Research on Chrysomelidae 3

Edited by Pierre Jolivet, Jorge Santiago-Blay & Michael Schmitt



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RESEARCH ARTICLE



Body size of Chrysomelidae (Coleoptera, Insecta) in areas with different levels of conservation in South Brazil

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Abstract

Body size is correlated with many species traits such as morphology, physiology, life history and abundance as well; it is one of the most discussed topics in macroecological studies. The aim of this paper was to analyze the body size distribution of Chrysomelidae, caught with Malaise traps during two years in four areas with different levels of conservation in the Araucaria Forest, Paraná, Brazil, determining if body size is a good predictor of abundance, and if body size could be used to indicate environmental quality. Body size was considered the total length of the specimen from the anterior region of head to the apex of abdomen/elytron. Measurements were taken for up to ten specimens of each species for each area and for all specimens of those species represented by fewer than ten individuals. The highest abundance and richness of Chrysomelidae were obtained in the lowest body size classes. This herbivorous group showed a trend toward a decrease in body size with increasing abundance, but body size was not a good predictor of its abundance. There was a trend toward a decrease in body size from the less to the most conserved areas; however, the definition of a pattern in successional areas not seems to be entirely clear.

Keywords

Abundance, biodiversity, body length, macroecology, Neotropical region, richness

Introduction

Potential ecological relationships between body size and structure of animal communities have been one of main focuses in ecological studies (Braun et al. 2004). Body size is correlated with many morphologic, physiologic, behavioral and ecologic traits, such as dispersal capacity, metabolic and digestive efficiency, reproduction rate, and generation time, as well as species abundance (Siemann et al. 1999, Brown 2003, White et al. 2007). In macroecological studies, the relationship between body size and abundance is one of the most studied topics, and reports mainly concern vertebrates (Krüger and McGavin 2000).

The relationship between body size and abundance is an essential link between individual and population level traits and the structure and dynamics of ecological communities (Woodward et al. 2005). According to White et al. (2007), there are four distinct, but interrelated, relationships between body size and abundance, which are generated by different combinations of processes and routinely confused. The relationships are: i) local size-density relationships which reflect processes influencing resource allocation among species; ii) individual size distributions which result from processes governing the distribution of individual sizes; iii) cross-community scaling relationships which are generated by general constraints, such as resource limitation, on the community as a whole; and iv) global size-density relationships which reflect ecological and evolutionary processes on large spatio-temporal scales.

Controversy has arisen regarding how body size and abundance are related, and concerning the ecological and evolutionary implications of these relationships. In this way, an early step in elucidating the factors that structure animal assemblages may be to understand how the body sizes of their component species are distributed (Blackburn and Gaston 1994, 1997). Hutchinson and MacArthur (1959) suggested that within a taxon there are more species of intermediate size than very large or very small ones, because they would be relatively more specialized and would utilize their resources better, since they would have a larger number of niches available. Following the energetic equivalence rule (EER) proposed by Damuth (1981, 1991) the amount of energy that a population of a species uses in the community is independent of its body size. Damuth (1981) found a slope of -0.75 for the relationship between population density and body size, and since body size scales with metabolic rate to the 0.75 power, the population density would compensate for the body size.

Another aspect about the body size that has been widely discussed is its use in the assessment of environmental quality. In general, richness and abundance are the variables most used to measure not only the diversity but also to assess the environmental quality of areas in different successional stages. Studies have shown that habitat type, management, succession and degradation level have a great influence on the body size of insects increasing or decreasing species body size along succession (Blake et al. 1994, Siemann et al. 1999, Brändle et al. 2000, Braun et al. 2004, Gaucherel et al. 2007). According to Siemann et al. (1999), this variation in size could be related to species efficiency-specialization to different habitats where large and efficient spe-

cies would be benefited in initial stages of succession while the small and specialized ones would be benefited in final stages of succession. In this way changes in species body size over the succession could be another important indicator of environmental changes and quality.

Phytophages represent about 45% of all described insect species (Frenzel and Brändle 2001). Among them, Chrysomelidae is one of the most diverse groups with more than 36,000 described species (Bouchard et al. 2009) and its body size has never been the focus of study. Thus, the first aim of this paper was to analyze the relationship between body size and abundance and between body size and richness in a Chrysomelidae community, to determine how these variables are related. Two applicable relationships proposed by White et al. (2007) were tested: the individual size distributions, regardless of the identity of species, and the local size-density relationships, since crosscommunity scaling relationships are more often used in studies of sessile communities and global size-density relationships needs, where data are generally on a wide geographic scale and from a larger number of groups. The second aim was to determine if there are differences in body size between areas at different levels of succession and if so how great.

Material and methods

The data came from the project Vila Velha (PROVIVE), which was developed in the Parque Estadual of Vila Velha (25°13'5.0"S; 50°2'26.9"W). This park is a conservation unit in the state of Paraná with an area of 3.122 ha, mainly covered by natural fields (steppe, grassy-woody) (Ziller 2000) associated with the Araucaria Forest at different levels of anthropic interference. The park is located in Ponta Grossa at an altitude of 880 m.

Of the five areas sampled during the PROVIVE project, the material from four areas was used in this study, one edge area and three with increasing conservation level. A brief description of these areas is as follows. More information could be found in Ganho and Marinoni (2003): a) Border, an edge area of transition between field and Araucaria Forest in intermediate stage of succession, maintained by mowing; b) Phase 1, area of about 15 ha, previously used for seasonal crops such as corn and beans, in natural regeneration since 1984. It was at an initial to intermediate level of succession; c) Phase 2, primary forest, changed by the removal of various plant species such as *Araucaria angustifolia* (Bert.) O. Ktze (Araucariaceae), *Ocotea porosa* (Nees & C. Mart.) Barroso (Lauraceae) and some Myrtaceae. Plant succession is at an intermediate to advanced stage; d) Phase 3, primary forest changed by selective cutting. It is the best preserved of all, showing a very similar flora to Phase 2 area, but with higher density of araucarias, epiphytes and lianas.

In each sampling area, a Malaise trap was placed and the caught material removed weekly from September 1999 to August 2001. As Malaise is a selective trap collecting flying insects, in this study Chrysomelidae assemblage is composed by species that fly from ground to 2m high and, because of the sampling effort, it was assumed that this trap sampled all species that occur in each sampling area.

The Coleoptera were mounted, labeled, and the chrysomelids identified to the lowest taxonomic level possible. The material is deposited in the Coleção de Entomologia Pe. J. S. Moure, Departamento de Zoologia, Universidade Federal do Paraná (DZUP).

All Chrysomelidae species sampled in each area were measured. The size was considered the total length of the specimen from the anterior region of the head (excluding antennae) to the apex of the abdomen or elytra (Morse et al. 1988). Therefore, the head (superior margin of eyes to the apical margin of labrum, in frontal view), the pronotum (in central region) and elytra/abdomen (sutural margin, in dorsal view) were measured separately. These three measures were summed, resulting in the length of each specimen. Measurements were made with a Wild-M5 stereomicroscope using an adjusted ocular micrometer.

According to Morse et al. (1988), the length of most beetle species varies little; the difference between the largest and the smallest specimen does not exceed 10%. Thus, following the methodology proposed by these authors, measurements were taken from a maximum of ten specimens of each species for each area or all specimens for those species represented by fewer than ten individuals.

The length values were grouped in arbitrarily established size classes (class 1: 1.0 to 2.99 mm, class 2: 3.0 to 4.99 mm, class 3: 5.0 to 6.99 mm and so on) and adjusted on a logarithmic scale, following Morse et al. (1988). This was done for all Chrysomelidae data and for each examined area separately. To determine the distribution of abundance of individuals, the identity of species was not taken into account, so one species may have individuals of more than one size class. The average size of each species was used to treat the distribution of species.

Correlation analyses were performed between size classes and abundance and, between size classes and richness.

A regression analysis was performed to determine the influence of body size on the abundance of Chrysomelidae. The dependent variable was the abundance of each species and the independent variable its average size. The slope obtained was visually compared to that proposed by Damuth (1981). This analysis was performed for each area separately and subsequent for all areas combined.

To examine if there were differences in body size of the Chrysomelidae community in each area, ANOVA (5% significance) was performed based on all measured values. This analysis was also used only for those species recorded in all areas. In addition, ANOVA was used to determine if the size of species varied in areas with different succession levels. For this, species that occurred at least in two areas and that had at least six specimens sampled were selected. Each species was analyzed separately, totaling 15 species that met these prerequisites.

The normality of data was previously tested by the Kolmogorov-Smirnov test and data were log transformed. The analyses were performed using the STATISTICA program 8.0 (StatSoft. Inc. 2007).

Results

During the two years 2,650 specimens of 254 Chrysomelidae species were sampled and, 1,217 specimens were measured (Table 1).

The Chrysomelidae size class histogram showed a tendency toward a decrease in abundance with increase in body size (Fig. 1), where the pattern of Chrysomelidae distribution of abundance was a polygonal type with a tail to the right. The same pattern was observed for the richness distribution. The highest frequencies of both abundances and richness were in class 2, with chrysomelids measuring from 3.0 to 4.99 mm.

The distribution of abundance in each area also showed a tendency toward a decrease in abundance with increasing body size, with the highest frequencies in class 2. However, in Phase 1 a higher abundance of Chrysomelidae was in class 3, from 5.0 to 6.99 mm and, in Phase 3, unlike the other, showed the highest abundance in class 6, from 11.0 to 12.99 mm (Fig. 1).

Regarding species richness, this followed the distribution pattern of abundance, with the largest number of species occurring in smaller size classes. Border area had the same number of species in classes 2 and 3. Notice that class 6 to all Chrysomelidae and class 5 of Phase 2 (Fig. 1) there are no values of richness. It happened because there are no species that fit in these size classes, i.e., the average species size fitted in other size class. However, as the specimens have a range of size, some values fitted in different size classes.

Table 1. Body size (mm) (mean \pm SD) of the Chrysomelidae community, trapped with Malaise in four areas with different conservation levels, in Ponta Grossa, Paraná, Brazil. Values followed by the same letter do not differ significantly (P < 0.05). (n) number of specimens measured, (S) richness and (N) abundance.

	Body size	n	S	N
Border	6.23 ± 2.42a	391	134	484
Phase 1	5.63 ± 2.86b	267	78	742
Phase 2	4.75 ± 1.94c	317	88	1010
Phase 3	5.38 ± 2.50b	242	70	414
Total	-	1,217	254	2,650

Table 2. Correlation between size class and abundance (N) and between size class and richness (S) of Chrysomelidae trapped with Malaise in four areas with different conservation levels, in Ponta Grossa, Paraná, Brazil. Values followed by * showed significant correlation (P < 0.05).

Areas	N	S
Border	-0,47	-0,49
Phase 1	-0,70*	-0,67*
Phase 2	-0,67*	-0,64*
Phase 3	-0,53	-0,52



Figure I. Size Frequency of specimens (N) and species (S) of Chrysomelidae total and in each area, with different conservation levels, in Ponta Grossa, Paraná, Brazil.

In all areas, there was a negative correlation between body size and abundance and between body size and richness, but only in Phase 1 and Phase 2 these correlations were significant (Table 2).

Studying the influence of body size on abundance, it was possible to show that the model was significant (b = -0.46, r = 0.16, P < 0.01) only when data from all areas are included (Fig. 2). Even so, body size explained only 2.56% of Chrysomelidae abundance. Moreover, the slope was -0.46.

The Border area, which is an ecotone between a field and Araucaria Forest and which is influenced more by human activity, was the place where the species reached the highest body sizes, 6.23 mm on average, and it was the only area with size class 7, with chrysomelids measuring from 13.0 to 15.0 mm. In this same area was sampled the higher number of species. In contrast, Phase 2 which is an intermediate stage of conservation, showed the smallest size, 4.75 mm on average, with the maximum size occurring in class 5 and, where was registered the higher abundance. The lowest richness as well as the lowest abundance was in Phase 3 (Table 1).

There was a significant decrease ($F_{3, 1213} = 28.7$, P < 0.05) in chrysomelid body size in areas less conserved, Border and Phase 1 to Phase 2 (Table 1). However, in Phase 3, which is the best conserved area, size was significantly greater than that of Phase 2 and



Figure 2. Relation between body size (log) and abundance (log) of Chrysomelidae, trapped with Malaise in four areas with different conservation levels in Ponta Grossa, Paraná, Brazil (closed circles = observed data, line = linear model adjusted).

did not differ significantly from that of Phase 1. There was no difference in body size of the Chrysomelidae community when only the species common to all areas were analyzed.

While determining if species common to at least two of the studied areas showed variation in body size, it was found that of the 15 species examined, eight had an increase in body size from an area less conserved to one better conserved, but for only two of them, *Trichaltica elegantula* Baly, 1876 and Hispini sp.9, this increase was significant. Four species showed a decrease in body size from an area less conserved to a better conserved, but this difference was not significant in any of the cases. *Acanthonycha costatipennis* Jacoby, 1905 and Eumolpinae sp.1 showed a significant increase in body size from the edge area to an area of intermediate level of conservation, followed by a significant decrease in size in the most conserved area, Phase 3, regarding to compared to the edge (Table 3).

Discussion

The highest richness and abundance was recorded in smaller size classes, with the highest number of species and specimens ranging from 3.0 to 4.99 mm in length

	Border	Phase 1	Phase 2	Phase 3
Acanthonycha chloroptera		5,19±0,80a	5,65±0,46a	
Acanthonycha costatipennis	4,96±0,72 a		5,84±0,28 b	5,07±0,59 b
Dinaltica gigia		5,15±0,31a	4,89±0,29a	
Heikertingerella ferruginea	3,74±0,36a		3,68±0,21a	3,78±0,16a
Monoplatus ocularis	3,92±0,25a	3,82±0,22a	3,72±0,14a	
Neothona prima		2,20±0,13a	2,33±0,11a	
Omophoita octoguttata	10,11±0,77a	10,41±0,62a		
Phyllotrupes violaceomaculatus		7,80±0,52a	7,96±0,64a	
Trichaltica elegantula			2,40±0,18 a	2,65±0,15 b
Hispini sp.7		6,90±0,44a		7,04±0,41a
Hispini sp.9	5,97±0,30 a	6,25±0,19 b		
Eumolpinae sp.1	5,00±0,40 a	5,80±0,31 b		5,47±0,25 b
Eumolpinae sp.6	4,88±0,33a		5,05±0,40a	
Eumolpinae sp.14	8,29±0,52a			8,22±0,53a
Eumolpinae sp.15		7,73±0,49a	7,63±0,55a	7,33±0,58a

Table 3. Body size (mm) (mean \pm SD) of Chrysomelidae species common to at least two of the four areas with different levels of conservation and which have at least six specimens collected in Ponta Grossa, Paraná, Brazil. Averages followed by the same letter in line do not differ significantly (P < 0.05).

(Fig. 1). This value was very near to that found for Chrysomelidae fauna by different authors using different collecting methods and in different habitats. Basset and Samuelson (1996), in studying the arboreal community in Papua New Guinea using several collecting methods, recorded the majority of species ranging from 2.8 to 3.3 mm. Pinheiro et al. (1998) who carried out their study in the Brazilian savanna using nets, found the highest frequencies at the same body size class interval as observed here. These authors also recorded a negative correlation between body size and abundance and between body size and richness for Coleoptera, similar to the results obtained here for the Chrysomelidae.

According to Blackburn and Gaston (1997) there are three different species distribution patterns, linear negative, non-linear negative and polygonal. The Chrysomelidae exhibited a polygonal distribution of abundance. Similar results were obtained by Krüger and McGavin (2000), analyzing a local community of insects collected from *Acacia*. They also found a negative relationship between size and abundance as in this paper.

In fact, according to Blackburn and Gaston (1997), distribution patterns of abundance are strongly influenced by the scale of study. Polygonal relations are usually obtained when unique areas are sampled trying to estimate the abundance of all species of a taxon that occur there, usually using a single and consistent method. In contrast, a negative linear relationship is obtained from compiled data from a great variety of published papers, which generally deal with one or a few species that occupy large geographic areas and whose density is estimated using a wide range of methods. These patterns, according to the authors, are not mutually exclusive and may indicate a clear relationship between abundance and body size at different spatial scales.

According to Morse et al. (1985), an inverse relationship between size and abundance, especially for herbivorous insects, would be linked to the fractal structure of plants. The fractal theory predicts that area or length becomes disproportionately large with a decrease in the unit of measure. Thus, the consequence of the fractal nature of the environment for the species body size distribution occurs due the existence of a more usable space for smaller animals, so species of smaller size should be more represented in nature, as they could subdivide the habitat and coexist in greater numbers.

However, the fractal structure of environment cannot alone explain the shape of the size distribution, since the smallest size class is not always the most numerous, but this may be a mechanism that accounts for the shape of distribution (Kozlowski and Gawelczyk 2002). Although, the distribution pattern of Chrysomelidae abundance is in accordance with those found for other local insect communities, their explanation in terms of ecological processes involved is complex and cannot be summarized in a simple cause and effect relationship.

Size is a poor predictor of Chrysomelidae abundance. Other variables such as availability and quality of food resources, presence of predators/parasitoids, intra- and interspecific competition and climatic factors should have a greater influence on the abundance of this group.

Several authors have found that body size is a poor predictor of population densities on a local scale (Morse et al. 1988, Blackburn et al. 1993, Blackburn and Gaston 1997, White et al. 2007). Furthermore, data obtained here did not support the EER, indicating that larger species use the most available resources. Brown and Maurer (1986) also showed that the greater abundance of small-sized species is not sufficient to compensate for their lower rates of energy use per individual.

It is important to stress that EER as calculated here is not recommended by White et al. (2007). According to these authors, data obtained on a local scale represent a small portion of data needed to test EER, and consequently, only the lower limits of species distribution would be included in the calculations. EER provides global patterns, which are not strictly ecological, but has an important evolutionary component. On the other hand, processes at local scales are more influenced by the partition of resources within the community (Allen et al. 2006, White et al. 2007).

Many features of organisms are correlated with animal body size, but especially life history, ability of dispersion and efficiency, and feeding specialization are linked to succession, so that changes in body size during plant succession may be an important indicator of environmental changes (Siemann et al. 1999). The Chrysomelidae exhibited a trend toward a decrease in body size from Border area, Phase 1, Phase 2 (Table 2); however, the pattern still seems to be unclear, due to the increase in the most conserved area, Phase 3. Besides, in the richest area (Border) the spectrum of body size measurements is very high comparing to the lowest rich area (Phase 3). Consequently, there is a high probability of increasing the body size in the richest area since increasing the spectrum usually increases the average. On the other hand, in Phase 2 where the second richest value was found, the spectrum has no influence since it was found the smallest size. Furthermore, we could not methodologically limit the number of species to eliminate some possible spectrum effect because it would change the composition of the local fauna and, although it seems to have a gradient relating the number of species with body size, the higher number of species alone does not explain the size found.

In the literature, there are different results, some of them show the same tendency as in this study, such as those of Siemann et al. (1999) and Braun et al. (2004). Siemann et al. (1999) studied the dynamic of arthropods in areas with different succession stages and found that, among the analyzed guilds (parasites, predators, herbivores and detritivores), only the herbivores had a significant decrease in body size with increase in age of area. According to these authors, the explanation for decreasing body size of herbivores is the tradeoff between efficiency and specialization.

There are environmental changes that could favor different species at different stages of succession. In early succession, plants have few defenses, high growth rates and low proportion of carbon and nitrogen in their tissues (Tilman 1990). As large animals have greater digestive and absorption efficiency due to larger guts, they may be able to overcome the small herbivores. In later succession, plants are less palatable, have lower growth rates and higher proportion of carbon and nitrogen in their tissues. Since smaller species may perceive greater levels of heterogeneity, small herbivores may be ablest to specialize on certain plants or parts of plants such as growing leaf tips or phloem cells, which have better nutritional quality, prevailing over the large and efficient herbivores (Siemann et al. 1999).

Braun et al. (2004) also found larger body sizes in less conserved areas, even working on a Coleoptera predator group. They studied the Carabidae fauna of areas in regeneration after the closure of a fertilizer factory. According to them, before the factory closure, there were few herbivorous species, which were large and generalists, and thus prey for large Carabidae. With the factory closure, there was a reduction of local pollution, allowing a recovery of vegetation. Thus, with the increase in primary production, there was an increase in immigration of herbivores expanding the food availability for carabids. Furthermore, the authors suggested that habitat structure must have also influenced the Carabidae body size, interfering with foraging efficiency. Early stages of succession and more open areas favored large species which are more efficient at traveling over larger distances in a patchy environment compared to later stages with denser vegetation, where smaller and more agile species may be favored.

Other studies, however, have found opposite results. Blake et al. (1994) reported that both habitat type and management level had a significant influence on Carabidae body size, and concluded that disturbed habitats support a smaller body size fauna. Brändle et al. (2000) observed that in succession areas, there was dominance of macropterous Carabidae species of small size in early stages and brachypterous species of larger size in later stages of succession. Gaucherel et al. (2007), also studying Carabidae, recorded that the intensification of agriculture has a greater impact on large-sized species, so that small species predominate in more disturbed areas.

As these results conflict with those obtained here and mainly do not deal with herbivorous insects but predators, it appears that the efficiency-specialization hypothesis proposed by Siemann et al. (1999) seems to be the most consistent explanation for the decrease in body size of Chrysomelidae in the most conserved areas, at least for this data set.

Among the 15 species examined, only four showed significant variations in body size among the different areas, and consequently, it was not possible to establish a consistent pattern between body size and level of conservation when species were analyzed separately. However, interesting information was obtained. Unlike what was determined for the entire Chrysomelidae community where the edge area had the highest average body size, for three species that showed significant differences in body size among areas (*A. costatipennis*, Hispini sp.9 and Eumolpinae sp.1), the Border was the area where these species had the smallest body size. These species did not contribute to explaining the Chrysomelidae pattern, where it was not possible to know which species most influenced the pattern.

Conclusions

The Chrysomelidae, an essentially phytophagous group, showed a trend toward a decrease in abundance with increasing body size, in a negative polygonal relation. Furthermore, a greater number of chrysomelid species collected by Malaise traps occurred in smaller body size classes; species ranged from 1.0 to 15.0 mm in length and most of them measured between 3.0 and 4.99 mm.

The results presented here seem to follow the pattern found for several animal groups, where body size is a poor predictor of abundance. Other factors such as availability of food, metabolic efficiency, host plant specificity and/or parts of the plant, predation, parasitism and climate should act more on the Chrysomelidae community determining the size of species populations.

It was demonstrated that there is a change in body size of Chrysomelidae communities in areas with different levels of conservation. There was a trend toward a decrease in body size of the less to the most conserved areas. The Border area, which is an ecotone and more influenced by human activity, had larger chrysomelid body sizes. However, the definition of a pattern in successional areas did not seem to be entirely clear, due to significant increase in body size of a later succession stage in relation to one of the others areas in an intermediate successional stage. Nevertheless, the results suggest that degrading the habitats, the small and specialized species would be at risk of disappearing.

The fractal characteristic of the environments, mainly the plants, may be one of the operating mechanisms in Chrysomelidae community. It would explain the higher richness and abundance of this group into smaller size classes, but it should not be considered the only explanation. Other factors, such as those already mentioned could be interfering in the ecological processes that generate such patterns.

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References

- Allen CR, Garmestani AS, Havlicek TD, Marquet PA, Peterson GD, Restrepo C (2006) Patterns in body mass distributions: shifting among alternative hypotesis. Ecology Letters 9: 630–643. doi: 10.1111/j.1461-0248.2006.00902.x
- Basset Y, Samuelson GA (1996) Ecological characteristics of an arboreal community of Chrysomelidae in Papua New Guinea. In: Jolivet P, Cox ML (Eds) Chrysomelidae Biology: Ecological Studies. Academic Publishing, Amsterdam, The Netherlands, 243–262.
- Blackburn TM, Brown VK, Doube BM, Greenwood JJD, Lawton JH, Stork NE (1993) The relationship between abundance and body size in natural animal assemblages. Journal of Animal Ecology 62: 519–528. doi: 10.2307/5201
- Blackburn TM, Gaston KJ (1994) Animal body size distributions: patterns, mechanisms and implications. Trends in Ecology and Evolution 9: 471–474. doi: 10.1016/0169-5347(94)90311-5
- Blackburn TM, Gaston KJ (1997) A critical assessment of the form of the interspecific relationship between abundance and body size in animals. Journal of Animal Ecology 66: 233–249. doi: 10.2307/6025
- Blake S, Foster GN, Eyre MD, Luff ML (1994) Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. Pedobiologia 38: 502–512.
- Bouchard P, Grebennikov VV, Smith ABT, Douglas H (2009) Biodiversity of Coleoptera. In: Foottit RG, Adler PH (Eds) Insect biodiversity: science and society. Blackwell Publishing, Oxford, 265–301. doi: 10.1002/9781444308211.ch11
- Brändle M, Durka W, Altmoos M (2000) Diversity of surface dwelling beetle assemblages in open-cast lignite mines in Central Germany. Biodiversity and Conservation 9: 1297–1311.
- Braun SD, Jones TH, Perner J (2004) Shifting average body size during regeneration after pollution - a case of study using ground beetle assemblages. Ecological Entomology 29: 543–554. doi: 10.1111/j.0307-6946.2004.00643.x
- Brown JH (2003) Macroecología. Fondo de Cultura Económica, Mexico, 397p.
- Brown JM, Maurer B (1986) Body size, ecological dominance and Cope's rule. Nature 324: 248–250. doi: 10.1038/324248a0
- Damuth J (1981) Population density and body size in mammals. Nature 290: 699–700. doi: 10.1038/290699a0
- Damuth J (1991) Of size and abundance. Nature 351: 268-269. doi: 10.1038/351268a0

- Frenzel M, Brändle R (2001) Hosts as habitats: faunal similarity of phytophagous insects between host plants. Ecological Entomology 26: 594–601. doi: 10.1046/j.1365--2311.2001.00355.x
- Ganho NG, Marinoni RC (2003) Fauna de Coleoptera no Parque Estadual de Vila Velha, Ponta Grossa, Paraná, Brasil. Abundância e riqueza das famílias capturadas através de armadilhas armadilha Malaise. Revista Brasileira de Zoologia 20: 727–736. doi: 10.1590/ S0101-81752003000400028
- Gaucherel C, Burel F, Baudry J (2007) Multiscale and surface pattern analysis of the effect of landscape pattern on carabid beetles distribution. Ecological Indicators 7: 598–609. doi: 10.1016/j.ecolind.2006.07.002
- Hutchinson GE, MacArthur RH (1959) A theoretical ecological model of size distributions among species of animals. The American Naturalist 93: 117–125. doi: 10.1086/282063
- Kozlowski J, Gawelczyk AT (2002) Why are species' body size distributions usually skewed to the right? Functional Ecology 16: 419–432. doi: 10.1046/j.1365-2435.2002.00646.x
- Krüger O, McGavin GC (2000) Macroecology of local insect communities. Acta Oecologica 21: 21–28. doi: 10.1016/S1146-609X(00)00112-0
- Linzmeier AM, Ribeiro-Costa CS (2009) Spatio-temporal dynamics of Alticini (Coleoptera, Chrysomelidae) in a fragment of Araucaria Forest in the state of Parana, Brazil. Revista Brasileira de Entomologia 53: 294–299. doi: 10.1590/S0085-56262009000200013
- Linzmeier AM, Ribeiro-Costa CS, Marinoni RC (2006) Fauna de Alticini (Newman) (Coleoptera, Chrysomelidae, Galerucinae) em diferentes estágios sucessionais na Floresta com Araucária do Paraná, Brasil: diversidade e estimativa de riqueza de espécies. Revista Brasileira de Entomologia 50: 101–109. doi: 10.1590/S0085-56262006000100015
- Morse DR, Lawton JH, Dodson MM, Williamson MH (1985) Fractal dimension of vegetation and the distribution of arthropod body lengths. Nature 314: 731–733. doi: 10.1038/314731a0
- Morse DR, Stork NE, Lawton JH (1988) Species number, species abundance and body length relationships of arboreal beetles in Bornean lowland rain forest trees. Ecological Entomology 13: 25–37. doi: 10.1111/j.1365-2311.1988.tb00330.x
- Pinheiro F, Diniz IR, Kitayama K (1998) Comunidade local de Coleoptera em Cerrado: Diversidade de espécies e tamanho do corpo. Anais da Sociedade Entomológica do Brasil 27: 543–550. doi: 10.1590/S0301-80591998000400006
- Siemann E, Haarstad J, Tilman D (1999) Dynamics of plant and arthropod diversity during old field succession. Ecography 22: 406–414. doi: 10.1111/j.1600-0587.1999.tb00577.x
- StatSoft, Inc. (2007) STATISTICA (data analysis software system), version 8.0. www.statsoft. com
- Tilman D (1990) Constraints and tradeoffs: toward a predictive theory of competition and succession. Oikos 58: 3–15. doi: 10.2307/3565355
- White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ (2007) Relationships between body size and abundance in ecology. Trends in Ecology and Evolution 22: 323–330. doi: 10.1016/j. tree.2007.03.007

- Woodward G, Ebenman B, Emmerson M, Montoyas JM, Olesens JM, Valido A, Warren PH (2005) Body size in ecological networks. Trends in Ecology and Evolution 20: 402–409. doi: 10.1016/j.tree.2005.04.005
- Ziller SR (2000) A Estepe Gramíneo-Lenhosa no Segundo Planalto do Paraná: Diagnóstico Ambiental com Enfoque à Contaminação Biológica. PhD thesis, Paraná, Brazil, Universidade Federal do Paraná.

RESEARCH ARTICLE



Altitudinal and temporal distribution of *Plagiometriona* Spaeth, 1899 (Coleoptera, Chrysomelidae, Cassidinae) in a tropical forest in southeast Brazil

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Abstract

Species richness and abundance of seven *Plagiometriona* species on their host plants were studied along a single trail in the mountainous Serra dos Órgãos National Park in the State of Rio de Janeiro, Brazil. Six sites were chosen along an altitudinal gradient ranging from 1300 m to 2050 m, where all Solanaceae host plants were inspected in search of adults every two months from June 2006 to June 2007. Species richness did not vary clearly with altitude, but abundance increased up to 1800 m, where the highest mean host plant density was found, and abruptly decreased at the last elevational site. Most species showed a restricted distribution and just one occurred across the entire gradient. For at least four species, altitudinal distribution seems to be strongly related to host plant availability, while for the others it is difficult to access which factors are decisive, due to their low numbers. Only in October all species were found in the field, although February was the month with the highest total abundance. Over the course of the study, the greatest abundances were recorded from October to February, comprehending the hottest and rainiest months, and the lowest abundances were found from June to August, which include the coldest and driest months. Thus, species seasonal distribution, supported by other studies in the same area, seems to be related to the local climate.

Keywords

Species richness, abundance of individuals, population fluctuation, host plant, altitude, phenology, Chrysomelidae, Cassidinae, Solanaceae.

