wesmaeli* (Boheman, 1855)
Published records. El Salvador, without further data (Berry 1959). SANTA ANA: Lago de Coatepeque, 19/VII/????, C. F. & S. Hevel leg. (Chaboo 2002).

71. *Uroplata sculptilis* Chapuis, 1877 new record (Fig. 2F)
Specimens examined. LA PAZ: Volcan San Vicente, Finca La Paz, 1/VIII/1959, 1 spec., J. Bechyné leg. (RBINS). SAN SALVADOR: San Salvador, 14–30/VI/1959, 1 spec., J. Bechyné leg. (RBINS).

72. *Xenochalepus* (*Neochalepus*) *contubernalis* (Baly, 1885)
Published records. SAN SALVADOR: San Salvador env., 17/VIII/1958, 3 spec. (Uhmann 1961).

Specimens examined. LA LIBERTAD: Tamanique, 4/V/1960, 6 spec., J. Bechyné leg. (RBINS, 2 LSC). SAN SALVADOR: San Salvador, 19/VI/1959, 1 spec., J. Bechyné leg. (LSC). SANTA ANA: Cerro Verde, 15/II/1960, 1 spec., J. Bechyné leg. (RBINS); Volcan San Diego, 22–24/VI/1959, 4 spec., J. Bechyné leg. (RBINS, 1 LSC).

73. *Xenochalepus* (s. str.) *omogerus* (Crotch, 1873)

Published records. El Salvador, without further data (Berry 1959). LA LIBERTAD: Santa Tecla (Berry and Salazar 1957). SAN SALVADOR: San Salvador env., 17/VIII/1958, 3 spec. (Uhmann 1961).

Specimens examined. AHUACHAPÁN: Apaneca, 14.–15/VII/1959, 5 spec., 15/VII/1959, 1 spec., J. Bechyné leg. (RBINS, 2 LSC). CUSCATLÁN: Hacienda Colima, 22/VII/1959, 1 spec., J. Bechyné leg. (RBINS). LA PAZ: Volcan San Vicente, Finca La Paz, 1/VIII/1959, 1 spec., J. Bechyné leg. (LSC). SANTA ANA: Volcan San Diego, 22–24/VI/1959, 1 spec., J. Bechyné leg. (LSC).

74. *Xenochalepus* (s. str.) *rufithorax* (Baly, 1885)

Published records. CUSCATLÁN: El Rosario (Berry and Salazar 1957). SAN SALVADOR: San Salvador env., 20/IX/1958, 1 spec. (Uhmann 1961: 20).

Specimens examined. SAN SALVADOR: El Salvador, 12/VII/1959, 2 spec., J. Bechyné leg. (RBINS, LSC).

Remarks. Berry and Salazar (1957) published this species under the name *Xenochalepus rufithorace sanguineus* Baly, which is wrong spelling. He must have meant *X. sanguinosus* (Baly, 1885), which is considered a synonym of *X. rufithorax*.

Subfamily Chrysomelinae

1. *Calligrapha argus* Stål, 1859

Published records. AHUACHAPÁN: Apaneca, 4500 ft, 7–12/IX/2002, D. Marqua, Calligrapha argus Stål J. Gómez-Zurita det. 2011 (Gómez-Zurita 2015). LA LIBERTAD: Tamanique, 1000 m, 5/XII/1971, S. & L. Steinhausen, Calligrapha argus Stål J. Gómez-Zurita det. 2011 (Gómez-Zurita 2015). LA UNIÓN: No. 444–7813, 15/VI/54, M.S.V. (Gómez-Zurita 2015). Volcan Conchagua, 27–29/V/1958, O.L. Cartwright, Calligrapha argus Stål J. Gómez-Zurita det. 2011 (Gómez-Zurita 2015). SANTA ANA: Metapán, No. 444–2806, 5/VII/1954, M.S.V. (Gómez-Zurita 2015).

Remarks. Bechyné and Bechyné (1965a) also report *C. argus* from El Salvador, but do not state specific localities.

2. *Calligrapha bajula* Stål, 1860 new record (Fig. 3A)

Specimens examined. SAN SALVADOR: El Boquerón, 3/VII/1959, Leg. J. Bechyné, Det. J. Gómez-Zurita, 1 spec. (RBINS).

Remarks. For a full inventory of the *Calligrapha* spec. in the RBINS collections, one should consult Merckx et al. (2018), where the records cited here from El Salvador are also included.

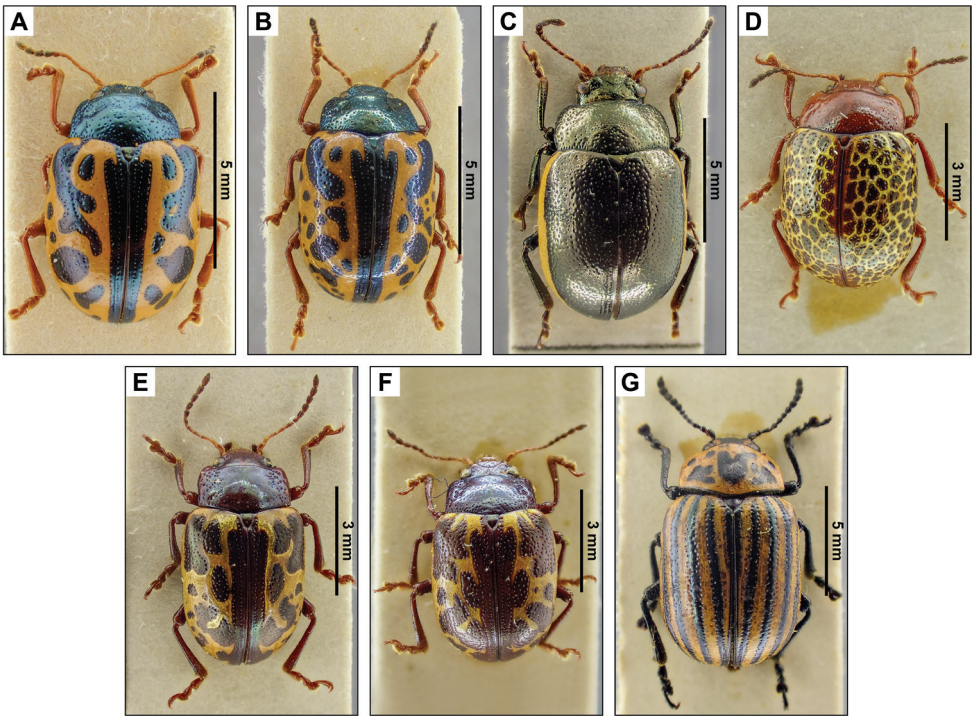

Figure 3. Dorsal pictures of the species of Chrysomelinae from El Salvador currently present in the collections of the RBINS. **A** *Calligrapha bajula* **B** *C. fulvipes* **C** *C.* (*Zygospila*) *championi* **D** *C.* (*Zygospila*) *guttulosa* **E** *C.* (*Zygospila*) *piceicollis* **F** *C.* (*Zygospila*) *signatipennis* **G** *Leptinotarsa undecimlineata*. High resolution images can be found at http://collections.naturalsciences.be/ssh-entomology.

3. *Calligrapha diversa* Stål, 1859

Published records. SANTA ANA: No. 444.2813, 5/VII/1954, Col. M.S.V., Calligrapha diversa Stål J. Gómez-Zurita det. 2011 (Gómez-Zurita 2015).

4. *Calligrapha fulvipes* Stål, 1859 (Fig. 3B)

Published records. CUSCATLÁN: El Rosario (Berry 1957). SAN SALVADOR: 10/VI/1951 (Bechyné 1954); Volcan Santa Ana, 1600–1700 m, 3/VIII/1951 (Bechyné 1954).

Specimens examined. SAN SALVADOR: El Boquerón, 3/VII/1959, Leg. J. Bechyné, Det. J. Bechyné, 40 spec. (RBINS).

Remarks. Bechyné and Bechyné (1965a) also report *C. fulvipes* from El Salvador, but do not state specific localities. Most possibly this originates from the localities from Bechyné (1954) which are cited here. For a full inventory of the *Calligrapha* spec. in the RBINS collections, one should consult Merckx et al. (2018), where the records cited here from El Salvador are also included.

5. *Calligrapha multiguttata* Stål, 1859

Published records. AHUACHAPÁN: Apaneca, MIZA0040488, 13.860000°N, 89.801110°W, 17/VIII/1959, J. Bechyné & B. Bechyné coll., Calligrapha multiguttata St. J. Bechyné det. (Gómez-Zurita 2016).

6. *Calligrapha nupta* Stål, 1859 new record

Specimens examined. SAN SALVADOR: El Boquerón, 3/VII/1959, Leg. J. Bechyné, Det. J. Gómez-Zurita, 1 spec. (RBINS).

Remarks. For a full inventory of the *Calligrapha* species in the RBINS collections, one should consult Merckx et al. (2018), where the records cited here from El Salvador are also included.

7. *Calligrapha ramulifera* Stål, 1859

Published records. CUSCATLÁN: Rosario, Cuzcatlan, n°631–39, 17/VII/1955, Col. M.S.V. (Gómez-Zurita 2015). LA LIBERTAD: Los Chorros (Berry 1957); Los Chorros, 700 m, 4/VI/1972, S. & L. Steinhausen, *Calligrapha ramulifera* Stål J. Gómez-Zurita det. 2011 (Gómez-Zurita 2015). SAN SALVADOR: 25/II/1920, E.S.C.A., K.A. Salman collector, *Calligrapha ramulifera* Stål EAC'27 (Gómez-Zurita 2015). SANTA ANA: San Isidro, Cerro Verde 1000 m, 2/VI/1972, S. & L. Steinhausen, 2563, *Calligrapha ramulifera* Stål J. Gómez-Zurita det. 2011 (Gómez-Zurita 2015). UNKNOWN PROVINCE: Landaverde, S. & L. Steinhausen, *Calligrapha ramulifera* Stål Det. J. Watts 1993 (Gómez-Zurita 2015). Servicios Técnicos Cafetalería, El Salvador C.A. [one with: 14–E–42], (Gómez-Zurita 2015).

8. *Calligrapha suboculata* Stål, 1859

Published records. SANTA ANA: San Isidro, Cerro Verde, 1000 m, 11/VI/1972, S. & L. Steinhausen coll., *Calligrapha suboculata* Stål J. Gómez-Zurita det. 2011 (Gómez-Zurita, 2018).

9. *Calligrapha (Zygospila) bigenera* (Stål, 1859)

Published records. LA LIBERTAD: Santa Tecla, (Berry 1957).

10. *Calligrapha (Zygospila) championi* (Jacoby, 1879) new record (Fig. 3C)

Specimens examined. SAN SALVADOR: 19/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 4 spec., (RBINS)

11. *Calligrapha (Zygospila) dulcis* (Stål, 1859)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

12. *Calligrapha (Zygospila) guttulosa* (Stål, 1859) new record (Fig. 3D)

Specimens examined. SANTA ANA: Cerro Verde, 16/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 22 spec. (RBINS).

13. *Calligrapha (Zygospila) piceicollis* (Stål, 1859) (Fig. 3E)

Published records. LA LIBERTAD: Santa Tecla (Berry 1957). SAN SALVADOR: La Toma de Aguilares (Berry 1957).

Specimens examined. LA LIBERTAD: Hacienda Chanmico, 20/VI/1960, Leg. J. Bechyné, Det. J. Bechyné, 8 spec. (RBINS).

14. *Calligrapha (Zygospila) signatipennis* (Stål, 1859) (Fig. 3F)
Published records. SAN SALVADOR: 23/IV/1951 and 11/VII/1951, (Bechyné 1954).
Specimens examined. SAN SALVADOR: El Boquerón, 9/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 5 spec. (RBINS).
15. *Chrysomela depressa* Suffrian, 1858
Published records. SAN SALVADOR: San Salvador (Berry 1957).
16. *Leptinotarsa flavitarsis flavitarsis* Guérin, 1855
Published records. CUSCATLÁN: Volcan San Vicente, Finca El Carmen, 1300 m, 11–16/VI/1951 (Bechyné 1954). Hacienda Buena Vista, 1200 m, Volcan Izalco, 26/VII/1951 (Bechyné 1954). LA LIBERTAD: Los Chorros (Berry 1957).
17. *Leptinotarsa undecimlineata* (Stål, 1859) new record (Fig. 3G)
Specimens examined. SANTA ANA: Cerro Verde, 3/I/1960, Leg. J. Bechyné, Det. J. Bechyné, 28 spec. (RBINS).
18. *Plagiodera aeneiventris* Stål, 1860
Published records. CUSCATLÁN: El Rosario, (Berry, 1957).
19. *Stilodes atromaculata* (Stål, 1859)
Published records. LA LIBERTAD: Los Chorros (Berry 1957).
Remarks. Berry and Salazar (1957) mentions this species under its synonym *Deuterocampta atromaculata*.

Subfamily Cryptocephalinae

1. *Babia* (s. str.) *quadriguttata* Lacordaire, 1848
Published records. LA LIBERTAD: Santa Tecla (Berry and Salazar 1957).
2. *Chlamisus maculipes* (Chevrolat, 1835)
Published records. CUSCATLÁN: El Rosario (Berry and Salazar 1957).
3. *Chlamisus pardalis* (Lacordaire, 1848)
Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.
4. *Cryptocephalus trizonatus* Suffrian, 1858
Published records. LA LIBERTAD: Santa Tecla (Berry and Salazar 1957).
5. *Griburius albilabris* (Suffrian, 1852)
Published records. CUSCATLÁN: El Rosario (Berry and Salazar 1957).
6. *Lexiphanes bimaculatus* (Jacoby, 1880)
Published records. CUSCATLÁN: El Rosario (Berry and Salazar 1957).
7. *Megalostomis dimidiata* Lacordaire, 1848
Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.
8. *Megalostomis pyropyga* Lacordaire, 1848
Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

Subfamily Eumolpinae

1. ***Brachypnoea cretifera*** **(Lefèvre, 1875) new record (Fig. 4A)**
   Specimens examined. SANTA ANA: Cerro Verde, 16/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 61 spec. (RBINS).
2. ***Brachypnoea lateralis lateralis*** **(Jacoby, 1881) new record (Fig. 4B)**
   Specimens examined. SANTA ANA: Cerro Verde, 16/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 39 spec. (RBINS).
3. ***Brachypnoea lefevrei lefevrei*** **(Jacoby, 1878) new record (Fig. 4C)**
   Specimens examined. SANTA ANA: Cerro Verde, 16/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 21 spec. (RBINS).
4. ***Brachypnoea viridis*** **(Jacoby, 1878) new record (Fig. 4D)**
   Specimens examined. SAN SALVADOR, 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 48 spec. (RBINS).
5. ***Chalcophana cincta*** **Harold, 1874 (Fig. 4E)**
   Published records. CUSCATLÁN: El Rosario (Berry 1957).
   Specimens examined. LA LIBERTAD: Comasagua, 3/VII/1959, Leg. J. Bechyné, Det. J. Bechyné, "No Type!", 4 spec. (RBINS). SAN SALVADOR: 23/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, 41 spec. (RBINS), 8/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, 12 spec. (RBINS).
6. ***Chrysodinopsis cupriceps*** **Lefèvre, 1877 new record (Fig. 4F)**
   Specimens examined. SAN SALVADOR: 24/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 14 spec. (RBINS).
7. ***Colaspis freyi*** **Bechyné, 1950 new record (Fig. 4G)**
   Specimens examined. SAN SALVADOR: 10/IX/1959, Leg. J. Bechyné, Det. J. Bechyné, 11 spec. (RBINS), 11/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 12 spec. (RBINS), 19/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 10 spec. (RBINS), 9/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 17 spec. (RBINS).
   Remarks. In the RBINS, these spec. are labeled as *Maecolaspis freyi*. However, all species within *Maecolaspis* Bechyné, 1950 have been placed into *Colaspis* Fabricius, 1801; see Flowers (1996).
8. ***Colaspis impressa*** **Lefèvre, 1877**
   Published records. CUSCATLÁN: El Rosario (Berry 1957).
9. ***Colaspis inconspicua*** **Jacoby 1890**
   Published records. CUSCATLÁN: El Rosario (Berry 1957).
10. ***Colaspis inconstans*** **(Lefèvre, 1878) new record (Fig. 4H)**
    Specimens examined. SAN SALVADOR: Guazapa, 11/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 14 spec. (RBINS).
    Remarks. In the RBINS, these spec. are labeled as *Maecolaspis inconstans*. However, all species within *Maecolaspis* Bechyné, 1950 have been placed into *Colaspis* Fabricius, 1801; see Flowers (1996).
11. ***Colaspis lebasi*** **(Lefèvre, 1878) (Fig. 4I)**
    Published records. SAN SALVADOR: 10/VI/1951 (Bechyné 1954).

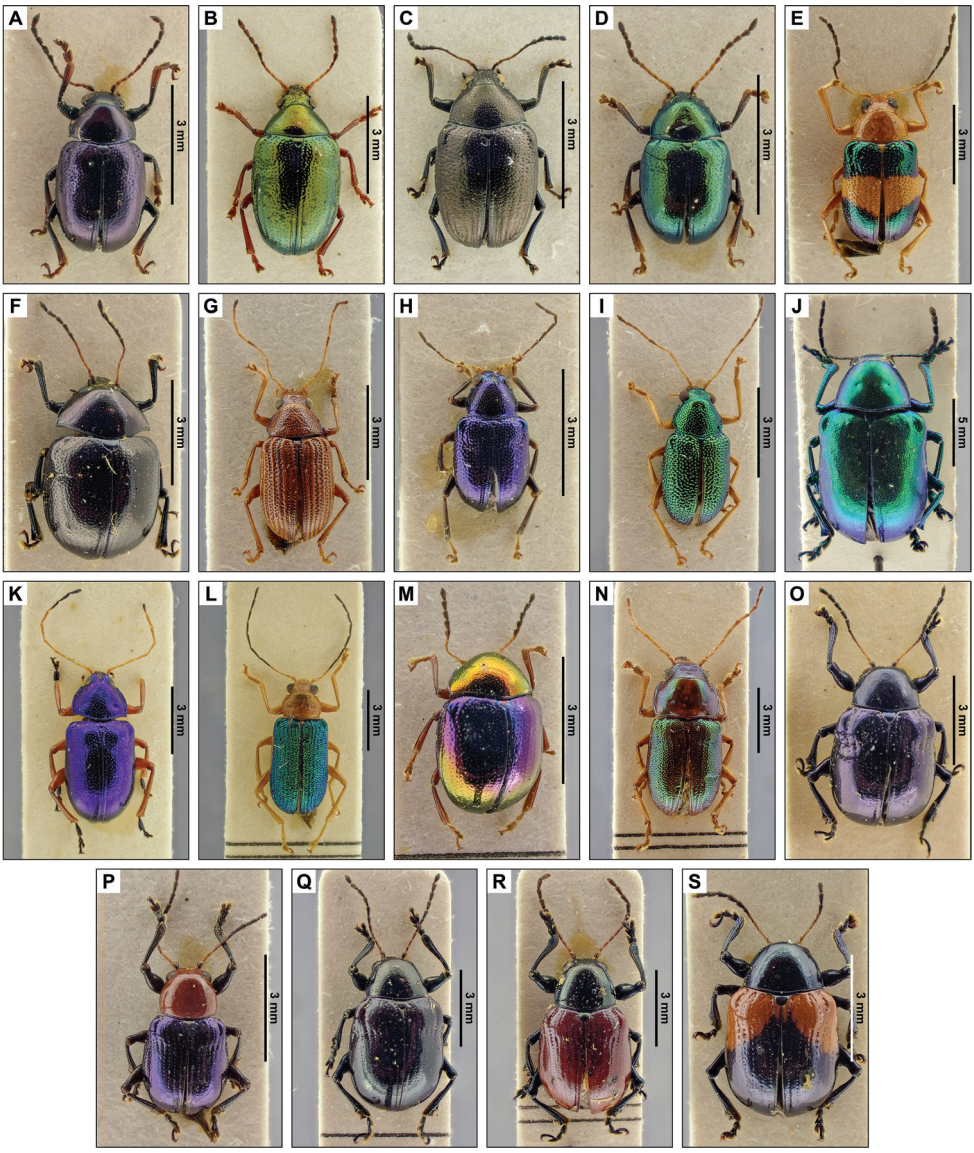

Figure 4. Dorsal pictures of the species of Eumolpinae from El Salvador currently present in the collections of the RBINS. Pictures of *nomina nuda* spec.s are not depicted. **A** *Brachypnoea cretifera* **B** *B. lateralis lateralis* **C** *B. lefeivrei lefeivrei* **D** *B. viridis* **E** *Chalcophana cincta* **F** *Chrysodinopsis cupriceps* **G** *Colaspis freyi* **H** *C. inconstans* **I** *C. lebasi* **J** *Eumolpus robustus* **K** *Nodocolaspis impressa* **L** *Prionodera hirtipennis* **M** *Spintherophyta corusca* **N** *Talurus rugosus* **O** *Typophorus limbatus* **P** *Typophorus mexicanus* **Q** *Typophorus nigritus obliquus* var. a **R** *Typophorus nigritus obliquus* var. b **S** *Typophorus nigritus obliquus* var. c. High resolution images can be found at http://collections.naturalsciences.be/ssh-entomology.

Specimens examined. SAN SALVADOR: 19/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 9 spec. (RBINS).

Remarks. In the RBINS, these spec. are labeled as *Maecolaspis lebasi*. However, all species within *Maecolaspis* Bechyné, 1950 have been placed into *Colaspis* Fabricius, 1801; see Flowers (1996). Bechyné (1955) also states El Salvador under distribution of *C. lebasi* but does not add additional records.

12. *Colaspis melancholica* Jacoby, 1881

Remarks. Flowers (1996) states El Salvador under this species distribution, but does not give specific localities.

13. *Colaspis suturalis* Lefèvre, 1878

Published records. SAN SALVADOR: Toma de Aguilares (Berry 1957).

14. *Colaspis zilchi* (Bechyné, 1954)

Published records. SAN SALVADOR: 30/IV–5/V/1951 (Bechyné 1954).

Specimens examined. SAN SALVADOR: 19/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 21 spec. (RBINS).

Remarks. These spec. are labeled as *Maecolaspis zilchi*. However, all species within *Maecolaspis* Bechyné, 1950 have been placed into *Colaspis* Fabricius, 1801; see Flowers (1996).

15. *Deuteronoda suturalis suturalis* Lefèvre, 1878

Remarks. Bechyné and Bechyné (1965b) state El Salvador under this species distribution, but do not give any specific localities.

16. *Eumolpus robustus* (Horn, 1885) new record (Fig. 4J)

Specimens examined. SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 4 spec. (RBINS).

17. *Fidia unistriata* Jacoby, 1882

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

18. *Freudeita melancholica* (Jacoby, 1881)

Remarks. Bechyné and Bechyné (1969b) state El Salvador under this species distribution, but do not give any specific localities.

19. *Glyptoscelis chontalensis* Jacoby, 1882

Remarks. Flowers (1996) states El Salvador under this species distribution, but does not give specific localities.

20. *Habrophora maculipennis* Jacoby, 1882

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

21. *Metachroma vittipennis* Blake, 1970

Remarks. Flowers (1996) states El Salvador under this species distribution, but does not give specific localities.

22. *Nodocolaspis impressa* (Lefèvre, 1877) new record (Fig. 4K)

Specimens examined. LA LIBERTAD: Hacienda Argentina, 11/IX/1959, Leg. J. Bechyné, Det. J. Bechyné, 5 spec. (RBINS).

Remarks. In Flowers (1996), this species is listed under *Colaspis* Fabricius, 1801. However, *Nodocolaspis* Bechyné, 1949 is not listed here as a synonym of *Colaspis*. The correct placement of this species thus remains uncertain for the authors.

23. *Prionodera hirtipennis* Jacoby, 1881 new record (Fig. 4L)
Specimens examined. SAN SALVADOR: El Boquerón, 25/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 24 spec. (RBINS).

24. *Promecosoma nobilitatum* Lefèvre, 1877
Published records. SAN SALVADOR: 30/IV–5/V/1951 (Bechyné 1954).

25. *Spintherophyta corrusca* (Lefèvre, 1877) new record (Fig. 4M)
Specimens examined. SAN SALVADOR: El Boquerón, 25/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, 15 spec. (RBINS), 24/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 15 spec. (RBINS).

26. *Talurus rugosus* (Jacoby, 1882) (Fig. 4N)
Published records. CUSCATLÁN: El Rosario; SONSONATE: Santa Cruz Porrillo (Berry 1957).
Specimens examined. LA UNIÓN: Cutuco, 3/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 32 spec. (RBINS). SAN SALVADOR: 19/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 26 spec. (RBINS), 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 1 spec. (RBINS).

27. *Typophorus limbatus* Jacoby, 1891 new record (Fig. 4O)
Specimens examined. LA LIBERTAD: Hacienda Argentina, 19/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 44 spec. (RBINS).

28. *Typophorus mexicanus* (Jacoby, 1882) new record (Fig. 4P)
Specimens examined. SAN SALVADOR: El Boquerón, 9/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 48 spec. (RBINS).

29. *Typophorus nigritus obliquus* Baly, 1859 new record (Fig. 4Q,R,S)
Specimens examined. SAN SALVADOR: Cartagena, 19/V/1959, Leg. J. Bechyné, Det. J. Bechyné, 24 spec. (RBINS), 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 26 spec. (RBINS).

Subfamily Galerucinae – Alticini

1. *Acallepitrix anila* Bechyné & Bechyné, 1963
Published records. LA LIBERTAD: Los Chorros, 25/VI/1959 (Bechyné and Bechyné 1963).

2. *Acallepitrix clypeata heteronitens* Bechyné & Bechyné, 1963
Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 27/IX/1959 (Bechyné and Bechyné 1963).

3. *Acallepitrix estebania* Bechyné & Bechyné, 1963 (Fig. 5A)
Published records. AHUACHAPÁN: Apaneca, 14–17/VIII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Hacienda Argentina, 4/IV/1960 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VI/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 16/VI/1959 (Bechyné and Bechyné 1963), Capital, 20/VIII/1959 (Bechyné and Bechyné 1963); Cerro San

Jacinto, 17/IX/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 23/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. LA LIBERTAD: Hacienda Argentina, 4/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 5 spec. (RBINS).

4. ***Acallepitrix hylophila*** **Bechyné & Bechyné, 1963**

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963).

5. ***Acallepitrix iris*** **Bechyné & Bechyné, 1963**

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1963).

6. ***Acallepitrix morazanica*** **Bechyné & Bechyné, 1963**

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963). SAN VICENTE: Volcan San Vicente, 1–10/VIII/1959 (Bechyné and Bechyné 1963).

7. ***Acallepitrix orbitalis*** **Bechyné & Bechyné, 1963**

Published records. SAN SALVADOR: Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1963). SAN VICENTE: Volcan San Vicente, 1–10/VIII/1959 (Bechyné and Bechyné 1963).

8. ***Acallepitrix persuavis*** **Bechyné & Bechyné, 1963**

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963).

9. ***Acallepitrix ponderosa*** **Bechyné & Bechyné, 1963**

Published records. LA LIBERTAD: Hacienda Chanmico, 16/VI/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 9/VI/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 22–24/VI/1959 (Bechyné and Bechyné 1963).

10. ***Acallepitrix rubrifrons*** **Bechyné & Bechyné, 1963**

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 11/VI/1959 (Bechyné and Bechyné 1963).

11. ***Acanthonycha jacobyi*** **Bechyné, 1959**

Published records. SAN SALVADOR: 11/VI/1959, 30/VI/1959, 6/VII/1959 (Bechyné and Bechyné 1960).

12. ***Acrocyum interposita*** **(Bechyné & Bechyné, 1963)**

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 12/VI/1959 (Bechyné and Bechyné 1963).