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Introduction

Chrysomelidae is one of the richest families of Coleoptera, comprised of almost 37,000 described species (Jolivet 1988). Species are almost exclusively phytophagous in habit and associated with host plants in a large number of Angiosperm families (Jolivet and Petitpierre 1976). The subfamily Cassidinae *s.l.*, i.e. including both "cassidoid" (tortoise beetles) and "hispoid" (hispines) forms (Staines 2002, Chaboo 2007, Bouchard et al. 2011) is the second largest subfamily within the chrysomelids, with 312 genera and approximately 6,000 species (Borowiec 1999, Staines 2004).

The majority of Cassidinae are specialized feeders (narrowly oligophagous), with few species which could be considered either truly monophagous or polyphagous in habits. In the neotropical region, cassidoid Cassidinae are mainly associated with host plants in the dicotyledenous families Convolvulaceae, Asteraceae, Bignoniaceae, Boraginaceae, Lamiaceae and Solanaceae. It is interesting to note how few potential plant families present in any particular area are actually exploited by these beetles. Of those plant families that are, most are members of a single clade of Eudicotyledonaes (Jolivet and Hawkeswood 1995, Soltis et al. 2011).

It is believed that multiple factors, operating across a hierarchy of spatial and temporal scales, shape species distributions (Levin 1992). Insect species distributions are influenced by abiotic factors (e.g. rainfall, humidity and temperature), biotic (e.g. host plants, predators/parasitoids), and by their physiology (Price 1975, Szukecki 1987). Recently, great focus is being given to the role of temperature due to the rising concern on how climatic change will affect species distribution (Bale et al. 2002, Battisti et al. 2006).

Nogueira-de-Sá et al. (2004) reviewed population phenology of Cassidinae *s.str.* in tropical and subtropical areas in Brazil and described different phenological patterns. Tropical cassidines tend to occur throughout the year and are little influenced by climatic factors and more influenced by host plant availability. In contrast, in subtropical areas the majority of species present a distinct period of reproduction and adults commonly overwinter in diapause. Reproduction of most of these species was observed only during the warmest and most humid seasons, as indicated by Wolda (1978, 1980).

On tropical mountains, abiotic factors are likely to have even greater effects on community structure, so patterns of population fluctuation similar to subtropical and even temperate regions may emerge, with occurrence periods of insects well defined throughout the year. Increasing altitude brings lower temperatures, increased precipitation (rain or snow), lower partial pressure of gases, higher wind speed and turbulence, and greater extremes in radiation input (Barry 1992). Combined, these factors may produce a general decrease in the structural complexity of insect habitats, as well as variation in the nutritional quality and availability of host plants. Phytophagous insects could well respond to these variations in host quality with changes in rates of growth, survival and fecundity (Hodkinson 2005).

Hodkinson (2005), in a review of terrestrial insects along elevational gradients, clearly shows that trends in species richness and abundance of individuals are variable, decreasing with increasing altitude (e.g. Wolda 1987, Fernandes and Lara 1993), increasing (e.g. Sota 1994, Romero and Avila 2000), peaking at middle elevation (e.g. Janzen 1973, Janzen et al. 1976, McCoy 1990), or showing no altitudinal trend (e.g. Casson and Hodkinson 1991). Many processes may explain species richness declines with increasing altitude, including reduced habitat area at high elevations, reduced resource diversity, increasingly unfavorable environments and reduced primary productivity (Lawton et al. 1987).

There are only few studies with Brazilian Chrysomelidae on elevational gradients, and data obtained so far show that abundance and richness patterns vary with altitude among study areas. Ribeiro et al. (1994) and Carneiro et al. (1995), working on the same gradient, found a tendency of increasing richness and abundance with increasing altitude and suggested that harsh climatic conditions on the mountain base might be responsible for this pattern. Flinte et al. (2009), studying chrysomelids on another gradient, did not record a clear variation of richness, but found a peak of abundance at an intermediate altitude. In this paper, we describe the altitudinal and temporal distribution of seven *Plagiometriona* Spaeth, 1899 (Cassidinae: Cassidini) species across the same elevational gradient in the State of Rio de Janeiro, Brazil, and focus on how elevational changes (specifically rainfall and temperature) and host plants can influence their distribution.

Material and methods

Study area

Our study was conducted in Serra dos Órgãos National Park (22°32'S and 43°07'W), which encompasses an area of 20,024 ha, extending over four counties in southeast Brazil, State of Rio de Janeiro (Fig. 1A), within the tropical Atlantic domain. The climate is marked by mild summers, winters of high precipitation and temperature reduction with altitude (Castro 2008). The Park undergoes a superhumid period most of the year, marked by an intense rainfall, especially from November to March (mean of 458.2 mm monthly rainfall), while the drier season (though still humid) extends from June to August (mean of 48.8 mm monthly rainfall). The coldest months are between May and August (mean temperature of 16.4 °C), and the hottest fall in the period from December to March (mean temperature of 21.1 °C) (Flinte et al. 2009; Fig. 1B). Unfortunately, the meteorological station which provided the climatic data cited above was only installed in the Park in the middle of the present study, preventing proper correlation analysis with beetle richness and abundance. Four different types of vegetation, related to altitude, can be found in the Park (Rizzini 1954, Veloso et al. 1991): lower montane forest (below 800 m), montane (600–1500 m), high-montane



Figure 1. A Location of Serra dos Órgãos National Park in the State of Rio de Janeiro, Brazil and **B** climatic diagram (meteorological station at 980 m altitude, from the National Institute of Meteorology), compiled for the period of January 2007 to December 2008. Striped area= humid period; Black area= superhumid period.

(1500–2000 m) and high altitude grasslands, named *campos de altitude* (over 2000 m), characterized by shrubs, herbs and grasses.

Surveys were conducted at six sites of different altitudes (approximately 1300 m, 1500 m, 1600 m, 1700 m, 1800 m and 2050 m) in Teresópolis County, specifically on the *Pedra do Sino* trail, which has an altitudinal variation of more than 1000 m, ranging from 1100 m to 2263 m. Accordingly, the two lowest sites are found in montane forest, the highest occupies the high altitude grasslands, with intermediate sites in highmontane forest. Trail conditions (incident light, tree cover, humidity) were undoubtedly different from the interior of the forest, but these varied nevertheless along the chosen sites with changing phytophysiognomies. Besides, although host plant characteristics will probably not be the same, open areas such as clearings and trails may be preferable over intact canopy forest, since many Cassidinae, including various *Plagiometriona* species, are associated with secondary growth plants (Windsor, 1992). Flinte et al. (2009), studying Chrysomelidae along the same trail but at only three elevational sites, and with data from two meteorological stations at 980 m and 2140 m altitude, found lower rainfall volume at the latter, and a decrease of 0.61°C for each 100 m altitude, which means a difference of ca. 4.6°C between the lowest and highest sites of the present study.

Study beetle species

Within a wider project on Chrysomelidae diversity and distribution started in 2005 in the Park, seven Cassidinae species were chosen for the present study: *Plagiometriona ambigena* (Boheman, 1855) (Fig. 2A), *P. dodonea* (Boheman, 1855) (Fig. 2B), *P. dorsosignata* (Boheman, 1855) (Fig. 2C), *P. sahlbergi* (Boheman, 1855) (Fig. 2D), *P. stillata* (Boheman, 1855) (Fig. 2E), *P. tredecimguttata* (Boheman, 1862) (Fig. 2F) and *Plagiometriona* sp. 7 (Fig. 2G), all of which present very similar patterns of elytral coloration, form and body size. Within these species, the biggest individuals belong to *P. dorsosignata* and the smallest to *P. stillata* (mean of 69 and 52 mm, respectively; n= 10 each species). Some of these species (*P. dodonea*, *P. dorsosignata*, *P. stillata* and *P. tredecimguttata*) were also studied by Flinte et al. (2009) on the same altitudinal gradient, however using different methodologies.

To describe species richness on each plant species and altitude, only adults were considered because eggs, larvae and pupae of the studied *Plagiometriona* are very similar to each other and to other species of the same genus not mentioned here, but which can be found on the same plant species (this problem was already described by Flinte et al. 2009). Although immature stages are more sensitive to abiotic changes than adults, which limits our conclusions on the relative importance of such factors over beetle abundance, any factor affecting immatures would be reflected in adult abundance, not compromising the description of the temporal and spatial patterns considered here.

Adult individuals of the focal *Plagiometriona* species fed one or more of seven different Solanaceae species: *Aureliana fasciculata* Sendtn., *Capsicum mirabile* Mart., *Solanum campaniforme* Roem. & Schult., *Solanum enantiophyllanthum* Bitter, *Solanum megalochiton* Mart., *Solanum swartzianum* Roem. & Schult. (Solanoideae: Solaneae) and *Cestrum bracteatum* Link & Otto (Cestroideae: Cestreae) (Table 1).

Because the host plants *Aureliana fasciculata* and *Solanum campaniforme* had very similar vegetative forms, it was not possible to reliably distinguish them in the field outside their reproductive season. Therefore, data from beetles associated with these plants were grouped in the present study.

Beetles were deposited in the collection of the Laboratório de Ecologia de Insetos at the Federal University of Rio de Janeiro, but some specimens were also deposited in the collection of the Department of Biodiversity and Evolutionary Taxonomy, Institute of Zoology, University of Wroclaw, Poland. After curation, plants were deposited in the Herbarium of the Federal University of Rio de Janeiro and in the Rio de Janeiro Botanical Garden.

Temporal and altitudinal distribution

Surveys were conducted every two months from June 2006 to June 2007 by Sama de Freitas and one additional of four undergraduation students. At each site, two transects of 200 m \times 0.5 m (length \times width) were made, one at each side of the border of the trail. Within each transect, host plants were carefully surveyed for adults of the focal *Plagiometriona* species, and the number of individuals per plant and the number of each plant species was recorded in every site.

To obtain mean plant density for each altitude, we summed the number of plant individuals of each species in the transect per month, and divided that number by the number of surveys (seven months). In order to describe the temporal distribution of the species we considered the total abundance of each species per survey. Finally, beetle altitudinal distribution was calculated from the total number of adults sampled over the course of the study for each species and elevational site. Host plant quality was not considered in this study.



Figure 2. Species studied at the Serra dos Órgãos National Park: *Plagiometriona ambigena* A *P. dodonea*B *P. dorsosignata* C *P. sahlbergi* D *P. stillata* E *P. tredecimguttata* F and *Plagiometriona* sp. 7 G

Table 1. Host plant records based on larval "no choice" feeding tests for the seven *Plagiometriona* species in the study (from Flinte et al. 2008).

Host plants / Cassidines	aA. fasciculat	eC. mirabil	mC. bracteatu	eS. campaniform	mS. enantiophy- llanthu	nS. megalochito	mS. swartzianu
P. ambigena						х	х
P. dodonea		x		х			
P. dorsosignata	x						
P. sahlbergi			х				
<i>Plagiometriona</i> sp. 7			х				
P. stillata		x		x			
P. tredecimguttata	x	x		x	x		

Results and discussion

Spatial distribution of host plants

At no altitudinal site did all seven host plant species co-occur. Plant richness was highest with five species co-occurring at 1600 m, 1700 m and 1800 m, and lowest at 1300 m and 2050 m where only two and three species co-occurred, respectively (Fig. 3). *Aureliana fasciculata / S. campaniforme* occurred along the whole elevational gradient, while the other species were more restricted in their altitudinal distribution. In general, host plant density was highest at 1800 m for all species, except *S. swartzianum*, which showed higher density at 1600 m.

Occurrence of *Plagiometriona* spp. on their host plants

Our field observations were consistent with the data presented by Flinte et al. (2008) (Table 1), showing restricted feeding habits for the seven focal *Plagiometriona* species. *Plagiometriona dorsosignata, P. sahlbergi, P. stillata* and *Plagiometriona* sp.7 were associated with only a single host plant, while *P. ambigena, P. dodonea* and *P. tredecimguttata* were locally oligophagous, having two or three related hosts (Table 2).

Except for *P. ambigena*, the other oligophagous species showed a clear preference for one of their host plants, with more than 50% of individuals being recorded on a single host species (Table 2). Because plants on the border of the trail are sometimes very close to each other, some individuals were eventually found on non-host plants, probably during dispersal or because of disturbances that may take place during the inspection of the feeding plants. Thus, very low percentage values of occurrence on "new" host plants were not considered true associations and must be confirmed by laboratory rearing. The occurrence of *P. stillata* on only one of its described hosts in field may be an artifact due to the small number of individuals this species ever observed during the study period.

Temporal and altitudinal distribution of *Plagiometriona* spp.

Abundance of the seven focal species varied considerably along the year. The lowest values were recorded in June, gradually increasing until peaking in February and then decreasing again (Table 3). Thus, the peak happens in the middle of the summer, when precipitation and temperatures are high, while the low numbers occur during months of lower rainfall and milder temperatures (Fig. 1B).

In spite of the low number of studied species, changes in species richness could also be observed during the period; in June 2006 and 2007 and April 2007 just three of the four most abundant species were found in the field and only in October all seven species were recorded together (Table 3). Once again, the lowest numbers occur



Figure 3. Mean host plant density of the studied *Plagiometriona* species at different altitudes.

in the coldest and driest months, and the highest during the rainy season with warmer temperatures.

Three species, *P. dorsosignata*, *P. sahlbergi* and *P. tredecimguttata* were the most abundant species during the study. Also, *Plagiometriona dorsosignata* and *P. tredecimguttata* were the only two species present in all surveyed months. Although *Plagiometriona* sp. 7 occurred practically throughout the year, the total number of individuals recorded was very small, with the exception of the February survey when its abundance was the highest observed. *Plagiometriona ambigena*, *P. dodonea* and *P. stillata* were rarely observed over the entire study (Table 3). The two latter were only recorded once and in October.

Plagiometriona dorsosignata, P. sahlbergi, and *P. tredecimguttata* numbers varied similarly during the study period. Their abundance was very low in June 2006, peaked in February 2007 and decreased again in April (Fig. 4). Increasing numbers during the study may reflect temperature and precipitation increases, since the highest numbers of individuals were found from October to February, comprehending the warmest and most rainy months, while the lowest were recorded from June to August, the coldest and driest period (Fig. 1B). This increase in cassidine activity during the warm and rainy season was also described by Nogueira-de-Sá et al. (2004), in a review of the subfamily's phenology in Brazil. As seasonal changes in temperature are very slight in

Host plants / Cassidines	eA. fasciculata / S. campaniform	eC. mirabil	mC. bracteatu	mS. enantiophy- llanthu	nS. megalochito	mS. swartzianu
P. ambigena					50.0	50.0
P. dodonea	33.3	66.7				
P. dorsosignata	100.0					
P. sahlbergi	1.5*		98.5			
Plagiometriona sp. 7	3.7 *	3.7 *	92.6			
P. stillata		100.0				
P. tredecimguttata	70.9	25.5		2.9		0.7*

Table 2. Relative adult occurrence (in percentage) of the seven *Plagiometriona* species associated with Solanaceae at the study site.

* Plant species on which adult individuals were found in field during the present study, but larval feeding was not recorded in the laboratory by Flinte et al. (2008).

Table 3. Abundance (per month and total) of the seven *Plagiometriona* species studied from June 2006 to June 2007 at the study site, and species richness per month. Darker shade in gray indicates the month in which the most abundant species had the highest numbers of individuals.

Months /		20	06			Total		
Cassidines	J	A	0	D	F	A	J	abundance
P. ambigena	0	1	1	0	2	0	0	4
P. dodonea	0	0	3	0	0	0	0	3
P. dorsosignata	4	16	6	15	24	3	2	70
P. sahlbergi	3	15	30	22	58	9	0	137
Plagiometriona sp. 7	0	2	1	3	19	0	2	27
P. stillata	0	0	1	0	0	0	0	1
P. tredecimguttata	4	10	26	37	39	18	7	141
Total abundance	11	44	68	77	142	30	11	363
Species richness	3	5	7	4	5	3	3	

the tropics, it is believed that the seasonal distribution of rainfall exerts a greater influence on insect population dynamics (Delinger 1986, Wolda 1988). However, on an altitudinal gradient, temperature variation has a decisive influence even in the tropics, as every 1000 m altitude results in a decrease in temperature of about 6°C (Odgen and Powell 1979).

Most insect species living in temperate zones become active during spring and summer, overwintering in diapause (Wolda 1988). In the tropics, even though seasons are not as well defined, some beetle species also show activity peaks, as the chrysomeline *Platyphora anastomozans* (Medeiros and Vasconcellos-Neto 1994), which is more abundant between October and May, overwintering in diapause. An activity peak was also recorded for the three most abundant species of our study, *P. dorsosignata, P. sahlbergi* and *P. tredecimguttata*, although no evidence of diapause was found, at least for adults.



Figure 4. Population fluctuation of *P. dorsosignata*, *P. sahlbergi* and *P. tredecimguttata* from June 2006 to June 2007 at the study site.

Changes in community composition per elevational site were observed with increasing altitude. Considering the small number of study species, richness showed no clear pattern with altitude, starting with three species at the three lowest sites, to four species at intermediate elevations (1700 m and 1800 m), and decreasing to two species at the highest site (Table 4).

Significant differences occurred in the spatial distribution of *Plagiometriona* species along the altitudinal gradient; with some species, such as *Plagiometriona* sp. 7 and *P. stillata* restricted to a single altitude, while others showed a wide elevational distribution, *P. tredecimguttata* being the most remarkable example, occurring on all six elevational sites. Most species were restricted in their altitudinal range, occurring at two, three or four sites, normally adjacent to each other (Table 4).

A general increase in the total abundance of beetles throughout the altitudinal gradient was recorded, the highest numbers of individuals being found at 1700 m and 1800 m, 61 and 252, respectively, followed by a sharp decrease in abundance at the highest site (Table 4). This pattern was evident in the distributions of each of the three most numerous species.

Plagiometriona sp. 7 and *P. sahlbergi* feed on the same host plant, *Cestrum* bracteatum, which was observed from 1600 to 2050 m. The highest density of *C. bracteatum* occurred at 1800 m (Fig. 5A), where 57.3% (n= 557) of all its individuals were recorded. At this site we also observed the highest abundance of *P. sahlbergi*, which was found at the same altitudinal range as its host plant (Fig. 5A).

Table 4. Abundance of the seven *Plagiometriona* species at the different altitudinal sites, number of species per altitude and total of sites in which each species was recorded at the study area. Darker shade in gray indicates the altitudinal sites in which the most abundant species had the highest numbers of individuals.

Altitudes / Cassidines	1300 m	1500 m	1600 m	1700 m	1800 m	2050 m	Total abundance	Total sites
P. ambigena	0	0	3	1	0	0	4	2
P. dodonea	2	1	0	0	0	0	3	2
P. dorsosignata	0	2	0	41	27	0	70	3
P. sahlbergi	0	0	5	4	96	32	137	4
<i>Plagiometriona</i> sp. 7	0	0	0	0	27	0	27	1
P. stillata	1	0	0	0	0	0	1	1
P. tredecimguttata	1	14	7	13	103	3	141	6
Total abundance	4	17	15	61	252	35	383	
Species richness	3	3	3	4	4	2		

Thus, spatial distribution of *P. sahlbergi* along the elevational gradient seems to be greatly influenced by the availability of its host plant. Individuals of *Plagiometriona* sp. 7 were only found at 1800 m (Fig. 5B), suggesting that their occurrence may be responding to the high density of their host at this altitude. Meanwhile, at the highest elevational site, where plant density is still considerable, the species absence may be explained by the lack of physiological adaptations necessary to survive at such altitudes. With increasing altitude, abiotic factors such as temperature and precipitation can influence physiological and morphological changes in insect populations in the short term (e.g. variations in the life cycle, fecundity and size of individuals) and over evolutionary time (e.g. such as high numbers of apterous or brachypterous individuals, polymorphisms) (Hodkinson 2005, Chown and Klok 2003).

Plagiometriona ambigena, P. dodonea and *P. stillata* were restricted to a small altitudinal range, occurring at only one or two sites, while their host plants showed broader distribution along the elevational gradient (Fig. 5C, D and E, respectively). Thus, it is possible that these three species also have low tolerance to the harsher climatic conditions at higher sites, which prevent them from having a wider altitudinal range. Another possibility may be sampling error, in that their small numbers prevented us from recording them at different altitudes.

Plagiometriona tredecimguttata occurred throughout the entire elevational gradient of the study (Fig. 5F), but not in even numbers. Low abundances were recorded at the lowest and highest sites of the gradient, with numbers peaking at 1800 m. In this way, species density increased with altitude to 1800 m, after which it decreased, following variation in host plant density (Fig. 5F). Therefore, the distribution of *P. tredecimgut-tata* appears strongly related to host availability.

Plagiometriona dorsosignata was found from 1500 m to 1800 m, with its abundance peaking at 1700 m (Fig. 5G). Its host plant *A. fasciculata* is potentially distrib-



Figure 5. Altitudinal distribution of the seven *Plagiometriona* species (bars) and their host plants (lines) from June 2006 to June 2007 at the study site: *P. sahlbergi* **A** *Plagiometriona* sp. 7 **B** *Plagiometriona ambigena* **C** *P. dodonea* **D** *P. stillata* **E** *P. tredecimguttata* **F** and *P. dorsosignata*.

uted along the entire length of the transect, but more densely between 1700 m and 1800 m, where the beetle is also more abundant.

A general pattern observed within the seven study species seems to be the complete or near absence of most of the species at the highest altitudinal site. Temperatures below 0°C are commonly recorded at the highest elevations in the Park (Castro 2008), demanding morphological and, specially, physiological adaptations to enable beetle survival (Gaston and Chown 1999). Climatic factors, in particular temperature, may thus influence beetles directly or indirectly via host plant. Although host plant quality was not analyzed here, plant availability appears to be a decisive factor, clearly influencing the altitudinal distribution of four out of the seven chrysomelids studied. However, even in the case of the other three species, host plant influence cannot be discarded, since the number of these beetles was very low. In that way, differences in numbers of individuals and species composition along the altitudinal gradient may depend on host plant availability, but also on species coping differently with varying abiotic conditions related to altitude. Naturally, the role of competing species, predators and parasitoids cannot be ruled out as another force determining the distribution of the species. According to Hodkinson (2005), knowledge of tritrophic interaction between host plant, herbivorous insect and predators/parasites, although rare, may improve the understanding of population dynamics along altitudinal gradients. Unfortunately, we are only beginning our research on insect distribution along such gradients in the tropics and much work still remains to clarify the factors underlying species distribution.

Flinte et al. (2009), studying 12 Chrysomelidae species, being eight cassidines (including *P. dorsosignata, P. dodonea, P. stillata* and *P. tredecimguttata*), along the same trail one year later, found that species richness did not vary clearly with altitude, but recorded a distinct abundance peak at mid-elevational sites (1600-1800 m). Furthermore, both species richness and abundance showed a drastic reduction during the driest and coldest months, and high numbers when temperature and rainfall increased. Flinte et al. (2010) also described the altitudinal and seasonal pattern in abundance of another related Cassidinae in the same gradient, *Plagiometriona forcipata* (= *P. emarcida*) which feeds on *Solanum lhotskyanum*. Their findings support the well defined seasonal distribution already known for the area, however, both adults and larvae showed higher numbers of individuals at the high- (2000-2100 m) than at the mid-elevation site (1600-1800 m). Although dealing with another species on a different host plant, this suggests that immature stages may respond similarly as adults to changing factors related to altitude.

Since many Cassidinae are associated with host plants on open habitats (Windsor 1992), surveys conducted on trails with a genera composed by many sun-loving species, such as *Plagiometriona*, may be a good indicator of the spatial and temporal distribution of the group. There is no doubt that descriptive studies such as the one presented here are an important starting point to widen our knowledge on cassidine ecology.

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References

- Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Coulson JC, Farrar J, Good JG, Harrington R, Hartley SE, Jones TH, Lindroth RL, Press MC, Syrmnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8: 1–16. doi: 10.1046/j.1365–2486.2002.00451.x
- Barry RG (1992) Mountain climatology and past and potencial future climatic changes in mountain regions – a review. Mountain Research and Development 12: 71–86. Stable url: http://www.jstor.org/stable/3673749
- Battisti A, Stastny M, Buffo E, Larsson S (2006) A rapid altitudinal range expansion in the pine processionary moth produced by the 2003 climatic anomaly. Global Change Biology 12: 662–671. doi: 10.1111/j.1365–2486.2006.01124.x
- Borowiec L (1999) A World Catalogue of the Cassidinae. Biologica Silesiae, Wroclaw, 476 pp.
- Bouchard P, Bousquet Y, Davies AE, Alonso-Zarazaga MA, Lawrence JF, Lyal CHC, Newton AF, Reid CAM, Schmitt M, Ślipiński SA, Smith ABT (2011) Family-group names in Coleoptera (Insecta). ZooKeys 88: 1–972. doi: 10.3897/zookeys.88.807
- Carneiro MA, Ribeiro SP, Fernandes GW (1995) Artrópodos de um gradiente altitudinal na Serra do Cipó, Minas Gerais, Brasil. Revista Brasileira de Entomologia 39(3): 597–604. url: http://www.icb.ufmg.br/big/leeb/publicacoes/1995.Carneiro.Ribeiro.Fernandes.pdf
- Casson DS, Hodkinson ID (1991) The Hemiptera (Insecta) communities of tropical rain forest in Sulawesi. Zoological Journal of the Linnean Society 102: 253–275. doi: 10.1111/ j.1096–3642.1991.tb00002.x
- Castro EBV (coord) (2008) Plano de Manejo do Parque Nacional da Serra dos Órgãos. Brasília, Instituto Chico Mendes de Conservação da Biodiversidade, Portaria ICMBio nº 45.
- Chaboo CS (2007) Biology and phylogeny of the Cassidinae Gyllenhal sensu lato (tortoise and leaf-mining beetles) (Coleoptera: Chrysomelidae). American Museum of Natural History, New York, 250 pp. doi: 10.1206/0003–0090(2007)305[1:BAPOTC]2.0.CO;2

- Chown SL, Klok CJ (2003) Altitudinal body size clines: latitudinal effects associated with changing seasonality. Ecography 26: 445–455. Stable Url: http://www.jstor.org/stable/3683569
- Delinger DL (1986) Dormancy in tropical insects. Annual Review of Entomology 31: 239–264. doi: 10.1146/annurev.en.31.010186.001323
- Fernandes GW, Lara ACF (1993) Diversity of Indonesian gall-forming herbivores along altitudinal gradients. Biodiversity Letters 1: 186–192. Stable url: http://www.jstor.org/stable/2999743
- Flinte V, Macedo VM, Monteiro FR (2008) Tortoise beetles (Chrysomelidae: Cassidinae) of a tropical rain forest in Rio de Janeiro, Brazil. In: Jolivet P, Santiago-Blay J, Schmitt M (Eds) Research on Chrysomelidae, vol. 1. Brill, Leiden, 194–209.
- Flinte V, Macedo VM, Monteiro FR (2009) Chrysomelids and their host plants along an altitudinal gradient in a tropical Atlantic Rain Forest in Rio de Janeiro, Brazil. In: Jolivet P, Santiago-Blay J, Schmitt M (Eds) Research on Chrysomelidae, vol. 2. Brill, Leiden, 31–56.
- Flinte V, Windsor D, Sekerka L, Macedo MV, Monteiro RF (2010) Plagiometriona emarcida (Boheman, 1855) and Plagiometriona forcipata (Boheman, 1855) (Coleoptera: Chrysomelidae: Cassidinae), a single species differing in larval performance and adult phenotype. Journal of Natural History 44: 891–904. doi: 10.1080/00222930903528230
- Gaston KJ, Chown SL (1999) Elevation and climatic tolerance: a test using dung beetles. Oikos 86: 584–590. Stable Url: http://www.jstor.org/stable/3546663
- Hodkinson ID (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. Biological Reviews 80: 489–513. doi: 10.1017/S1464793105006767
- Janzen D (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. Ecology 54: 687–708. Stable url: http://www.jstor. org/stable/1935359
- Janzen DH, Ataroff M, Farinas M, Reyes S, Rincon N, Soler A, Soriano P, Vera M (1976) Changes in the arthropod community along an elevational transect in the Venezuelan Andes. Biotropica 8: 193–203. Stable url: http://www.jstor.org/stable/2989685
- Jolivet P, Petitpierre E (1976) Selection trofique et evolution chromossomic chez les Chrysomelinae (Coleopters: Chrysomelidae). Acta Zoologica 66: 59–90.
- Jolivet P (1988) Food habits and food selection of Chrysomelidae. Bionomics and evolutionary Perspectives. In: Jolivet P, Petitpierre E, Hsiao TH (Eds) Biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, 1–24. doi: 10.1007/978-94-009-3105-3_1
- Jolivet P, Hawkwswood TJ (1995) Host-plants of Chrysomelidae beetles of the world an: essay about the relationships between leaf beetles and their food-plants. Backhuys Publishers, Leiden, 281 pp.
- Lawton JH, Macgarvin M, Heads PA (1987) Effects of altitude on the abundance and species richness of insect herbivores on bracken. Journal of Animal Ecology 56: 147–160. Stable url: http://www.jstor.org/stable/4805
- Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. Ecology 73: 1943–1967. doi: 10.2307/1941447
- McCoy ED (1990) The distribution of insects along elevational gradients. Oikos 58: 313–322. Stable url: http://www.jstor.org/stable/3545222

- Medeiros L, Vasconcellos-Neto J (1994) Host plant and seasonal abundance patterns os some Brazilian Chrysomelidae. In: Jolivet P, Cox ML, Petitpierre E (Eds) Novel aspects of the biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, 185–189. doi: 10.1007/978-94-011-1781-4_11
- Nogueira-de-Sá F, Medeiros L, Macedo MV (2004) Phenology of populatios of tortoise beetles (Cassidinae) in Brazil. In: Jolivet P, Santiago-Blay JA, Schmitt M (Eds) New Developments in the Biology of Chrysomelidae. SPB Academic Publishing, The Hague, 647–658.
- Ogden J and Powell JA (1979) A quantitative description of the forest vegetation on an altitudinal gradient in the Mount Field National Park, Tasmania, and a discussion of its history and dynamics. Australian Journal of Ecology 4: 293–325. doi: 10.1111/j.1442– 9993.1979.tb01220.x
- Price PW (1975) Insect Ecology. John Wiley & Sons, New York, 514 pp.
- Ribeiro SP, Carneiro MAA, Fernandes GW (1994) Distribuition of *Brachpnoea* (Coleoptera: Chrysomelidae) in na altitudinal gradient in a brazilian savanna vegetation. Phytophaga 6: 28–33.
- Rizzini CT (1954) Flora Organensis: lista preliminar das Cormophyta da Serra dos Órgãos. Volume XIII. Arquivos do Jardim Botânico do Rio de Janeiro, Rio de Janeiro.
- Romero AE, Avila JM (2000) Effect of elevation and type of habitat on the abundance and diversity of Scarabaeoid dung beetle (Scarabaeoidea) assemblages in a Mediterranean area from Southern Iberian Peninsula. Zoological Studies 39: 351–359. url: http://zoolstud. sinica.edu.tw/Journals/39.4/351–359.pdf
- Soltis DE, Smith SA, Cellinese N, Wurdack KJ, Tank DC, Brockington SF, Refulio-Rodriguez NF, Walker JB, Moore MJ, Carlsward BS, Bell CD, Latvis M, Crawley S, Black C, Diouf D, Xi Z, Rushworth CA, Gitzendanner MA, Sytsma KJ, Qiu Y, Hilu KW, Davis C C, Sanderson MJ, Beaman RS, Olmstead RG, Judd WS, Donoghue MJ, Soltis PS (2011) Angiosperm phylogeny: 17 genes, 640 taxa. American Journal of Botany 98:704–730. doi: 10.3732/ajb.1000404
- Sota T (1994) Variation of carabid life cycles along climatic gradients: an adaptive perspective for life history evolution under adverse conditions. In: Danks HV (Ed) Insect life-cycle polymorphism. Kluwer Academic Publishers, The Netherlands, 91–112.
- Staines CL (2002) The New World tribes and genera of hispines (Coleoptera: Chrysomelidae: Cassidinae). Proceedings of the Entomological Society of Washington 104(3): 721–784. url: http://cat.inist.fr/?aModele=afficheN&cpsidt=13796188
- Staines CL (2004) Cassidinae (Coleoptera, Chrysomelidae) and Zingiberales: a review of the literature. In: Jolivet P, Santiago-Blay JA, Schmitt M (Eds) New Developments in the Biology of Chrysomelidae. SPB Academic Publishing, The Hague, 307–310.
- Szujecki A (1987) Ecology of Forest Insects. Junk Publishers, Boston, 600 pp.
- Veloso HP, Rangel-Filho ALR, Lima JCA (1991) Classificação da vegetação brasileira adaptada a um sistema universal. Fundação Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro.
- Windsor DM, Riley EG, Stockwell HP (1992) An introduction to the biology and systematics of Panamanian tortoise beetle (Coleoptera: Chrysomelidae: Cassidinae). In: Quintero D

and Aiello A (eds) Insects of Panama and Mesoamerica: selected studies. Oxford University Press, Oxford, 372–391.