13. ***Alagoasa acutangula*** **(Jacoby, 1886) (Fig. 5B)**

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1959). LA LIBERTAD: Comasagua, 1/VII/1959 and 3/VII/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 20/VI/1959

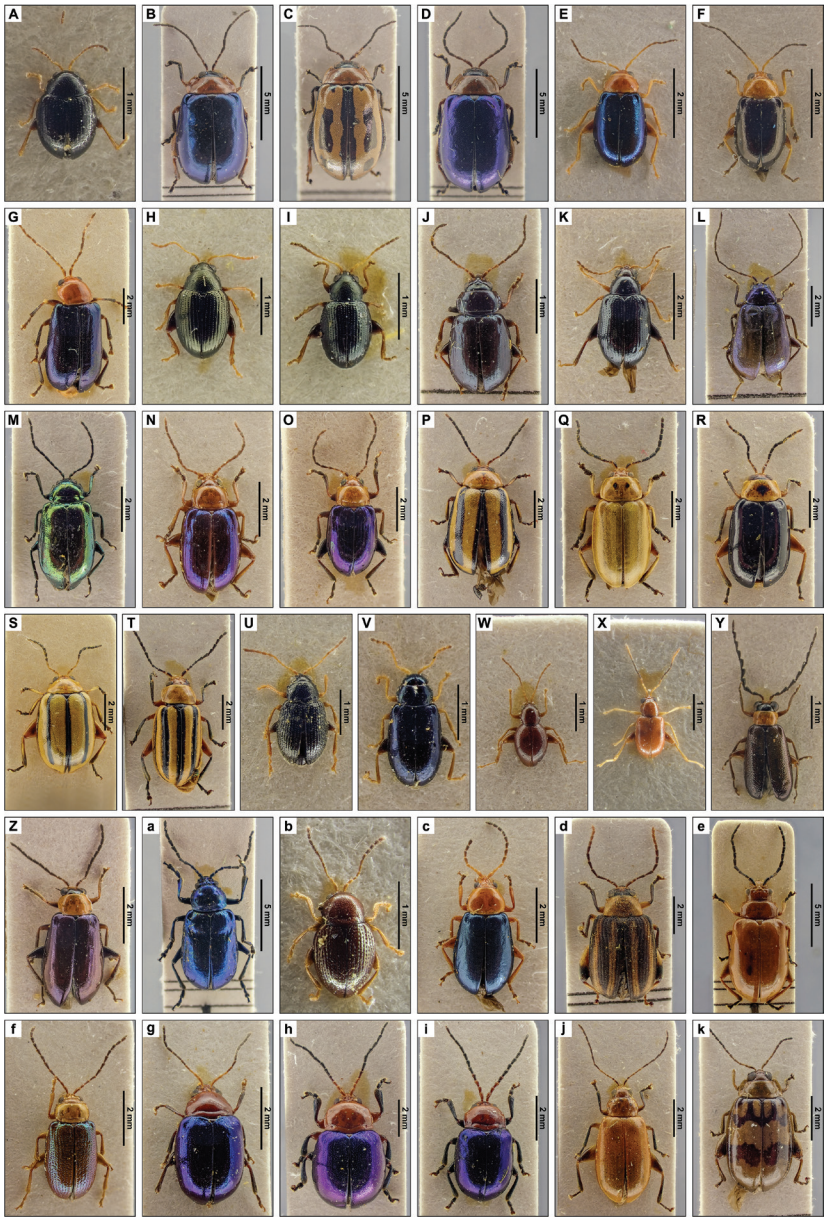

Figure 5. Dorsal pictures of the species of Galerucinae – Alticini from El Salvador currently present in the collections of the RBINS. Pictures of *nomina nuda* spec.s are not depicted. **A** *Acallepitrix estebania* **B** *Alagoasa acutangula* **C** *A. bipunctata* **D** *A. ceracollis* **E** *Ayalaia minor* **F** *A. salvadorensis* **G** *Cacoscelis guazapa* **H** *Chaetocnema fulvicornis* **I** *C. mexicana* **J** *Chalatenanganya quadrifida* **K** *Cyrsylus recticollis* **L** *Deuteraltica longicornis* **M** *Diphaltica trifiniensis* **N** *Diphaulaca cordobae* **O** *D. wagneri* **P** *Disonycha brevilineata* **Q** *D. figurata* **R** *D. nigrita* **S** *D. ovata* **T** *D. recticollis* **U** *Epitrix hirtula* **V** *Genaphthona transversicollis* **W** *Longitarsus berryi* **X** *L. varicornis* **Y** *Lupraea fulvicollis* **Z** *L. portilloi* **a** *Macrohaltica salvadorensis* **b** *Oreinodera aptera* **c** *Phrynocepha laevicollis* **d** *Physimerus femoralis* **e** *Platiprosopus acutangulus* **f** *Plectotetra surquia* **g** *Syphrea balneria* **h** *S. pretiosa* **i** *S. quintanillai* **j***Systena variabilis* **k** *Walterianella venustula*. High resolution images can be found at http://collections.naturalsciences.be/ssh-entomology.

and 2/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. SAN SALVADOR: 13/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 10 spec. (RBINS).

Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

14. ***Alagoasa bipunctata*** **(Chevrolat, 1834) (Fig. 5C)**

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963). CUSCATLÁN: Hacienda Colima, 27/VII,1959, (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 8/VI/1959, 13/VI/1959, 20/VI/1959, 6/VII/1959, 20/VII/1959, 24/VII/1959, 11/VIII/1959, 23/V/1960, (Bechyné and Bechyné 1963); Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1963); Hacienda Argentina, 17/VI/1959 and 20/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 22–24/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 20 spec. (RBINS).

15. ***Alagoasa ceracollis*** **(Say, 1835) (Fig. 5D)**

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Los Chorros, 27/VI/1959 (Bechyné and Bechyné 1963); Comasagua, 1/VII/1959 and 3/VII/1959 (Bechyné and Bechyné 1963); Hacienda Argentina, 17/VI/1959 (Bechyné and Bechyné 1963). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: 10/VI/1951, 21/VI/1951, 23/VI/1951, 13/VIII/1951, 15/IX/1951 (Bechyné 1954); Capital, 7/VI/1959, 20/VI/1959, 30/VI/1959, 28/VII/1959, 24/I/1960, 7/VI/1959, 23/V/1960 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 23/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 18 spec. (RBINS).

16. ***Alagoasa decemguttata*** **(Fabricius, 1801)**

Published records. CUSCATLÁN: El Rosario (Berry 1957). SONSONATE: San Julián (Berry 1957).

17. ***Alagoasa extrema*** **(Harold, 1880)**

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 24/IV/1960 (Bechyné and Bechyné 1963); Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1963).

18. ***Alagoasa paraphana*** **Bechyné & Bechyné, 1963**

Published records. LA LIBERTAD: Comasagua, 1/VII/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963).

19. ***Alagoasa seriata*** **(Baly, 1878)**

Published records. CHALATENANGO: La Palma, 7–8/VII/1959 (Bechyné and Bechyné 1963). CUSCATLÁN: El Rosario (Berry 1957). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 20/VI/1959, 30/VI/1959, 6/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 22/VI/1959 (Bechyné and Bechyné 1963).

Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

20. ***Alagoasa virgata*** **(Harold, 1880)**

Published records. CUSCATLÁN: El Rosario (Berry 1957).

21. ***Allochroma coccineum*** **Clark, 1860**

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

22. ***Altica brevis*** **(Harold, 1875)**

Published records. AHUACHAPÁN: Hacienda Monte Cristo, 2200 m, 4–8/VI/1951 (Bechyné 1954).

23. ***Asphaera abdominalis*** **(Chevrolat, 1835)**

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963).

24. ***Asphaera reichei*** **(Harold, 1876)**

Published records. LA PAZ: Volcan San Vicente. Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: El Salvador, IX/1950, Mertens (Bechyné 1954). SANTA ANA: Cerro Verde, 16/V/1960 (Bechyné and Bechyné 1963).

25. ***Ayalaia minor*** **Bechyné & Bechyné, 1960 (Fig. 5E)**

Published records. AHUACHAPÁN: Apaneca, 14–17/VI/1959 (Bechyné and Bechyné 1960). LA LIBERTAD: Hacienda Argentina, 20/VII/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959, (Bechyné and Bechyné 1960). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: Capital, 8/VI/1959, 19/VI/1959, 20/VII/1959, 20/VIII/1959 (Bechyné and Bechyné 1960); Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1960); El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1960).

Specimens examined. LA PAZ: Volcan San Vicente, Finca La Paz, 1/VIII/1959, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 19 spec. (RBINS).

26. ***Ayalaia salvadorensis*** **Bechyné & Bechyné, 1960 (Fig. 5F)**

Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1960). LA LIBERTAD: Hacienda Argentina, 17/VI/1959, 20/VII/1959, 16/V/1960 (Bechyné and Bechyné 1960). SAN SALVADOR: Capital, 19–20/VI/1959 (Bechyné and Bechyné 1960); El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 22–24/VI/1959, (Bechyné and Bechyné 1960).

Specimens examined. LA LIBERTAD: Hacienda Argentina, 16/V/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 51 spec. (RBINS).

27. *Blepharida godmani* Jacoby 1885

Published records. LA LIBERTAD: Hacienda Argentina, 19/V/1960, J. & B. Bechyné (Furth 1998).

28. *Blepharida suturalis* Jacoby, 1885

Published records. LA LIBERTAD: Hacienda Argentina, 19/V/1960, (Furth 1998). SAN SALVADOR: El Salvador, A. Martinez Cuestas (Furth 1998); San Salvador, 30/IV–5/V/1951 (Bechyné 1954); Capital, 3/V/1960, 16/V/1960, 18/V/1960, (Bechyné and Bechyné 1963); Guazapa, 11/V/1960 (Bechyné and Bechyné 1963), 9–19/V/1958, O. L. Cartwright, at light (Furth 1998). SANTA ANA: Volcan San Diego, 22/VI/1959 (Bechyné and Bechyné 1963).

29. *Cacoscelis guazapa* Bechyné & Bechyné, 1960 (Fig. 5G)

Published records. SAN SALVADOR: Guazapa, 25/IV/1960 (Bechyné and Bechyné 1960).

Specimens examined. SAN SALVADOR: Guazapa, 25/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, 57 spec. (RBINS).

30. *Capraita maculata* (Harold, 1876)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Cerro Verde, 16/V/1960, (Bechyné and Bechyné 1963).

31. *Centralaphthona desmodita* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: Capital, 15/VI/1959, 27/VI/1959, 20/VII/1959, 20/VIII1959 (Bechyné and Bechyné 1960).

32. *Centralaphthona deyrollei* (Baly, 1877)

Published records. SAN SALVADOR: El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1960).

33. *Centralaphthona diversa* (Baly, 1877)

Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1960). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). SAN SALVADOR, 11/VI/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 23–24/VI/1959 (Bechyné and Bechyné 1960).

34. *Centralaphthona durri* Bechyné & Bechyné, 1960

Published records. LA LIBERTAD: Hacienda Argentina, 17/VI/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 13/VI/1959 and 19/VI/1959 (Bechyné and Bechyné 1960).

35. *Centralaphthona gaetana* Bechyné & Bechyné, 1960

Published records. SAN SALVADOR: 3/X/1959 (Bechyné and Bechyné 1960).

36. *Centralaphthona lessmanni* Bechyné & Bechyné, 1960

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 19/VI/1959 (Bechyné and Bechyné 1960).

37. *Centralaphthona nemorivaga* Bechyné & Bechyné, 1960

Published records. SAN SALVADOR: Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1960).

38. *Centralaphthona obscuripennis* (Jacoby, 1885)
Published records. SAN SALVADOR: 7/VI/1959 (Bechyné and Bechyné 1960).

39. *Centralaphthona orbitifera* Bechyné & Bechyné, 1960
Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1960).

40. *Centralaphthona peripherica* Bechyné & Bechyné, 1960
Published records. MORAZÁN: Perquín, 22/IV/1959, (Bechyné and Bechyné 1960). SAN SALVADOR: 20/VIII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Trifinio, 11/X/1959 (Bechyné and Bechyné 1960).

41. *Centralaphthona perpetualis* Bechyné & Bechyné, 1960
Published records. LA LIBERTAD: Hacienda Argentina, 17/VI/1959 (Bechyné and Bechyné 1960).

42. *Centralaphthona primordialis* Bechyné & Bechyné, 1960
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

43. *Centralaphthona selecta* Bechyné & Bechyné, 1960
Published records. SANTA ANA: Volcan San Diego, 23–29/VI/1959 (Bechyné and Bechyné 1960).

44. *Centralaphthona xanthochrysa* Bechyné & Bechyné, 1960
Published records. SANTA ANA: Volcan San Diego, 29/VI/1959 (Bechyné and Bechyné 1960).

45. *Chaetocnema acrolabris* Bechyné & Bechyné, 1963
Published records. SANTA ANA: Trifinio, 11/X/1959 and 13/X/1959 (Bechyné and Bechyné 1963).

46. *Chaetocnema arcifera* Bechyné & Bechyné, 1963
Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 11/VI/1959 (Bechyné and Bechyné 1963); Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963).

47. *Chaetocnema bellorhina* Bechyné & Bechyné, 1963
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963).

48. *Chaetocnema confinis* Crotch, 1873
Published records. King and Saunders (1984) mention this species being present in El Salvador, but do not state specific records.

49. *Chaetocnema diegoana* Bechyné & Bechyné, 1963
Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 23–24/VI/1959 (Bechyné and Bechyné 1963).

50. *Chaetocnema fulvicornis* Jacoby, 1885 new record (Fig. 5H)
Specimens examined. SAN SALVADOR: El Boquerón, 9/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 66 spec. (RBINS).

51. ***Chaetocnema guija*** **Bechyné & Bechyné, 1963**
Published records. SANTA ANA: Volcan San Diego, 22/VI/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963).

52. ***Chaetocnema itica*** **Bechyné & Bechyné, 1963**
Published records. SAN SALVADOR: Capital, 6/VIII/1959 (Bechyné and Bechyné 1963).

53. ***Chaetocnema jacinta*** **Bechyné & Bechyné, 1963**
Published records. SAN SALVADOR: Cerro San Jacinto, 17/XI/1959 (Bechyné and Bechyné 1963).

54. ***Chaetocnema lagunaria*** **Bechyné & Bechyné, 1963**
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963).

55. ***Chaetocnema leptocephala*** **Bechyné & Bechyné, 1963**
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963).

56. ***Chaetocnema mexicana*** **Baly, 1877 (Fig. 5I)**
Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Hacienda Chanmico, 3/IX/1959 (Bechyné and Bechyné 1963); Hacienda Argentina, 20/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Guazapa, 11/V/1960 (Bechyné and Bechyné 1963). SANTA ANA: Volcan Diego, 22–23/VI/1959 (Bechyné and Bechyné 1963); Trifinio, 14/X/1959 (Bechyné and Bechyné 1963).
Specimens examined. SAN SALVADOR: Guazapa, 11/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 102 spec. (RBINS).

57. ***Chaetocnema nepotica*** **Bechyné & Bechyné, 1963**
Published records. MORAZÁN: Perquín, 23/IX/1959 (Bechyné and Bechyné 1963).

58. ***Chaetocnema obtusilabris*** **Bechyné & Bechyné, 1963**
Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 22/VI/1959 (Bechyné and Bechyné 1963).

59. ***Chaetocnema perquinensis*** **Bechyné & Bechyné, 1963**
Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 19/VI/1959, 28/VII/1959, 27/IX/1959 (Bechyné and Bechyné 1963); El Boquerón, 20/VIII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Trifinio, 14/X/1959 (Bechyné and Bechyné 1963).

60. ***Chaetocnema sitarina*** **Bechyné & Bechyné, 1963**
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963).

61. ***Chaetocnema vega*** **Bechyné & Bechyné, 1963**
Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 22/VI/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1963).

62. *Chalatenanganya quadrifida* Bechyné & Bechyné, 1963 (Fig. 5J)

Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Comasagua, 1/VII/1959 and 3/VII/1959 (Bechyné and Bechyné 1963); Los Chorros, 29/VI/1959 (Bechyné and Bechyné 1963); Hacienda Argentina, 20/VII/1959 and 18/V/1960 (Bechyné and Bechyné 1963). LA UNIÓN: Cutuco, 2–4/VI/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 12/VI/1959, 16/VI/1959, 30/VI/1959 (Bechyné and Bechyné 1963); El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963); Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 23–24/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. LA LIBERTAD: Hacienda Argentina, 18/V/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 53 spec. (RBINS).

63. *Cyrsylus recticollis* Jacoby, 1891 (Fig. 5K)

Published records. LA LIBERTAD: Comasagua, 1/VII/1959 and 3/VII/1959 (Bechyné and Bechyné 1963). MORAZÁN: Perquín, 25/IX/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 6/VI/1959, 11/VI/1959, 18–19/VI/1959, 21/VII/1959, 27/IX/1959, (Bechyné and Bechyné 1963); Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1963); Guazapa, 10/IV/1960 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1963). USULUTÁN: Berlín, V/1898, A. & F. Solari (Bechyné 1957).

Specimens examined. LA LIBERTAD: Santa Tecla, 28/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, 24 spec. (RBINS); Tamanigue, 4/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 25 spec. (RBINS).

64. *Deuteraltica longicornis* (Jacoby, 1891) (Fig. 5L)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).SAN SALVADOR: Capital, 8/VI/1959 (Bechyné and Bechyné 1960); El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1960).

Specimens examined. SAN SALVADOR: El Boquerón, 9/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 53 spec. (RBINS).

Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

65. *Dinaltica anilina* Bechyné & Bechyné, 1963

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963).

66. *Diphaltica trifiniensis* Bechyné & Bechyné, 1960 (Fig. 5M)

Published records. SANTA ANA: Trifinio, 11/X/1959 and 6–8/III/1960 (Bechyné and Bechyné 1960).

Specimens examined. SANTA ANA: Trifinio, 6/III/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 51 spec. (RBINS).

67. *Diphaulaca aulica aulica* Barber, 1941

Published records. SAN SALVADOR, 5/VII/1951 (Bechyné 1954).

Specimens examined. UNKNOWN PROVINCE: Cristobal, 20/V/1959, Leg. J. Bechyné, Det. J. Bechyné, 13 spec. (RBINS).

Remarks. The RBINS spec. are labeled as *D. panama*, which is currently a junior synonym of *D. aulica aulica* (Olivier, 1808); see Furth and Savini (1996). The record from Bechyné (1954) names this species as *Diphaulaca aulica* (Olivier, 1888).

68. *Diphaulaca aulica cordobae* Barber, 1941 (Fig. 5N)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960). CUSCATLÁN: Hacienda Colima, 22/VII/1959 (Bechyné and Bechyné 1960). LA LIBERTAD: Hacienda Chanmico, 3/IX/1959 and, 20/VI/1960 (Bechyné and Bechyné 1960); Hacienda Argentina, 15/VI/1959, and 20/VII/1959 (Bechyné and Bechyné 1960); Los Chorros, 29/VI/1959 (Bechyné and Bechyné 1960); Comasagua, 1/VII/1959 and 3/VII/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). LA UNIÓN: Cutuco, 2–4/VI/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: Capital, 7/VI/1959, 11/VI/1959, 13/VI/1959, 15/VI/1959, 19/VI/1959, 20/VI/1959, 20/VII/1959, 24/VII/1959, 28/VII/1959, 20/VIII/1959, 24/IV/1960 (Bechyné and Bechyné 1960); Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1960); Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1960); El Boquerón, 10/VI/1959 and 20/VIII/1959 (Bechyné and Bechyné 1960); Guazapa, 10/IX/1959 and 25/IV/1960 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 22–24/VI/1959 (Bechyné and Bechyné 1960).

Specimens examined. LA LIBERTAD: Comasagua, 1/VII/1959, Leg. J. Bechyné, Det. J. Bechyné, 31 spec. (RBINS). LA UNIÓN: Cutuco, 3/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 24 spec. (RBINS).

69. *Diphaulaca salvadorensis* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960).LA LIBERTAD: Los Chorros, 29/VI/1959 (Bechyné and Bechyné 1960). SAN SALVADOR, 7/VI/1959, 15/VI/1959, 12/VII/1959, 21/VII/1959 (Bechyné and Bechyné 1960).

70. *Diphaulaca wagneri* Harold, 1875 (Fig. 5O)

Published records. AHUACHAPÁN, Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960). CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1960).LA LIBERTAD: Comasagua, 1/VII/1959 and 3/VII/1959 (Bechyné and Bechyné 1960).SAN SALVADOR: Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1960); El Boquerón, 10/VI/1959 and 20/VIII/1959 (Bechyné and Bechyné 1960).

Specimens examined. CHALATENANGO: La Palma, 9/VII/1959, Leg. J. Bechyné, Det. J. Bechyné, 11 spec..

71. *Disonycha brevilineata* Jacoby, 1884 (Fig. 5P)

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Hacienda Chanmico, 20/VI/1960 (Bechyné and Bechyné 1963); Comasagua, 3/VII/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 30/VI/1959, 6–7/VII/1959, 28/VII/1959, 23/V/1960 (Bechyné and Bechyné 1963); Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 23–24/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. LA LIBERTAD: Hacienda Chanmico, 20/VI/1960, Leg. J. Bechyné, Det. J. Bechyné, 10 spec. (RBINS); Santa Tecla, 28/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, 25 spec. (RBINS); Tamanigue, 4/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 5 spec. (RBINS). SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 8 spec. (RBINS). SANTA ANA: Volcan San Diego, 23/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 13 spec. (RBINS).

Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

72. *Disonycha brunneofasciata* Jacoby, 1884

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963).

73. *Disonycha collata* (Fabricius, 1801)

Published records. SAN SALVADOR: Capital, 24/IV/1960 (Bechyné and Bechyné 1963).

74. *Disonycha dorsata* Harold, 1880

Published records. CUSCATLÁN: El Rosario (Berry 1957).

75. *Disonycha figurata* Jacoby, 1884 (Fig. 5Q)

Published records. SANTA ANA: Hacienda Los Planes, 1800 m, Metapan Mts., 24–25/VIII/1951 (Bechyné 1954).

Specimens examined. SAN SALVADOR: 19/VI/1960, Leg. J. Bechyné, Det. J. Bechyné, 39 spec. (RBINS).

Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

76. *Disonycha fumata labiata* Jacoby, 1901

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: El Boquerón, 10/VI/1959 and 20/VIII/1959 (Bechyné and Bechyné 1963).

77. *Disonycha glabrata* (Fabricius, 1781)

Published records. LA LIBERTAD: Los Chorros, 26/VI/1959, (Bechyné & Bechyné, 1963); Comasagua, 3/VII/1959, (Bechyné & Bechyné, 1963); Santa Tecla (Berry 1957). SANTA ANA: Volcan San Diego, 22–29/VI/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 12/VI/1959, 15/VI/1959, 27/VI/1959, 30/VI/1959 (Bechyné and Bechyné 1963).

78. *Disonycha guatemalensis* Jacoby, 1884

Published records. CUSCATLÁN: Hacienda Colima, 22/VII/1959 (Bechyné and Bechyné 1963).

79. *Disonycha mexicana* Jacoby, 1884

Published records. CHALATENANGO: La Palma, 7/VII/1959, (Bechyné and Bechyné 1963). LA LIBERTAD: Comasagua, 3/VII/1959 (Bechyné and Bechyné 1963). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1963); Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963).

80. *Disonycha militaris* Jacoby, 1884

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR, 13/VIII/1951 (Bechyné 1954).

Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

81. *Disonycha nigrita* Jacoby, 1884 (Fig. 5R)

Published records. CUSCATLÁN: Hacienda Colima, 22/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Comasagua, 1/VII/1959 and 3/VII/1959 (Bechyné and Bechyné 1963); Hacienda Chanmico, 3/IX/1959 and, 20/VI/1960 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 6/VII/1959 and 28/VII/1959 (Bechyné and Bechyné 1963); Lago Ilopango, 29/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 23/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. LA LIBERTAD: Hacienda Chanmico, 20/VI/1960, Leg. J. Bechyné, Det. J. Bechyné, 8 spec. (RBINS).

Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

82. *Disonycha ovata* Blake, 1931 (Fig. 5S)

Published records. AHUACHAPÁN: Los Ausoles, 26/I/1960 (Bechyné and Bechyné 1963). CHALATENANGO: La Palma, 7–8/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Comasagua, 3/VII/1959 (Bechyné and Bechyné 1963); Santa Tecla (Berry 1957). SAN SALVADOR: Capital, 8/VI/1959, 19/VI/1959, 6/VII/1959, 20/VII/1959, 3/X/1959, 23/V/1960 (Bechyné and Bechyné 1963); El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963); Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963).

Specimens examined. SAN SALVADOR: Cerro San Jacinto, 17/IX/1959, Leg. J. Bechyné, Det. J. Bechyné, 5 spec. (RBINS), 13/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 5 spec. (RBINS), 22/I0/1959, Leg. J. Bechyné, Det. J. Bechyné, 4 spec. (RBINS), 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 5 spec. (RBINS).

83. *Disonycha quinquelineata* (Latreille, 1881)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). CUSCATLÁN: Volcan San Vicente, Finca El Carmen, 1300 m, 11–16/VI/1951 (Bechyné 1954). SAN SALVADOR: 23/VI/1951 (Bechyné 1954).

84. *Disonycha recticollis* (Jacoby, 1884) (Fig. 5T)

Published records. AHUACHAPÁN: Apaneca, 27/I/1959 and 14–17/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963); San Salvador (Berry 1957).

Specimens examined. AHUACHAPÁN: Apaneca, 15/VII/1959, Leg. J. Bechyné, Det. J. Bechyné, 24 spec. (RBINS).

85. *Disonycha scriptipennis* (Jacoby, 1884)

Published records. SAN SALVADOR: Capital, 28/VII/1959 (Bechyné and Bechyné 1963).

86. *Disonycha steinheili* Harold, 1876
Published records. SAN SALVADOR: El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963).

87. *Disonycha trifasciata* Clark, 1865
Published records. LA LIBERTAD: Comasagua, 3/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 12/VI/1959, 20/VII/1959, 28/VII/1959 (Bechyné and Bechyné 1963). Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 26/VI/1959 (Bechyné and Bechyné 1963).

88. *Disonycha vera* Bechyné & Bechyné, 1963
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 8/VI/1959 (Bechyné and Bechyné 1963).

89. *Epitrix anahoria* Bechyné & Bechyné, 1960
Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1960). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1960).

90. *Epitrix angelina* Bechyné & Bechyné, 1960
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

91. *Epitrix apanecana* Bechyné & Bechyné, 1960
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960). LA LIBERTAD: Comasagua, 3/VII/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: El Boquerón 10/VI/1959, (Bechyné and Bechyné 1960).

92. *Epitrix atripes silvicola* Bechyné & Bechyné, 1960
Published records. SANTA ANA: Trifinio, 11–15/X/1959 (Bechyné and Bechyné 1960).

93. *Epitrix auricoma* Bechyné & Bechyné, 1960
Published records. SANTA ANA: Trifinio, 13/X/1959 (Bechyné and Bechyné 1960).

94. *Epitrix dilaticornis* Jacoby, 1885
Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960).

95. *Epitrix hirtula* Harold, 1875 (Fig. 5U)
Published records. SAN SALVADOR: El Boquerón, 9/V/1960 (Bechyné and Bechyné 1960). SANTA ANA: Trifinio, 11–15/X/1959 (Bechyné and Bechyné 1960).
Specimens examined. SAN SALVADOR: El Boquerón, 9/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 53 spec., (RBINS).

96. *Epitrix integralis* Bechyné & Bechyné, 1960
Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

97. *Epitrix lacustris* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: Capital, 20/VIII/1959 (Bechyné and Bechyné 1960); Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1960).

98. *Epitrix nicolina* Bechyné & Bechyné, 1960

Published records. SAN SALVADOR: 13/VI/1959 and 20/VII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 23/VI/1959 (Bechyné and Bechyné 1960).

99. *Epitrix ninfa* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca (Laguna de las ninfas), 14–17/VII/1959 (Bechyné and Bechyné 1960). LA LIBERTAD: Hacienda Argentina, 20/VII/1959 (Bechyné and Bechyné 1960).

100. *Epitrix nycteroptera* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Trifinio, 11/X/1959 (Bechyné and Bechyné 1960).

101. *Epitrix perquinensis* Bechyné & Bechyné, 1960

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960).