- Wolda H (1978) Fluctuations in abundance of tropical insects. American Naturalist 112: 1017–1045. Stable url: http://www.jstor.org/stable/2460346
- Wolda H (1987) Altitude, habitat and tropical insect diversity. Biological Journal of the Linnean Society 30: 313–323. doi: 10.1111/j.1095–8312.1987.tb00305.x
- Wolda H (1988) Insect seasonality: why? Annual Review of Ecology and Systematics 19: 1–18. Stable url: http://www.jstor.org/stable/2097145
RESEARCH ARTICLE



Rhyparida foaensis (Jolivet, Verma & Mille, 2007), comb. n. (Coleoptera, Chrysomelidae) and implications for the colonization of New Caledonia

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Abstract

The study of external morphology of the New Caledonian leaf beetle *Dematochroma foaensis* Jolivet, Verma & Mille (Chrysomelidae, Eumolpinae, Colaspoidini) substantiates its new combination into the genus *Rhyparida* Baly (Chrysomelidae, Eumolpinae, Nodinini). The species is redescribed here to highlight characters important for suprageneric diagnosis. This is the second species of Nodinini found in New Caledonia, otherwise rich in species of Colaspoidini, raising questions about the paucity of *Rhyparida* and this tribe in New Caledonian fauna, when they are dominant in surrounding archipelagoes, and very rich in potential source areas such as Australia and New Guinea. Some alternative explanations for this pattern are advanced, serving as alternative hypotheses until our knowledge on the ecology of these species improves or supported phylogenetic scenarios become available for this group.

Keywords

Rhyparida, Dematochroma, New Caledonia, island disharmony, new combination

Introduction

Generic attributions of New Caledonian Eumolpinae are currently in need of revision. Montrouzier (1861) and Fauvel (1862) described two medium sized species of Eumolpinae from the archipelago as *Edusa laboulbenei* Montrouzier and *Chalcoplacis antipodum* Fauvel, respectively. Chapuis (1874) described another New Caledo-

nian species within his "Colaspitae" and under a new genus, Thasycles cordiformis Chapuis, which was later synonymised with Montrouzier's taxon (Lefevre 1876). Finally, Lefèvre (1885) ranked the two recognized New Caledonian taxa into the genus Dematochroma Baly, characterized by the species D. picea Baly, 1864, an endemic eumolpine from Lord Howe island in the so-called Lord Howe Rise, a marine ridge separated from the Norfolk Ridge, the oceanic feature where New Caledonia belongs to (Keast 1996). The three species have markedly divergent external appearance, perhaps as much as to be treated as different genera (Fig. 1). Heller (1916) acknowledged the differences between the forms from New Caledonia and Lord Howe, highlighting the insufficient justification by Lefèvre (1885) to place them together, and preferred to treat them in different genera-against the choice of Clavareau (1914)-maintaining Chapuis' name Thasycles for the Neocaledonian taxa. In fact, he described under Thasycles six new species of Eumolpinae, again markedly divergent among each other and from either previously described taxon (see also Gómez-Zurita in press). In the absence of explicit diagnostic characters, his decision to rank species so different under the same generic name was mostly based on the relatively large size of these species and perhaps the prejudice of a fauna evolved in isolation from one or at most few ancestors. In the same tradition, Pierre Jolivet and his coauthors (Jolivet et al. 2007a,b,c, 2009) described many New Caledonian eumolpine beetles, recovering the generic name Dematochroma, whereby the distinguishing feature to place the new species under this genus is mainly their moderate size (5–9 mm long; Jolivet et al. 2007b).

Size as a systematic criterion is liable to taxonomic confusion. In my initial steps to understand the systematic structure of New Caledonian Eumolpinae above the species level, both using morphological and DNA-based criteria, stood out one example in need of additional study. The 6 mm long species described as Dematochroma foaensis Jolivet, Verma & Mille, 2007a: 43 belongs into a distantly related suprageneric rank compared to Dematochroma or most other New Caledonian Eumolpinae. Indeed, after Stethotes bertiae Jolivet, Verma & Mille, 2007b: 81 it is the second representative reported from this archipelago as belonging into the tribe Nodinini, as opposed to Colaspoidini, where Dematochroma and most other New Caledonian species appear to belong. The species shows highly divergent characters as compared to Dematochroma sensu auctorum or any other Eumolpinae in New Caledonia. These include the lack of dorsal longitudinal groove on pygidium, meso- and metatibiae with preapical emargination, and bifid claws. A closer analysis of morphology of several specimens showed it to present the characters considered by previous authors to diagnose the genus Rhyparida Baly, 1861 (e.g., Gressitt 1969). Thus, herein, I propose the name Rhyparida foaensis (Jolivet, Verma & Mille), comb. n. The original diagnosis for the species was succinct and lacked mention to those systematic characters important for the recognition of the species and its correct placement in the system of Eumolpinae. Thus, a redescription is provided below, with illustrations of male and female genitalia for the first time, as well as a discussion about the presence of this isolated Nodinini in New Caledonia.



Figure I. Habitus of three species of *Dematochroma* **a** Male holotype of *D. piceum* Baly from Lord Howe Island (N.H.M., London) **b** male of *D. laboulbenei* (Montrouzier) from Thio, New Caledonia (voucher no. IBE-JGZ-NC-0112; I.B.E., Barcelona), and **c** male of *D. antipodum* (Fauvel) from L'Aoupinié, New Caledonia (voucher no. IBE-JGZ-NC-0144; I.B.E., Barcelona). Scale bar = 5 mm.

Taxonomy

Redescription of Rhyparida foaensis (Jolivet, Verma & Mille)

Rhyparida foaensis (Jolivet, Verma & Mille)

http://species-id.net/wiki/Rhyparida_foaensis

Material examined. Type material: (1) Holotype, one male, La Foa, 21°44S, 165°54E, 10 February 2004, M'bouéri R. M. leg. (Museum National d'Histoire Naturelle, Paris); (2) Paratype, one female, Ouégoa, Mandjélia, 20.39683°S, 164.53218°E, 787m, 7–8 February 2005, S. Cazères & C. Mille leg. (Museum National d'Histoire Naturelle, Paris). Other material: (3) two females, Caavatch (=Kaavac), 5 February 1977, Dr. J. Balogh leg. (Hungarian Natural History Museum, Budapest); (5) three females, Province Sud, Camp Brun, 14 March 1994, on *Melaleuca quinquenervia*, M. Schöller leg. (M. Schöller coll., Berlin); (4) one female, Province Nord, Hienghene 20.69545°S, 164.94274°E 24m, 8 April 2008, J. Gómez-Zurita leg. (J. Gómez-Zurita coll., voucher no. NC-0110, Institute of Evolutionary Biology, Barcelona).

Description. *Habitus* (Fig. 2). Body stout, elongated oval (6.1 mm long, 3.4 mm wide), moderately convex. Ground color orange testaceous, with infuscate head sutures, inverted triangle on frons, apical antennal segments, margins and discal markings on pronotum, scutellum, elytral suture, humeri, medially for short distance on



Figure 2. Habitus of *Rhyparida foaensis* (Jolivet, Verma & Mille). Scale bar = 5 mm.

third and seventh elytral intervals, apex of femora, basal half of tibiae, episterna and ventral thoracic segments; mandibles black.

Head large, deeply inserted into pronotum, nearly to upper eye margin; surface very delicately microreticulated; vertex weakly convex, very finely, rather densely and homogeneously punctured, with very fine median longitudinal impression, becoming progressively larger, on depressed longitudinal area on frons, joined apically to transversally widely obtuse fronto-clypeal suture. Clypeus wider than long, subtrapezoidal, depressed apically, with deep median semicircular apical emargination, flanked laterally by shortly produced denticles; surface microreticulated, with larger, deeper punctures than those on vertex, bearing minute, very fine setae anteriorly. Labrum as long as wide; surface finely microreticulated; sides feebly convergent towards round anterior angles; apex depressed and weakly emarginated; anterior angles with one pair of nearly adjacent fine golden setae; two setae anteriorly on disc. Genae very short, with some fine setae below eye margin. Eyes very big, dorsoventrally elongated; deeply emarginated at inner border for antennal insertion; supraocular margin furrowed, furrow not surpassing eye margin above, with long, yellowish dorsal seta. Space for antennal insertion concave, slightly raised dorsally above clypeus level; microreticulated, unpunctured, with one anterior, oblique fine golden seta. Antennae long and slender, reaching basal third of elytra; scape long, weakly flattened and arched antero-posteriorly; second antennomere elongated, slightly clavate, weakly curved, 0.66x as long as first; third segment straight, as long as second; antennomeres 4–5 subcylindrical, slightly shorter than scape, narrow and slender; 6–10 as long as scape, slightly widened towards apex, densely setose; apical antennomere longest, sharply pointed and paler at apex. Maxillary palpi short, slender; apical palpomere elongated, subconical.

Pronotum transverse, 0.58× as long as wide between posterior angles, shorter than head, transversally convex, especially at anterior angles; posterior border weakly bisinuated with weakly projecting median lobe, finely margined with premarginal line of dense dot-like impressions; posterior angles laterally projecting as small teeth continuing basal margin, with large apical setigerous pore; anterior border nearly straight, finely margined at sides, with margin broader and more imprecisely defined at middle; anterior angles laterally and slightly obliquely projecting as small teeth with large setigerous pore at apex; sides broadly curved, wider behind middle; lateral margins relatively wide, flat, glossy, with internal row of dense round impressions; pronotal surface delicately microreticulated, rather uniformly and densely covered by shallow, moderate punctures, smaller, almost disappearing near borders. Anterior border of hypomeron more or less straight, regularly continuing profile of anterior border of pronotum with that of prosternum, both remaining largely separated by anterior margin of hypomeron (see Fig. 4f in Gressitt 1967); hypomera finely alutaceous, unpunctured, with shallow, wavy longitudinal impressions on disc; posterior border of hypomera surrounding procoxae posteriorly for 2/3 of their width, joining apex of prosternal process laterally, enclosing procoxal cavities behind. Prosternum narrow, slightly convex before coxae; anterior border with slightly raised broad margin and weakly emarginated medially; very finely alutaceous, with scattered, fine long yellowish setae; prosternal process broad, as wide as base of femora between coxae, progressively widening apically, following contour of coxae to join posterior border of hypomera; apex of prosternal process straight, twice as wide as width between coxae. Procoxae ovoid, slightly transverse. Combined mesanepisternum and mesepimeron subtrapezoidal, transverse, finely alutaceous, unpunctured. Mesoventrite relatively long, glossy, unpunctured; process long, spatula-like, apex convex, glossy, with few scattered very fine yellowish setae. Metanepisterna long, finely microreticulated, with scattered minute punctures and very fine, short recumbent whitish setae. Metaventrite as long as first abdominal ventrite; disc below level of mesosternal process, glossy, nearly unpunctured; sides finely alutaceous, with scattered minute punctures and very fine, short whitish setae; posterior border with short median notch.

Scutellum as long as broad at base, sides straight, weakly divergent at basal 2/3, curved at obtuse angle to obtusely pointed apex; surface finely alutaceous, unpunctured. Elytra slightly broader than base of pronotum; humeri round, slightly callose; sides very feebly curved, with maximum width behind middle, and regularly curved to broadly round apex; margins feebly explanate, entirely visible from above; surface shiny, with dense unordered minute punctures and regular series of strong punctures separated at most by distance equal to their diameter; short scutellar striae of some 14 punctures starting before middle of scutellum and obliquely directed to suture; sutural striae reaching from base of elytra to sutural angles, joining marginal striae at inner edge of explanate margin of elytra; four longitudinal discal striae from base of elytra joining successively to apical ends of ninth, eighth, seventh and sixth striae on preapical declivity of elytra; short premarginal posthumeral striae, curved and convergent with elytral margin before middle of elytra; space between striae 7 and 8, medially and at lateral declivity of elytra occupied by two additional shorter longitudinal striae convergent at both ends; darkened sutural interval, humeri, elongated spots medially on disc on third interval and more advanced at lateral declivity of elytra on seventh interval between stria 7 and internal row of additional posthumeral striae. Epipleura flat, unpunctured, shiny, broad basally and gradually narrowing toward apex; only visible laterally below humeri. Species fully winged.

Profemora spindle-shaped at basal 3/4, nearly cylindrical at apical quarter; extremely finely alutaceous with scattered minute punctures and very short appressed setae on basal 3/4 and coarser punctures and longer setae at apical 1/4. Protibiae very slightly curved inward, gradually widened toward apex; with several fine longitudinal ridges and longitudinal series of semierect golden setae at intervals; apex concave, obliquely cut for tarsal insertion, densely setose internally. Protarsi 0.6× as long as protibiae; first tarsomere slightly expanded laterally, longer than wide at concave apex; second shorter than first, triangular with broadly concave apex; third deeply and narrowly bilobed; fifth longer than tarsomeres 2-3, slender, subparallel, ventrally curved; claws bifid, weakly divergent, long, sharp, with short, sharp inner teeth. Median and hind legs very similar to anterior legs, but tibiae straight, with conspicuous preapical emargination externally, margined by fringe of erect golden setae and apex not densely setose internally. Abdominal ventrites finely microsculptured, shiny, narrow, strongly transverse, with posterior border increasing concavity from ventrites one to four, finely but more or less uniformly punctured and with very fine, short whitish setae; sides corrugated; anterior process between metacoxae of first abdominal ventrite broader than long, regularly curved; last abdominal ventrite very feebly emarginated.

Median lobe of the aedeagus (Fig. 3a,b) strongly bent at right angle near base, dorso-ventrally flattened and nearly straight at apical 2/3; sides slightly divergent, reaching maximum width at mid-level of ostium, feebly converging before abruptly tapering at obtuse angle before apex; apex anteriorly prolonged as blunt median triangular denticle curved dorsally; median dorsal flap broad, spatula-like, with short narrow base 0.5× as wide as broadest point medially, before regularly curved nearly semicircular apex. Spermatheca (Fig. 3c,d) U-shaped with pump slightly shorter than receptacle, gradually narrowing towards curved pointed apex; proximal end slightly broadened before narrow elongated basal appendix attached prebasally to very fine, transparent spermathecal duct; spermathecal gland apparently attached to spermathecal duct distally from spermatheca at 1.5× its length.

Diversity and distribution of Rhyparida

As it occurs with most Eumolpinae genera, the objective limits of *Rhyparida* need to be revised and it is possible that profound changes will affect the systematics of the group (C.A.M. Reid, Australian Museum, pers. comm.). However, before this revision is attempted, following the latest treatments of the genus by several specialists, it is possible to draw some preliminary conclusions about the diversity and biogeography of the genus. Clavareau's (1914) catalogue lists 166 species of Rhyparida, an increase of 34.3% over the account by Lefevre (1885), thirty years earlier. Today, there are 361 species recognized as belonging into the genus *Rhyparida*, which appear predominantly distributed in Australia (110 species) and the main island of New Guinea (99 species). The remaining species are mostly distributed in the Philippines (32 species), Sulawesi (18 species) and many other islands of Indonesia, as well as in several archipelagoes of the Micronesia and Melanesia (Fig. 4). Very few species occur in continental South East Asia. Interestingly, the genus had not been reported so far from New Caledonia, despite all other surrounding archipelagoes having several species, including Fiji with ten recognized taxa (Bryant and Gressitt 1957), and that the genus reaches as far east as Samoa (Gressitt 1957).

It is largely elusive understanding why such a diverse genus like *Rhyparida* is so rare in New Caledonia, considering the old age of the island, its relatively large size, its ecological diversity and its relative proximity to species-rich source areas such as New Guinea and Australia, as compared to Fiji, for instance, comparatively rich in species of *Rhyparida*. Island disharmony is a well-known biogeographic pattern, and very common in the case of insects in Pacific islands (see Gillespie and Roderick 2002). Thus, Rhyparida could represent one more example of biased composition of an island community. But perhaps the attention should be on Fiji and a disharmonic excess of Nodinini, not only *Rhyparida* but several other genera as well, compared to surrounding archipelagoes (Bryant and Gressitt 1957). Fiji supports in turn a comparatively poor Colaspoidini fauna, highly diverse in New Caledonia. In any case, in the absence of a reconstruction for the evolutionary history of this group, whatever explanation we attempt at these patterns remains speculative. Chance determines that island biotas are a non-representative sample of their continental counterparts, and the classical mechanistic justification of differential odds for initial colonization of an island invokes dispersal capabilities of the species in potential sources (Grant 1998). We do not have any reason to believe a priori that Rhyparida is less suited for transoceanic dispersal compared to other eumolpines such as Dematochroma, which have reached, successfully colonized and radiated in New Caledonia. For instance, all New Caledonian eumolpines, including Rhyparida foaensis, are winged, the same as their continental relatives. And of course, the presence of the genus in Samoa argues against inherent limitations to dispersal potential.

If differences in ability for dispersal compared to other eumolpines are not obvious, another possibility is that successfully colonizing *Rhyparida* (or other Nodinini for that matter) were outcompeted by local stable populations of Colaspoidini, in this



Figure 3. Male (a dorsal b lateral) and female c, d genitalia of *Rhyparida foaensis* (Jolivet, Verma & Mille).

case. Again, and considering the generally eclectic ecologies of these animals, their notable success in similar geographic scenarios also rich in other eumolpines, and the diversity of suitable habitats offered by New Caledonian ecosystems, it is difficult to admit that such a fierce antagonism and exclusion can affect settlement chances for representatives of an entire beetle tribe.

Yet another possibility is that ecological requirements for Nodinini, or *Rhyparida* in particular, are actually stricter than considered *a priori*, and not available in New Caledonia, compared to the mainland or surrounding oceanic islands. This hypothesis could be evaluated examining for instance the association of *Rhyparida* species to specific soils, types of vegetation or specific plants throughout its range and confirming the absence (or rarity) of these conditions in New Caledonia, remarkable and quite unique for its geologic and mineral characteristics (Jaffré 1993; Morat 1993). However, perhaps the importance of host plants in this specific case of island disharmony could be neglected, since *Rhyparida* appears in the literature associated to many different hosts, most of them or their relatives present in New Caledonia. Species of *Rhyparida* have



Figure 4. Distribution and diversity of *Rhyparida* Baly species worldwide.

been reported as feeding on dicot Anacardiaceae (Sapindales), Asteraceae (Asterales), Dilleniaceae (Dilleniales), Loganiaceae (Gentianales), Malvaceae (Malvales), Moraceae (Rosales) and Rhizophoraceae (Malpighiales), and monocot Arecaceae (Arecales), Pandanaceae (Pandanales), and Poaceae (Poales) (Bryant and Gressitt 1957; Chûjô and Kimoto 1961; Gressitt 1955, 1967), with species like *R. coriacea* Jacoby and *R. carolina* Chûjô found and explicitly reported on many hosts (Gressitt 1955, 1967). Indeed, as it occurs with many eumolpines, it is possible that *Rhyparida* species are polyphagous as root feeding larvae, but also as adults (Jolivet and Verma 2002). If this were the case, they would have a high colonization potential of new habitats, particularly those offering such a diverse range of potential hosts as New Caledonia, but also intermediate islands along their possible colonization routes. The host or hosts of *R. foaensis* are not known, but some of the specimens available for study were collected on the so-called *niaouli*, a dominant shrub in savannah-like environments in the south of Grande Terre currently included in the genus *Melaleuca* (Myrtales: Myrtaceae), very diverse in Australia and with a similar range as the genus *Rhyparida*.

A last possibility about the paucity of Nodinini in New Caledonia and worth consideration here is that there may be several species in the archipelago still awaiting discovery. Considering the intense sampling in the recent past and the conspicuous characters diagnosing this tribe, although it is likely that new species will be discovered, it appears improbable that the catalogue of New Caledonian Nodinini will grow to a number of species comparable to that found in Fiji or even Samoa, the later with at least eight species among *Rhyparida, Stethotes* and *Stygnobia* (Gressitt 1957).

The number of questions that this intriguing pattern suggest and the few, speculative answers available, highlight the importance of further research on New Caledonian fauna, from biodiversity and ecological surveys to phylogenetic analyses which will help understanding the history of colonization and diversification on this remote biodiversity hotspot.

Replacement names for the genus Rhyparida

During the course of this study, several homonyms were detected affecting the genus *Rhyparida* Baly, which need name replacements to avoid ambiguity. *Rhyparida leana* nom. n. (after Arthur Mills Lea) is proposed as replacement name for the Australian species *Rhyparida apicipennis* Lea, 1915, name preoccupied by a species from Fergusson Island (Papua New Guinea) described by Jacoby (1898). Both Lea (1915) and Weise (1922) used the name *R. pallidula* to describe species from Australia and the Philippines, respectively; the name *Rhyparida weiseana* nom. n. (after Julius Weise) is suggested to replace Weise's younger taxon. Finally, Lea (1915) named an Australian species using the same name, *R. prosternalis*, previously proposed by M. Jacoby for a species found in Indonesian Papua (Jacoby 1894); Lea's name is thus replaced here by *Rhyparida reiterata* nom. nov. (from post-classical Latin *reiteratus* = repeated).

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References

Bryant GE, Gressitt JL (1957) Chrysomelidae of Fiji (Coleoptera). Pacific Science 11: 3–91. Chapuis F (1874) Genera des Coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes. Tome X. Famille des Phytophages. Librairie Encyclopédique de Roret, Paris, 455 pp.

- Chûjô M, Kimoto S (1961) Systematic catalog of Japanese Chrysomelidae (Coleoptera). Pacific Insects 3: 117–202.
- Clavareau H (1914) Chrysomelidae: 11. Eumolpinae. Pars 59. Coleopterorum Catalogus (S. Schenkling Ed.). W. Junk, Berlin, 215 pp.
- Fauvel A (1862) Coléoptères de la Nouvelle-Calédonie, recueillis par M. E. Déplanche, chirurgien de la Marine Impériale, 1858-59-60 (1ère Partie). Notices Entomologiques, A. Hardel, Caen, 68 pp.
- Gillespie RG, Roderick GK (2002) Arthropods on islands: Colonization, speciation, and conservation. Annual Review of Entomology 47: 595–632. doi: 10.1146/annurev. ento.47.091201.145244
- Gómez-Zurita J (in press) Revision of New Caledonian species of Eumolpinae described by K. M. Heller (Coleoptera: Chrysomelidae). Zootaxa.
- Grant PR (1998) Patterns on islands and microevolution. In: Grant PR (Ed) Evolution on Islands. Oxford Univ. Press, Oxford, 1–17.
- Gressitt JL (1955) Insects of Micronesia. Coleoptera: Chrysomelidae. Insects of Micronesia 17: 1–60.
- Gressitt JL (1957) Chrysomelidae of Samoa (Coleoptera). Proceedings of the Hawaiian Entomological Society 16: 241–258.
- Gressitt JL (1967) Chrysomelid beetles from the Papuan subregion, 4 (Eumolpinae, 2). Pacific Insects 9: 295–340.
- Gressitt JL (1969) Chrysomelid beetles from the Papuan subregion, 6 (Eumolpinae, 4). Pacific Insects 11: 1–31.
- Heller KM (1916) Die K\u00e4fer von Neu-Caledonien und den benachbarten Inselgruppen. In: Sarasin F, Roux J (Eds) Nova Caledonia, Zoologie, Vol. II, L. III. C. W. Kreidels Verlag, Wiesbaden, 229–364.
- Jacoby M (1894) Descriptions of new genera and species of phytophagous Coleoptera obtained by W. Doherty in the Malayan archipelago. Novitates Zoologicae 1: 267–330.
- Jacoby M (1898) New species of Phytophagous Coleoptera from Australia and the Malayan regions. Annales de la Société entomologique de Belgique 42: 350–380.
- Jaffré T (1993) The relationship between ecological diversity and floristic diversity in New Caledonia. Biodiversity Letters 1: 82–87. doi: 10.2307/2999751
- Jolivet P, Verma KK (2002) Biology of Leaf Beetles. Intercept, Andover, 332 pp.
- Jolivet P, Verma KK, Mille C (2007a) New species of Eumolpinae from the genera *Dematochro-ma* Baly, 1864 and *Taophila* Heller, 1916 from New Caledonia (Coleoptera, Eumolpinae). Revue française d'Entomologie (N.S.) 29: 33–47.
- Jolivet P, Verma KK, Mille C (2007b) New genera and species of Eumolpinae from New Caledonia (Coleoptera, Chrysomelidae). Revue française d'Entomologie (N.S.) 29: 77–92.
- Jolivet P, Verma KK, Mille C (2008) New species of *Dematochroma* and *Colaspoides* from New Caledonia (Coleoptera, Chrysomelidae, Eumolpinae). Nouvelle Revue d'Entomologie (N.S.) 24 [2007]: 195–200.
- Jolivet P, Verma KK, Mille C (2010) Eumolpinae recently collected in New Caledonia and Vanuatu (Coleoptera, Chrysomelidae). Nouvelle Revue d'Entomologie (N.S.) 26 [2009]: 3–17.

- Keast A (1996) Pacific biogeography: Patterns and processes. In: Keast A, Miller SE (Eds) The origin and evolution of Pacific island biotas, New Guinea to Eastern Polynesia: patterns and processes. SPB Academic Publishers, Amsterdam, 477–512.
- Lea AM (1915) Notes on Australian eumolpides (Coleoptera, Chrysomelidae), with descriptions of new species. Transactions and Proceedings of the Royal Society of South Australia 39: 102–339.
- Lefèvre E (1876) Descriptions d'eumolpides nouveaux ou peu connus. Revue et Magasin de Zoologie Pure et Appliquée (3e Sér.) 4: 278–311.
- Lefèvre E (1885) Eumolpidarum hucusque cognitarum catalogus, sectionum conspectu systematico, generum sicut et specierum nonullarum novarum descriptionibus adjunctis. F. Hayez, Impr. Acad. Roy. Belgique, Bruxelles, 172 pp.
- Montrouzier X (1861) Essai sur la faune entomologiqe de la Nouvelle-Calédonie (Balade) et des îles des Pins, Art, Lifu, etc. Annales de la Société entomologique de France (4ème sér.) 1: 265–306.
- Morat P (1993) Our knowledge of the flora of New Caledonia: endemism and diversity in relation to vegetation types and substrates. Biodiversity Letters 1:72–81. doi: 10.2307/2999750
- Weise J (1922) Chrysomeliden der Philippinen, III. The Philippine Journal of Science 21: 423–490.

RESEARCH ARTICLE



Hispines (Chrysomelidae, Cassidinae) of La Selva Biological Station, Costa Rica

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Abstract

Survey work from 1992–2001 identified 139 species of hispines at the lowland part of La Selva Biological Station, Costa Rica. The tribe Cephaloleiini was the most speciose with 58 species (41.7%) followed by the Chalepini with 55 (39.5%). The fauna is most closely related to that in South America but with some genera which are more speciose in the Nearctic Region. Plant associations are known for 88 (63.3%) of the species but many of these are merely collecting records, not host plant associations. The first plant associations are reported for *Alurnus ornatus*, *A. salvini*, and *Acentroptera nevermanni*.

Keywords

Chrysomelidae, hispine, La Selva Biological Station

Introduction

Hispines comprise half of the subfamily Cassidinae (sensu lato) in the family Chrysomelidae within the order Coleoptera (Staines 2002b). Until recently, most authors treated the group as a separate subfamily but recent work has shown that there is no biological or morphological reason to retain sub-familial status (Staines 2002b). The combined subfamily consists of 6000 species placed in 42 tribes (Staines 2002b). See Staines (2002b) for a detailed history of the classification of the two groups.

The combination of the Hispinae with the Cassidinae (s. str.) has created difficulty in having a handy term to use for these beetles. Several have been proposed but they

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are cumbersome. Until an easily used term is coined for this group, I continue to use "hispines" in the traditional sense of the genera and species in the former subfamily Hispinae (see Seeno and Wilcox 1982 for a list of genera).

The adult hispine head is opisthognathous, prominent, visible from above, at least to behind the eyes. The frons is prominent, exposed or rarely retracted. The antennae are not retractable and are closely inserted between the eyes. The pronotum is narrower than the elytra; it is more or less quadrangular or trapezoidal, with definite anterior angles which may have a small tubercle. The scutellum is always visible. The elytra lack lateral expansions or have reduced and discontinuous expansions. The margins are usually denticulate or with spines. Larvae are either leaf-miners or free living. They have eight pairs of abdominal spiracles which are well developed and dorsally placed; with the eighth abdominal segment terminal, and with free hind margin (Staines 2002b, 2006).

Ecologically, New World hispines fall into three feeding groups: external feeders; sheath, appressed or rolled-leaf feeders; and leaf-miners. In the Old World, some species have been reported as stem borers in herbaceous or semi-ligneous plants, but this has not been reported from the New World. The biology of few species has been studied; most are not associated with a host plant or plant family.

Methods

Study Area

La Selva Biological Station (10°26'N, 83°59'W) is located in the Atlantic tropical lowlands of Costa Rica and is adjacent to Braulio Carrillo National Park. It is about 100 km from San José. The station comprises 1600 hectares. Habitat is a mosaic of primary forest, early secondary pasture, young secondary forest, abandoned plantations, and selectively logged primary forest. The elevation varies from 35 to 137 m. The station is near the confluence of Rio Puerto Viejo and Rio Sarapiquí. It is owned and operated by the Organization for Tropical Studies (McDade and Hartshorn 1994).

Rainfall varies from 152.0 mm (March) to 480.7 mm (July) with a total 4 m per year. The dry season is short and not severe (Sanford et al. 1994).

There are 1744 plant species documented from La Selva. The most speciose families are Pteridophyta, Orchidaceae, Araceae, Rubiaceae, Melastomataceae, Fabaceae, and Piperace (Hartshorn and Himmel 1994).

The Arthropods of La Selva (ALAS) project was started in 1991 (http://viceroy. eeb.uconn.edu/ALAS/ALAS.html). An existing building on the station was remodeled as an entomology laboratory and four technicians were trained in the National Biodiversity Institute (INBio) six-month parataxonomist course. From 1992 until 2000 the project was funded by separate grants from the U.S. National Science Foundation (Biotic Surveys and Inventories Program). From 2001–2006 the focus of the project shifted to a transect survey from La Selva Biological Station to the summit of Volcan Barva. This paper deals only with the results at the La Selva Biological Station. Daily operations of ALAS were conducted by the parataxonmists under the direction of the principal investigators John T. Longino, Evergreen State College, and Robert K. Colwell, University of Connecticut. Over the course of the project there were over 100 collaborating taxonomists.

Survey Methods

The ALAS survey consisted of both structured and directed sampling. Structured sampling consisted of black-lights, Malaise and flight intercept traps, and canopy fogging (see Furth et al. 2003 for summary).

Passive black-lights were utilized from 1993 to 1999 at twelve sites, six on the ground and six in the canopy. Malaise traps were used at sixteen sites from 1993 to 2000. Specimens were collected directly into ethanol and the traps emptied every two weeks. Flight intercept traps were place at sixteen sites and samples were collected every two weeks.

Canopy fogging was conducted in 1993–1994, 1996, and 2000. Sixteen trees were fogged: six trees of the most common species at La Selva, six trees of an intermediate abundant species, and trees of six different species. The tree selected had large crowns with little crown overlap and with good climbing access.

Directed collecting for chrysomelids used beating, sweeping, visual observation, known host plant observation, and use of a mid-canopy shaker net.

Results and discussion

Species richness at La Selva

As of the end on 2001, a total of 139 hispine species have been collected at La Selva Biological Station (see Table 1).

Quantitative inventory by non-specialists using standard sampling techniques can capture about half of the fauna. Individual methods are needed to sample the rest of the community. Sweeping, beating, and host plant sampling are the best methods. Fogging, Berlese funnels, and Malaise traps capture a few species usually not otherwise collected but are not sufficient in themselves to indicate the actual fauna.

Major lineages

The most recent classification of hispines is by Würmli (1975) and Staines (2002b). There are 24 extant tribes of hispines, of which six have been found at La Selva (see Table 1).

Over 40% of the 139 hispine species and 25% of the genera are in the tribe Cephaloleiini. The Cephaloleiini is a New World tribe of 16 genera and 382 species (Staines 2002b). Over 200 species are in the genus *Cephaloleia* Chevrolat (Uhmann 1957, Staines 1996).

E					c 6
Iribe	Genus/Species	l'lant association	l'lant family	Ubservation	Keterences
Alurnini	Alurnus ornatus Baly	Chamaedorea sp.	Arecaceae	А	New observation
Alurnini	Alurnus salvini Baly	Chamaedorea sp.	Arecaceae	А	New observation
Arescini	Chelobasis bicolor Gray	Heliconia sp., H. latispatha Benth., H.	Heliconiaceae	L	Maulik 1937;
		tortuosa Griggs, H. cathaeta R. R. Smith			Strong 1977a, 1983;
		<i>Musa</i> sp.	Musaceae	L	Meskins et al. 2008
		Calathea latifolia Klotzsch	Marantaceae	L	
Arescini	Chelobasis perplexa Baly	Heliconia imbricata (Kuntze) Baker, H.	Heliconiaceae	L	Maulik 1932;
		latispatha, H. pogonantha Cuford.,			Strong and Wang 1977;
		H. irrasa R. R. Smith, H. mariae Hook.	Marantaceae	L	McKenna and Farrell 2005;
		Calathea insignis Hort. & Bull.			Meskins et al. 2008
Cephaloleiini	Aslamidium impurum	Calathea ovata Lindl., C. virginalis	Marantaceae	А	Bondar 1940; Spaeth 1938;
	(Boheman)	Linden, C. insignis, C. micans (Mathieru)			
		Koern.			
		<i>Heliconia</i> sp.	Heliconiaceae	А	Windsor et al. 1992
Cephaloleiini	<i>Cephaloleia aequilata</i> Uhmann	Unknown			
Cephaloleiini	Cephaloleia atriceps Pic	Unknown			
Cephaloleiini	Cephaloleia bella Baly	Heliconia imbricata	Heliconiaceae	А	Staines 1996
Cephaloleiini	Cephaloleia belti Baly	Calathea insignis, Calathea latifolia	Marantaceae	Α	Uhmann 1930; Maulik 1932;
		Klotzsch, C. lutea (Aubl.) GFW Mey.,			Strong 1977b,1982a; Meskins
		Ischnosiphon pruinosus Peterson			et al. 2008; Descampe et al.
		Heliconia imbricata, H. latispatha, H.	Heliconiaceae	Α, L	2008; García-Robledo et al.
		pogonantha, H. mariae, H. tortuosa,			2010
		Heliconia catheta, H. irrasa, H. vaginalis Benth H maneriana Peterson			
Cephaloleiini	Cephaloleia championi Baly	Heliconia sp.	Heliconiaceae	Α	Staines 1996
Cephaloleiini	Cephaloleia congener Baly	Heliconia latispatha, H. tortuosa	Heliconiaceae	А	Staines 1996
Cephaloleiini	<i>Cephaloleia consanguinea</i> Baly	Unknown			
Cephaloleiini	Cephaloleia costaricensis Uhmann	Chusquea simpliciflora Munro	Poaceae	U	Meskins et al. 2008

Table 1. Hispines known from La Selva Biological Station and their plant associations (**A**=adult plant feeding: **L**=larval host plant; **U**=unspecified).

E	•				
Iribe	Genus/Species	Plant association	l'lant tamily	Ubservation	Keterences
Cephaloleiini	Cephaloleia deficiens Uhmann	Unknown			
Cephaloleiini	Cephaloleia dilaticollis Baly	Calathea insignis, C. lutea, C. inocephala (Kuntze), H. Kennedy, Ischnosiphon pruinosus	Marantaceae	A	Staines 1996; McKenna and Farrell 2005; Meskins et al. 2008: Descampe et al. 2008:
		Renealmia sp., R. alpinia (Rottb.) Maas	Zingiberaceae	A, L	García-Robledo et al. 2010
Cephaloleiini	Cephaloleia disjuncta Staines	<i>Vitex copperi</i> Stanley	Verbenaceae	A	Staines 1998
Cephaloleiini	Cephaloleia distincta Baly	<i>Calathea</i> sp.	Marantaceae	А	Staines 1996
		Heliconia imbricata	Heliconiaceae	A	
Cephaloleiini	Cephaloleia dorsalis Baly	Costus sp., C. pulverulentus C. Presl., C.	Costaceae	A, L	Staines 1996; McKenna and Earrell 2005: Meekine et al
		Renealmin con	Zingiheraceae	A	2008: García-Robledo and
				4	Horvitz. 2009; García-Robledo et al. 2010
Cephaloleiini	<i>Cephaloleia elegantula</i> Baly	Unknown			
Cephaloleiini	Cephaloleia erichsonii Baly	Calathea gymnocarpa H. Kennedy, C.	Marantaceae	A	Staines 1996; Strong 1977a;
I		inocephala, C. leucostachys Hook., C.			McKenna and Farrell 2005;
		insignis, C. latifolia, C. lutea			Meskins et al. 2008; Descampe
		Heliconia sp., H. catheta, H. latispatha, H. mariae H. marinalis H. marneriana	Heliconiaceae	А	et al. 2008
Cenhaloleiini	Cephaloleia exigua Uhmann	Unknown			
Cephaloleiini	Cephaloleia fenestrata Weise	Ischnosiphon sp., I. cerotus Leos.,	Marantaceae	L	Staines 1996; Strong 1977a;
-		Pleiostachya pruinosa K. Schum.			Johnson 2004a
Cephaloleiini	<i>Cephaloleia flava</i> Uhmann	Unknown			
Cephaloleiini	<i>Cephaloleia fulvolimbata</i> Baly	Unknown			
Cephaloleiini	Cephaloleia heliconicae Uhmann	<i>Heliconia</i> sp.	Heliconiaceae	А	Staines 1996
		Calathea insignis	Marantaceae	S	
Cephaloleiini	<i>Cephaloleia histrionica</i> Baly	Unknown			
Cephaloleiini	<i>Cephaloleia lata</i> Baly	Chamaedorea tepejilote Lichm., C. wendlandiana Hemsl.	Arecaceae	А	McKenna and Farrell 2005; Meskins et al. 2008

Tribe	Genus/Species	Plant association	Plant family	Observation	References
Cephaloleiini	<i>Cephaloleia mauliki</i> Uhmann	<i>Heliconia</i> sp.	Heliconiaceae	Α	Uhmann, 1930; Maulik 1932,
		Calathea insignis	Marantaceae	А	1937
Cephaloleiini	Cephaloleia metallescens Baly	Bactris major Jacq., Chamaedorea wendlandiana	Arecaceae	U	Meskins et al. 2008
Cephaloleiini	Cephaloleia nevermanni Uhmann	Calathea insignis, C. macrosepala K. Schumann	Marantaceae	А	Uhmann 1930; Staines 1996
		Heliconia imbracata	Heliconiaceae	А	
Cephaloleiini	Cephaloleia nigricornis (Fabricius)	Unknown			
Cephaloleiini	<i>Cephaloleia ornatrix</i> Donckier	Heliconia sp.	Heliconiaceae	Α	Strong 1977a
Cephaloleiini	Cephaloleia placida Baly	<i>Renealmia</i> sp., <i>R. alpinia</i> (Rottb.) Maas	Zingiberaceae	A	Staines 1996; García-Robledo and Horvitz. 2009; García- Robledo et al. 2010
Cephaloleiini	Cephaloleia puncticollis Baly	Calathea insignis	Marantaceae	L	Uhmann 1930; Seifert and
		Heliconia imbricata, H. latispatha	Heliconiaceae	L	Seifert 1976; Staines 1996
		Musa sp.	Musaceae	L	
Cephaloleiini	<i>Cephaloleia quadrilineata</i> Baly	Heliconia imbricata, H. latispatha	Heliconiaceae	А	Staines 1996
Cephaloleiini	Cephaloleia reventazonica Uhmann	Heliconia latispatha	Heliconiaceae	А	Staines 1996
Cephaloleiini	Cephaloleia ruficollis Baly	Unknown			
Cephaloleiini	Cephaloleia sallei Baly	Heliconia sp., H. irrasa, H. catheta, H. latispatha, H. mariae, H. vaginalis	Heliconiaceae	L	Strong 1977a; Staines 2004a; McKenna and Farrell 2005;
		Renealmia strobilifera			Meskins et al. 2008; Descampe
		Calathea inocephala, C. latifolia, C. lutea,	Zingiberaceae	А	et al. 2008
		Ishnosiphon pruinosus	Marantaceae	Α	
Cephaloleiini	<i>Cephaloleia semivittata</i> Baly	Calathea marantifolia Standley	Marantaceae	А	Staines 1996
Cephaloleiini	<i>Cephaloleia splendida</i> Staines	Unknown			
Cephaloleiini	<i>Cephaloleia stevensi</i> Baly	<i>Heliconia</i> sp.	Heliconiaceae	А	Staines 1996; McKenna and
		Calathea micans, C. inocephala, C. latifolia, Ishnosiphon pruinosus	Marantaceae	А	Farrell 2005; Meskins et al. 2008

E			-		
Iribe	Genus/Species	Plant association	l'lant tamily	Ubservation	Keterences
Cephaloleiini	Cephaloleia sulciceps Baly	Unknown			
Cephaloleiini	<i>Cephaloleia suturalis</i> Baly	Costus malorticenus H. Wendl., Costus sp., C. pulperulentus	Costaceae	Α	Uhmann 1930; Maulik 1937; Meskins et al. 2008
Cephaloleiini	Cephaloleia tenella Baly	Unidentified	Areaceae	A	Staines 1996
Cephaloleiini	<i>Cephaloleia trimaculata</i> Baly	ginger lily, Renealmia sp.	Zingiberaceae	A	Uhmann 1950; McKenna and
4	х ч	Costus pulverulentus	Costaceae	А	Farrell 2005; Meskins et al. 2008
Cephaloleiini	<i>Cephaloleia trivittata</i> Baly	Calathea haamelii H. Kennedy, C. macrosebala	Marantaceae	А	Staines 1996
Cephaloleiini	Cephaloleia vicina Baly	Heliconia spp., H. latispatha, H. imbricata	Heliconiaceae	А	Strong 1977a, 1977b, 1981
		Calathea spp., Ischnospihon spp.	Marantaceae	А	
Cephaloleiini	Cephaloleia sp. 1	Unknown			
Cephaloleiini	Demotispa nevernanni Uhmann	Unknown			
Cephaloleiini	<i>Demotispa strandi</i> Uhmann	Spermacoce sp.	Rubiaceae	U	Flowers and Janzen 1997; Staines 2006a
		Calathea sp.	Marantaceae	A	
Cephaloleiini	Demotispa sp. 1	Unknown			
Cephaloleiini	Demotispa sp. 2	Unknown			
Cephaloleiini	Homalispa gracilis Baly	Unknown			
Cephaloleiini	<i>Homalispa nevernmanni</i> Uhmann	Oenocarpus panamanus Bailey	Arecaceae	U	Meskins et al. 2008
Cephaloleiini	Homalispa sp. 1	Unknown			
Cephaloleiini	Imatidium rufiventre Boheman	Inga marginata Willd.	Fabaceae	Α	Gilbert et al. 2001
Cephaloleiini	Imatidium thoracicum Fabricius	Calathea insignis, C. ovata, C. virginalis, C. lutena	Marantaceae	А	Spaeth 1938; Bondar 1940; Windsor et al. 1992; Meskins
		Heliconia latispatha, H. catheta, H. irrasa, H. wagneriana	Heliconiaceae	А	et al. 2008
Cephaloleiini	Solenispa leptomorpha (Baly)	Unknown			
Cephaloleiini	Stenispa graminicola Uhmann	Unknown			

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TIDE	Genus/opecies	r lant association	riant family	ODSELVATION	velerences
Cephaloleiini	<i>Stenispa sallei</i> Baly	Unknown			
Cephaloleiini	Stenispa vespertina Baly	Cyperus sp.	Cyperaceae	L	Bondar 1931b
Cephaloleiini	Stilpnaspis rubiginosus (Boheman)	Unknown			
Chalepini	Anisostena pilatei (Baly)	Unknown			
Chalepini	Baliosus productus (Baly)	Unidentified	Bignoniaceae	L	Hespenheide and Dang 1999
Chalepini	Baliosus sp.1	Urera bogataense ?	Urticaceae	L	Hespenheide and Dang 1999
Chalepini	Baliosus sp. 2	Unknown			
Chalepini	<i>Carinispa nevermanni</i> Uhmann	Malpighia glabra L., Bunchosia sp.	Malpighiaceae	L	Uhmann 1934; Flowers and Janzen 1997
Chalepini	Chalepus amiculus Baly	Unknown			
Chalepini	Chalepus angulosus Baly	Unknown			
Chalepini	Chalepus assmani Uhmann	Unknown			
Chalepini	Chalepus bellulus (Chapuis)	<i>Digitaria eriantha</i> Steud., <i>Oryza</i> sp.	Poaceae	L	Maes and Staines 1991; Staines 1997; Flowers and Janzen
				TT	1661
		Unidentified	Arecaceae	D	
		Phaseolus sp.	Fabaceae	U	
Chalepini	Chalepus brevicornis (Baly)	Unknown			
Chalepini	Chalepus consanguineus (Baly)	Lasiacis sp.Unidentified	Poaceae	L	Uhmann 1935; Hespenheide and Dang 1999
Chalepini	Chalepus digressus Baly	Lasiacis sp.	Poaceae	L	Memmott et al. 1993
Chalepini	Chalepus nigripictus Baly	Unknown			
Chalepini	<i>Chalepus pici</i> Descarpentries & Villiers	Unknown			
Chalepini	Chalepus similatus Baly	Unknown			
Chalepini	Chalepus tappesi Chapuis	Unknown			
Chalepini	Chalepus verticalis (Chapuis)	Phaseolus sp.	Fabaceae	U	Maes and Staines 1991
Chalepini	Chalepus sp. 1	Unknown			

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Tribe	Genus/Species	Plant association	Plant family	Observation	References
Chalepini	Chalepus sp. 2	Unknown			
Chalepini	Charistena ruficollis (Fabricius)	Zea mays L., Paspalum conjugatum Berg	Poaceae	U	Bondar 1931a; Schlottfeldt
		Glycine max (L.) Merr.	Fabaceae	U	1944; Maulik 1937; Maes and
		Coffea sp.	Rubiaceae	U	Staines 1991
Chalepini	<i>Euprionota aterrima</i> Guérin- Méneville	Unknown			
Chalepini	Glyphuroplata nigella Weise	Valota sp., Eriochloa gracilis (Fourn.) Hitchc.	Poaceae	L	Riley 1985; Hespenheide and Dang 1999
		Mimosa sp.	Fabaceae	U	0
Chalepini	Heptispa limbata (Baly)	Cassia grandis L., C. fruitcosa Mill., Inga sp., Machaerium sp.	Fabaceae	L	Uhmann 1934, 1937; Memmott et al. 1994;
		<i>Serjania</i> sp.	Sapindaceae	U	Hespenheide and Dang 1999
		Olyra latifolia	Poaceae	U	
Chalepini	Heterispa vinula (Erichson)	Triumfetta josefina Polak,	Tilaceae	L	Uhmann 1934, 1937; Maulik
		Apeiba membranacea Spruce ex. Benth.			1937; Hespenheide and Dang
		Guazuma ulmifolia L.	Sterculiaceae	L	1999; Casari and Teixeira 2004
		<i>Sida</i> sp. <i>S. rhombifolia</i> L., <i>S. carpinifolia</i> K. Schum.	Malvaceae	L	
		Infigofera sp.	Fabaceae	L	
Chalepini	Octhsipa bimaculata Uhmann	Stigmaphyllum lindenianum A. Juss.	Malphigiaceae	L	Hespenheide and Dang 1999
Chalepini	Octhispa decepta (Baly)	Stigmaphyllum lindenianum	Malphigiaceae	L	Hespenheide and Dang 1999
Chalepini	Octhispa elegantula Baly	Serjania sp., Paullinia sp.	Sapindaceae	L	Uhmann 1937; Hespenheide
		Pithecoctenium echinatum K. Schum.	Bignoniaceae	U	and Dang 1999
Chalepini	Octhispa elevata (Baly)	Paullinia sp.	Sapindaceae	L	Uhmann 1934; Maulik 1937;
		Pithecoctenium echinatum	Bignoniaceae	U	Hespenheide and Dang 1999
Chalepini	Octhispa haematopyga Baly	Colubrina spinosa Don. Sm.	Rhamnaceae	L	Hespenheide and Dang 1999
Chalepini	Octhispa nevernanni Uhmann	Ochroma lagopus Rowlee	Bombaceae	L	Hespenheide and Dang 1999
Chalepini	Oxychalepus alienus (Baly)	Centrosema macrocarpum Benth., Cassia	Fabaceae	L	Howers and Janzen 1997;
		Juurosa			

Tribe	Genus/Species	Plant association	Plant family	Observation	References
Chalepini	Oxychalepus posticatus (Baly)	Cassia oxyphylla Kunth., C. hayesiana Standl., C. fruticosa	Fabaceae	L	Uhmann 1937; Memmott et al. 1994; Hespenheide and Dang 1999
Chalepini	Oxyroplata nr. bellicosa Uhmann	Bamosteroa argentea Spreng.	Malphighiaceae	L	Uhmann 1937
Chalepini	Pentispa explanata (Chapuis)	Pithecoctenium sp.	Bignoniaceae	L	Uhmann 1934
Chalepini	Pentispa fairmairei (Chapuis)	Chusquea sp.	Poaceae	U	Uhmann 1937; Maulik 1937;
		Calea urticaefolia (P. Mill.) DC, C. axillaries DC., Vernonia mollis H.B.K.,	Asteraceae	L	Morris et al. 2004
		Verbesina sp., Eupatorium populifolium Hook. & Arn., Clibadium sp., Lepidaploa			
		tortuosa (L.) H. Rob.			
		Elephantopus spicatus Aubl., Malpighia glabra	Malpighiaceae	U	
		Serjania sp.	Sapindaceae	U	
Chalepini	Pentispa sp. 1	Unknown			
Chalepini	Pentispa sp. 2	Unknown			
Chalepini	Platocthispa championi (Baly)	Piper sp.	Piperaceae	L	Hespenheide and Dang 1999
Chalepini	Platocthispa emorsitans (Baly)	Calathea sp., Calathea insignis,	Marantaceae	U	Staines 2004a; Meskins et al.
		C. latifolia			2008
		Costus sp.	Costaceae	U	
		Heliconia catheta, H. irrasa, H. latispatha	Heliconiaceae	U	
Chalepini	Platocthispa sp. 1	Ochroma lagopus	Bombaceae	Г	Hespenheide and Dang 1999
Chalepini	Probaenia armigera (Baly)	<i>Piptocarpha chontalensis</i> Baker in Mart.	Asteraceae	L	Hespenheide and Dang 1999
Chalepini	<i>Probaenia pici</i> Uhmann	Mikania guaco Humb. & Bonpl.	Asteraceae	L	Hespenheide and Dang 1999
Chalepini	Probaenia sp. 1	Arrabidaea chica (Humb. & Bonpl.) Verl.	Bignoniaceae	Г	Hespenheide and Dang 1999
Chalepini	Sumitrosis amica (Baly)	Heliconica sp.	Heliconiaceae	L	Hespenheide and Dang 1999
Chalepini	Sumitrosis fryi (Baly)	Eupatorium populifolium	Asteraceae	L	Uhmann 1937
Chalepini	Sumitrosis instabilis (Baly)	Unknown			

Tribe	Genus/Species	Plant association	Plant family	Observation	References
Chalepini	Sumitrosis pallescens (Baly)	Chamaecrista fasciculata (Michx.) Greene, C. nictitans (L.) Moench.	Caesalpiniaceae	n	Cavey 1994
Chalepini	Sumitrosis terminatus (Baly)	Unidentified	Fabaceae	L	Hespenheide and Dang 1999
Chalepini	<i>Uroplata fusca</i> Chapuis	Pithecactenium echinatum, Arrabidaea mollisima Bureau & K. Schm.	Bignoniaceae	Γ	Uhmann 1934, 1937; Memmott et al. 1994
		Malpighia glabra	Malpighiaceae	n	
Chalepini	<i>Uroplata sculptilis</i> Chapuis	Clibadium aspersum DC, Synedrella nodiflora Gaertn.	Asteraceae	Г	Uhmann 1934, 1937; Hespenheide and Dang 1999
		Inga edalis Mart.	Fabaceae	L	1
		Gouania adenophora Pilg.	Rhamnaceae	L	
Chalepini	Uroplata sp. 1	Unknown			
Chalepini	<i>Uroplata</i> sp. 2	Unknown			
Chalepini	Xenochalepus amplipennis (Baly)	Unidentified	Fabaceae	L	Hespenheide and Dang 1999
Chalepini	Xenochalepus erythroderus (Chapuis)	Coussapoa nymphaeifolia Standll., C. villosa Poepp. & Endl., Cecropia insignis Liebm, Pourouma bicolor (Standl.) C.C. Berg & E.C. van Heusden	Cecropiaceae	Г	Hespenheide and Dang 1999
Chalepini	Xenochalepus rufithorax (Baly)	Unknown			
Prosopodontini	Prosopodonta distincta (Baly)	Unknown			
Prosopodontini	Prosopodonta dorsata (Baly)	Costus sp.	Costaceae	U	Uhmann 1930; Meskins et al.
		Chamaedorea wendlandiana, Gryosophila warscewiczii Bartl., Oenocarpus panamanus Bailey	Arecaceae	L	2008
Sceloenoplini	Acentroptera strandi Uhmann	Pentaclethra macroloba Kuntze	Fabaceae	U	New observation
Sceloenoplini	Ocnosispa humerosa Staines	Conceveiba pleiostemona Donn. Smith	Euphorbiaceae	А	Staines 2002a
Sceloenoplini	Pseudispa fulvolimbata (Baly)	Unknown			
Sceloenoplini	Sceloenopla antennata (Baly)	Unknown			
Sceloenoplini	Sceloenopla bicolorata Staines	Sterculia recordiana papyracea E. Taylor	Sterculiaceae	A	Staines 2002a
Sceloenoplini	Sceloenopla bidentata Staines	Unknown			

Tribe	Genus/Species	Plant association	Plant family	Observation	References
Sceloenoplini	Sceloenopla erudita (Baly)	Anthurium sp.	Araceae	L	Uhmann 1944; Hespenheide
		<i>Cupania</i> sp.	Sapindaceae	L	and Dang 1999
Sceloenoplini	Sceloenopla godmani (Baly)	<i>Clusia flava</i> Planch. & Triana	Clusiaceae	L	Hespenheide and Dang 1999
Sceloenoplini	Sceloenopla gracilenta (Baly)	Unknown			
Sceloenoplini	Sceloenopla lampyridiformis	Unidentified	Viscaceae	L	Staines 2002a
	Staines				
Sceloenoplini	Sceloenopla longula (Baly)	Unidentified	Araceae	L	Hespenheide and Dang 1999
Sceloenoplini	Sceloenopla lutena Staines	Virola koschnyi Warb.	Myristicaceae	Α	Staines 2002a
Sceloenoplini	Sceloenopla minuta Staines	Unknown			
Sceloenoplini	Sceloenopla multistriata Uhmann	Virola koschnyi	Myristicaceae	U	Staines 2002a; Maes 2004
		Phonadendron sp.	Loranthaceae	U	
		Persea americana P. Mill.	Lauraceae	U	
Sceloenoplini	Sceloenopla nevermanni Uhmann	Anthurium sp.	Araceae	L	Uhmann 1944; Hespenheide
		<i>Cupania</i> sp	Sapindaceae	L	and Dang 1999
Sceloenoplini	Sceloenopla nigropicta Staines	Virola koschnyi	Myristicaceae	А	Staines 2002a
Sceloenoplini	Sceloenopla obscurovittata (Baly)	Philodendron radiatum radiatum Schott, Monstera tennic K Koch	Araceae	L	Hespenheide and Dang 1999
Sceloenoplini	Sceloenopla proxima (Balv)	Unknown			
Sceloenoplini	Sceloenopla scherzeri (Baly)	Davilla nitida (Vahl) Kubitzki	Dilleniaceae	L	Bondar 1937; Hespenheide
		<i>Persea gratissima</i> Gaertn.	Lauraceae	L	and Dang 1999
Sceloenoplini	Sceloenopla subparallela (Baly)	Unknown			

At La Selva *Cephaloleia* is the most speciose genus with 44 species from La Selva. The biology of various *Cephaloleia* species has been studied by Strong (1977a, b, 1982a, 1983), Seifert and Seifert (1976), Strong and Wang (1977), Auerbach and Strong (1981), and Morrison and Strong (1981). Since the only identification aid available to these workers was Baly (1885), which covered less than half of the species known from Central America, some of the published names are not associated with the correct species. However the published information does give valuable data on the general biology and ecology of *Cephaloleia* species. Staines (2004a) attempted to associate the biological data with the correct species. Additional biological work and host plant associations have been done by Johnson (2004a, b), Johnson and Horvitz (2005), McKenna and Farrell (2005), Descampe et al. (2008), Meskins et al. (2008), García-Robledo & Horvitz (2009, *in press*), and García-Robledo et al. (2010).

Cephaloleia eggs are flat, with a thin chorion; hence they are subject to desiccation. Eggs are laid on host surfaces. Oviposition sites vary among beetle species and host plant. The most common oviposition sites are leaf surfaces, petioles of immature leaves or inflorescence bracts. Eggs hatch in 10 to 20 days. Larvae begin feeding immediately upon the part of the plant on which the egg was laid. Cephaloleia larvae have a water penny-like appearance. They are flat and well adapted to moving between the wet surfaces of Zingiberales leaves, stems, and flowers. Larvae grow very slowly and go through up to eight molts depending on the size of the species and the part of the plant fed on. During their development, larvae of leaf and stem-feeding species utilize several leaves or even leaves on adjacent plants. Inflorescence-feeding larvae are restricted to a single inflorescence. Larvae of Cephaloleia species feed on the plant by dragging their mandibles across the plant surface while they crawl forward. This results in an irregularly shaped feeding scar and a trail of frass. Pupation occurs above ground, usually on the stalk of the host plant and lasts about 20 days. Adult Cephaloleia are found in the same habitat as larvae and cause similar feeding damage. Several different Cephaloleia species as well as other genera may utilize the same leaf, so larval associations require rearing (Strong 1977a, b, 1982a, 1983; Strong and Wang 1977; Auerbach and Strong 1981; and Morrison and Strong 1981).

Seven other genera of Cephaloleiini containing 14 species are known from La Selva. Most of these species are poorly known and not associated with their host plant.

The tribe Arescini consists of four genera and 17 species from the Neotropics (Staines 2002b). One genus and two species are known from Mesoamerica. None of the genera have been revised and little work has been done on the biology. *Chelobasis bicolor* Gray and *C. perplexa* Baly are found at La Selva. Strong (1977a, 1983) reported the larval host plants of *C. bicolor* as *Heliconia latispatha* Benth. and *H. tortuosa* Griggs (Heliconiaceae). Strong (1983) reported on the biology of this species indicating that eggs are laid on wet, tender tissue of the host plant and hatch in about 20 days. Larvae begin feeding in rolled leaves immediately after hatching. Development is slow, requiring at least eight months until pupation. Larvae require more than one leaf-roll to complete development and move from maturing leaf-rolls to more tender ones at night. If they are between leaf-rolls at daylight, they hide between the petiole and stalk

until nightfall. Adults are polymorphic (in color and size) and long-lived; in mark-recapture studies adults were found 18 months after marking.