102. *Epitrix thoracolysa* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Volcan San Diego, 27/VI/1959 (Bechyné and Bechyné 1960).

103. *Epitrix triangularis* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Trifinio, 11–14/X/1959 (Bechyné and Bechyné 1960).

104. *Epitrix vincentina* Bechyné & Bechyné, 1960

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960).

105. *Genaphthona transversicollis* (Jacoby, 1885) (Fig. 5V)

Published records. AHUACHAPÁN: Apaneca, 14–17/VIII/1959, (Bechyné & Bechyné, 1960). CHALATENANGO: La Palma, 7/VII/1959, (Bechyné & Bechyné, 1960). LA LIBERTAD: Hacienda Argentina, 17/VI/1959, (Bechyné & Bechyné, 1960). Hacienda Argentina, 30/IX/1959, (Bechyné & Bechyné, 1960). Comasagua, 1/VII/1959, (Bechyné & Bechyné, 1960). SAN SALVADOR: Capital, 9/VI/1959, 12/VI/1959, 19/VI/1959, 31/IX/1959 (Bechyné and Bechyné 1960). El Boquerón, 10/VI/1959 and 20/VIII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 29/VI/1959, (Bechyné & Bechyné, 1960). Trifinio, 10/X/1959 (Bechyné & Bechyné, 1960).

Specimens examined. LA LIBERTAD: Hacienda Argentina, 18/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 54 spec. (RBINS).

106. *Genaphthona virkkii* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

107. *Heikertingerella allopantha* Bechyné & Bechyné, 1960

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 12/VI/1959, 20/VIII/1959,

27/IX/1959, 30/IX/1959, (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 23/VI/1959 (Bechyné and Bechyné 1960).

108. *Heikertingerella brachycaula* Bechyné & Bechyné, 1960

Published records. SANTA ANA : Trifinio, 11/X/1959 (Bechyné and Bechyné 1960).

109. *Heikertingerella brachygena* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Trifinio, 14/X/1959 (Bechyné and Bechyné 1960).

110. *Heikertingerella hamagira* Bechyné & Bechyné, 1960

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960).

111. *Heikertingerella irrahetai* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Volcan San Diego, 29/VI/1959 (Bechyné and Bechyné 1960).

112. *Heikertingerella macrogena* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca, 14–17/?/1959 (Bechyné and Bechyné 1960). CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: Capital, 15/VI/1959, 19/VI/1959, 20/VII/1959 (Bechyné and Bechyné 1960); Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1960).

113. *Heikertingerella siliconia* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

114. *Heikertingerella trifiniensis* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Trifinio, 14/X/1959 (Bechyné and Bechyné 1960).

115. *Heikertingerella variabilis* (Jacoby, 1885)

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 6/VII/1959 (Bechyné and Bechyné 1960).

116. *Heikertingerella xanthocarya* Bechyné & Bechyné, 1960

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: Guazapa, 10/IX/1959 (Bechyné and Bechyné 1960). SANTA ANA: Trifinio, 14/X/1959 (Bechyné and Bechyné 1960).

117. *Longitarsus argopterus* Bechyné & Bechyné, 1960

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960).

118. *Longitarsus asteriscus* Bechyné & Bechyné, 1960

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 20/VII/1959 (Bechyné and Bechyné 1960).

119. *Longitarsus berryi* Bechyné & Bechyné, 1960 (Fig. 5W)

Published records. SANTA ANA: Trifinio, 11–14/X/1959 and 8–9/III/1960 (Bechyné and Bechyné 1960).

Specimens examined. SANTA ANA: Trifinio, 8/III/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 52 spec. (RBINS).

120. *Longitarsus columbicus centroamericanus* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). SAN SALVADOR, 19/VI/1959, 20/VII/1959, 27/VII/1959 (Bechyné and Bechyné 1960).

121. *Longitarsus gerodontus* Bechyné & Bechyné, 1960

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960).

122. *Longitarsus orphanus* Bechyné & Bechyné, 1960

Published records. MORAZÁN: Perquín, 25/VIII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Trifinio, 11/X/1959 (Bechyné and Bechyné 1960).

123. *Longitarsus perichromus* Bechyné & Bechyné, 1960

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). MORAZÁN: Perquín, 28/IX/1959 (Bechyné and Bechyné 1960).

124. *Longitarsus scurrilis* Bechyné & Bechyné, 1960

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960).

125. *Longitarsus seraphinus* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

126. *Longitarsus somaticus* Bechyné & Bechyné, 1960

Published records. SAN SALVADOR: 15/VI/1959 and 20/VIII/1959 (Bechyné and Bechyné 1960).

127. *Longitarsus sparnus* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

128. *Longitarsus varicornis* Suffrian, 1868 (Fig. 5X)

Published records. SANTA ANA: Volcan San Diego, 29/VI/1959 (Bechyné and Bechyné 1960).

Specimens examined. LA LIBERTAD: Hacienda San Diego, 28/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, 61 spec. (RBINS).

129. *Luperaltica cayetunya* (Bechyné & Bechyné, 1960)

Published records. SANTA ANA: Volcan San Diego, 22–24/VI/1959 (Bechyné and Bechyné 1960); Trifinio, 10–14/X/1959 (Bechyné and Bechyné 1960).

130. *Luperaltica sylvia* (Bechyné & Bechyné, 1960)

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960). LA LIBERTAD: Hacienda Argentina, 20/VII/1959 (Bechyné and Bechyné 1960); Comasagua, 3/VII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: Capital, 8/VI/1959, 11/VI/1959, 13/VI/1959, 18–19/VI/1959, 6/VII/1959, 28/VII/1959 (Bechyné and Bechyné 1960); El Boquerón, 10/VI/1956 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 29/VI/1959 (Bechyné and Bechyné 1960).

131. *Luperaltica ustulata centralis* (Bechyné, 1955)

Published records. LA LIBERTAD: Comasagua, 3/VII/1959 (Bechyné and Bechyné 1960).

132. *Lupraea acanthonychina* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1960).

133. *Lupraea fulvicollis* Jacoby, 1885 (Fig. 5Y)

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: Capital, 8/VI/1959, 11/VI/1959, 19/VI/1959, 21/VII/1959, 22/IX/1959, 1/I/1960 (Bechyné and Bechyné 1960); Hacienda Argentina, 20/VII/1959 (Bechyné and Bechyné 1960).

Specimens examined. SAN SALVADOR: 2/VII/1960, Leg. J. Bechyné, Det. J. Bechyné, 8 spec. (RBINS).

134. *Lupraea nigricollis* (Jacoby, 1891)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

135. *Lupraea portilloi* Bechyné & Bechyné, 1960 (Fig. 5Z)

Published records. SAN SALVADOR: 7/VI/1959, 8/VI/1959, 12/VI/1959, 13/VI/1959, 19/VI/1959, 21/VII/1959, 31/V/1960, 19/VI/1960 (Bechyné and Bechyné 1960).

Specimens examined. SAN SALVADOR: 31/V/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 34 spec. (RBINS).

136. *Lupraea santaneca* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1960).

137. *Lysathia comasagua* Bechyné & Bechyné, 1960

Published records. LA LIBERTAD: Comasagua, 3/VII/1959 (Bechyné and Bechyné 1960).

138. *Lysathia simplex* (Jacoby, 1891)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 24/VII/1959 and 20/VIII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1960).

139. *Lysathia volcanica* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1960).

140. *Macrohaltica salvadorensis* Bechyné & Bechyné, 1954 (Fig. 5a)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960), 9/VI/1926, Salman, K.A., USNM (Santisteban 2006); Laguna de la Ninfas, 1630 m, 18/VII/1951 (Bechyné 1954). LA LIBERTAD: Comasa-

gua, 1/VII/1959 (Bechyné and Bechyné 1960); Santa Tecla, ll/X/1956, Berry, RA., USNM (Santisteban 2006); Valiano, 5500 ft, Berry, RA., USNM (Santisteban 2006). CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 18/VII/1951 and 7/VIII/1950 (Bechyné 1954); El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1960); San Salvador, NHMW (Santisteban 2006); Volcán San Salvador USNM (Santisteban 2006). SAN VICENTE: Santa Cruz Porrillo, 14/X/1956, Berry, RA., USNM (Santisteban 2006). SANTA ANA: Hacienda Los Planes, 1800 m, Metapan Mts., 24–25/VIII/1951 (Bechyné 1954). Hacienda Los Planes, 2000 m, 30/X/1950 (Bechyné 1954); Trifinio, 12/X/1959 (Bechyné and Bechyné 1960), 12/XII/1956 and 14/VIII/1959 Berry, RA., USNM (Santisteban 2006); Volcán Santa Ana, 30/VIII/1956, Berry, RA.,USNM (Santisteban 2006); Laguna de las Ranas, 1750 m, 27/VI/1951 (Bechyné 1954); Volcan Santa Ana, W slope, 1600–1700 m, near Buenos Aires, 3/VIII/1951 (Bechyné 1954); Cerro Verde, 7/VIII/1964, Vega, J.C., Jr., TAMU (Santisteban 2006), 8/X/1956, Berry, RA, USNM (Santisteban 2006); 101.2 mi down from Cerro Verde summit, 20/VIII/1972, Hevel, GE & S, USNM (Santisteban 2006).

Specimens examined. AHUACHAPÁN: Apaneca, 15/VII/1959, Leg. J. Bechyné, Det. J. Bechyné, 20 spec. (RBINS).

141. *Monomacra dixira* Bechyné & Bechyné, 1963

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Cerro Verde, 16/V/1960 (Bechyné and Bechyné 1963).

142. *Monomacra guazapa* Bechyné & Bechyné, 1963

Published records. SAN SALVADOR: Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963).

143. *Monomacra variabilis* (Jacoby, 1884)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). CHALATENANGO: La Palma, 7–9/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Comasagua, 1/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 8/VI/1959, 13/VI/1959, 19/VI/1959, 20/VII/1959, 1/I/1960 (Bechyné and Bechyné 1963).

144. *Monomacra violacea* (Jacoby, 1884)

Published records. SAN SALVADOR: Capital, 6/VII/1959 (Bechyné and Bechyné 1963).

145. *Neothona quatuordecima* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960).

146. *Neothona quindecima* Bechyné & Bechyné, 1960

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 8/VI/1959, 6/VII/1959, 12–13/VII/1959, 24/VII/1959, 3/X/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1960).

147. *Neothona sedecima* Bechyné & Bechyné, 1960

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960).

148. *Neothona tredecima* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960).

149. *Omophoita affinis* (Jacoby, 1880)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960).

150. *Omophoita clerica* (Erichson, 1848)

Published records. Bechyné and Bechyné (1961) mention the occurrence of *O. clerica* in El Salvador, but do not give specific records.

151. *Omophoita punctulata* (Bechyné & Bechyné, 1963)

Published records. AHUACHAPÁN: Apaneca, 27/I/1960 (Bechyné and Bechyné 1963). CHALATENANGO: La Palma, 7–8/VII/1959 (Bechyné and Bechyné 1963).SAN SALVADOR: Capital, 1/I/1960 (Bechyné and Bechyné 1963); Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 22–29/VI/1959 (Bechyné and Bechyné 1963).

152. *Omophoita quadrinotata costaricensis* (Bechyné, 1955)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Comasagua, 1/VII/1959 (Bechyné and Bechyné 1963).

153. *Omophoita simulans* (Jacoby, 1892)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). CHALATENANGO: La Palma, 8/VII/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 20/VI/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 22/VI/1959 (Bechyné and Bechyné 1963).

154. *Oreinodera aptera* Bechyné & Bechyné, 1963 (Fig. 5b)

Published records. SANTA ANA: Trifinio, 11–13/X/1959 and 6/III/1960 (Bechyné and Bechyné 1963).

Specimens examined. SANTA ANA: Trifinio, 6/III/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 20 spec. (RBINS).

155. *Phrynocepha australis* Gilbert, 2011

Published records. CUSCATLÁN: Rosario (El Rosario), 15/VI/1953, No. 444-273, Col. M.S.V. (Gilbert 2011).

156. *Phrynocepha laevicollis* Jacoby, 1884 (Fig. 5c)

Published records. SAN SALVADOR: El Boquerón, 25/V/1960 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 22–24/VI/1959 (Bechyné and Bechyné 1960).

Specimens examined. SAN SALVADOR: El Boquerón, 25/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 52 spec. (RIBNS).

157. *Physimerus femoralis* Jacoby, 1886 (Fig. 5d)

Published records. SAN SALVADOR: Capital, 9/VI/1959, 12–13/VI/1959, 18/VI/1959, 6/VII/1959, 20/VII/1959 (Bechyné and Bechyné 1963); El Boquerón, 25/V/1960 (Bechyné and Bechyné 1963); Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963).

Specimens examined. SAN SALVADOR: El Boquerón, 25/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 28 spec. (RBINS), 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 17 spec. (RBINS).

Remarks. The examined spec. from the RBINS are labeled as *Thrasygoeus femoralis*, which has been synonymized with *Physimerus*; see Furth and Savini (1996).

158. *Platiprosopus acutangulus* (Chevrolat, 1834) (Fig. 5e)

Published records. LA LIBERTAD: Comasagua, 1/VII/1959 (Bechyné and Bechyné 1963); Santa Tecla (Berry 1957). LA UNIÓN: Cutuco, 2–4/VI/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 30/VI/1959, 28/VII/1959, 19/VI/1960 (Bechyné and Bechyné 1963); Lago Hopango, 24/VII/1959 (Bechyné and Bechyné 1963); Guazapa, 11/V/1960 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 22–29/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. LA UNIÓN: Cutuco, 4/VI/1959, Leg. J. Bechyné, Det. J. Bechyné, 15 spec. (RBINS). UNKNOWN PROVINCE: Cartagena, 19/V/1959, Leg. J. Bechyné, Det. J. Bechyné, 17 spec. (RBINS).

Remarks. The spec. in the RBINS are labeled as *Phyllotrupes acutangulus*, which has been synonymized with *Platiprosopus*; see Furth and Savini (1996).

159. *Plectotetra nigripes* Jacoby, 1884

Published records. SAN SALVADOR: El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963).

160. *Plectrotetra surquia* Bechyné & Bechyné, 1963 (Fig. 5f)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Cerro Verde, 16/V/1960 (Bechyné and Bechyné 1963).