Chelobasis perplexa is known to feed on *Calathea insignis* Hort. & Bull. (Marantaceae) and *H. imbricata* (Kuntze) Baker in Costa Rica (Maulik 1932). Strong & Wang (1977) and Auerbach and Strong (1981) reported *H. latispatha* as a larval host plant. The biology of this species is similar to that of *C. bicolor*.

The tribe Alurnini consists of six genera and 29 species (Staines 2002b) and contains some of the largest chrysomelids (25–45 mm). The tribe was revised by Fischer (1935) and I am in the process of revising it. Published life histories record various genera and species feeding on palms (Arecaceae) (Fischer 1935, Villacis Santos 1968, Macedo *et al.* 1994). Both Mesoamerican species, *Alurnus ornatus* Baly and *A. salvini* Baly, have been collected at La Selva. *Alurnus salvini* is the more commonly collected species.

The New World tribe Prosopodontini contains the genus *Prosopodonta* Baly with 26 species found from Nicaragua to Ecuador (Staines 2002b). The genus is in need of revision.

Two species, *P. distincta* (Baly) and *P. dorsata* (Baly), have been collected at La Selva. McCoy (1984, 1985) reported *P. dorsata* (as *Cheirispa*) adults and larvae feeding in accumulated leaf debris on the top of *Heliconia* leaves in Costa Rica and Ecuador. All other species of *Prosopodonta* have been reported as leaf-miners on various Arecaceae (Jolivet and Hawkeswood 1995). The photograph in McCoy (1984) is a *Prosopodonta* larvae (Maulik 1931). All other species of *Prosopodonta* are associated with Arecaceae and I have only found *P. dorsata* on unfurled palm fronds, never on *Heliconia*.

The tribe Sceloenoplini contains five genera and 299 species, with 154 species in the genus *Sceloenopla* Chevrolat (Staines 2002b). They are leaf-miners in a variety of plant families. This tribe is represented at La Selva by four genera and 20 species (see Table 1). There are 17 species of *Sceloenopla* known from La Selva. The biology is unknown for all species.

The tribe Chalepini consists of 55 genera and nearly 1000 species in the New World (Staines 2002b). Very few genera have been revised. All species studied are leaf-miners and appear to prefer dicots (Jolivet and Hawkeswood 1995). This tribe is represented at La Selva by 18 genera and 55 species (see Table 1). *Chalepus* is the most speciose genus with 14 species.

Habitat specificity

Hispines can be found in most non-aquatic habitats at La Selva. There are 46 species which feed on rolled leaves and inflorences of Zingiberales. This one feeding guild accounts for 33% of the hispine species known from La Selva.

Most hispines species seem to be restricted to understory to mid-canopy level plants. Work on hispines has shown many species to be monophagous or narrowly oligophagous. These species are found mostly in relation to their host plants. Other hispines are broadly oligophagous or polyphagous and can be found in many habitats.

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A continuing problem in inventory work is determining if the specimen collected was actually on its host plant or was a transient. Much of the earlier literature on host associations does not specify whether the insect was feeding as an adult, was breeding on the plant, or merely resting on it.

Relatively few species have only been collected from canopy fogging but these have been almost always undescribed species. Some of these species may actually be breeding in epiphytes rather than the fogged tree. *Calliaspis rubra* (Olivier) and *Acentroptera pulchella* Guérin-Méneville have been associated with bromeliads (Bromeliaceae) in South America (Lowman et al. 1996; Mantovani et al. 2005).

Biogeography

Most of the La Selva hispine fauna is closely related to South American species. Some species have distributions throughout the Neotropics such as *Aslamidium impurum* (Boheman), *Charistena ruficollis* (Fabricius), and *Imatidium thoracicum* Fabricius. However, the genera *Anisostena* Weise and *Glyphuroplata* Uhmann are most speciose in the Nearctic and the La Selva specimens are part of the southern extension of the genera (Staines 2002b). No La Selva hispines are exotic.

Many species appear to be Central American Atlantic lowland wet forest endemics but with congeners in South America. *Ocnosispa humerosa* Staines, *Sceloenopla bicolorata* Staines, *S. bidentata* Staines, *S. lutena* Staines, and *S. nigropicta* Staines appear to fall into this category.

Specimen identification

Of the 139 hispine species known from La Selva, 125 (89.9%) are described species with published names, one is a morphospecies which is known to be new, and 14 (11.2%) are morphospecies in groups whose taxonomy is too poorly known to determine whether they are new or not.

La Selva hispine species can be identified using the key to the genera in Staines (2002b). All genera and species of La Selva hispines are in the "hispines of La Selva" web site (http://viceroy.eeb.uconn.edu/ALAS/ALAS.html). This site includes a summary of hispines, species lists, keys to species, references to revisions and other taxonomic publications, and individual species accounts with images and natural history data.

Suggestions for future Research

What do hispines eat? A little more than half (63.3%) of La Selva hispines have any host plant association. Many of these have only been noted as being collected on a plant rather than actually feeding on it (listed as adult on Table 1). Since hispines are

intimately tied to their host plant, determining the food plant will give a much better picture of their distribution and abundance. Additional leaf-miner rearing work such as that of Hespenheide & Dang (1999) is needed to make larval host plant associations. Johnson (2004a, b), Johnson & Horvitz (2005), García-Robledo and Horvitz. (2009, *in press*), and García-Robledo et al. (2010) worked on the biology and ecology of several *Cephaloleia* species at La Selva.

What is the biology and ecology of hispines? Very little work has been done on the biology and ecology of La Selva hispines. Kirkendall (1984) studied the mating behavior of the North American *Odontota dorsalis* (Thunberg). Eberhard (1994) mentioned a hispine in his study of insect and spider courtship behavior. Staines and Staines (2001) and Flowers and Hanson (2003) suggested chrysomelids as potential indicator species assemblages for natural area monitoring. Farrell and Erwin (1988) showed that chrysomelids are a good indicator of local species richness. None of these ideas have been applied to hispines at La Selva.

What are the hispine host plant interactions? Strauss (1988) demonstrated that chrysomelids are a useful group for studing these interactions. Some work by Strong and his students (Strong 1977a, 1977b, 1981, 1982a, 1982b, Strong and Wang 1977), Horvitz and Schemske (2002), García-Robledo and Horvitz. (2009, *in press*), and García-Robledo et al. (2010) have added to our knowledge of this but much remains to be done.

How do pathogens, predators, and parasitoids influence hispine populations? Hispines are parasitized by various wasps and flies (Cox 1994) and mites (Santiago-Blay and Fain 1994). They also have a few recorded predators (Cox 1996) and pathogens (Balazuc 1988, Hazarika and Puzari 1990). Memmott and Godfray (1993), Memmott et al. (1993), and Lewis et al. (2002) developed food and parasitism webs for some hispine species. A great deal of work needs to be done on how these organisms interact and what effect they have on hispine populations and distribution.

How do hispine populations and distributions change over time? Staines (2004b) studied the changes in chrysomelid populations over time on Plummers Island, Maryland. With the baseline inventory data and local knowledge at La Selva, a similar project could be started.

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References

- Auerbach MJ, Strong DR (1981) Nutritional ecology of *Heliconia* herbivores: Experiments with plant fertilization and alternative hosts. Ecological Monographs 51: 63–83. doi: 10.2307/2937307
- Balazuc J (1988) Laboulbeniales (Ascomycetes) parasitic on Chrysomelidae. In: Jolivet P, Petitpeirre E, Hsaio TH (Eds) Biology of Chrysomelidae. Kluwer Academic Press, 389–398.
- Baly JS (1885) Hispidae. In: Godman FD, Salvin O (Eds) Biologia Centrali-Americana, Zoology, Insecta, Coleoptera, Phytophaga. 6(2): 1–124.
- Bondar G (1931a) Notas biologicas sobre alguns hispineos observados na Bahia. O Campo 2: 74–75.
- Bondar G (1931b) Notas biologicas sobre algnus Hispineos brasileiros. Correio Agricola Bahia 9: 134–137.
- Bondar G (1937) Notas entomologicas da Bahia (I). Revista de Entomologia Rio de Janeiro 7: 475–483.
- Bondar G (1940) Novas observações sobre *Himatidium neivai* Bondar, praga do coqueiro. O Campo 11(129): 26–27.
- Casari SA, Teizeira EP (2004) Immatures of *Heterispa vinula* (Erichson) and *Physocoryna scabra* Guérin-Méneville (Coleoptera, Chrysomelidae, Cassidinae, Chalepini). Revista Brasileira de Entomologia 48(4): 473–480.
- Cavey JF (1994) Annotated new distributional records for North American Chrysomelidae (Coleoptera). Coleopterists Bulletin 48: 1–9.
- Cox ML (1994) The Hymenoptera and Diptera parasitoids of Chrysomelidae. In: Jolivet PH, Cox ML, Petitpierre E (Eds) Novel aspects of the biology of Chrysomelidae. Kluwer Academic Press, 419–467.
- Cox ML (1996) Insect predators of Chrysomelidae. In: Jolivet PHA, Cox ML (Eds) Chrysomelidae Biology. Vol. 2: Ecological studies. SPB Academic Publishing. Amsterdam, 23–91.
- Descampe A, Meskins C, Pasteels J, Windsor D, Hance T (2008) Potential and realized feeding niches of Neotropical hispine beetles (Chrysomelidae, Cassidinae, Cephaloleiini). Environmental Entomology 37(1): 224–229. doi: 10.1603/0046-225X(2008)37[224:PARFN O]2.0.CO;2
- Eberhard WG (1994) Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. Evolution 48: 711–733. doi: 10.2307/2410481
- Farrell BD, Erwin TL (1988) Leaf-beetle community structure in an amazonian rainforest canopy. In: Jolivet P, Petitpierre E, Hsiao TH (Eds) Biology of Chrysomelidae. Kluwer Academic Publishers, 73–90.
- Fischer CR (1935) Os coleopteros phytophagos da tribu Alurnini, pragas das palmeiras (Chrysomelidae, Hispinae). Revista de Entomologica Rio de Janiero 5: 257–292.
- Flowers RW, Hanson PE (2003) Leaf beetle (Coleoptera: Chrysomelidae) diversity in eight Costa Rican habitats. In: Furth DG (Ed) Special topics in leaf beetle biology, Proceedings of the 5th International Symposium on the Chrysomelidae. Pensoft Publishers, 25–51.

- Flowers RW, Janzen, DH (1997) Feeding records of Costa Rican leaf beetles (Coleoptera: Chrysomelidae). Florida Entomologist 80: 334–366. doi: 10.2307/3495768
- Furth DG, Longino JT, Paniagua M (2003) Survey and quantitative assessment of flea beetle diversity in a Costa Rican rainforest (Coleoptera: Chrysomelidae: Alticinae). In: Furth DG (Ed) Special topics in leaf beetle biology. Proceedings of the Fifth International Symposium on the Chrysomelidae. Pensoft Publishers, 1–23.
- García-Robledo C, Horvitz CC (2009) Host plant scents attract rolled-leaf beetles to Neotropical gingers in a Central American tropical rain forest. Entomologia Experimentalis et Applicata 131: 115–120. doi: 10.1111/j.1570-7458.2009.00843.x
- García-Robledo C Horvitz CC (*in press*) Experimental demography of generalist and specialist insect herbivores on novel and native host plants. Journal of Animal Ecology.
- García-Robledo C, Horvitz CC, Staines CL (2010) Larval morphology and development, host plants, adult longevity, sexual dimorphism and notes on natural history in *Cephaloleia* rolled-leaf beetles (Coleoptera: Chrysomelidae: Hispinae). Zootaxa 2610: 50–68.
- Gilbert AJ, Andrews FE, Staines CL (2001) An unusual host record for *Imatidium* and new distributional records for *I. rufiventre* Boheman and *I. thoracicum* Fabricius (Coleoptera: Chrysomelidae: Hispinae: Cephaloleiini). Pan-Pacific Entomologist 77(4): 278–280.
- Hartshorn GS, Himmel BE (1994) Vegetation types and floristic patterns. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (Eds) La Selva: Ecology and natural history of a Neotropical rainforest. University of Chicago Press, 73–89.
- Hazarika LK, Puzari KC (1990) *Beauveria bassiana* (Bals.) Vuill. for biological control of rice hispa (RH) in Assam, India. International Rice Research Newsletter 15(1): 31.
- Hespenheide HA, Dang V (1999) Biology and ecology of leaf-mining Hispinae (Coleoptera, Chrysomelidae) of the La Selva Biological Station, Costa Rica. In: Cox ML (Ed) Advances in Chrysomelidae Biology 1. Backhuys Publishers, 375–389.
- Horvitz CC, Schemske DW (2002) Effects of plant size, leaf herbivory, local competition and fruit production on survival, growth and future reproduction of a neotropical herb. Journal of Ecology 90: 279–290. doi: 10.1046/j.1365-2745.2001.00660.x
- Johnson DM (2004a) Life history and demography of *Cephaloleia fenestrata* (Hispinae: Chrysomelidae: Coleoptera). Biotropica 36(3): 352–361.
- Johnson DM (2004b) Source-sink dynamics in a temporary heterogeneous environment. Ecology 85(7): 2037–2045. doi: 10.1890/03-0508
- Johnson DM, Horvitz CC (2005) Estimating postnatal dispersal: Tracking the unseen dispersers. Ecology 86(5): 1185–1190. doi: 10.1890/04-0974
- Jolivet P, Hawkeswood TJ (1995) Host-plants of Chrysomelidae of the world. Backhuys Publishers, Leiden.
- Kirkendall LR (1984) Long copulatory and post-copulatory 'escort' behaviour in the locust leafminer, *Odontota dorsalis* (Coleoptera: Chrysomelidae). Journal of Natural History 18: 905–919. doi: 10.1080/00222938400770791
- Lewis OT, Memmott J, LaSalle J, Lyal CHC, Whitefoord C, Godfray HCJ (2002) Structure of a diverse tropical forest insect-parasitoid community. Journal of Animal Ecology 71: 855–873. doi: 10.1046/j.1365-2656.2002.00651.x

- Lowman MD, Wittman PK, Murray D (1996) Herbivory in a bromeliad of the Peruvian rain forest canopy. Journal of the Bromeliad Society 46: 52–55.
- de Macedo MV, Monteiro RF, Lewinsohn TM (1994) Biology and ecology of *Mecistomela marginata* (Thunberg, 1821) (Hispinae: Alurnini) in Brazil. In: Jolivet PH, Cox ML, Petitpierre E (Eds) Novel aspects of the biology of Chrysomelidae. Kluwer Academic Publishers, 567–571.
- Maes JM (2004) Insectos asociados a algunos cultivos tropicales en el Atlantico de Nicaragua. Parte IV: Aguacate (*Persea americana*, Lauraceae). Revista Nicaragüense de Entomología 64(Supplemento 1, parte IV): 1–262.
- Maes JM, Staines CL (1991) Catalogo de los Chrysomelidae (Coleoptera) de Nicaragua. Revista Nicaragüense de Entomología 18: 1–53.
- Mantovani A, Magalháes N, Teixeira ML, Leitão G, Staines CL, Resendo B (2005) First report on host plants and feeding habits of the leaf beetle *Acentroptera pulchella* Guérin- Méneville (Chrysomelidae, Hispinae). In: Konstantinov AS, Penev L, Tishechkin A (Eds) Contributions to systematics and biology of insects: Papers celebrating the 80th birthday of I. K. Lopatin. Pensoft Publishers, 153–157.
- Maulik S (1931) On the structure of larvae of hispine beetles. Proceedings of the Zoological Society of London 1931: 1137–1162.
- Maulik S (1932) On the structure of larvae of hispine beetles-II. Proceedings of the Zoological Society of London 1932: 293–322.
- Maulik S (1937) Distributional correlation between Hispine beetles and their host plants. Proceedings of the Zoological Society of London, Series A 1937: 129-159.
- McCoy ED (1984) Colonization by herbivores of *Heliconia* spp. plants (Zingiberales: Heliconiaceae). Biotropica 16: 10–13. doi: 10.2307/2387887
- McCoy ED (1985) Interactions among leaf-top herbivores of *Heliconia imbracata* (Zingiberales: Heliconiaceae). Biotropica 17: 326–329. doi: 10.2307/2388596
- McDade LA, Hartshorn GS (1994) La Selva Biological Station. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (Eds) La Selva: Ecology and natural history of a Neotropical rainforest. University of Chicago Press, 6–14.
- McKenna DD, Farrell BD (2005) Molecular phylogenetics and evolution of host plant use in the Neotropical rolled leaf 'hispine' beetle genus *Cephaloleia* (Chevrolat) (Coleoptera: Cassidinae). Molecular Phylogenetics and Evolution 37: 117–131. doi: 10.1016/j. ympev.2005.06.011
- Memmott J, Godfray HCJ. (1993) Parasitoid webs. In: LaSalle J, Gauld ID (Eds) Hymenoptera and biodiversity. CAB International, 217–234.
- Memmott J, Godfray HCJ, Bolton B (1993) Predation and parasitism in a tropical herbivore. Ecological Entomology 18: 348–352. doi: 10.1111/j.1365-2311.1993.tb01111.x
- Memmott J, Godfray HCJ, Gauld ID (1994) The structure of a tropical host-parasitoid community. Journal of Animal Ecology 63: 521–540. doi: 10.2307/5219
- Meskins C, Windsor D, Hance T (2008) A comparison of hispine beetles (Coleoptera: Chrysomelidae) associated with three orders of monocot host plants in lowland Panama. International Journal of Tropical Insect Science 27(3/4): 159–171. doi: 10.1111/j.1365-2311.1981.tb00972.x

- Morrison G, Strong DR (1981) Spatial variations in egg density and the intensity of parasitism in a neotropical chrysomelid (*Cephaloleia consanguinea*). Ecological Entomology 6: 55–61.
- Riley EG (1985) Review of the North American species of *Glyphuroplata* Uhmann, 1940 (Coleoptera: Chrysomelidae: Hispinae). Journal of the Kansas Entomological Society 58: 428-436.
- Sanford RL, Paaby P, Luvall JC, Phillips E (1994) Climate, geomorphology, and aquatic systems. In: McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS (Eds) La Selva: Ecology and natural history of a Neotropical rainforest. University of Chicago Press, 3–33.
- Santiago-Blay JA, Fain A (1994) Phoretic and ectoparasitic mites (Acari) of the Chrysomelidae. In: Jolivet PH, Cox ML, Petitpierre E (Eds) Novel aspects of the biology of Chrysomelidae. Kluwer Academic Publishers, 407–417.
- Schlottfeldt CS (1944) Insetos encontrados em plantas cultivadas e communs- Viçosa, Minas Gerais. Revista Ceres 6(32): 108–127.
- Seeno TN, Wilcox JA (1982) Leaf beetle genera (Coleoptera: Chrysomelidae). Entomography 1: 1–221.
- Seifert RP, Seifert FH (1976) A community matrix of *Heliconia* insect communities. American Naturalist 110: 461–483. doi: 10.1086/283080
- Spaeth F (1938) Die Gattung *Himatidium* Fabr. (Col. Cassidinae). Revista de Entomología Rio de Janiero 9: 305–317.
- Staines CL (1996) The genus *Cephaloleia* (Coleoptera: Chrysomelidae) in Central America and the West Indies. Special Publication No. 3 of the Revista de Biología Tropical, 87 pp.
- Staines CL (1997) The Hispinae (Coleoptera: Chrysomelidae) of Nicaragua. Revista Nicaragüense de Entomología 37/38: 1–65.
- Staines CL (2002a) Nomenclatural notes and new species of Sceloenoplini (Coleoptera: Chrysomelidae: Cassidinae). Zootaxa 89: 1–32.
- Staines CL (2002b) The New World tribes and genera of hispines (Coleoptera: Chrysomelidae: Cassidinae). Proceedings of the Entomological Society of Washington 104(3): 721–784.
- Staines CL (2004a) Cassidines and Zingiberales: A review of the literature. In: Jolivet P, Santiago-Blay JA, Schmitt M (Eds) New contributions to the biology of Chrysomelidae. SPB Academic Publishing, 307–319.
- Staines CL (2004b) Changes in the chrysomelid community (Coleoptera) over a ninety-five year period on a Maryland river island. In: Jolivet P, Santiago-Blay JA, Schmitt M (Eds) New contributions to the biology of Chrysomelidae. SPB Academic Publishing, 613–622.
- Staines CL (2006) The hispine beetles (Coleoptera: Chrysomelidae: Cassidinae) of America north of Mexico. Virginia Museum of Natural History Special Publication Number 13, 178 pp.
- Staines CL, Staines SL (2001) The leaf beetles (Insecta: Coleoptera: Chrysomelidae): Potential indicator species assemblages for natural area monitoring. In: Therres GD (Ed) Proceedings of Conservation of biological diversity: A key to restoration of the Chesapeake Bay ecosystem and beyond. Maryland Department of Natural Resources, 233–244.
- Strauss SY (1988) The Chrysomelidae: a useful group for investigating herbivore-herbivore interactions. In: Jolivet P, Petitpierre E, Hsiao HS (Eds) Biology of Chrysomelidae. Kluwer Academic Press, 91–105.

- Strong DR (1977a) Rolled-leaf hispine beetles (Chrysomelidae) and their Zingiberales host plants in Middle America. Biotropica 9: 156–169. doi: 10.2307/2387878
- Strong DR (1977b) Insect species richness: Hispine beetles of *Heliconia latispatha*. Ecology 58: 573–582. doi: 10.2307/1939006
- Strong DR (1981) The possibility of insect communities without competition: Hispine beetles on *Heliconia*. In: Denno RF, Dingle H (Eds) Insect life history patterns habitat and geographic variation. Springer-Verlag, 183–194.
- Strong DR (1982a) Potential interspecific competition and host specifity: Hispine beetles on *Heliconia*. Ecological Entomology 7: 217–220. doi: 10.1111/j.1365-2311.1982.tb00660.x
- Strong DR (1982b) Harmonious coexistence of hispine beetles on *Heliconia* in experimental and natural communities. Ecology 63: 1039–1049. doi: 10.2307/1937243
- Strong DR (1983) Chelobasis bicolor (Abejón de Platanillo, Rolled Leaf Hispine). In: Janzen DH (Ed) Costa Rican Natural History. University of Chicago Press, 708–711.
- Strong DR, Wang MD (1977) Evolution of insect life histories and host plant chemistry: Hispine beetles on *Heliconia*. Evolution 31: 854–862. doi: 10.2307/2407447
- Uhmann E (1930) Hispinen aus Costa Rica aus der Ausbeute der Herrn. Ferd. Nevermann. 20. Beitrag zur Kenntnis der Hispinen (Col. Chrys.). Folia Zoologica et Hydrobiologica 1: 209–256.
- Uhmann E (1934) Hispinen-Minen aus Costa Rica. 48. Beitrag zur Kenntnis der Hispinen (Col.: Chrysomelidae). Arbeiten über physiologische und angewandte Entomologie aus Berlin-Dahlem 1: 272–277.
- Uhmann E (1935) Neue Hispinen aus Costa Rica. II. Teil. 52. Beitrag zur Kenntnis der Hispinen (Col. Chrys.). Entomologische Blätter 31: 103–106.
- Uhmann E (1937) Hispinen-Minen aus Costa Rica. II. Teil. 62. Beitrag zur Kenntnis der Hispinen (Coleoptera: Chrysomelidae). Arbeiten über physiologische und angewandte Entomologie aus Berlin-Dahlem 4: 61–66.
- Uhmann E (1944) Hispinen-Minen aus Costa Rica (Coleoptera: Chrysomelidae). 104. Beitrag zur Kenntnis der Hispinen. Arbeiten über physiologische und angewandte Entomologie aus Berlin-Dahlem 11: 59–61.
- Uhmann E (1950) Hispinae aus dem Britischen Museum. V. Teil. 129. Beitrag zur Kenntnis der Hispinae (Coleopt. Chrysom.). Annals and Magazine of Natural History (12)3: 324–337. doi: 10.1080/00222935008654055
- Uhmann E (1957) Coleopterorum Catalogus Supplementa. Chrysomelidae: Hispinae, Hispinae Americanae. W. Junk. s'Gravenhage. pars 35(1): 1–153.
- Villacis Santos J (1968) Algunas características biológicas y etológicas del *Alurnus humeralis* Rosenberg "gusano chato o cogollero" de la palma africana. Turrialba 18: 115–128.
- Windsor DM, Riley EG, Stockwell HP (1992) An introduction to the biology and systematics of Panamanian Tortoise Beetles (Coleoptera: Chrysomelidae: Cassidinae). In: Quintero D, Aiello A (Eds) Insects of Panama and Mesoamerica, Selected studies. Oxford University Press, 372–391.
- Würmli M (1975) Gattungmonographie der altweltlichen Hispinen (Coleoptera: Chrysomelidae: Hispinae). Entomologische Arbeiten aus dem Museum G. Frey 26: 1–83.

RESEARCH ARTICLE



Cytogenetics, cytotaxonomy and chromosomal evolution of Chrysomelinae revisited (Coleoptera, Chrysomelidae)^{*}

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Abstract

Nearly 260 taxa and chromosomal races of subfamily Chrysomelinae have been chromosomally analyzed showing a wide range of diploid numbers from 2n = 12 to 2n = 50, and four types of male sexchromosome systems. with the parachute-like ones Xy_p and XY_p clearly prevailing (79.0%), but with the XO well represented too (19.75%). The modal haploid number for chrysomelines is n = 12 (34.2%) although it is not probably the presumed most plesiomorph for the whole subfamily, because in tribe Timarchini the modal number is n = 10 (53.6%) and in subtribe Chrysomelina n = 17 (65.7%). Some well sampled genera, such as *Timarcha, Chrysolina* and *Cyrtonus*, are variable in diploid numbers, whereas others, like *Chrysomela, Paropsisterna, Oreina* and *Leptinotarsa*, are conservative and these differences are discussed. The main shifts in the chromosomal evolution of Chrysomelinae seems to be centric fissions and pericentric inversions but other changes as centric fusions are also clearly demonstrated. The biarmed chromosomes at least. A significant negative correlation between the haploid numbers and the asymmetry in size of karyotypes (r = -0.74) has been found from a large sample of 63 checked species of ten different genera. Therefore, the increases in haploid number are generally associated with a higher karyotype symmetry.

Keywords

chromosomes, leaf-beetles, diploid numbers, modal numbers, sex-chromosome systems, intrageneric evolution, karyotype symmetry

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Introduction

The subfamily Chrysomelinae is a large cosmopolitan taxon of nearly 2000 species (Farrell 1998) or even 3000 worldwide species (Reid et al. 2009), in some 133 genera (Daccordi 1994). They are mostly round and highly convex leaf-beetles, living mainly in temperate regions of Australia and South America, but well represented also in the Holarctic region (Daccordi 1982). A very interesting feature of the species in this subfamily is a striking ecological specialisation, due to their trophic selection on plants usually belonging to the same botanic family, and very often even, on one or a few closely related plant genera (Jolivet and Hawkeswood 1995). Chrysomelinae has been characterized as a fixed taxonomic group which can be distinguished by many apomorphic characters of adults and larvae (Chen 1935). Recent molecular and morphological studies support their monophyletic origin (Duckett et al. 2004; Farrell and Sequeira 2004), although a much larger sampling on 30 species indicates paraphyly of *Timarcha* with regard to the other chrysomelines (Gómez-Zurita et al. 2008).

The current cytogenetic findings in this subfamily cover a total of 259 taxa and chromosomal races, that is between 8,6% and 13.0% of those described, which have been surveyed at least with the first level of chromosomal knowledge, usually called α -karyology (White 1978), basically referred to diploid numbers and sex-chromosome systems. Since our first published list of karyologically checked taxa of Chrysomelinae along with the remaining leaf beetles (Petitpierre et al. 1988), and their rough chromosomal evolution (Petitpierre and Segarra 1985) based upon 165 species, new findings have been added in the last 25 years (Petitpierre 1999a, 1999b; Petitpierre and Garneria 2003; Gómez-Zurita et al. 2004; Petitpierre and Grobbelaar 2004; Petitpierre et al. 2004; Petitpierre and Elgueta 2006; Petitpierre and Mikhailov 2009), which deserve further approach and discussion in order to improve our views on the cytogenetic evolution and cytotaxonomy of this subfamily.

Material and methods

The cytogenetic data were mostly obtained by testis dissection of adult or pupa male specimens, which were fixed, teased, squashed, and finally treated by using conventional staining procedures. A great majority of the cells used for these analyses were in meiotic metaphase I stages, which provide the male meioformula, so including the number of autosomal bivalents, male sex-chromosome system, and the possible presence of accessory chromosomes. In addition, less than 50% of the analysed species were also studied in their karyotype architecture from spermatogonial cells in mitotic metaphases or, more seldom, from meiotic metaphase II cells. These more in-depth analyses, gave up worth information on the size and shape of all chromosomes of specific karyotypes, at this second level of cytogenetic resolution known as ß-karyology (White 1978).
Other cytogenetic findings of an even much finer resolution, such as those on genome size, C and/or Ag-banding, and fluorescent *in-situ* hybridization (FISH), have been reported in so few species that they should not be discussed in the frame of this contribution.

Although all the recent and also ancient authors accept the reality of the subfamily Chrysomelinae, the number and names of its tribes and subtribes differ strikingly among them. Thus, very recently, Kippenberg (2010) for instance, proposes five tribes and nine subtribes, based principally on the poorly sampled pupal morphology, whereas Daccordi (1994) and Riley et al. (2002) consider only two tribes, Timarchini and Chrysomelini, the former with one and the latter with four subtribes, and Reid (2002) states four tribes, each one with only one subtribe except Gonioctenini with two. We shall follow here a mixed criterion taken from these latter authors with a few changes according with my own opinions, thereby, we assume the tribes Timarchini and Chrysomelini, the former with the subtribe Timarchina only, and the latter with five subtribes: Entomoscelina (= Phyllocharitina *sensu* Reid 2002), Chrysolinina, Doryphorina, Gonioctenina and Chrysomelina.

Chromosome numbers and sex-chromosome systems

The Chrysomelinae show a wide variation of diploid chromosome numbers and meioformulas, from 2n = 12 and 5 + neo XY, respectively, in the South American *Doryphora quadrisignata* (Vidal, 1984), to 2n = 50 and $24 + Xy_p$ in the European *Chrysolina rufoaenea* (Petitpierre and Mikhailov, 2009). These shifts in number are almost always due to structural chromosome rearrangements, because only a few polyploidy parthenotes have been recognized to date, all of them restricted to the genus *Calligrapha*, (Robertson 1966, Smith and Virkki 1978). The range of variation of haploid numbers for the total 259 taxa and chromosomal races in the 38 examined genera, shows an almost continuous list of numbers (fig. 1A) but with a modal one of n = 12 (34.2%), followed by three others of n = 10 and n = 17 (both with 9.6%), and n = 20 (7.6%).

Conversely, the parachute-like sex-chromosome system (Xy_p), of a non-chiasmate nature, is clearly prevailing in the subfamily (79.0%) as shown in fig. 1B. This system consists mostly of a large X and a small y-chromosome, looking such as this configuration at metaphase I, or more rarely, two large X and Y chromosomes (XY_p), held together by a non-nucleolar argyrophilic substance (Virkki 1984; Postiglioni and Brum-Zorrilla 1988; Virkki et al. 1991). The Xy_p is probably the most plesiomorphous condition in Chrysomelinae, as it is for the whole beetles of the suborder Polyphaga (Smith 1951; Smith, 1952; Smith and Virkki, 1978), while the others so far checked in the subfamily, the XO (19.75%) and neoXY or XY systems (1.2%) (fig. 1B), are certainly derived from the former.

Although the modal number of n = 12 chromosomes has been found in five out of the six reported subtribes, it is very seldom in Timarchina (fig. 2A) and Chrysomelina (fig. 6A), and it does not occur to date in the poorly surveyed Entomoscelina, with



Figures 1–3. Basic chromosomal data on higher taxa of Chrysomelinae

only seven analyzed species (Petitpierre and Grobbelaar 2004, Petitpierre unpublished), belonging to five among the 27 described genera (Daccordi, 1994). Consequently, it can not be presently taken as the presumed ancestral number for the whole subfamily, despite being probably this for the subtribes Chrysolinina (fig. 3A), Gonioctenina (fig. 5A), and less reliably for the Doryphorina (fig. 4A).

The Timarchina subtribe shows a striking modal value of n = 10, and $9 + Xy_p$ meioformula (figs. 2A-2B), which are the modal and presumably the possible plesiomorphous state for this group, as well as for the whole beetles of the suborder Polyphaga (Smith 1952; Smith and Virkki 1978; Angus et al. 2007). However, some caution should be exerted before assuming the previous point, because the two most ancestral extant subgenera of Timarcha, Americanotimarcha and Metallotimarcha, both on morphological and molecular grounds (Iablokof-Khnzorian 1966; Jolivet 1989; Gómez-Zurita et al. 2000; Gómez-Zurita 2004), comprise only species showing the highest diploid numbers found in the genus, 2n = 38 and 2n = 44 (Petitpierre and Jolivet, 1976, Jolivet and Petitpierre 1992; Petitpierre, unpublished). If these high numbers were the possible plesiomorphous condition for the chromosomal evolution in *Tima*rcha, how could have derived all the common 20-chromosome species by independent processes? The most parsimonious view would be assuming a hypothetic stem species for the genus, represented with a karyotype of 20-chromosomes, from which the ancient ancestors of the three extant subgenera would have splitted. The Americanotimarcha and Metallotimarcha through multiple chromosome fissions, followed by pericentric inversions and/or chromatin accretions of uniarmed elements, to recover some of them later to their ancient biarmed condition, while within the species-rich *Timarcha* s.str. subgenus much more conservative events of chromosomal shifts had presumably occurred in the karyological origin of most species.

The subtribe Doryphorina displays a 2n(3) = 35 modal chromosome number and 17 + XO meioformula (figs. 4A–4B), but this can be attributed to a biased sampling on the species of *Leptinotarsa*, all but one sharing these values (Hsiao and Hsiao 1983). Nevertheless, the species of the remaining eight genera of analyzed Doryphorina, out of the two closely related in the genus *Labidomera*, have karyotypes of much lower chromosome numbers, namely, n = 12 in six species of five different genera, *Desmogramma*, *Leucocera*, *Strichosa*, *Platyphora* and *Zygogramma*, a fact which could possibly hint towards the supposed most plesiomorphous karyotype condition for this subtribe too, as we have assumed before.

On the contrary, in subtribe Chrysomelina the modal number and meioformula are 2n = 34 and $16 + Xy_p$, respectively (Figs. 6A and 6B), shared by 65.7% of the 35 surveyed species in twelve genera, and we assumed that this should possibly be the ancestral condition (Petitpierre and Segarra, 1985) for this taxon, but with our present enlarged screening of species and genera, it is more uncertain due to the absence of this $2n = 34(Xy_p)$ karyotype and meioformula in half of the twelve sampled genera.

If we study the α -karyology of chrysomelines at the genus level, we find genera with high chromosomal diversity, as measured by standard deviation (SD) of their male diploid chromosome numbers, for example *Chrysolina* with SD = 8.67 in 72 sampled taxa and chromosomal races, *Timarcha* with SD = 4.33 in 42 taxa, and *Cyrtonuss* with SD = 6.33 in 15 taxa, whereas other genera have zero or a low diversity such as *Paropsisterna* with SD = 0 in 10 taxa, *Chrysomela* with SD = 0 in 9 taxa, *Oreina* with SD = 1.15 in 12 taxa, and *Leptinotarsa* with SD = 2.77 in 16 taxa. The differences between "variable" and "conservative" genera in their chromosome numbers, were ten-



Figures 4–6. Basic chromosomal data on higher taxa of Chrysomelinae

tatively explained according with the ability for dispersal of flying vs. flightless species genera, and the number of host-plant families they are able to feed, being both characters in a presumed relationship with the size of local populations and thereby with the chances of fixation for new chromosomal shifts (Petitpierre et al. 1993). Under these premises, the genera with flying species and feeding on only one or two plant-families would presumably constitute larger local populations and, consequently, they are less able to fix new chromosomal mutations by random genetic drift and/or inbreeding

than those genera of flightless species and feeding on a good number of plant families as particular habitats to live and breed for each beetle species. *Timarcha* and *Cyrtonus* consist of apterous species only, most *Chrysolina* have wings but are flightless, and these three genera feed on six, one, and seven plant families respectively, and they share high heterogeneities of diploid numbers (SD > 4.0); on the contrary, *Paropsisterna, Chrysomela* and *Leptinotarsa* have flying species, the first two feeding on a unique plant family each and the third on three, but *Oreina* has some species completely unable to fly and others flying very seldom, in spite of being chromosomally "conservative" as the previous three genera (SD ≤ 4.0), and feeding on two plant families only (Petitpierre et al. 1993). Hence, these two features alone can not account for all the observed intrageneric variation in diploid chromosome numbers of these chrysomelines.

Evolution of chromosomal architecture

The chromosomes may show a huge variable morphology in size and shape, some species have karyotypes made of very few chromosomes of a large size while others have karyotypes of many small chromosomes and there are not evidences of any advantages of ones over others, although minute chromosomes are more easily lost at meiosis if a chiasma fails to be formed, and very large acro- or telocentric chromosomes can be cut across before they have been properly separated at anaphase (Sumner 2003). Anyway, chromosomes are elements of the genetic system that may supply worth features to explain evolution among closely related species (White 1973, King 1993).

Some 80 among the 259 presently know taxa or chromosomal races of chrysomelines have been examined at the level of ß-karyology i.e. by identifying size and shape of individual chromosomes in each karyotype. Such kind of studies have been mainly carried out in certain genera, the North American Calligrapha (Robertson 1966) and Leptinotarsa (Hsiao and Hsiao 1983), and the Holarctic Timarcha (Petitpierre 1970, 1976; Gómez-Zurita et al. 2006), and the Palaearctic Chrysolina (Petitpierre 1981, 1983, 1999a, 1999b; Petitpierre et al. 2003; Petitpierre and Mikhailov 2009) and Cyrtonus (Petitpierre and Garneria 2003). The karyotypes of chrysomelines are usually composed of meta- or submetacentric chromosomes as occur mostly in all groups of Coleoptera (Smith and Virkki 1978; Virkki 1984). This means that the shifts in number due to centric fissions, should necessarily rebuild the emerging acrocentric chromosomes into biarmed ones by pericentric inversions or heterochromatin accretions (Virkki 1984; Virkki and Santiago-Blay 1993), and this secondary metacentry has been described in diphasic chromosomes of several beetle species (Virkki 1984). Taking into account the biarmed shape of most chromosomes in chrysomelines, and in other beetles in general, it is evident that the number of major chromosome arms (FN = fundamental number) could not remain constant and increase accordingly with the diploid number. Nevertheless, many species of high diploid numbers have at least a few acrocentric or subacrocentric chromosomes, which may be the ancient survivors of primary shifts by centric fissions. For instance, the Nearctic Timarcha intricata with 2n

= 44 has 15 of such autosome pairs (Petitpierre and Jolivet, 1976; Petitpierre, 1988a), Leptinotarsa lineolata, L. behrensi and L. decemlineata (the potato beetle), all with 2n $(\mathcal{E}) = 35$, have seven, four and three, respectively (Hsiao and Hsiao 1983), the Palaearctics Timarcha pimelioides with 2n = 28 has five (Petitpierre 1976, 1988), Chrysolina gypsophilae with 2n = 32 has three (Petitpierre 1999b), Ch. diluta with 2n = 36 and *Ch. haemoptera* with 2n = 40 have four (Petitpierre 1988), *Ch. lepida* with 2n = 42 has six, whereas its closely related Ch. fuliginosa, also with 2n = 42, has none (Petitpierre 1999a). The extreme cases are those of the European Ch. carnifex and Ch. interstincta both with 2n = 40 and having only acrocentric chromosomes, contrary to Ch. helopi*oides* with $2n \left(\bigcirc \right) = 47$ and lacking any of them (Petitpierre 1981; Petitpierre 1999a; Petitpierre and Segarra 1985; Petitpierre et al. 2004). In conclusion, the FN even in species having similar numbers as the latter, can be strikingly distinct, FN = 40 in Ch. carnifex and Ch. interstincta, and FN = 94 in Ch. helopioides. Additional examples of frequent increases of acrocentric chromosomes in Polyphaga beetles associated with high diploid numbers are those which have been reported in Buprestidae (Karagyan and Lachowska 2007) and in Curculionidae (Lachowska et al. 1998).

Karyotypes can also be classified as symmetrical in size when all chromosomes have similar magnitudes, and asymmetrical when there are two clearly distinct size classes, and these two alternatives can also be applied to chromosome shape, uniarmed chromosomes for asymmetrical and biarmed ones for symmetrical karyotypes (Stebbins 1971; White 1973).

For the sake of simplicity we should only consider here the asymmetry vs. symmetry in chromosome size but not in shape. The karyotypes of Chrysomelinae offer examples of both types but more often of intermediate states, that is, with chromosomes of gradually decreasing sizes. In order to measure the degree of asymmetry of a karyotype we have used the standard deviation (SD) of each chromosome relative length with respect to the averaged % length taken from the total complement length (TCL) (Petitpierre and Segarra 1985). Here again we use this parameter but measuring the % of each chromosome length at mitotic metaphase with regard to the haploid TCL including the X but not the Y-chromosome, therefore, treating identically the species with or without a Y-chromosome. In this sense, we have calculated the SDs of asymmetry in 63 species and subspecies, whose karyotypes were mostly published, from the following ten genera of chrysomelines: the Holarctic Timarcha (Petitpierrre 1970, 1976), and the Nearctics or Palaearctics Calligrapha (Robertson 1966), Chrysolina (Petitpierre 1983, 1999a, 1999b; Petitpierre and Segarra 1985; Petitpierre et al. 2004), Oreina (Petitpierre 1999a), Cyrtonus (Petitpierre and Segarra 1985; Petitpierre and Garneria 2003), Leptinotarsa and Labidomera (Hsiao and Hsiao 1983), Phratora (Petitpierre and Segarra 1985), and the Neotropical Araucanomela (Petitpierre and Elgueta 2006) and Henicotherus (Petitpierre unpublished).

These cytogenetic results are reported in Table 1 and they were used to obtain the coefficient of correlation (r) between these two cytological parameters, haploid chromosome number and SD of karyotype asymmetry, which was clearly negative with a highly significant likelihood, r = -0.74 (P > 0.99). In brief, the increase in haploid

	n	DS		n	DS
Timarcha balearica	11	3.57	Cyrtonus cobosi	14	3.36
T. calceata	15	2.30	C. contractus	14	2.19
T. cyanescens	10	4.71	C. elegans	14	2.11
T. erosa vermiculata	10	6.28	C. plumbeus	14	2.29
T. fallax	10	4.66	Oreina ludovicae	12	3.32
T. intermedia	10	3.41	Calligrapha alni	12	3.73
T. lugens	10	4.02	C. amator	12	3.42
T. marginicollis	10	4.09	C. bidenticola	12	3.32
T. pimelioides	14	4.01	C. californica corepsivora	12	4.76
T. recticollis	10	4.72	C. confluens	12	3.32
T. rugosa	13	3.45	C. multipunctata bigsbyana	12	3.39
T. sicelidis	10	5.27	C. philadelphica	12	3.14
T. strangulata	14	1.68	C. pnirsa	12	3.41
Ch. affinis baetica	12	1.65	C. pruni	12	3.95
Ch. americana	12	1.98	C. rowena	12	3.42
Ch. bankii	12	2.12	C. verrucosa	12	3.16
Ch. bicolor	12	1.60	Labidomera clivicollis	17	2.36
Ch. carnifex	20	1.29	L. suturella	16	2.11
Ch. coerulans	12	3.05	Leptinotarsa behrensi	18	1.84
Ch. costalis	12	2.54	L. decemlineata	18	1.51
Ch. femoralis	12	1.65	L. defecta	18	1.83
Ch. gypsophilae	16	2.76	L. haldemani	18	1.38
Ch. haemoptera	20	1.54	L. heydeni	18	1.52
Ch. helopioides	24	1.51	L. juncta	18	1.20
Ch. herbacea	12	2.56	L. lineolata	18	1.62
Ch. hyperici	19	1.37	L. peninsularis	18	1.83
Ch. kuesteri	11	5.41	L. rubiginosa	18	1.36
Ch. latecincta	12	4.74	L. texana	18	1.45
Ch. umbratilis	15	3.08	L. tumamoca	18	1.55
Phratora tibialis	17	1.63	L. typographica	18	1.48
Henicotherus porteri	14	2.14	L. undecimlineata	17	2.67
			Araucanomela wellingtonensis	14	4.49

Table 1. Haploid chromosome number (n) and SD of karyotype asymmetry

chromosome number is generally associated with a decrease in asymmetry, or in other words, the karyotypes are more symmetrical when they have more chromosomes, a clear trend which has also been reported in other beetles like the weevils (Curculionidae) by Lachowska et al. (1998). This does not mean at all an evident polarity towards increases in chromosome number by centric fissions, although it seems to be the more feasible trend in leaf beetles (Petitpierre and Segarra, 1985; Virkki, 1970, 1988; De Julio et al. 2010). Nevertheless, some well-established examples in chrysomelines support the reverse shifts in number by centric fusions: a) the origin of chiasmatic sex-chromosome systems neo-XY from the non-chiasmatic Xy_p or XY_p imply a translocation between an autosome and the X-chromosome, with the loss or fusion of the y-chromosome. The karyotype with the lowest number reported to date in chrysomelines, that of *Doryphora quadrisignata*, with 5 + neo XY meioformula (Vidal 1984), has probably arisen by a centric fusion of this previous type plus several further fusions between autosomes, b) the meioformula of *Timarcha aurichalcea*, 8 + neoXY, the lowest one so far found in this genus, has been clearly demonstrated to be due to an all-arm translocation between a X-chromosome and one autosome bearing the rDNA loci, by fluorescent *in situ* hybridization (FISH) using a ribosomal DNA probe (Gómez-Zurita et al. 2004), and c) the origin of the strikingly asymmetric karyotype of *Chrysolina* (*Stichoptera*) *kuesteri* with 2n = 22 chromosomes (Petitpierre 1983), can be presumably explained from a 24-chromosome species of the same subgenus, such as *Ch. latecincta*, because the largest autosome of the former has 21.30% of the complement length while that of the latter has 16.46% only, therefore, a centric fusion between this largest autosome and a smaller one of *Ch. latecincta*, or any other karyologically similar species of the subgenus *Stichoptera*, may have given rise after fixation to the largest autosome pair of *Ch. kuesteri* (Petitpierre, 1999b).

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References

- Angus RB, Wilson CJ, Mann DJ (2007) A chromosomal analysis of 15 species of Gymnopleurini, Scarabaeini and Coprini (Coleoptera: Scarabaeidae). Tijdsch voor Entomologie 150: 201–211.
- Chen S (1935) Recherches sur les Chrysomelinae de la Chine et du Tonkin. Annals de la Societé entomologique de France 104: 127–158.
- Daccordi M (1983) Quelques réflexions sur la distribution des Chrysomelinae (Col. Chrysomelidae). Bulletin de la Societé entomologique de France 88: 448–451.
- Daccordi M (1994) Notes for phylogenetic study of Chrysomelinae, with descriptions on new taxa and a list of all the known genera (Coleoptera: Chrysomelidae, Chrysomelinae). Proceedings of the Third International Symposium on Chrysomelidae, Beijing 1992, Backhuys Publications, Leiden, The Netherlands, 60–84.
- De Julio M, Rodrigues-Fernandes F, Costa C, Almeida MC, Cella D (2010). Mechanisms of karyotype differentiation in Cassidinae *sensu lato* (Coleoptera, Polyphaga, Chrysomelidae) based on seven species of the Brazilian fauna and an overview of the cytogenetic data. Micron 41: 26–38. doi: 10.1016/j.micron.2009.07.013
- Duckett CN, Gillespie JJ, Kjer KM (2004) Relationships among the subfamilies of Chrysomelidae inferred from small subunit ribosomal DNA and morphology, with special emphasis on the relationship among the flea beetles and the Galerucinae. In: Jolivet P, Santiago-Blay

J, Schmitt M (Eds) New Developments in the Biology of Chrysomelidae. SPB Academic Publications, The Hague, The Netherlands, 3–18.

- Farrell B (1998) "Inordinate" fondness explained: why there are so many beetles? Science 281: 555–559. doi: 10.1126/science.281.5376.555
- Farrell B, Sequeira AS (2004) Evolutionary rates in the adaptive radiation of beetles on plants. Evolution 58: 1984–2001.
- Gómez-Zurita J (2004) Molecular systematics and time-scale for the evolution of *Timarcha*, a leaf beetle genus with a disjunct Holartic distribution. Molecular Phylogenetics and Evolution 32: 647–665. doi: 10.1016/j.ympev.2004.02.009
- Gómez-Zurita J, Juan C, Petitpierre E (2000) The evolutionary history of the genus *Tima-rcha* (Coleoptera, Chrysomelidae) inferred from mitochondrial COII gene and partial 16S rDNA sequences. Molecular Phylogenetics and Evolution 14: 304–317. doi: 10.1006/mpev.1999.0712
- Gómez-Zurita J, Pons J, Petitpierre E (2004) The evolutionary origin of a novel karyotype in *Timarcha* (Coleoptera, Chrysomelidae) and general trends of chromosome evolution in the genus. Journal of Zoological Systematics and Evolutionary Research 42: 332–341. doi: 10.1111/j.1439-0469.2004.00267.x
- Gómez-Zurita J, Garnería I, Petitpierre E (2007) Molecular phylogenetics and evolutionary analysis of body shape in the genus *Cyrtonus*. Journal of Zoological Systematics and Evolutionary Research 45: 317–328.
- Gómez-Zurita J, Hunt T, Vogler AP (2008) Multilocus ribosomal RNA phylogeny of the leaf beetles (Chrysomelidae). Cladistics 24: 34–50. doi: 10.1111/j.1096-0031.2007.00167.x
- Hsiao TH, Hsiao C (1983) A chromosomal analysis of *Leptinotarsa* and *Labidomera* species (Coleoptera: Chrysomelidae). Genetica 60: 139–150. doi: 10.1007/BF00127500
- Iablokoff-Khnzorian SM (1966) Considérations sur l'édéage des Chrysomelidae et son importance phylogénique. L'Entomologiste 22: 115–136.
- Jolivet P (1989) A propos des *Timarcha* nord-americaines (Col. Chrysomelidae). L'Entomologiste 45: 27–34.
- Jolivet P, Hawkeswood TJ (1995) Host-plants of Chrysomelidae of the world. Backhuys Publications, Leiden, The Netherlands.
- Jolivet P, Petitpierre E (1992) Notes on Timarcha. Chrysomela Newsletter 26: 2.
- Karagyan GH, Lachowska D (2007) Karyotypes of five species of jewel beetles and presumptive ancestral state of karyotypes of the subfamilies Polycestinae, Chrysochroinae and Buprestinae (Insecta: Coleoptera: Buprestidae). Comparative Cytogenetics 1: 121–1276.
- King M (1993) Species evolution: the role of chromosomal change. Cambridge University Press, Cambridge (UK).
- Kippenberg H (2010) Chrysomelinae, In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera Vol. 6 Chrysomeloidea. Apollo Books, Stenstrup, Denmark, 390–443.
- Lachowska D, Holecova M, Rozek M (1998) Karyotypic data on weevils (Coleoptera, Curculionidae). Folia biologica (Kraków) 46: 129–136.
- Petitpierre E (1970) Cytotaxonomy and evolution in *Timarcha* Latr. (Coleoptera, Chrysomelidae). Genética Ibérica 22: 67–120.

- Petitpierre E (1976) Further cytotaxonomical and evolutionary studies on the genus *Timarcha* Latr. (Coleoptera: Chrysomelidae). Genética Ibérica 28: 57–81.
- Petitpierre E (1981) New data on the cytology of *Chrysolina* Mots. and *Oreina* Chevr. (Coleoptera, Chrysomelidae). Genetica 54: 265–272. doi: 10.1007/BF00135045
- Petitpierre E (1983) Karyometric differences among nine species of the genus *Chrysolina* Mots. (Coleoptera, Chrysomelidae). Canadian Journal of Genetics and Cytology 25: 33–39.
- Petitpierre E (1988) Cytogenetics, Cytotaxonomy and Genetics of Chrysomelidae. In: Jolivet P, Petitpierre E, Hsiao TH (Eds) Biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, The Netherlands, 131–159. doi: 10.1007/978-94-009-3105-3_9
- Petitpierre E (1999a) The cytogenetics and cytotaxonomy of *Chrysolina* Mots. and *Oreina* Chevr. (Coleoptera, Chrysomelidae). Hereditas 131: 55–62. doi: 10.1111/j.1601-5223.1999.00055.x
- Petitpierre E (1999b) The cytogenetics and cytotaxonomy of the subgenus *Stichoptera* of *Chrysolina* (Coleoptera, Chrysomelidae). In: Sobti RC, Yadav JS (Eds) Some aspects on the insight in Insect Biology, Narendra Publishing House, Delhi, India, 181–188.
- Petitpierre E, Elgueta M (2006) A cytogenetic study on three Chilean species of Chrysomelinae (Coleoptera, Chrysomelidae). Folia biologica (Kraków) 54: 87–91. doi: 10.3409/173491606778557464
- Petitpierre E, Garnería I (2003) A cytogenetic study of the leaf beetle genus *Cyrtonus* (Coleoptera, Chrysomelidae). Genetica 119: 193–199. doi: 10.1023/A:1026010102779
- Petitpierre E, Grobbelaar E (2004) A chromosome survey of three South African species of Chrysomelinae (Coleoptera: Chrysomelidae). African Entomology 12: 123–124.
- Petitpierre E, Jolivet P (1976) Phylogenetic position of the American *Timarcha* Latr. (Coleoptera, Chrysomelidae) based on chromosomal data. Experientia 32: 157–158. doi: 10.1007/ BF01937739
- Petitpierre E, Mikhailov Yu (2009) Chromosomal evolution and trophic affiliation in the genus *Chrysolina* (Coleoptera: Chrysomelidae). In: Jolivet P, Santiago-Blay J, Schmitt M (Eds) Research on Chrysomelidae Vol. 2. Brill, Leiden – Boston, 225–234.
- Petitpierre E, Segarra C (1985) Chromosomal variability and evolution of Chrysomelidae (Coleoptera), particularly that of Chrysomelinae and Palearctic Alticinae. Entomography 3: 403–426.
- Petitpierre E, Segarra C, Yadav CS, Virkki N (1988) Chromosome numbers and meioformulae of Chrysomelidae. In: Jolivet P, Petitpierre E, Hsiao TH (Eds) Biology of Chrysomelidae. Kluwer Academic Publishers, Dordrecht, The Netherlands, 161–186. doi: 10.1007/978-94-009-3105-3_10
- Petitpierre E, Segarra C, Juan C (1993) Genome size and chromosomal evolution in leaf beetles (Coleoptera, Chrysomelidae). Hereditas 119: 1–6. doi: 10.1111/j.1601-5223.1993.00001.x
- Petitpierre E, Kippenberg H, Mikhailov Yu, Bourdonné JC (2004) Karyology and cytotaxonomy of the genus *Chrysolina* Motschulsky (Coleoptera, Chrysomelidae). Zoologischer Anzeiger 242: 347–352. doi: 10.1078/0044-5231-00108

- Postiglioni A, Brum-Zorrilla N (1988) Non-relationship between nucleolus and sex chromosome system Xy_p in *Chelymorpha variabilis* Boheman (Coleoptera: Chrysomelidae). Genetica 77: 137–141. doi: 10.1007/BF00057764
- Reid CAM (2002) A new genus of Chrysomelinae from Australia (Coleoptera: Chrysomelidae). Coleopterists Bulletin 56: 589–596.
- Reid CAM, Jurado-Rivera JA, Beatson M (2009) A new genus of Chrysomelinae from Australia (Coleoptera: Chrysomelidae). Zootaxa 2207: 53–66. doi: 10.1649/0010-065X(200 2)056[0589:ANGOCF]2.0.CO;2
- Riley EG, Clark SM, Flowers RW, Gilbert AJ (2002) Family 124. Chrysomelidae Latreille (1802) (Chrysomelinae). In: Arnett RH, Thomas MC, Skelley PE, Frank JH (Eds) American Beetles Vol. 2, CRC Press, Boca Raton, Florida, 648–653.
- Robertson JG (1966) The chromosomes of bisexual and parthenogenetic species of *Calligrapha* (Coleoptera: Chrysomelidae) with notes on the sex-ratio, abundance and egg number. Canadian Journal of Genetics and Cytology 8: 695–732.
- Smith SG (1951) Evolutionary changes in the sex chromosomes of Coleoptera. Genetica 25: 522–524. doi: 10.1007/BF01784837
- Smith SG (1952) The cytology of some tenebrionid beetles (Coleoptera). Journal of Morphology 91: 325–364. doi: 10.1002/jmor.1050910206
- Smith SG, Virkki N (1978) Coleoptera In: Animal Cytogenetics Vol. 3 Insecta 5. Borntraeger, Berlin.
- Stebbins GL (1971) Chromosomal Evolution in Higher Plants. Edward Arnold Publishers Ltd., London.
- Sumner AT (2003) Chromosomes: organization and function. Blackwell Publishing.
- Vidal OR (1984) Chromosome numbers of Coleoptera from Argentina. Genetica 65: 235–239. doi: 10.1007/BF00122910
- Virkki N (1984) Chromosomes in Evolution of Coleoptera. In: Sharma AK, Sharma A (Eds) Chromosomes in Evolution of Eukaryotic groups, Vol. 2, CRC Press, Boca-Raton, Florida.
- Virkki N, Santiago-Blay J (1993) Trends of karyotype evolution in neotropical Oedionychina (Coleoptera: Chrysomelidae: Alticinae) Hereditas 119: 263–283. doi: 10.1111/j.1601-5223.1993.00263.x
- Virkki N, Mazzella C, Denton A (1991) Silver staining of the coleopteran Xy_p sex bivalent. Cytobios 67: 45–63.
- White MJD (1973) Animal Cytology and Evolution, 3rd ed. Cambridge University Press, Cambridge, UK.
- White MJD (1978) Modes of Speciation. W H Freeman, San Francisco.

RESEARCH ARTICLE



The adipokinetic hormone family in Chrysomeloidea: structural and functional considerations^{*}

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Abstract

The presented work is a hybrid of an overview and an original research paper on peptides belonging to the adipokinetic hormone (AKH) family that are present in the corpora cardiaca of Chrysomeloidea. First, we introduce the AKH/red pigment-concentrating hormone (RPCH) peptide family. Second, we collate the available primary sequence data on AKH peptides in Cerambycidae and Chrysomelidae, and we present new sequencing data (from previously unstudied species) obtained by liquid-chromatography coupled with ion trap electrospray ionisation mass spectrometry. Our expanded data set encompasses the primary structure of AKHs from seven species of Cerambycidae and three species of Chrysomelidae. All of these species synthesise the octapeptide code-named Peram-CAH-I (pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide). Whereas this is the sole AKH peptide in Cerambycidae, Chrysomelidae demonstrate a probable event of AKH gene duplication, thereby giving rise to an additional AKH. This second AKH peptide may be either Emppe-AKH (pGlu-Val-Asn-Phe-Thr-Pro-Asn-Trp amide) or Peram-CAH-II (pGlu-Leu-Thr-Phe-Thr-Pro-Asn-Trp amide). The peptide distribution and structural data suggest that both families are closely related and that Peram-CAH-I is the ancestral peptide. We hypothesise on the molecular evolution of Emppe-AKH and Peram-CAH-II from the ancestral peptide due to nonsynonymous missense single nucleotide polymorphism in the nucleotide coding sequence of prepro-AKH. Finally, we review the biological significance of the AKH peptides as hyperprolinaemic hormones in Chrysomeloidea, i.e. they cause an increase in the circulating concentration of proline. The mobilisation of proline has been demonstrated during flight in both cerambycid and chrysomelid beetles.

Keywords

Cerambycidae, Chrysomelidae, adipokinetic hormone, structure elucidation, mass spectrometry, phylogenetic relatedness

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I. The adipokinetic hormone (AKH)/red pigment-concentrating hormone (RPCH) family of peptides: general background information

Peptides belonging to the AKH/ RPCH family are produced in neurosecretory cells of either the corpora cardiaca (CC) of insects or of the X-organ cells in the eyestalks of decapod crustaceans (see reviews by Gäde 1997; Gäde et al. 1997b; Gäde and Marco 2006). In crustaceans, the classical effect of RPCH is the concentrating movement of pigment granules in integument cells causing a blanching appearance of the whole body (see review by Rao 2001). In insects, AKHs classically control the mobilisation of fuels for active muscular exertion, such as flight, swimming or running (see reviews by Gäde 2004; Gäde and Marco 2009). Such metabolites can be lipids, carbohydrates or the amino acid proline, and the neuropeptides involved in this action are then generally referred to as adipokinetic (lipid-mobilising), hypertrehalosaemic (increase in the level of the haemolymph sugar, trehalose) or hyperprolinaemic (increase of haemolymph proline levels). After release of the neuropeptides from the CC into the haemolymph during flight for example, they bind to G-protein-coupled receptors, which are known from a limited number of insects to date, and in turn activate either a triacylglycerol lipase or a glycogen phosphorylase in the fat body via diverse second messenger systems (see review by Gäde and Auerswald 2003). Whereas only two structurally different octapeptides are known from Crustacea (Fernlund and Josefsson 1972; Christie et al. 2008; Marco and Gäde 2010), about 50 isoforms are known from various insect species (Gäde 2009; Gäde and Simek 2010; Marco et al. 2011). These peptides have the following common structural characteristics: a chain length of 8-10 amino acids, post-translationally modified termini (the N-terminus contains a pyroglutamate residue and the C-terminus is carboxyamidated), at least two aromatic amino acids (at position 4 and 8), a glycine residue at position 9, and largely, but not exclusively, the peptides are uncharged with only 4 of the 50 odd members having a charged asparagine residue at position 7 (Gäde 2009).