Specimens examined. SANTA ANA: Cerro Verde, 16/V/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 58 spec. (RBINS).

161. *Podaltica harrietta* Bechyné & Bechyné, 1963

Published records. LA LIBERTAD: Hacienda Argentina, 17/VI/1959 (Bechyné and Bechyné 1963).

162. *Resistenciana cardiophora* Bechyné & Bechyné, 1960

Published records. SAN SALVADOR: El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1960).

163. *Resistenciana ornata* (Jacoby, 1884)

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 6/VII/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 23/VI/1959 (Bechyné and Bechyné 1963).

164. *Styrepitrix boqueronica* Bechyné & Bechyné, 1963

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 29/VI/1959 (Bechyné and Bechyné 1963).

165. *Syphrea arevaloi* Bechyné & Bechyné, 1960

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 8/VI/1959, 20/VI/1959, 12/VII/1959, 24/VII/1959, 20/VIII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 29/VI/1959 (Bechyné and Bechyné 1960).

166. *Syphrea arhenia* Bechyné & Bechyné, 1960

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960).

167. *Syphrea balnearia* Bechyné & Bechyné, 1960 (Fig. 5g)

Published records. LA LIBERTAD: Los Chorros, 29/VI/1959 (Bechyné and Bechyné 1960); San Andrés, 15/VI/1959 (Bechyné and Bechyné 1960); Hacienda Chanmico, 20/VI/1960 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: El Boquerón, 16/VI/1959 and 20/VIII/1959 (Bechyné and Bechyné 1960).

Specimens examined. LA LIBERTAD: Hacienda Chanmico, 20/VI/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 3 spec. (RBINS).

168. *Syphrea chrysoderma* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Volcan San Diego, 22–29/VI/1959 (Bechyné and Bechyné 1960).

169. *Syphrea frígida* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960).

170. *Syphrea fulvitarsis* Jacoby, 1891

Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VII/1959 (Bechyné and Bechyné 1960). SAN SALVADOR: 11/VI/1959, 13/VI/1959, 19/VI/1959, 30/VI/1959, 6/VII/1959, 20/VII/1959 (Bechyné and Bechyné 1960). LA LIBERTAD: Comasagua, 1/VII/1959 and 3/VII/1959 (Bechyné and Bechyné 1960).

171. *Syphrea idiolepis* Bechyné & Bechyné, 1960

Published records. LA LIBERTAD: Comasagua, 1/VII/1959 (Bechyné and Bechyné 1960). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1960).

172. *Syphrea palaciosi* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1960).

173. *Syphrea palomita* Bechyné & Bechyné, 1960

Published records. SANTA ANA: Volcan San Diego, 23/VI/1959 (Bechyné and Bechyné 1960).

174. *Syphrea pretiosa* Baly, 1876 (Fig. 5h)

Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1960). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1960).

Specimens examined. CHALATENANGO: La Palma, 9/VII/1959, Leg. J. Bechyné, Det. J. Bechyné, 9 spec. (RBINS).

175. *Syphrea quintanillai* Bechyné & Bechyné, 1960 (Fig. 5i)

Published records. LA LIBERTAD: Los Chorros, 29/VI/1959 (Bechyné and Bechyné 1960); Hacienda Chanmico, 20/VI/1960 (Bechyné and Bechyné 1960). SAN SALVADOR: Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1960); Capital, 30/VI/1959 (Bechyné and Bechyné 1960).

Specimens examined. LA LIBERTAD: Hacienda Chanmico, 20/VI/1960, Leg. J. Bechyné, Det. J. Bechyné, Paratype, 15 spec. (RBINS).

176. *Syphrea rufobadia* Bechyné & Bechyné, 1960

Published records. SAN SALVADOR: Capital, 13/VI/1959 and 30/VI/1959 (Bechyné and Bechyné 1960); Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1960).

177. *Syphrea suntia* Bechyné & Bechyné, 1960

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1960).

178. *Syphrea teapensis* Jacoby, 1891

Published records. SAN SALVADOR: Capital, 19–20/VI/1959 (Bechyné and Bechyné 1960); Guazapa, 10/IX/1959 (Bechyné and Bechyné 1960). SANTA ANA: Volcan San Diego, 23–29/VI/1959 (Bechyné and Bechyné 1960).

179. *Systena candella* Bechyné & Bechyné, 1963

Published records. LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963).

180. *Systena costifera* Bechyné & Bechyné, 1963

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 12/VI/1959 (Bechyné and Bechyné 1963).

181. *Systena elongatula* Csiki, 1939

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963); La Palma, 9/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Santa Tecla, 28/IX/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 20/VIII/1959 (Bechyné and Bechyné 1963). El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1960). SANTA ANA: Trifinio, 17/X/1959 (Bechyné and Bechyné 1963).

182. *Systena guija* Bechyné & Bechyné, 1963

Published records. CHALATENANGO: La Palma, 9/VII/1959 (Bechyné and Bechyné 1963). CUSCATLÁN: Hacienda Colima, 22/VII/1959 (Bechyné and Bechyné 1963). MORAZÁN: Perquín, 27/IX/1959 (Bechyné and Bechyné 1963).

SAN SALVADOR: Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 23–29/VI/1959 (Bechyné and Bechyné 1963).

183. *Systena lepontina* Bechyné & Bechyné, 1963

Published records. CHALATENANGO: La Palma, 8/VII/1959 (Bechyné and Bechyné 1963). LA LIBERTAD: Comasagua, 3/VII/1959 (Bechyné and Bechyné 1963); Los Chorros, 29/VI/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 7–8/VI/1959, 18–19/VI/1959, 30/VI/1959, 3/V/1960, 15/V/1960, 18/V/1960 (Bechyné and Bechyné 1963).

184. *Systena melanosterna* Bechyné & Bechyné, 1963

Published records. CHALATENANGO: La Palma, 7/VII/1959 and 9/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Cerro San Jacinto, 17/IX/1959 (Bechyné and Bechyné 1963).

185. *Systena pectoralis* Clark, 1865

Published records. CHALATENANGO: La Palma, 7/VII/1959 (Bechyné and Bechyné 1963).

186. *Systena sulcatula* Bechyné & Bechyné, 1963

Published records. LA LIBERTAD: Comasagua, 1/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963).

187. *Systena thoracica* Jacoby, 1884

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963); Los Ausoles, 26/I/1960 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 24/VI/1959 (Bechyné and Bechyné 1963).

188. *Systena variabilis* Jacoby, 1884 (Fig. 5j)

Published records. CHALATENANGO: La Palma, 7–8/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 23/V/1960 (Bechyné and Bechyné 1963); El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963). SANTA ANA: Volcan San Diego, 27/VI/1959 (Bechyné and Bechyné 1963).

Specimens examined. SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 30 spec. (RBINS).

Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

189. *Temnocrepis trifiniensis* Bechyné & Bechyné, 1963

Published records. SANTA ANA: Trifinio,11–13/V/1959 (Bechyné and Bechyné 1963).

190. *Trichaltica variabilis* Jacoby, 1885

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 19/VI/1960 (Bechyné and Bechyné 1963).

191. *Trifiniocola freundi* Bechyné & Bechyné, 1963

Published records. SANTA ANA: Trifinio, 10–14/X/1959 and 8–9/III/1960 (Bechyné and Bechyné 1963).

192. *Walterianella biarcuata* (Chevrolat, 1834)

Published records. MORAZÁN: Perquín, 22/IX/1959 (Bechyné and Bechyné 1963).

193. *Walterianella exocosta* Bechyné & Bechyné, 1963

Published records. SAN SALVADOR: Captital, 1/I/1960, 24/IV/1960, 15/V/1960, 23/V/1960 (Bechyné and Bechyné 1963); Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963).

194. *Walterianella hypocrita* (Jacoby, 1886)

Published records. CUSCATLÁN: El Rosario (Berry 1957).

195. *Walterianella inscripta* (Jacoby, 1886)

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

196. *Walterianella sublineata* (Jacoby, 1886)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: El Boquerón, 10/VI/1959 (Bechyné and Bechyné 1963). USULUTÁN: Alegría, 27/II/1960 (Bechyné and Bechyné 1963).

197. *Walterianella tenuicincta* (Jacoby, 1886)

Published records. AHUACHAPÁN: Apaneca, 14–17/VII/1959, (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 8/IX/1959 (Bechyné and Bechyné 1963).

198. *Walterianella venustula* (Schaufuss, 1874) (Fig. 4k)

Published records. LA LIBERTAD: Hacienda Argentina, 15/VI/1959 and 17/VI/1959 (Bechyné and Bechyné 1963). LA PAZ: Volcan San Vicente, Finca La Paz, 1–10/VIII/1959 (Bechyné and Bechyné 1963). SAN SALVADOR: Capital, 11/VI/1959, 19/VI/1959, 30/VI/1959, 28/VII/1959, 24/IV/1960, 29/IV/1960 (Bechyné and Bechyné 1963); Lago Ilopango, 24/VII/1959 (Bechyné and Bechyné 1963); Guazapa, 10/IX/1959 (Bechyné and Bechyné 1963). SANTA ANA: Trifinio, 14/X/1959 (Bechyné and Bechyné 1963).

Specimens examined. SAN SALVADOR: 24/IV/1960, Leg. J. Bechyné, Det. J. Bechyné, 63 spec. (RBINS).

Subfamily Galerucinae excl. Alticini

1. *Acalymma semicoerulea* (Jacoby, 1887) new record (Fig. 6A)

Specimens examined. SAN SALVADOR: Cerro San Jacinto, 17/IX/1959, Leg. J. Bechyné, Det. J. Bechyné, 11 spec. (RBINS), 2/VII/1960, Leg. J. Bechyné, Det. J. Bechyné, 10 spec. (RBINS).

2. *Acalymma trivittata* (Mannerheim, 1843)

Published records. LA LIBERTAD: Santa Tecla (Berry 1957).

3. *Amphelasma nigrolineatum* (Jacoby, 1878) new record (Fig. 6B)

Specimens examined. SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 7 spec. (RBINS). SANTA ANA: Trifinio, 6/III/1960, Leg. J. Bechyné, Det. J. Bechyné, 12 spec. (RBINS).

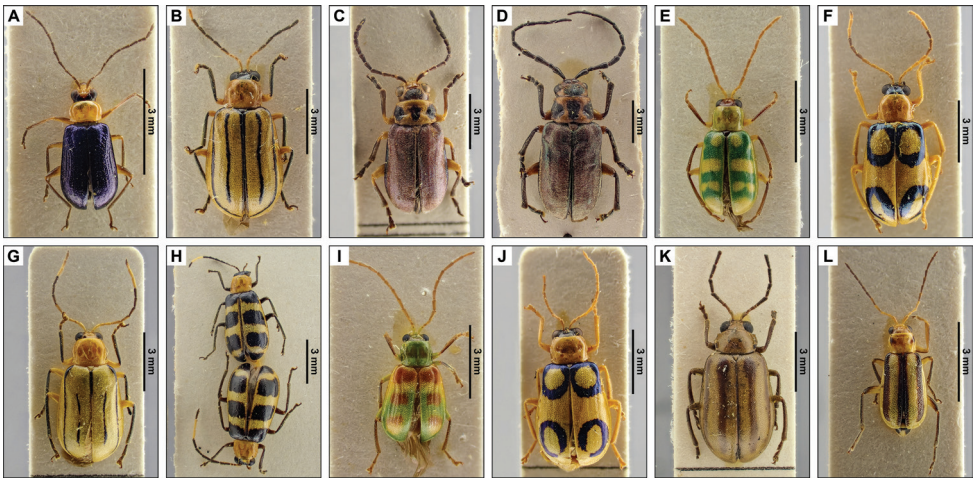

Figure 6. Dorsal pictures of the species of Galerucinae excluding Alticini from El Salvador currently present in the collections of the RBINS. **A** *Acalymma semicaerulea* **B** *Amphelasma nigrolineatum* **C** *Coraia clarki* **D** *C. maculicollis* **E** *Diabrotica balteata* **F** *D. circulata* **G** *D. curvilineata* **H** *D. pulchra* **I** *D. viridula* **J** *Neobrotica ornata* **K** *Pyesia detrita laevicollis*. High resolution images can be found at http://collections.naturalsciences.be/ssh-entomology.

4. *Cerotoma atrofasciata* Jacoby, 1879

Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

5. *Cerotoma ruficornis* (Olivier, 1791)

Published records. LA UNIÓN: La Unión (Jacoby 1880 – 1892).

6. *Coraia clarki* Jacoby, 1886 new record (Fig. 6C)

Specimens examined. LA LIBERTAD: Hacienda Argentina, 18/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 93 spec. (RBINS).

7. *Coraia maculicollis* Clark, 1865 new record (Fig. 6D)

Specimens examined. LA LIBERTAD: Hacienda Argentina, 18/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 4 spec., (RBINS).

8. *Diabrotica amecameca* Krysan & Smith, 1987

Remarks. Derunkov et al. (2013) list El Salvador under known distribution of *D. amecameca*, but do not give specific localities.

9. *Diabrotica balteata* LeConte, 1865 (Fig. 6E)

Published records. LA LIBERTAD: Santa Tecla (Berry 1957); San Andrés (Berry 1957). SAN SALVADOR: Aeropuerto de Ilopango (Berry 1957). SAN VICENTE: Santa Cruz Porrillo (Berry 1957).

Specimens examined. LA LIBERTAD: Zapotitan, 22/I/1960, Leg. J. Bechyné, Det. J. Bechyné, 11 spec. (RBINS). SAN SALVADOR: 1/I/1960, Leg. J. Bechyné, Det. J. Bechyné, 4 spec. (RBINS). UNKNOWN PROVINCE: Asino, Lago Ilopango, 24/VII/1959, Leg. J. Bechyné, Det. J. Bechyné, 8 spec. (RBINS).

10. *Diabrotica circulata* Harold, 1875 new record (Fig. 6F)

Specimens examined. SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 8 spec. (RBINS). SANTA ANA: Trifinio, 6/III/1960, Leg. J. Bechyné, Det. J. Bechyné, 13 spec. (RBINS).

11. *Diabrotica curvilineata* Jacoby, 1887 new record (Fig. 6G)

Specimens examined. SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 10 spec. (RBINS).

12. *Diabrotica litterata* (Sahlberg, 1823)

Published records. CUSCATLÁN: El Rosario (Berry 1957).

13. *Diabrotica porracea* (Harold, 1875)

Remarks. Derunkov et al. (2013) list El Salvador under known distribution of *D. porracea*, but do not give specific localities. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

14. *Diabrotica pulchra* (Sahlberg, 1823) (Fig. 6H)

Published records. CUSCATLÁN: El Rosario (Berry 1957).

Specimens examined. USULUTÁN: Alegría, 22/II/1960, Leg. J. Bechyné, Det. J. Bechyné, 26 spec. (RBINS).

Remarks. Derunkov et al. (2013) list El Salvador under known distribution of *D. pulchra*, but do not give specific localities. The record listed in Berry and Salazar (1957) is listed as *D. albosignata* which is a synonym of *D. pulchra*.

15. *Diabrotica salvadorensis* Derunkov et al., 2015

Published records. CUSCATLÁN: Rosario Cuscatlan, No 444–506B, 17/III/1955, Col. M.S.V. (Derunkov et al. 2015); Rosario Cuscatlan, No 444–218A, 20/XI/1953, Col. M.S. (Derunkov et al. 2015). LA UNIÓN: No 444–766A, 14/V/1954, Col. C.A.B. (Derunkov et al. 2015). SAN SALVADOR: No 714.210, 14/III/1957, Col. PAB, det. R.F. Smith 1963, *Diabrotica* n. sp. near *D. pulchra* (Sahlberg) (Derunkov et al. 2015). SANTA ANA: 6.0 km W. Hwy CA1 above Lago de Coatepeque, 853 mts., 1/VI/1973 (Derunkov et al. 2015). USULUTÁN: 4 miN Santiago de Maria, 29/VIII/1972, G.F.and S. Hevel. (Derunkov et al. 2015).

16. *Diabrotica spec.iosa spec.iosa* (Germar, 1824)

Remarks. Derunkov et al. (2013) list El Salvador under known distribution of *D. pulchra*, but do not give specific localities.

17. *Diabrotica viridula* (Fabricius, 1801) (Fig. 6I)

Published records. USULUTÁN: Berlín (Bechyné and Bechyné 1962).

Specimens examined. SAN SALVADOR: Cerro San Jacinto, 17/IX/1959, Leg. J. Bechyné, Det. J. Bechyné, 5 spec. (RBINS). USULUTÁN: Alegría, 22/II/1960, Leg. J. Bechyné, Det. J. Bechyné, 23 spec. (RBINS).

Remarks. Derunkov et al. (2013) also lists El Salvador under known distribution of *D. viridula*, but does not give specific localities. Bechyné and Bechyné (1969a) state that *D. viridula* is common in San Salvador. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records as well.

18. ***Exora detrita*** **(Fabricius, 1801)**
Published records. CUSCATLÁN: Finca El Carmen, 1300 m, Volcan San Vicente, 11–16/VI/1951 (Bechyné 1954).

19. ***Exora encaustica*** **Harold, 1875**
Published records. LA LIBERTAD: Santa Tecla (Berry 1957).
Remarks. Bechyné and Bechyné (1962) list El Salvador under species distribution, but do not give specific localities.

20. ***Exora obsoleta*** **(Fabricius, 1801)**
Published records. SAN SALVADOR: 22/VII/1951 (Bechyné 1954).
Remarks. Bechyné and Bechyné (1962) also list El Salvador under species distribution, but do not give specific localities. This thus might be a reference to the locality listed above.

21. ***Gynandrobrotica nigrofasciata*** **(Jacoby, 1878)**
Published records. CUSCATLÁN: El Rosario (Berry 1957). LA LIBERTAD: Los Chorros (Berry 1957).

22. ***Gynandrobrotica variabilis*** **(Jacoby, 1887)**
Published records. CUSCATLÁN: El Rosario (Berry 1957).

23. ***Monocesta ducalis*** **Clark, 1865**
Published records. SAN SALVADOR: 8/VII/1951 (Bechyné 1954).
Remarks. Berry (1959) also mentions this species as being present in El Salvador, but does not give specific records.

24. ***Monocesta jansoni*** **Jacoby, 1886**
Published records. LA LIBERTAD: Santa Tecla (Berry 1957).

25. ***Monolepta bipartita*** **Jacoby, 1888**
Published records. CUSCATLÁN: El Rosario (Berry 1957).

26. ***Neobrotica ornata*** **Jacoby, 1887 new record (Fig. 6J)**
Specimens examined. SAN SALVADOR: 23/V/1960, Leg. J. Bechyné, Det. J. Bechyné, 5 spec. (RBINS).

27. ***Pyesia detrita laevicollis*** **(Jacoby, 1887) (Fig. 6K)**
Specimens examined. SAN SALVADOR: 1/I/1960, Leg. J. Bechyné, Det. J. Bechyné, 1 spec. (RBINS), 1/I/1960, Leg. J. Bechyné, Det. J. Bechyné, 25 spec. (RBINS).
Remarks. Bechyné and Bechyné (1962) list El Salvador under species distribution, but do not give specific localities.

28. ***Trichobrotica sexplagiata*** **(Jacoby, 1878) new record**
Specimens examined. SAN SALVADOR: 27/II/1959, Leg. J. Bechyné, Det. J. Bechyné, 20 spec. (RBINS).

Subfamily Lamprosomatinae

1. ***Lamprosoma splendidum*** **Lacordaire, 1848**
Remarks. Berry (1959) mentions this species as being present in El Salvador, but does not give specific records.

Discussion

The digitization of the Bechyné collection in the RBINS revealed that there were a total of 2797 individual specimens sorted into 89 species. Among these were ten apparent nomina nuda which could not be found in any publication from J. Bechyné: *Antitypona* sp. (Manuscript species – Eumolpinae), *Brachypnoea* sp. *1* (Manuscript species – Eumolpinae), *Brachypnoea* sp. *2* (Manuscript species – Eumolpinae), *Hylax* sp. (Manuscript species – Eumolpinae), *Percolaspis* sp. *1* (Manuscript species – Eumolpinae), *Percolaspis* sp. *2* (Manuscript species – Eumolpinae), *Phanaeta* sp. (Manuscript species – Eumolpinae), *Chaetocnema* sp. (Manuscript species – Galerucinae, Alticini), *Phyllotreta* sp. (Manuscript species – Galerucinae, Alticini) and *Walterianella* sp. (Manuscript species – Galerucinae, Alticini). These are species which Bechyné either forgot to formerly describe, did not have time to describe, or the validity of which he questioned. Regarding the former list, the authors believe that *Walterianella* sp. (Manuscript species) could just be a variation of *W. venustula* (Schaufuss) which it closely resembles, but this should be confirmed by comparison with the type material and especially the structure of the genital structures. These and all of the other "paratypes" of the *nomina nuda* should be examined and revised in the future by experts.

The study of relevant literature led to a checklist of 385 species known from El Salvador. A total of 43 species from these 309 were also present in the collections in the RBINS. Material from the Bechyné collection added a further 33 species (excluding the ten *nomina nuda*) to the literature-based checklist of chrysomelids. This leads to a preliminary checklist of a total of 420 species of Chrysomelidae currently known for El Salvador (see table 1 for a full overview). Incorporated were also records from Berry and Salazar (1957) and Berry (1959), references which were frequently overlooked in the past.

Surprisingly few records of the subfamilies Criocerinae, Lamprosomatinae, and Cryptocephalinae could be found, despite their high prevalence in Central America. This is most likely due to the fact that most chrysomelid research in El Salvador has been done by J. and B. Bechyné, who focused mostly on Eumolpinae and Galerucinae including Alticini (of which respectively 16, 9, and 2 species could be newly added to the El Salvador checklist by Bechyné's collection in the RBINS). The latter are relatively well represented in comparison with the currently known number of species from neighbouring countries (see Furth and Savini (1996)), mainly because of the extensive work of the Bechynés.

We noted a strong bias towards collection efforts in the departments San Salvador (182 species), La Libertad (105 species) and Santa Ana (114 species), and to a lesser extent in the districts Ahuachapán (54 species), La Paz (50 species) and Chalatenango (46 species). No records from San Miguel or Cabañas could be found. Future surveys in the country should thus also be focussed on the two latter departments.

Conclusions

Our study reveals a preliminary total of 420 species of Chrysomelidae known to El Salvador. However, this number should be approached with caution, since the taxonomy of some subfamilies is not yet fully clear (e.g., Eumolpinae), some subfamilies seem to lack sampling effort in the country (e.g., Cryptocephalinae, Criocerinae and Lamprosomatinae), and in general there has been little study on the fauna of El Salvador, possibly due to its political instability and safety issues for field research (Bourgois 2001). Nonetheless, we believe that this checklist, although almost certainly incomplete, will serve as a baseline for further study in the area.

Acknowledgements

We greatly acknowledge Pol Limbourg for logistic support, and we thank the Scientific Service Heritage (Patrick Semal) of the Royal Belgian Institute for Natural Sciences, Brussels for the support hosting the pictures online through the Virtual Collections platform. We would also like to thank Florence Trus for providing the full drawer pictures which were added to the online database. Anouk D'Hont is thanked for her help in constructing the data tables and for final adjustments. Shawn Clark (BYU), Jesús Gómez-Zurita (CSIC), and David Furth (SMNH) are greatly acknowledged for a first stage review of the paper, for adding species records and for sharing their expertise. Jan Mertens is sincerely thanked for delivering the species plates for the manuscript. We would like to thank Alanna Rebelo for a grammar and spelling check of this manuscript. We also acknowledge the two reviewers. This work was partly financed by the Ministry of Culture of the Czech Republic (DKRVO 2019-2023/5.I.a, National Museum, 00023272).

References

Baly JS, Champion GC (1885–1894) Insecta. Coleoptera. Phytophaga (part). Cassididae & Hispidae. In: Godman FD, Salvin O (Eds) Biologia Centrali Americana, Volume VI, Part 2. Taylor & Francis, London, 249 pp. [+ 13 pls]

Bechyné J (1954) Chrysomeloidea aus El Salvador (Ins. Col. Phytophaga). Senckenbergiana 34: 293–296.

Bechyné J (1955) Reise des Herrn G. Frey in Südamerika: Eumolpidae (Col. Phytophaga). Entomologische Arbeiten aus der Museum G. Frey 6: 569–657.

Bechyné J, Bechyné B (1960) Beiträge zur Kenntnis der Salvadorenischen Chrysomeloidea (Col. Phytophaga). Pesquisas, Seria Zoologia 6: 5–73.

Bechyné J, Bechyné B (1962) Liste der bisher in Rio Grande do Sul gefundenen Galeruciden. Pesquisas, Seria Zoologia 15: 5–68.

Bechyné J, Bechyné B (1963) Beitrag zur Kenntnis der Salvadorenischen Chrysomeloidea (Col. Phytophaga) 1. Fortsetzung. Iheringia, Seria Zoologia 31: 1–79.

Bechyné J, Bechyné B (1965a) Notes sur les Chrysomelidae s. str. de Venezuela et des pays limitrophes (Col. Phytophaga). Revista de la Facultad de Agronomia de Maracay 3: 44–110. https://doi.org/10.3406/linly.1958.7945

Bechyné J, Bechyné B (1965b) Notes sur les Chrysomeloidea captures par le Dr. W. A. Egler au Rio Jari (Bresil: Para/Amapa) en 1961 (Col. Phytophaga). Boletim do Museu Paraense Emilio Goeldi 53: 1–44. https://doi.org/10.1590/s1981-81222009000100018

Bechyné J, Bechyné B (1969a) Die Galerucidengattungen in Südbrasilien. Iheringia, Zoologia 36: 3–110.

Bechyné J, Bechyné B (1969b) Notas sobre Phytophaga americanos (Coleoptera). Revista de la Facultad de Agronomia de Maracay 5: 5–64.

Berry PA, Salazar M (1957) Lista de Insectos Clasificados de El Salvador. Boletin Técnico de Ministerio de Ministerio de Agricultura y Ganadería (El Salvador) 21: 5–134.

Berry PA (1959) Segunda Lista de Insectos Clasificados de El Salvador. Boletin Técnico de Ministerio de Ministerio de Agricultura y Ganadería (El Salvador) 25: 1–89.

Blackwelder RE (1946) Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 4. Bulletin of the United States National Museum 185: 551–925. https://doi.org/10.5479/si.03629236.185.4

Boheman CH (1850) Monographia Cassididarum. Tomus Primus. Officina Norstedtiana, Holmiae, 452 pp. [+ 4 pls]0 https://doi.org/10.5962/bhl.title.8973

Boheman CH (1854) Monographia Cassididarum. Tomus Secundus. Officina Norstedtiana, Holmiae, 506 pp. [+ 2 pls]

Boheman CH (1855) Monographia Cassididarum. Tomus Tertius. Officina Norstedtiana, Holmiae, 543 pp. [+ 1 pl]

Boheman CH (1862) Monographia Cassididarum. Tomus Quartus. (Supplementum). Officina Norstedtiana, Holmiae, 504 pp.

Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CH, Newton AF, Reid CA, Schmitt M, Slipiński SA, Smith AB (2011) Family-group names in Coleoptera (Insecta). ZooKeys 88: 1–972. https://doi.org/10.3897/zookeys.88.807

Bourgois P (2001) The power of violence in war and peace: Post-Cold War lessons from El Salvador. Ethnography 2: 5–34. https://doi.org/10.1177/14661380122230803

Bridwell JC (1929) A preliminary generic arrangement of the palm bruchids and allies with description of new species. Proceedings of the Entomological Society of Washington 31(8): 141–160.

Clavareau H (1913) Chrysomelidae: 1. Sagrinae, 2. Donaciinae, 3. Orsodacninae, 4. Criocerinae. In: Junk W, Schenkling S (Ed.) Coleopterorum Catalogus, Pars 51. Berlin, 103 pp.

Clavareau H (1913) Chrysomelidae: 5. Megascelinae, 6. Megalopodinae, 7. Clytrinae, 8. Cryptocephalinae, 9. Chlamydinae, 10. Lamprosominae. In: Junk W, Schenkling S (Ed.) Coleopterorum Catalogus, Pars 53. Berlin, 278 pp.