The primary structure of peptides from the AKH/RPCH family have been used as an additional data set to aid in the construction of phylogenies in insect orders (Gäde 1989; Gäde et al. 1994, 1997a, 2003a,b; Gäde and Simek 2010; Kodrik et al. 2010). Despite the few character states, these structures supported, for example, a high-level phylogeny for Odonata (Gäde and Marco 2005; Gäde et al. 2011) when used in conjunction with published ideas on Odonata phylogenies (see, for example, Bechly 1996; Misof 2000; Ware et al. 2007; Dumont et al. 2010).

In the present study we focus on the AKHs from certain beetle families, namely the superfamily Chrysomeloidea. Here, we review the previously published data on AKHs in this superfamily and add hitherto unpublished structural data on AKHs of more species from the two subfamilies, Chrysomelidae and Cerambycidae, with the aim of drawing preliminary conclusions on the putative value of this data set for scientific speculation on relatedness of these families. We also review the current knowledge on the function of AKHs in both subfamilies with respect to the control of substrate availability, especially the amino acid proline.

2. The AKH/RPCH peptide family in Chrysomeloidea

The order Coleoptera constitutes the most species-rich taxon on Earth with approximately 350 000 described species and comprises, therefore, about 40 % of all insect species and about 25 % of all animal species (Hammond 1992; Grove and Stork 2000). About 75 % of beetle species are phytophagous and within these "Phytophaga" two superfamilies, Curculionoidea and Chrysomeloidea, are especially diverse and total about 130 000 species. The Chrysomeloidea is usually divided in five families (Crowson 1981) of which the Cerambycidae (longhorn beetles) and Chrysomelidae (leaf beetles) are the most radiated ones with about 35 000 species each. In the current work, we have compiled an AKH data base using seven cerambycid and three chrysomelid species.

2.1. Insects included in the current data set

The cerambycids *Ceroplesis capensis* Linnaeus, 1764 and *Promeces longipes* (Olivier, 1795) were collected in September 2009 and 2010 in the Cedarberg close to Clanwilliam, South Africa, while the eucalyptus borer *Phoracantha recurva* Newman, 1840 was found in the cellar of a house in Cape Town, S. Africa after the purchase and storage of logs from eucalyptus trees which were apparently infested with borer larvae and pupae (2009). The chrysomelid *Chrysolina kuesteri* (Helliesen, 1912) was collected at the beginning of November 2007 in a vineyard in Frickenhausen, Germany. The cerambycid *Leptura maculata* Poda, 1761 and the chrysomelid *Chrysolina fastuosa* Scopoli, 1763 were collected in June 2011 in the forest adjacent to the campus of the University of Konstanz in Germany. For collection details of the cerambycids *Ceroplesis thunbergii* Fåhraeus, 1872, *Phryneta spinator* (Fabricius, 1792) and *Morimus funereus* Mulsant, 1863, see Gäde and Auerswald (2000; 2001), and for the chrysomelid *Leptinotarsa decemlineata* Say, 1824, see Gäde and Kellner (1989) and Gäde (1999).

2.2 Structure elucidation and diversity of AKHs

We followed standard laboratory procedures to identify and obtain the primary structure of AKHs from the CC of Chrysomeloidea species. In all cases, the CC were dissected into 80% methanol and extracts were prepared by sonification according to Gäde et al. (1984). AKH peptides from *C. thunbergii*, *P. spinator*, *L. decemlineata* and *M. funereus* were then purified by reversed-phase high performance liquid chromatography (RP-HPLC) as outlined in Gäde (1985) and identified in biological assays; finally, material from active fractions were sequenced by the Edman degradation technique (see Gäde and Kellner 1989; Gäde and Auerswald 2000).

For the remaining species: C. capensis, P. longipes, P. recurva, L. maculata, C. kuesteri and C. fastuosa, peptide material in the CC extracts were analysed directly by liquid chromatography-mass spectrometry (LC-MS) using a quadropole ion trap mass spectrometer equipped with an electrospray ionisation (ESI) source (instruments and methods as described in detail elsewhere (see Kodrik et al. 2010). This strategy has been employed successfully for a number of other insect species (see for example Gäde et al. 2003a, 2009; Gäde and Simek 2010), and produces clean, easily interpretable data for which only a fraction of gland material is required when compared with enzymatic degradation techniques. For the current study, the mass spectrometry results are exemplarily illustrated from a CC extract of a cerambycid, *C. capensis* (Figs 1–2), and of a chrysomelid, *C. kuesteri* (Figs 3–5).

The total ion chromatogram of about 0.5 pair equivalent of CC from C. capensis showed one peak of interest at a retention time of 5.40 min (Fig. 1A); this peak displays inter alia an ion with highest abundance at m/z 973.5 for the $[M + H]^+$ ion (Fig. 1B). The primary sequence of the peptide was deduced from the MS² spectrum obtained by collision-induced dissociation (CID) of the precursor shown in Fig. 2. The characteristic y-type and b-type product ions, in conjunction with diagnostic ions (i.e. y-NH₂, y-2NH₃ and b-H₂O) enabled the assignment of an $[M + H]^+$ ion as a member of the AKH family (see inset in Fig. 2). Although the alignment of the first two amino acids cannot be inferred from the recorded MS² spectrum, we know from the general signature structure of AKHs that pyroglutamate is typically at the N-terminus, which leaves only a valine residue at position two to fill the gap of the measured 99 atomic mass units. Thus, the sequence of the AKH synthesised in the CC of C. capensis is assigned as pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide which is identical to that of Peram-CAH-I (Periplaneta americana-cardioacceleratory hormone-I), which was found for the first time in the cockroach Periplaneta americana (Linnaeus, 1758) (Scarborough et al. 1984; Witten et al. 1984).

The total ion chromatogram of about 0.8 pair equivalent of CC from *C. kuesteri* show three peaks of interest at retention times of 5.02 min (highest abundance), 5.23 min (lowest abundance) and 5.36 min (intermediate abundance) (Fig. 3A); these peaks display ions at m/z 973.5, 1031.5 and 987.5, respectively for the $[M + H]^+$ ions (Figs 3B-D). The MS² spectra obtained by CID of the respective precursors were recorded. Because the spectrum for $[M + H]^+$ at m/z 973.4 was almost identical to the one for *C. capensis* (Fig. 2), the data are not illustrated here, and the underlying AKH was easily assigned as Peram-CAH-I. The MS² spectrum for $[M + H]^+$ at m/z 987.5 is given in Fig. 4; the interpretation was straightforward, and a peptide with the primary structure of pGlu-Val-Asn-Phe-Thr-Pro-Asn-Trp amide was assigned, which had previously been found in the CC of the mantid *Empusa pennata* (Thunberg, 1815) called Emppe-AKH (Gäde 1991). The third peptide with $[M + H]^+$ at m/z 1031.5 was assigned as a C-terminal Gly-extended non-amidated form of Peram-CAH-I by its MS² spectrum (Fig. 5).

In the cases detailed above, the assigned amino acid sequence of the native AKHs was confirmed by comparing the retention times, the $[M + H]^+$ ions and the respective CID-MS² spectra with those of the appropriate synthetic peptides; chromatographic and mass spectral properties were always identical (data not shown). For use in such confirmatory studies, synthetic peptides Peram-CAH-I and -II (*Periplaneta americana*)



Figure 1. LC-MS analysis of an extract from the corpora cardiaca of *Ceroplesis capensis*. Material from the CC of the cerambycid beetle, *Ceroplesis capensis* was extracted with 80% methanol and analysed by LC-MS. **A** The total ion chromatogram **B** A full scan positive electrospray ionisation (ESI) mass spectrum of the peak shown in (**A**) with a retention time of 5.40 min.



Figure 2. The collision-induced dissociation ESI mass spectrum of an AKH peptide in *Ceroplesis capensis*, and its deduced amino acid sequence. The CID MS²-ESI spectrum of the ion MH⁺ (m/z 973.5) in Fig. 1B. The inset shows the assigned peptide sequence (corresponding to that of Peram-CAH-I), together with the theoretical calculated masses for b-type and y-type diagnostic fragment ions which are observed in the MS² mass spectrum.



Figure 3. LC-MS analysis of an extract from the corpora cardiaca of *Chrysolina kuesteri*. Material from the CC of the chrysomelid beetle, *Chrysolina kuesteri* was extracted with 80% methanol and analysed by LC-MS. (A) The total ion chromatogram. Full scan positive ESI mass spectra of the peaks shown in (**A**) with a retention time of 5.02 min (**B**), 5.23 min (**C**) and 5.36 min (**D**).



Figure 4. The collision-induced dissociation ESI mass spectrum of an AKH peptide in *Chrysolina kuesteri*, and its deduced amino acid sequence. The CID MS² ESI spectrum of the ion MH⁺ at *m*/z 987.5 (see Fig. 3D). The inset shows the sequence of the assigned peptide (corresponding to that of Emppe-AKH), together with the theoretical calculated masses for b-type and y-type diagnostic fragment ions which are observed in the MS² mass spectrum.



Figure 5. The collision-induced dissociation ESI mass spectrum of an additional putative AKH peptide in *Chrysolina kuesteri*, and its deduced amino acid sequence. The CID MS² ESI spectrum of the ion MH⁺ at *m*/z 1031.5 (see Fig. 3C). The inset shows the sequence of the assigned peptide (corresponding to an intermediate processing form of Peram-CAH-I, i.e. a non-amidated nonapeptide with a Gly residue at position 9). Also shown are the theoretical calculated masses for b-type and y-type diagnostic fragment ions which are observed in the MS² mass spectrum.

cardioacceleratory hormone-I and -II) had been purchased from Peninsula Laboratories Inc. (now Bachem Americas Inc., California, USA), while the peptide Emppe-AKH (*Empusa pennata* adipokinetic hormone) had been custom-synthesised by Dr. R. de Milton (Medical School, UCT, South Africa).

2.3 Primary sequence diversity of AKHs

Table 1 summarises the structural information of AKHs in chrysomeloid beetles known previously from Edman sequencing (Gäde and Kellner 1989; Gäde and Auerswald 2000), and those (hitherto unpublished) that have recently been elucidated by employing direct analysis of the glandular extract via LC-ESI MS. Although mass spectra of AKHs are only shown for C. capensis and C. kuesteri in the current work, it should be noted that clear sequencing data were obtained for all chrysomeloid beetles studied in this way. Hence, the current study unambiguously identifies AKHs from the two large families of the Chrysomeloidea via a combined LC-MS approach in comparison with synthetic peptides. These results are very interesting and revealing. First, all AKH members are octapeptides, no decapeptide has been detected yet in any chrysomeloid beetle. In fact, the only decapeptide member sequenced from ANY beetle species to date is the peptide code-named Declu-CC (pGlu-Leu-Asn-Phe-Ser-Pro-Asn-Trp-Gly-Asn amide; *Decapotoma lunata*-CC) which is biosynthesised in the CC of members of blister beetles (Meloidae; Gäde 1995). Second, all investigated chrysomeloid species contain in their CC the peptide Peram-CAH-I (see Table 1). All 7 species of the Cerambycidae, spanning 6 genera, have this peptide as the only AKH member, whereas

Family	Species	Amino acid sequence	Code name of
			peptide
Cerambycidae	Phryneta spinator	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
	Ceroplesis thunbergii	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
	Ceroplesis capensis	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
	Promeces longipes	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
	Phoracantha recurva	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
	Morimus funereus	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
	Leptura maculata	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
Chrysomelidae	Leptinotarsa decemlineata	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
		pGlu-Leu-Thr-Phe-Thr-Pro-Asn-Trp amide	Peram-CAH-II
	Chrysolina kuesteri	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
		pGlu-Val-Asn-Phe-Thr-Pro-Asn-Trp amide	Emppe-AKH
	Chrysolina fastuosa	pGlu-Val-Asn-Phe-Ser-Pro-Asn-Trp amide	Peram-CAH-I
		pGlu-Val-Asn-Phe-Thr-Pro-Asn-Trp amide	Emppe-AKH

Table 1. Adipokinetic hormone sequences in Cerambycidae and Chrysomelidae. Primary sequences of peptides of the adipokinetic hormone family in the corpora cardiaca of various species belonging to the families Cerambycidae and Chrysomelidae.

the three species of Chrysomelidae representing two genera have Peram-CAH-I plus a second AKH peptide (see Table 1). Interestingly, the two species from the same genus (*Chrysolina kuesteri* and *C. fastuosa*) have the same AKH complement. Additionally, what appears to be an incompletely-processed form of Peram-CAH-I is also detected in the CC of *C. kuesteri* (see Fig. 5). Whether this non-amidated nonapeptide is biologically active, remains to be determined in the future.

From the data in Table 1, it seems that Peram-CAH-I is the ancestral peptide. We propose that the following molecular evolution (Fig. 6) may have occurred by conservative nucleotide substitutions involving nonsynonymous missense single nucleotide polyphemisms (SNPs) in the DNA:

- (1) T in position one of the genetic code for serine (S⁵) in Peram-CAH-I was replaced by A to code for threonine (T⁵) in Emppe-AKH;
- (2) G in position one of the genetic code for valine (V²) in Emppe-AKH was replaced by C to now code for leucine (L²) in Pyrap-AKH (*Pyrrhocoris apterus*adipokinetic hormone);
- (3) A in position two of the genetic code for asparagine (N³) in Pyrap-AKH was replaced by C and now codes for threonine (T³) in Peram-CAH-II (Fig. 6).

The proposed scenario outlined above, appears to be the most likely one. An alternative route may have involved the molecular change from Emppe-AKH to Peram-CAH-II via another intermediate peptide where N^3 in Emppe-AKH is first changed to T^3 ; we find this to be highly unlikely since none of the 50 completely known AKH structures, to date, has the combination of pGlu-Val-Thr at the N-terminus that is required from such an intermediate AKH.

The evolutionary steps proposed in Fig. 6 lead to the peptide Pyrap-AKH, which exists in certain heteropteran and homopteran bugs, in a pamphagid grasshopper and in the red flour beetle, *Tribolium castaneum* (Herbst, 1797) (Gäde 2009). In Chrysomelidae, however, this peptide has not yet been detected. With more chrysomelid beetles to be investigated for their complement of AKH peptides, the proposed hypothesis can be proven or refuted in the future. We would like to emphasise that AKH structures cannot be used as a sole tool for investigation into the phylogenies of Chrysomelidae. Phylogenies have been carried out based on morphological and molecular data (for example, Duckett et al. 2004; Gomez-Zurita et al. 2007) and these two pillars will certainly continue to be central in future investigations, with peptide structure and complement used in a supportive context.

2.4. Functional significance of AKH peptides

Previously, we conducted two sets of experiments to determine which substrate is mobilised by the secretion of an AKH in chrysomeloid beetles.

In the first set of experiments, we injected the cerambycid beetles, *C. thunbergii* and *P. spinator*, with their own CC extract or a low dose of the identified peptide,



Figure 6. Putative molecular evolution of adipokinetic peptides in chrysomeloid beetles. A proposed scheme of the molecular evolution of adipokinetic peptides to give rise to the different structures observed in investigated chrysomeloid beetles. The inset shows the genetic code for the respective amino acids involved. Differences in amino acids or code nucleotides are given in bold lettering.

Peram-CAH-I, in a synthetic form and measured the concentration of total lipids, total carbohydrates and proline in the haemolymph before injection and 90 min thereafter (Gäde and Auerswald 2000). In both beetles the crude CC extract, as well as the synthetic Peram-CAH-I peptide had a hypertrehalosaemic and hyperprolinaemic effect, i.e. significant increases in the concentration of carbohydrates and proline were measured. In the chrysomelid, *L. decemlineata*, it was shown that injection of conspecific CC extract had a hypertrehalosaemic effect (Gäde and Scheid 1986) and injection of low doses of synthetic endogenous peptides, Peram-CAH-I and -II, caused a significant increase in the proline concentration in the haemolymph (Gäde 1999).

In the second set of experiments we examined the effect of active flight on substrate levels in the haemolymph of chrysomeloid beetles. In this set-up, the beetles were tethered to a flight mill that was modified to allow lift-generating flight; after a 1 min period of such active flying, the beetle was detached from the mill and kept at rest. In both cerambycid species, C. thunbergii and P. spinator, a small but significant decrease in the concentration of carbohydrates was measured in the haemolymph upon 1 min of flight; there was, however no changes measured in the levels of total lipids. In contrast, the proline concentration in these cerambycid species diminished by 20 to 30 % upon 1 min of flight; following an hour of rest subsequent to a short period of active flight, however, the proline concentration returned to pre-flight levels in the haemolymph (Gäde and Auerswald 2000). In the chrysomelid beetle, L. decemlineata (Gäde 1999), we note very similar results, i.e. a decrease in the circulating proline concentration upon 1 min of flight and subsequent restoration of the pre-flight proline level (at rest) within 1 h of rest after the flight episode. The data indicate that AKH peptides are released during flight, which initiate substrate mobilisation for use by the active muscle tissue. During the restorative phase (resting after flight), the flight muscles are no longer active and, consequently, there is a build-up of the substrates in the haemolymph that were released from stored sources in the fat body (see Gäde 2004).

Based on these earlier investigations with chrysomeloid species, we have, thus, shown that proline is used in conjunction with carbohydrates as metabolic fuel to power flight activity (Gäde 1999; Gäde and Auerswald 2000; Gäde and Auerswald 2002). The pathway that involves proline, ultimately relies on the activation of a lipase which is necessary to provide acetyl-CoA units for the formation of proline from alanine (see Gäde and Auerswald 2003). This critical step in the process of supplying proline for metabolic use is under the regulatory control of members of the AKH family (Gäde and Auerswald 2003). We have, however, no information on the respective role played by multiple AKH peptides in fuel mobilisation in an individual insect, e.g. do both AKHs have the same potency and same action in chrysomelid beetles? Further, does the conserved AKH (Per-am-CAH-I) in cerambycid beetles hint at a conserved receptor structure? It still remains a biological curiosity as to why certain groups of insects have AKH gene duplication and others not. In conclusion, many more questions remain open in insect studies that may be addressed by additional investigations at different phylogenetic and physiological levels.

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References

- Bechly G (1996) Morphologische Untersuchungen an Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta: Pterygota: Odonata) unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. Petalura 2 (Special Volume): 1–402.
- Christie AE, Cashman CR, Brennan HR, Ma M, Sousa GL, Li L, Stemmler EA, Dickinson PS (2008) Identification of putative crustacean neuropeptides using *in silico* analyses of publicly accessible expressed sequence tags. General and Comparative Endocrinology 156: 246–264. doi: 10.1016/j.ygcen.2008.01.018
- Crowson RA (1981) The Biology of the Coleoptera. Academic Press, New York.
- Duckett CN, Gillespie JJ, Kjer KM (2004) Relationships among the subfamilies of Chrysomelidae inferred from small subunit ribosomal DNA and morphology, with special emphasis on the relationship among the flea beetles and the Galerucinae. In: Jolivet P, Santiago-Blay JA, Schmitt M (Eds) New Developments in the Biology of Chrysomelidae. SPB Academic Publishing, The Hague, 3–18.
- Dumont HJ, Vierstraete A, Vanfleteren JR (2010) A molecular phylogeny of the Odonata (Insecta). Systematic Entomology 35: 6–18. doi: 10.1111/j.1365-3113.2009.00489.x
- Fernlund P, Josefsson L (1972) Crustacean colour change hormone: amino acid sequence and chemical synthesis. Science 177: 173–175. doi: 10.1126/science.177.4044.173
- Gäde G (1985) Isolation of the hypertrehalosaemic factors I and II from the corpus cardiacum of the Indian stick insect, *Carausius morosus*, by reversed-phase high-performance liquid chromatography, and amino acid composition of factor II. Biological Chemistry Hoppe-Seyler 366: 195–199. doi: 10.1515/bchm3.1985.366.1.195
- Gäde G (1989) The hypertrehalosaemic peptides of cockroaches: a phylogenetic study. General and Comparative Endocrinology 75: 287–300. doi: 10.1016/0016-6480(89)90082-8
- Gäde G (1991) The adipokinetic neuropeptide of Mantodea: sequence elucidation and evolutionary relationships. Biological Chemistry Hoppe-Seyler 372: 193–201. doi: 10.1515/ bchm3.1991.372.1.193
- Gäde G (1995) Isolation and identification of AKH/RPCH family peptides in blister beetles (Meloidae). Physiological Entomology 20: 45–51. doi: 10.1111/j.1365-3032.1995.tb00799.x
- Gäde G (1997) The explosion of structural information on insect neuropeptides. In: Herz W, Kirby GW, Moore RE, Steglich W, Tamm C (Eds) Progress in the Chemistry of Organic Natural Products. Springer-Verlag, Wien, 71: 1–128.
- Gäde G (1999) Control of proline as flight substrate in long-horned and leaf beetles by AKH/ RPCH neuropeptides. In: Roubos E, Wendelaar Bonga SE, Vaudry H, de Loof A (Eds) Recent Developments in Comparative Endocrinology and Neurobiology. Shaker Publishing, Maastricht, 308–310.
- Gäde G (2004) Regulation of intermediary metabolism and water balance of insects by neuropeptides. Annual Reviews of Entomology 49: 93–113.
- Gäde G (2009) Peptides of the adipokinetic hormone/ red pigment-concentrating hormone family. A new take on biodiversity. Trends in Comparative Endocrinology and Neurobiology Annual New York Academy of Science 1163: 125–136.

- Gäde G, Auerswald L (2000) Flight substrates and their regulation by a member of the AKH/ RPCH family of neuropeptides in Cerambycidae. Journal of Insect Physiology 46: 1567–1576.
- Gäde G, Auerswald L (2001) Neurohormonal control of proline metabolism in beetles. In: Goos HJTh, Rastogi RK, Vaudry H, Pierantoni R (Eds) Perspective in Comparative Endocrinology: Unity and Diversity. Monduzzi Editore S.p.A., Italy, 443–453.
- Gäde G, Auerswald L (2002) Beetles' choice proline for energy output. Control by AKHs. Comparative Biochemistry and Physiology B 132: 117–128. doi: 10.1016/S1096-4959(01)00541-3
- Gäde G, Auerswald L (2003) Mode of action of neuropeptides from the adipokinetic hormone family. General and Comparative Endocrinology 132: 10–20. doi: 10.1016/S0016-6480(03)00159-X
- Gäde G, Auerswald L, Šimek P, Marco HG, Kodrik D (2003a) Red pigment-concentrating hormone is not limited to crustaceans. Biochemical and Biophysical Research Communications 309: 967–973. doi: 10.1016/j.bbrc.2003.08.107
- Gäde G, Grandcolas P, Kellner R (1997a) Structural data on hypertrehalosaemic neuropeptides from *Cryptocercus punctulatus* and *Therea petiveriana*: how do they fit into the phylogeny of cockroaches? Proceedings of the Royal Society London B. 264: 763–768. doi: 10.1098/rspb.1997.0108
- Gäde G, Goldsworthy GJ, Kegel G, Keller R (1984) Single step purification of locust adipokinetic hormones I and II by reversed-phase high-performance liquid chromatography and the amino-acid composition of the hormone II. Hoppe Seyler's Zeitschrift für physiologische Chemie 365: 393–398. doi: 10.1515/bchm2.1984.365.1.393
- Gäde G, Hoffmann K-H, Spring JH (1997b) Hormonal regulation in insects: facts, gaps and future directions. Physiological Reviews 77: 963–1032.
- Gäde G, Kellner R (1989) The metabolic neuropeptides of the corpus cardiacum from the potato beetle and the American cockroach are identical. Peptides 10: 1287–1289. doi: 10.1016/0196-9781(89)90023-5
- Gäde G, Marco HG (2005) The adipokinetic hormones of Odonata: a phylogenetic approach. Journal of Insect Physiology 51: 333–341. doi: 10.1016/j.jinsphys.2004.12.011
- Gäde G, Marco HG (2006) The invertebrate AKH/RPCH family. In: Kastin AJ (Ed) The Handbook of Biologically Active Peptides. Elsevier, Amsterdam, 189–192.
- Gäde G, Marco HG (2009) Peptides of the adipokinetic hormone/red pigment-concentrating hormone family with special emphasis on Caelifera: primary sequences and functional considerations contrasting grasshoppers and locusts. General and Comparative Endocrinology 162: 59–68. doi: 10.1016/j.ygcen.2008.06.007
- Gäde G, Marco HG, Desutter-Grandcolas L (2003b) A phylogenetic analysis of the adipokinetic neuropeptides of Ensifera. Physiological Entomology 28: 283–289. doi: 10.1111/j.1365-3032.2003.00344.x
- Gäde G, Reynolds SE, Beeching JR (1994) Molecular evolution of peptides of the AKH/RPCH family. In: Davey KG, Peter RE, Tobe SS (Eds) Perspectives in Comparative Endocrinology, National Research Council of Canada, Ottawa, 119–128.
- Gäde G, Scheid M (1986) A comparative study on the isolation of adipokinetic and hypertrehalosaemic factors from insect corpora cardiaca. Physiological Entomology 11: 145–157. doi: 10.1111/j.1365-3032.1986.tb00401.x

- Gäde G, Simek P (2010) A novel member of the adipokinetic peptide family in a "living fossil", the ice crawler *Galloisiana yuasai*, is the first identified neuropeptide from the order Grylloblattodea. Peptides 31: 372–376. doi: 10.1016/j.peptides.2009.10.016
- Gäde G, Simek P, Fescemyer HW (2011) Adipokinetic hormones provide inference for the phylogeny of Odonata. Journal of Insect Physiology 57: 174–178. doi: 10.1016/j.jin-sphys.2010.11.002
- Gäde G, Simek P, Marco HG (2009) The first identified neuropeptide in the insect order Megaloptera: A novel member of the adipokinetic hormone family in the alderfly *Sialis lutaria*. Peptides 30: 477–482. doi: 10.1016/j.peptides.2008.07.022
- Gomez-Zurita J, Hunt T, Kopliku F, Vogler A (2007) Recalibrated tree of leaf beetles (Chrysomelidae) indicates independent diversification of angiosperms and their insect herbivores. PLoS ONE 2 (4): e360. doi: 10.1371/journal.pone.0000360
- Grove SJ, Stork NE (2000) An inordinate fondness for beetles. Invertebrate Taxonomy 14: 733–739. doi: 10.1071/IT00023
- Hammond PM (1992) Species inventory. In: Groombridge B (Ed.) Global Diversity, Status of the Earth's Living Resources. Chapman and Hall, London, 17–39.
- Kodrík D, Marco HG, Šimek P, Socha R, Štys P, Gäde G (2010) The adipokinetic hormones of Heteroptera: a comparative study. Physiological Entomology 35: 117–127. doi: 10.1111/j.1365-3032.2009.00717.x
- Marco HG, G\u00e4de G (2010) Biological activity of the predicted red pigment-concentrating hormone of *Daphnia pulex* in a crustacean and an insect. General and Comparative Endocrinology 166: 104–110. doi: 10.1016/j.ygcen.2009.08.002
- Marco HG, Šimek P, Gäde G (2011) The first decapeptide adipokinetic hormone (AKH) in Heteroptera: a novel AKH from a South African saucer bug, *Laccocoris spurcus* (Naucoridae, Laccocorinae). Peptides 32: 454–460. doi: 10.1016/j.peptides.2010.10.015
- Misof B (2000) Diversity of Anisoptera (Odonata): inferring speciation processes from patterns of morphological diversity. Zoology 105: 355–365. doi: 10.1078/0944-2006-00076
- Rao KR (2001) Crustacean pigmentary-effector hormones: chemistry and functions of RPCH, PDH, and related peptides. American Zoologist 41: 364–379. doi: 10.1668/0003-1569(2001)041[0364:CPEHCA]2.0.CO;2
- Scarborough RM, Jamieson GC, Kalish F, Kramer SJ, McEnroe GA, Miller CA, Schooley DA (1984) Isolation and primary structure of two peptides with cardioacceleratory and hyperglycemic activity from the corpora cardiaca of *Periplaneta americana*. Proceedings of the National Academy of Sciences, USA 81: 5575–5579. doi: 10.1073/pnas.81.17.5575
- Ware J, May M, Kjer K (2007) Phylogeny of the higher Libelluloidea (Anisoptera: Odonata): an exploration of the most speciose superfamily of dragonflies. Molecular Phylogeny and Evolution 45: 289–310. doi: 10.1016/j.ympev.2007.05.027
- Witten JL, Schaffer MH, O'Shea M, Cook JC, Hemling ME, Rinehart KL (1984) Structures of two cockroach neuropeptides assigned by fast atom bombardment mass spectrometry. Biochemical and Biophysical Research Communications 124: 350–358. doi: 10.1016/0006-291X(84)91560-2

RESEARCH ARTICLE



Biology of Blepharida-group flea beetles with first notes on natural history of Podontia congregata Baly, 1865 an endemic flea beetle from southern India (Coleoptera, Chrysomelidae, Galerucinae, Alticini)*

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Abstract

The biology, host plants, and pest status of *Podontia* Dalman, 1824 species are reviewed. Natural history of *Podontia congregata* Baly, 1865 a flea beetle endemic to southern India, is reported for the first time. It is distributed from the Western Ghats Mountains westward to the plains. Clusiaceae is reported as a new host plant family for *Blepharida*-group species, with *Garcinia gummi-gutta* (L.) N. Robson (Clusiaceae) as the host plant for *P. congregata*. Pentatomid bugs attack the larvae but not eggs, pupae, or adults. A new egg parasitoid species, *Ooencyrtus keralensis* Hayat and Prathapan, 2010 (Hymenoptera: Encyrtidae), was discovered. Aspects of *P. congregata* host selection, life cycle, and larval fecal defenses are consistent with its inclusion in the *Blepharida*-genus group.

Keywords

Leaf beetles, Podontia congregata, Pest, Garcinia, Clusiaceae, India

Introduction

The *Blepharida*-group of genera consists of robust and brightly colored flea beetles (Figs 1–10). Furth (1998) lists 16 genera in the *Blepharida*-group, which are united

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by characters of the eye shape, metatibial, aedeagal, and spermathecal morphology. Medvedev (1999) added three new genera, *Asiophrida* Medvedev, *Blepharella* Medvedev, and *Furthia* Medvedev from the Oriental region, making 19 genera in total. The *Blepharida*-group has a primarily Old World tropical distribution, with the exception of *Euplectroscelis* Crotch being endemic to Mexico (Furth 1992; Furth and Lee 2000). We follow Furth and Lee (2000: 27, Table 1) on the composition of the *Blepharida*group genera as this is the most recent discussion of these genera, building from his morphological and classificatory discussions (Furth 1992, 1998) and pointing out the limitations of catalogue phylogenies. A modern phylogenetic analysis of relationships among these taxa and with other flea beetles is badly needed.