Clavareau H (1914) Chrysomelidae: 11. Eumolpinae. In: Junk W, Schenkling S (Ed.) Coleopterorum Catalogus, Pars 59. Berlin, 215 pp.

Derunkov A, Konstantinov A, Tishechkin A, Hartje L, Redford AJ (2013) Diabrotica ID: Identification of *Diabrotica* species (Coleoptera: Chrysomelidae) from North and Central America. https://doi.org/10.12976/jib/2015.3.2 [Accessed 03/01/2018]

Drew LW (2011) Are We Losing the Science of Taxonomy? As need grows, numbers and training are failing to keep up. BioScience 61: 942–946. https://doi.org/10.1525/bio.2011.61.12.4

Flowers WR (1996) La subfamilia Eumolpinae (Coleoptera: Chrysomelidae) en América Central Revista de Biología Tropical, Special volume no. 2: 1–59.

Furth DG (1998) Revision of the New World *Blepharida* (Coleoptera: Chrysomelidae: Alticinae). Memoirs of the Entomological Society of Washington 21: 1–109.

Furth DG (2006) The current status of knowledge of the Alticinae of Mexico (Coleoptera: Chrysomelidae). Bonner zoologische Beiträge 54(4): 209–237.

Furth DG (2013) Diversity of Alticinae in Oaxaca, Mexico: A preliminary study (Coleoptera, Chrysomelidae). ZooKeys 332: 1–32. https://doi.org/10.3897/zookeys.332.4790

Furth DG, Savini V (1996) Checklist of the Alticinae of Central America, including Mexico (Coleoptera: Chrysomelidae). Insecta Mundi 10(1–4): 45–68.

Gilbert AJ (2011) A review and clarification of the alticine genera *Hemiphrynus* Horn 1889 and *Phrynocepha* Baly 1861 (Coleoptera: Chrysomelidae: Galerucinae: Alticini). Insecta Mundi 200: 1–57.

Gómez-Zurita J (2015) Systematic revision of the genus Calligrapha Chevrolat (Coleoptera: Chrysomelidae, Chrysomelinae) in Central America: The group of *Calligrapha argus*. Stål. Zootaxa 3922: 1–71. https://doi.org/10.11646/zootaxa.3922.1.1

Gómez-Zurita J (2016) Systematic revision of *Calligrapha* Chevrolat (Coleoptera: Chrysomelidae) with pale spots on dark elytra and description of two new species. Zootaxa 4072: 61–89. https://doi.org/10.11646/zootaxa.4072.1.3

Gómez-Zurita J (2018) Systematic revision of Central American *Calligrapha* Chevrolat of the subgenus *Erythrographa* subgen. nov. (Coleoptera: Chrysomelidae, Chrysomelinae). Zootaxa 4531 (1): 001–058. https://doi.org/10.11646/zootaxa.4531.1.1

Heikertinger F, Csiki C (1939) Chrysomelidae: Halticinae I. In: Junk W, Schenkling S (Ed.) Coleopterorum Catalogus, Pars 59. 's-Gravenhage, 336 pp.

Heikertinger F, Csiki C (1940) Chrysomelidae: Halticinae II. In: Junk W, Schenkling S (Ed.) Coleopterorum Catalogus, Pars 59. 's-Gravenhage, 337–635.

Jacoby M (1880–1892) Insecta. Coleoptera. Phytophaga (part). In: Godman FD, Salvin O (Eds) Biologia Centrali Americana, Volume VI, Part 1. Taylor & Francis, London, 625 pp.

Jacoby M (1888–1892) Insecta. Coleoptera. Phytophaga (part). In: Godman FD, Salvin O (Eds) Biologia Centrali Americana, Volume VI, Part 1, Supplement. Taylor & Francis, London, 374 pp. [+ 43 pls]

Johnson CD (1979) New host records for *Acanthoscelides* (Coleoptera: Bruchidae). Pan-Pacific Entomologist 55(1): 61–71.

Johnson CD (1990) Systematics of the Seed Beetle Genus *Acanthoscelides* (Bruchidae) of Northern South America. Transactions of the American Entomological Society 116(2): 297–618.

Johnson CD, Kingsolver JM (1973) A revision of the genus *Sennius* of North and Central America (Coleoptera: Bruchidae). Technical Bulletin of the United States Department of Agriculture 1462: 1–135.

Johnson CD, Kingsolver JM (1976) Systematics of *Stator* of North and Central America (Coleoptera: Bruchidae). Technical Bulletin of the United States Department of Agriculture 1537: 1–101.

King ABS, Saunders JL (1984) The invertebrate pests of annual food crops in Central America. Overseas Develoment Administration, London, 166 pp.

Kingsolver JM (1969) A new species of Neotropical seed weevil affecting pigeon peas, with notes on two closely related species (Coleoptera: Bruchidae: Bruchinae). Proceedings of the Entomological Society of Washington 71(1): 50–55.

Kingsolver JM (1970a) Synopsis of the genus *Pygiopachymerus* Pic, with notes on its relationships to other genera (Coleoptera: Bruchidae: Bruchinae). Proceedings of the Entomological Society of Washington 72(1): 37–42.

Kingsolver JM (1970b) The identity of a bruchid feeding in seeds of *Cassida grandis* L. (Leguminosae) (Coleoptera: Bruchidae: Bruchinae). Proceedings of the Entomological Society of Washington 72(2): 203–206.

Kingsolver JM (1980) Eighteen new species of Bruchidae, principally from Costa Rica, with host records and distributional notes (Insecta: Coleoptera). Proceedings of the Biological Society of Washington 93(1): 229–283.

Kingsolver JM (1988): Biosystematics of the genus *Merobruchus* of continental North America and the West Indies (Coleoptera: Bruchidae). Technical Bulletin of the United States Department of Agriculture 1744: 1–63.

Kingsolver JM (1990) Biosystematics of the genus *Zabrotes* of America North of Mexico (Coleoptera: Bruchidae). Transactions of the American Entomological Society 116(1): 135–174.

Kingsolver JM, Johnson CD (1978) Systematics of the genus *Mimosestes* (Coleoptera: Bruchidae). Technical Bulletin of the United States Department of Agriculture 1590: 1–106.

Kingsolver JM, Whitehead DR (1974a) Classification and comparative biology of the seed beetle genus *Caryedes* Hummel (Coleoptera: Bruchidae). Transactions of the American Entomological Society 100(4): 341–436.

Kingsolver JM, Whitehead DR (1974b) Biosystematics of Central American species of *Ctenocolum*, a new genus of seed beetles (Coleoptera: Bruchidae). Proceedings of the Biological Society of Washington 87(27): 283–312.

Kingsolver JM, Whitehead DR (1976) The North and Central American species of *Meibomeus* (Coleoptera: Bruchidae: Bruchinae). Technical Bulletin of the United States Department of Agriculture 1523: 1–54.

Kleinschmidt B, Kölsch G (2011) Adopting Bacteria in Order to Adapt to Water—How Reed Beetles Colonized the Wetlands (Coleoptera, Chrysomelidae, Donaciinae). Insects 2: 540–554. https://doi.org/10.3390/insects2040540

Livia C (2006) Diversity and economic importance of the leaf beetles (Coleoptera, Chrysomelidae) in the republic of Moldova. Bulletin of University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca Agriculture 62: 184–187. https://doi.org/10.15835/buasvmcn-agr:1594

Maes JM, Staines CL (1991) Catalogo de los Chrysomelidae (Coleoptera) de Nicaragua. Revista Nicaraguense de Entomologia 18: 1–53.

Mancía JE, Cortéz MR (1975) Lista de insectos clasificados encontrados en el cultivo del fríjol, *Phaseolus vulgaris* L. Siades 4(4): 120–136.

Merckx J, Van Roie M, Gómez-Zurita J, Dekoninck W (2018) From theory to practice: a photographic inventory of museum collections to optimize collection management. Biodiversity Informatics 13: 38–48. https://doi.org/10.17161/bi.v13i0.7036

Mertens J, Van Roie M, Merckx J, Dekoninck W (2017) The use of low cost compact cameras with focus stacking functionality in entomological digitization projects. ZooKeys 712: 141–154. https://doi.org/10.3897/zookeys.712.20505

Monrós F (1960) Los generos de Chrysomelidae (Coleoptera). Opera Lilloana 3: 1–337. [+ 3 pls]

Pic M (1913) Bruchidae. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus, Pars 55. Berlin, 74 pp.

Rodrigues JMS, Mermudes JRM (2016) New records and distributional notes for the Neotropical genus *Isotes* Weise, 1922 (Insecta, Coleoptera, Chrysomelidae, Galerucinae). Check-List 12(1): 1848. https://doi.org/10.15560/12.1.1848

Romero J, Johnson CD, Kingsolver JM (1996) Revision of the genus *Amblycerus* of the United States and Mexico (Coleoptera: Bruchidae: Amblycerinae). Technical Bulletin of the United States Department of Agriculture 1845: 1–166.

Scherer G (1962) Bestimmungsschlüssel der neotropischen Alticinen-Genera. Entomologische Arbeiten aus dem Museum G. Frey 13(2): 497–607.

Seeno TA, Scherer G, Corwin KS (1976) Jan Bechyné. Necrology and bibliography. Entomologische Arbeiten aus dem Museum G. Frey 27: 1–69.

Spaeth F (1914) Chrysomelidae: 16. Cassidinae. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus, Pars 62. Berlin, 182 pp.

Teran AL, Kingsolver JM (1977) Revisión del género *Megacerus* (Coleoptera: Bruchidae). Opera Lilloana 25: 1–287.

Uhmann E (1960) Über Hispinae (Ins. Col.) des Senckenberg-Museums. II. Teil. 204. Beitrag zur Kenntnis der Hispinae (Chrysomelidae). Senckenbergiana Biologica 41(5–6): 303–305. https://doi.org/10.1080/00222935708655969

Uhmann E (1961) Hispinae aus Verschiedenen Erdteilen. 202. Beitrag zur Kenntnis der Hispinae (Coleoptera, Chrysomelidae). Pesquisas, Seria Zoologia 10: 1–63. https://doi.org/10.1080/00222935708655969

Vencl F, Levy A, Geeta R, Keller G, Windsor D (2004) Observations on the natural history, systematics and phylogeny of the Criocerinae of Costa Rica and Panama. In: Jolivet P, Santiago-Blay JA, Schmitt M (Eds) New developments in the biology of Chrysomelidae. SPB Academic Publishing, The Hague, 423–454.

Weise J (1911) Chrysomelidae: Hispinae. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus, Pars 35., Berlin, 94 pp. https://doi.org/10.4039/ent43107-3

Weise J (1916) Chrysomelidae: 12 Chrysomelinae. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus, Pars 68., Berlin, 255 pp.

Weise J (1924) Chrysomelidae: 13 Galerucinae. In: Junk W, Schenkling S (Eds) Coleopterorum Catalogus, Pars 78., Berlin, 225 pp.

Whitehead DR, Kingsolver JM (1975a) Megasenius, a new genus for *Acanthoscelides muricatus* (Sharp) (Coleoptera: Bruchidae), a seed predator of *Cassida grandis* L. (Caesalpiniaceae) in Central America. Proceedings of the Entomological Society of Washington 77(4): 460–465.

Whitehead DR, Kingsolver JM (1975b) Biosystematics of the North and Central American species of *Gibbobruchus* (Coleoptera: Bruchidae: Bruchinae). Transactions of the American Entomological Society 101(2): 167–225.

Windsor DM, Dury GJ, Frieiro-Costa FA, Lanckowsky S, Pasteels JM (2013) Subsocial Neotropical Doryphorini (Chrysomelidae, Chrysomelinae): new observations on behavior, host plants and systematics. ZooKeys 332: 71–93. https://doi.org/10.3897/zookeys.332.5199

Supplementary material 1

Table S1. Species and genera count per subfamily for El Salvador and each of El Salvador's departments

Authors: Martijn Van Roie, Frederik De Wint, Ayse Güngor, Charlotte Huyghe, Wouter Dekoninck, Lukáš Sekerka

Data type: species data

Explanation note: Species given for department "Unknown" are species counts for which there were country records only.

Link: https://doi.org/10.3897/zookeys.856.32017.suppl1

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Accepted Papers: Same as above, but ''In press'' appears instead the page numbers.

Electronic Journal Articles: Mallet J, Willmott K (2002) Taxonomy: renaissance or Tower of Babel? Trends in Ecology and Evolution 18 (2): 57-59. doi: 10.1016/S0169-5347(02)00061-7.

Paper within conference proceedings: Orr AG (2006) Odonata in Bornean tropical rain forest formations: Diversity, endemicity and applications for conservation management. In Cordero Rivera A (Ed) Forest and Dragonflies. Fourth WDA International Symposium of Odonatology, Pontevedra (Spain), July 2005. Pensoft Publishers, Sofia-Moscow, 51-78.

Book chapters: Mayr E (2000) The biological species concept. In: Wheeler QD, Meier R (Eds) Species Concepts and Phylogenetic Theory: A Debate. Columbia University Press, New York, 17-29.

Books: Goix N, Klimaszewski J (2007) Catalogue of Aleocharine Rove Beetles of Canada and Alaska. Pensoft Publishers, Sofia-Moscow, 166 pp.

Book with institutional author: International Commission on Zoological Nomenclature (1999) International code of zoological nomenclature. Fourth Edition. London: The International Trust for Zoological Nomenclature.

PhD thesis: Dalebout ML (2002) Species identity, genetic diversity and molecular systematic relationships among the Ziphiidae (beaked whales). PhD thesis, Auckland, New Zealand: University of Auckland.

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Volume 8 of *Research on Chrysomelidae* (RoC8) presents again examples of the attractiveness and the diversity of Chrysomelidae (sensu lato) as subjects of scientific research. The seven papers included here cover taxonomy, ecology, faunistics as well as phylogenetics. Four of these papers (Geiser, Gikonyo et al., Salvi et al., Wendorff and Schmitt) are extended versions of talks presented to the Third European Symposium on the Chrysomelidae, held on 5 July, 2018, in Naples, Italy within the frame of the 11th European Congress of Entomology.

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