Species in the *Blepharida*-group are documented most commonly on host plants in the Anacardiaceae, Bignoniaceae, Burseraceae, and Sapindaceae (Table 1). However, there are several single species records from Apocynaceae, Caesalpiniaceae, Elaeocarpaceae, Fabaceae, Lythraceae, Meliaceae, Moraceae, and Verbenaceae, which raise interesting questions about diet evolution as well as the distinct possibility of questionable host reports. Additionally, Furth (1998) indicated how the lack of reference sources in Jolivet and Hawkeswood (1995) could mislead about true chrysomelid-plant associations. Host chemistry may likely have played an important role in the co-evolution of *Blepharida* Chevrolat (73 species; Figs 2–3) with their hosts in *Bursera* Jacq. ex L. (Burseraceae) (Becerra 1997, 2003, 2004a, b, 2007; Becerra and Venable 1999; Becerra et al. 2001). Host acquired secondary metabolites also appear to contribute to the effectiveness of an unusual larval fecal defense in *Blepharida* (Morton 1997; Morton and Vencl 1998; Vencl and Morton 1998, 1999).

Furth and Lee (2000) provided a morphological synthesis of the *Blepharida*-group, and reported that morphological data for immature stages were available for only nine species in *Blepharida* Chevrolat, *Diamphidia* Gerstaecker, *Euplectroscelis* Crotch, *Ophrida* Chapuis, and *Podontia* Dalman. Within this broader group, Takizawa (2005) recognized a *Podontia*-genus group comprised of *Blepharida* (Figs 2–3), *Ophrida* (Fig. 6), and *Podontia* (Figs 7–9), based on larval setal patterns and deposition of eggs in rows. Chaboo et al. (2007) added data for three more species in the southern African genera *Diamphidia* and *Polyclada* Chevrolat and Lee and Cheng (2007) added data for two Taiwanese species—*Ophrida spectabilis* (Baly) and *Podontia lutea* (Olivier) (Figs 6 and 8 respectively).

In *Blepharida*, *Diamphidia*, *Podontia*, and *Polyclada*, larvae retain their feces directly on the dorsum. This coating acts as a deterrent to attacking enemies such as ants (Vencl and Morton 1998, 1999). The fecal coat may also serve to moderate body temperature or to reduce water loss but the functions have not been tested. Fecal retention and the dorsally-positioned anus represent complex characters supporting the monophyly of the *Blepharida*-group (Paterson 1943).

The genus *Podontia* Dalman 1824 (Figs 7–9) comprises 14 Asian species ranging from Indonesia to Indo-China, with one species occurring in northern Australia (Baly 1865; Heikertinger and Csiki 1940). *Podontia* adults are distinguished from other *Blepharida*-group species by bifurcate prosternum, saddle-shaped mesosternum and strongly inwardly curved bifid tarsal claws (Medvedev 1999; Becerra 2004a). *Podontia* larvae vary in the presence and shapes of meso and metathoracic tubercles (Kimoto and

Species	Host plant	Reference	
Asiophrida Medvedev			
Asiophrida marmorea	Anacardiaceae: <i>Spondias</i> L. <i>s</i> p.	Furth and Lee 2000	
(Wiedemann)	Apocynaceae: <i>Holarrhena</i> <i>pubescens</i> Wall. (= <i>antidysenterica</i> (L.) Wall)	Stebbing 1914; Maulik 1926; Takizawa 1978; Medvedev 1999	
	Burseraceae: <i>Garuga pinnata</i> Roxb.	Mathew and Mohandas 1989	
	<i>Garuga</i> Roxb. sp.	Medvedev 1999	
Asiophrida (Trichophrida) hirsuta (Wiedemann)	Burseraceae: <i>Boswellia serrata</i> Roxb. ex Colebr.	Stebbing 1914; Maulik 1926; Scherer 1969; Medvedev 1999	
Asiophrida scaphoides	Anacardiaceae: Rhus L.	Medvedev 1999	
(Baly)	Burseraceae: Canarium L.	Medvedev 1999	
Blepharida	Anacardiaceae	Furth 1999; Furth and Lee 2000	
Chevrolat	Anacardiaceae: Cotinus Mill.	Jolivet and Hawkeswood 1995	
	<i>Rhus</i> L. sp.	Jolivet and Hawkeswood 1995; Scherer 1973; Furth 1998	
	Schinus L. sp.	Jolivet and Hawkeswood 1995	
	Burseraceae	Furth 1999; Furth and Lee 2000; Newbold et al. 2007	
	<i>Bursera</i> Jacq. ex L.	Becerra and Venable 1999; Becerra et al. 2009; Noge and Becerra 2009; Becerra 1994, 1997, 2003, 2007; Jolivet and Hawkeswood 1995; Becerra and Venable 1999; Jolivet and Verma 2002; Becerra et al. 2009	
	Bursera schlechtendalii Engl.	Becerra 1994; Becerra and Venable 1990; Becerra et al. 2001	
	Burseraceae: <i>Commiphora</i> Jacq. sp.	Becerra 2003	
	Sapindaceae: <i>Allophylus</i> L. sp.	Jolivet and Hawkeswood 1995	
	Matayba Aubl.	Jolivet and Hawkeswood 1995	
Blepharida alternata	Bursera arborea L. Riley	Furth 1998; Becerra 2007	
Jacoby	Bursera attenuata L. Riley	Furth 1998; Evans et al. 2000; Becerra et al. 2001, Becerra 2004a, b; 2007	
	Bursera bicolor Engl.	Becerra 2004a, b, 2007	
	<i>Bursera chemapodicta</i> Rzed. & E. Ortiz	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007	
	<i>Bursera citronella</i> McVaugh & Rzed.	Becerra 2007	
	Bursera cuneata Engl.	Becerra 2004a, b, 2007	
	Bursera excelsa Engl.	Becerra 2004a, b, 2007	
	Bursera fragilis S. Watson	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007	

Table 1. Host plants of species of the *Blepharida*-group. Known questionable records are indicated by "(?)". Plant names follow the International Plant Names Index (2011).

Species	Host plant	Reference
	Bursera heteresthes Bullock	Becerra 2007
	<i>Bursera instabilis</i> McVaugh & Rzed.	Becerra 1997, 2004a, b, 2007; Furth 1998; Evans et al. 2000; Becerra et al. 2001
	Bursera palmeri S. Watson	Furth 1998; Becerra 2004a, b, 2007
	Bursera submoniliformis Engl.	Furth 1998: Becerra 2004a, b, 2007
Blepharida atripennis	Bursera epinnata (Rose) Engl	Furth 1998: Lee 1999: Furth and Lee 2000
Horn	Bursera odorata T.S. Brandeg	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera ruticola Pérez-Navarro	Becerra 2004a, b, 2007
<i>Blepharida balyi</i> Bryant	<i>Bursera copallifera</i> (Sessé & Moc. ex DC.) Bullock	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	Bursera bipinnata (DC.) Engl.	Furth 1998; Becerra and Venable 1999; Becerra 2004a, b, 2007
	Bursera discolor Rzed.	Furth 1998; Becerra 2004a, b, 2007; Becerra and Venable 1999
	Bursera diversifolia Rose	Furth 1998; Becerra 2004a, b, 2007
	Bursera Jacq. ex L. sp.	Furth 1998
<i>Blepharida bryanti</i> Furth	Bursera excelsa (Kunth) Engl.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, 2007
<i>Blepharida condrasi</i> (Weise)	<i>Rhus tripartita</i> (Ucria) Grande	Furth and Young 1988
Blepharida conspersa	Bursera epinnata (Rose) Engl.	Furth 1998; Becerra 2004a, b, 2007
(Horn)	Bursera filicifolia T. S. Brandeg.	Furth 1998; Becerra 2004a, b, 2007
	Bursera hindsiana Engl. in DC.	Becerra 2004a b, 2007
<i>Blepharida flavocostata</i> Jacoby	<i>Bursera aspleniifolia</i> T. S. Brandeg.	Furth 1998; Evans et al. 2000; Becerra and Venable 1999; Becerra et al. 2001; Becerra 2003, 2004a, b. 2007
	Bursera bicolor Engl.	Becerra 2003
	Bursera biflora (Rose) Standl.	Furth 1998; Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera bipinnata (DC.) Engl.	Becerra 2004a, b, 2007
	Bursera bonetii Rzed.	Furth 1998; Becerra and Venable 1999; Becerra 2003, 2004a, b, 2007
	<i>Bursera copallifera</i> (DC.) Bullock	Furth 1998; Evans et al. 2000; Becerra et al. 2001
	<i>Bursera hintonii</i> Bullock	Furth 1998; Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	<i>Bursera sarukhanii</i> Guevera & Rzed.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera schlechtendalii Engl.	Furth 1998
	Bursera submoniliformis Engl.	Furth 1998; Becerra and Venable 1999; Becerra 2003, 2004a, b, 2007
	<i>Bursera velutina</i> Bullock	Furth 1998; Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007
	Bursera xochipalensis Rzed.	Becerra 2004a, b

Species	Host plant	Reference
Blepharida florhi	Bursera bipinnata (DC.) Engl.	Furth 1998; Becerra and Venable 1999;
Jacoby		Becerra 2004a, b, 2007
Blepharida gabrielae	Bursera aptera Ramirez	Evans et al. 2000; Becerra et al. 2001
Furth	Bursera discolor Rzed.	Furth 1998; Evans et al. 2000; Becerra et al.
		2001; Becerra 2004a, b, 2007
	<i>Bursera fagaroides</i> Engl.	Furth 1998; Evans et al. 2000; Becerra et al.
		2001; Becerra 2004a, b, 2007
	<i>Bursera paradoxa</i> Guevera & Rzed.	Furth 1998; Evans et al. 2000; Becerra et al. 2001; Becerra 2004a, b, 2007
	<i>Bursera trifoliolata</i> Bullock	Furth 1998; Evans et al. 2000; Becerra et al. 2001: Becerra 2004a b. 2007
	Bursera Jaca ex L sp	Furth 1998
Blepharida	Anacardiaceae:	Furth 1998: Becerra 2004a b
hinchahuevosi Furth	Pseudosmodingium perniciosum (Kunth) Engl.	
Blepharida humeralis	Bursera submoniliformis Engl.	Furth 1998; Becerra and Venable 1999;
Furth		Becerra 2004a, b, 2007
Blepharida irrorata	Sapindaceae: Allophylus cominia	Brunner et al. 1975; Furth 1998; Takizawa
Chevrolat	Sw.	2003; Becerra 2004a
	Allophylus occidentalis Radlk.	Brunner et al.1975; Furth 1998; Takizawa
		2003; Becerra 2004a
	<i>Matayba</i> Aubl.	Wolcott 1936; Furth 1998; Takizawa 2003;
		Becerra 2004a
	Bursera simaruba (L.) Sarg.	Furth 1998; Takizawa 2003; Becerra 2004a
Blepharida johngi	Bursera glabrifolia (Kunth) Engl.	Furth 1998; Becerra 2004a, 2007
Furth	Bursera Jacq. ex L. sp.	Furth 1998
Blepharida judithae	Bursera ariensis (Kunth)	Furth 1998; Becerra and Venable 1999;
Furth	McVaugh & Rzed.	Becerra 2004a, b, 2007
Blepharida lineata	Bursera crenata P. G. Wilson	Furth 1998; Evans et al. 2000; Becerra and
Furth		Venable 1999; Becerra et al. 2001; Becerra
	Primana dantiaulata MaVarrah	Recommend Veneble 1000; Evene et al. 2000;
	& Rzed	Becerra et al. 2001: Becerra 2003, 2004a b
		2007
	Bursera kerberi Engl.	Evans et al. 2000; Becerra et al. 2001;
		Becerra 2004a, b, 2007
	<i>Bursera trimera</i> Bullock	Furth 1998; Evans et al. 2000; Becerra and
		Venable 1999; Becerra et al. 2001; Becerra
		2003, 2004a, b, 2007
Blepharida	Bursera submoniliformis Engl.	Furth 1998
maculicollis Furth	Bursera xochipalensis Rzed.	Becerra 2004a
Blepharida marginalis	Rhus natalensis Bernh. ex	Furth and Young 1988
Weise	Krauss, <i>Rhus tripartita</i> DC.,	
	<i>Rhus vulgaris</i> Meikle	
Blepharida	Bursera infernidialis Guevera &	Furth 1998; Becerra and Venable 1999;
<i>melanoptera</i> (Fall)	Rzed.	Becerra 2004a, b, 2007
	Bursera laxiflora S. Watson	Furth 1998; Becerra 2004a, b, 2007

Species	Host plant	Reference
Blepharida	Bursera aptera Ramirez	Furth 1998; Evans et al. 2000; Becerra et al.
<i>multimaculata</i> Jacoby	-	2001; Becerra 2007
	Bursera discolor Rzed.	Furth 1998; Evans et al. 2000; Becerra and
		Venable 1999; Becerra et al. 2001
	Bursera fagaroides (Kunth) Engl.	Furth 1998; Evans et al. 2000; Becerra et al.
		2001; Becerra 2004a, b, 2007
	Bursera fagaroides var. purpusii	Becerra and Venable 1999
	(Brandegee) McVaugh & Rzed.	
	<i>Bursera paradoxa</i> Guevera &	Furth 1998; Becerra and Venable 1999
	Rzed.	
	<i>Bursera trifoliolata</i> Bullock	Furth 1998; Becerra and Venable 1999
	Bursera Jacq. ex L. sp.	Furth 1998
Blepharida natalensis	<i>Rhus lancea</i> L.f.	Becerra 2004b
Baly	Rhus zeyheri Sond.	Scherer 1973
Blepharida	Rhus L. sp.	Becerra 2004b
nigromaculata Jacoby		-
Blepharida	Rhus L. sp.	Paterson 1943
nigrotesselata Baly		D 2007
Blepharida pallida	Bursera arborea (Rose) Riley	Becerra 2007
Ыаке	Bursera aloexylon (Scheide ex	Furth 1998; Becerra 2007
	Schlecht.) Engl.	P 2007
	Bursera bipinnata (DC.) Engl.	Becerra 2007
	Bursera coyucensis Bullock	Furth 1998; Becerra 2004a, b, 2007
	Bursera cuneata (Schlecht.) Engl.	Furth 1998
	Bursera excelsa (Kunth) Engl.	Becerra 2007
	Bursera glabrifolia Engl.	Becerra 2007
	Bursera grandifolia (Schlecht.)	Furth 1998; Evans et al. 2000; Becerra and
	Engl.	Venable 1999; Becerra et al.2001; Becerra
	Ramana hatavethas Bullock	Eurth 1998, Bacarra 1997, 2007
	Pumung instabilis MaVauch 87	Pagame 2007
	Baed	Becella 2007
	Bursera kerheri Engl	Becerro 2007
	Bursera penicillata (DC) Engl	Becerra 2007
	Bursera sarcapada P.C. Wilson	Becerra 2007
	Physical surveyour 1. G. witson	Scherer 1973
Rlepharida parallela	Bursera discolar Rzedowski	Furth 1998: Becerra 2004a b 2007
Furth	Bursera schlachten dalii Engl	Furth 1998: Becerra and Venable 1999:
	Dursera serveemenaanti Liigi.	Becerra 2003, 2004a, b. 2007
Rlepharida rhois	Anacardiaceae: Catinus abavatus	Furth 1998: Becerra 2004a b
(Forster)	Raf. Sullivan	
· · · ·	Rhus L.	Peterson 1953: Takizawa 1978: Furth 1998.
		1999; Becerra 2004b
	Rhus aromatica Aiton	Mignot 1971; Scherer 1973; Furth 1998
	Rhus copallina Linnaeus	Mignot 1971; Frost 1973; Furth 1998; Lee
		1999; Furth and Lee 2000
	Rhus cotinus Nutt.	Riley 1874; Furth 1998

Species	Host plant	Reference	
	Rhus microphylla Engl.	Furth 1998	
	Rhus trilobata Nutt.	Furth 1998	
	Rhus typhina Linnaeus	Mignot 1971; Scherer 1973; Frost 1973; Furth 1998	
	Rhus vernix Linnaeus	Mignot 1971; Frost 1973	
	Rhus L. spp.	Takizawa 1978; Becerra 2004a, b	
	<i>Schinus terebinthifolius</i> Raddi	Frost 1972, 1973; Takizawa 1978; Furth 1998; Becerra 2004a, b	
	Schinus L. sp.	Mignot 1971; Frost 1972, 1973	
	Apocynaceae: <i>Catharanthus</i> (= <i>Vinca</i>) roseus (L.) G. Don	Frost 1972	
	Pinaceae: Pinus palustris Mill.	Mignot 1971; Frost 1972	
	Rosaceae: strawberry	Mignot 1971	
Blepharida sacra	Rhus natalensis Bernh. ex Krauss	Furth and Young 1988	
(Weise)	<i>Rhus tenuinervis</i> Engl. & Gilg. (non-host)	Furth and Young 1988	
	Rhus tripartita DC.	Furth 1982, 1985, 2004; Furth and Young 1988; Lee 1999; Furth and Lee 2000	
	Rhus vulgaris Meikle	Furth and Young 1988	
Blepharida	Bursera aptera Ramirez	Furth 1998; Becerra 2004a, b, 2007	
<i>schlechtendalii</i> Furth	Bursera heteresthes Bullock	Furth 1998	
	Bursera schlechtendalii Engl.	Furth 1998; Evans et al. 2000; Becerra and Venable 1990, 1999; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007	
<i>Blepharida singularis</i> Jacoby	<i>Bursera</i> Jacq. ex L.sp.	Furth 1998; Becerra 2004a	
<i>Blepharida</i> sonorstriata Furth	<i>Bursera laxiflora</i> S. Watson	Furth 1998; Becerra 2004a, b, 2007	
<i>Blepharida sparsa</i> (Clark)	<i>Bursera kerberi</i> Engl.	Becerra 1997; 2004a, b; Furth 1998; Evans et al. 2000; Becerra and Venable 1999; Becerra et al. 2001; Becerra 2003, 2007	
	Bursera submoniliformis Engl.	Furth 1998; Becerra 2004a, b, 2007	
	Bursera Jacq. ex L.sp.	Furth 1998	
<i>Blepharida unami</i> Furth	<i>Bursera fagaroides</i> (H. B. K.) Engl.	Furth 1998; Becerra 2004a	
	Bursera Jacq. ex L. sp.	Furth 1998	
<i>Blepharida variegatus</i> Furth	Bursera submoniliformis Engl.	Furth 1998	
<i>Blepharida verdea</i> Furth	<i>Bursera lancifolia</i> (Schlecht.) Engl.	Furth 1998; Becerra 2003, 2004a, b, 2007	
	<i>Bursera morelensis</i> Ramirez	Furth 1998; Becerra and Venable 1999; Evans et al. 2000; Becerra et al. 2001; Becerra 2003, 2004a, b, 2007	
	Bursera rzedowskii C. A.Toledo	Furth 1998; Becerra 2003, 2004a, b, 2007	
<i>Blepharida vittata</i> Baly	<i>Rhus</i> L. sp.	Becerra 2004b	

Species	Host plant	Reference	
Blepharida xochipala	Bursera mirandae C.A. Toledo	Furth 1998; Becerra 2004a, b, 2007	
Furth	<i>Bursera</i> Jacq. ex L.sp.	Furth 1998	
<i>Blepharida</i> sp.	Bursera cuneata (Schlecht.) Engl.	Evans et al. 2000; Becerra et al. 2001	
<i>Blepharida</i> sp.	Bursera schlechtendalii Engl.	Becerra and Venable 1990; Becerra 1994	
<i>Blepharida</i> sp.	Pseudoosmodingium perniciosum (Kunth) Engl.	Furth 1999	
<i>Blepharida</i> sp.1	Bursera glabrifolia Engl.	Becerra 2004b, 2007	
<i>Blepharia</i> sp. 2	<i>Bursera chemapodicta</i> Rzed. & Ortiz	Becerra 2004b, 2007	
Blepharida sp. 3	Bursera vejar-vazquezii Miranda	Becerra 2004b, 2007	
<i>Blepharida</i> sp. 4	Bursera biflora (Rose) Standl.	Becerra 2004b, 2007	
	Bursera longipes (Rose) Standl.	Becerrra 2004b, 2007	
<i>Blepharida</i> sp. 5	Bursera xochipalensis Rzed.	Becerra 2004b, 2007	
<i>Blepharida</i> sp. 1a	<i>Rhus</i> L. sp., <i>Commiphora</i> Jacq. sp.	Becerra 2004b	
<i>Blepharida</i> sp. 2a	Bignoniaceae: <i>Rhizogum</i> ebovatum?	Becerra 2004b	
<i>Blepharida</i> sp. 3a	Commiphora mollis (Oliv.) Engl.	Becerra 2004b	
<i>Blepharida</i> sp. 6	<i>Bursera ribana</i> Rzed. & Calderón	Becerra 2007	
<i>Blepharida</i> sp. 7	Bursea suntui C.A. Toledo	Becerra 2007	
<i>Crimissa</i> Stål	Anacardiaceae (?)	Furth and Lee 2000	
	Anacardiaceae: <i>Anacardium</i> L.; <i>Mangifera</i> L.	Jolivet and Hawkeswood 1995	
<i>Crimissa cruralis</i> Stål	Anacardium occidentale L.	Bastos 1975; Bastos 1977b; Bastos and Vieira 1977a, b; Santos and Vieira 1977; Sales and Pereira 1978; Bastos et al. 1979; Sales et al. 1981; Tandon and Verghese 1985; Marques et al. 1992	
Crimissa sp.	Anacardium occidentale L.	Santos 1972	
	Bignoniaceae	Jolivet and Hawkeswood 1995	
Diamphidia	Burseraceae	Furth and Lee 2000	
Gerstaecker	Commiphora Jacq. sp.	Jolivet and Hawkeswood 1995; Furth 1998, 1999; Becerra 2003	
<i>Diamphidia femoralis</i> Gerstaecker	Commiphora Jacq. sp.	Becerra 2004b; Chaboo et al. 2007	
Diamphidia	Commiphora Jacq. sp.	Chaboo et al. 2007	
<i>nigroornata</i> Stål	<i>Commiphora africana</i> (A. Rich.) Engl.	Becerra 2004b	
	Commiphora angolensis Engl.	Neuwinger and Scherer 1976; Neuwinger 1996	
	Commiphora glandulosa Schinz	Becerra 2004b	
<i>Diamphidia simplex</i> Péringuey	<i>Commiphora africana</i> (A. Rich.) Engl.	Roodt 1993; Nonaka 1996	
Diamphidia	Commiphora africana (A. Rich.)	Neuwinger and Scherer 1976; Neuwinger	
<i>vittatipennis</i> Baly	Engl.	1996; Becerra 2004b	
	<i>Commiphora tenuipetiolata</i> Engl.	Becerra 2004b	

Species	Host plant	Reference
<i>Diamphidia</i> sp.	<i>Sclerocarya caffra</i> Sond.	Furth and Lee 2000
Elithia Chapuis	Anacardiaceae	Furth and Lee 2000
Euplectroscelis	Burseraceae	Furth and Lee 2000
Crotch	<i>Bursera</i> Jacq. ex L. sp.	Furth 1998
	Bursera microphylla A. Gray	Becerra 2004a
Euplectroscelis xanti	Bursera microphylla A. Gray	Becerra 2004b, 2007
Crotch	Bursera odorata Brandegee	Furth and Lee 2000
Notozona Chevrolat	Anacardiaceae (?)	Furth and Lee 2000
	<i>Rhus</i> L. sp. (?)	Furth 1998
	Burseraceae	Furth and Lee 2000
	Bursera Jacq. ex. L. sp.	Becerra 2004a
Notozona histrionica	Bursera simaruba (L.) Sarg.	Becerra 2004b, 2007
Chevrolat		
Notozona	Bursera simaruba (L.) Sarg.	Flowers and Janzen 1997
nicaraguensis Jaq.		
<i>Ophrida</i> Chapuis	Anacardiaceae	Furth 1998; Furth and Lee 2000
	Apocynaceae	Jolivet and Hawkeswood 1995
	Burseraceae	Furth 1998; Furth and Lee 2000
	Boswellia Roxb. ex. Colebr.,	Jolivet and Hawkeswood 1995
0.1.11.1.	Canarium L., Garuga Roxb.	C 11: 101/ D 1010 10/1
Stebbing	Boswellia serrata Roxb.	Stebbing 1914; Beeson 1919, 1941; Takizawa 1978
<i>Ophrida nigrovaria</i> (MacLeay)	<i>Canarium australianum</i> F. Muell.	Furth 1998
<i>Ophrida scaphoides</i> (Baly)	Anacardiaceae: <i>Rhus succedanea</i> L.	Kimoto and Takizawa 1997
	Burseraceae: Canarium L.	Medvedev and Dap 1982
Ophrida spectabilis	Anacardiaceae: Rhus chinensis	Yang et al.1997; Bilun 1998a; Wang et al.
(Baly)	Mill.; Gall nut, Sumac	1998; Wu et al. 1999; Lee and Cheng 2007
	Rhus punjabensis J.L. Stewart	Wang et al. 1998
	<i>Rhus trichocarpa</i> Miq.	Zhang and Yang 2008
	Rhus verniciflua Stokes	Zhang and Yang 2008
Oprhida xanthospilota (Baly)	Continus coggygria Scop.	Zhao 1985; Furth 1998; Zhang and Yang 2008
<i>Podontia</i> Dalman	Anacardiaceae	Furth 1998; Furth and Lee 2000
	Anacardiaceae: <i>Mangifera</i> L., <i>Rhus</i> L., <i>Spondias</i> L., <i>Toxicodendron</i> Mill.	Jolivet and Hawkeswood 1995
	Rhus L.	Becerra 2003
	Burseraceae	Furth 1998; Furth and Lee 2000
	Burseraceae: Canarium L.	Jolivet and Hawkeswood 1995
	Caesalpiniaceae (?)	Jolivet and Hawkeswood 1995
	Elaeocarpaceae: <i>Elaeocarpus</i> L. sp.	Jolivet and Hawkeswood 1995
	Moraceae: Ficus L. sp. (?)	Jolivet and Hawkeswood 1995
	Theaceae: Thea L. sp. (?)	Jolivet and Hawkeswood 1995

Species	Host plant	Reference	
Podontia affinis	Anacardiaceae: <i>Spondias</i> L. sp.	Kalshoven 1951	
(Gröndal)	Spondias dulcis Forster	Mohamedsaid 1989, 2004; Medvedev 1999	
<i>Podontia congregata</i> Baly	Clusiaceae: <i>Garcinia gummi-gutta</i> (L.) N. Robson	New Family Record, this paper	
Podontia dalmani	Meliaceae: Melia L. sp.	Medvedev 1999	
Baly	Caesalpiniaceae	Medvedev and Dap 1982; Medvedev 1999	
Podontia lutea	Canarium L. sp.	Medvedev and Dap 1982; Medvedev 1999	
(Olivier)	Anacardiaceae: <i>Rhus</i> L. sp.	Hsu 1934a, b; Furth 1998; Medvedev 1999	
	Rhus succedanea L.	Chujo 1935; Takizawa 1978; Kimoto and Takizawa 1997	
	Toxicodendron Mill. sp.	Medvedev and Dap 1982; Medvedev 1999	
Podontia quatuor-	Anacardiaceae: Mangifera L. sp.	Furth 1998	
decimpunctata (L.)	<i>Spondias</i> L. sp.	Kalshoven 1951; Takizawa 1978; Medvedev 1999	
	<i>Spondias cyatherea</i> Sonn.	Yunus and Hua 1980; Daulmerie 1994; Furth 1998	
	Spondias dulcis Forster	Corbett and Yusope 1921; Maulik 1926; Bose 1953; Scherer 1969; Pramanik and Basu 1973; Mohamedsaid 1989, 2004; Singh and Misra 1989; Baksha 1997; Medvedev 1999	
	Spondias pinnata (L.f.) Kurz (= Spondias mangifera Willd.)	Barlow 1900; Maxwell-Lefroy 1909; Stebbing 1914; Beeson 1919, 1941; Bose 1953; Scherer 1969; Pramanik and Basu 1973; Husain and Ahmad 1977; Sardar and Mondal 1983; Singh and Misra 1989; Howlader 1993; Baksha 1997; Deka and Kalita 1999, 2002a - d, 2003, 2004; Hossain et al. 2004	
	Burseraceae: Canarium L.	Yunus and Hua 1980; Furth 1998	
	Moraceae: <i>Ficus elastica</i> Roxb. ex Hornem.	Stebbing 1914; Beeson 1919, 1941; Scherer 1969; Baksha 1997; Singh and Misra 1989	
	Ficus L.	Medvedev 1999	
	"fruit trees" (native & imported)	Fletcher 1920, 1921; Susainathan 1923	
	Lythraceae: <i>Duabanga</i> <i>grandiflora</i> Walp	Singh and Misra 1989; Baksha 1997	
	Lythraceae: <i>Duabanga</i> sonneratioides Buch.	Ahmad 1939; Beeson 1941; Bose 1953	
	Lythraceae: <i>Sonneratia apetala</i> BuchHam.	http://banglapedia.search.com.bd/ HT/B_0385.html	
Podontia soriculata (Swartz)	Thea boheae (?)	Swartz 1808; Gressitt and Kimoto 1963	
Polyclada Chevrolat	Anacardiaceae	Roodt 1993; Jolivet and Hawkeswood 1995; Furth 1998; Furth and Lee 2000	
	Pseudospondias Engl.	Jolivet and Hawkeswood 1995	
	Rhus L.	Shaw et al. 1963	
	<i>Sclerocarya caffra</i> Sond.	Jolivet and Hawkeswood 1995; Shaw et al. 1963	
Species	Host plant	Reference	
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	<i>Sclerocarya birrea</i> (A.Richt.) Hochst.	Roodt 1993; Furth 1998; Chaboo et al. 2007	
	Burseraceae: Commiphora Jacq.	Furth 1999	
	Fabaceae: <i>Dalbergia</i> L. sp. (?)	Jolivet and Hawkeswood 1995	
	Verbenaceae: <i>Clerodendrum</i> L. sp. (?)	Jolivet and Hawkeswood 1995	
<i>Polyclada flexuosa</i> Baly	<i>Sclerocarya birrea</i> sub. sp. <i>caffra</i> Sonder	Shaw et al. 1963; Neuwinger and Scherer 1976; Neuwinger 1996	
<i>Procalus</i> Clark	Anacardiaceae	Jerez 1995; Furth and Lee 2000; Jolivet and Verma 2002	
	<i>Lithraea</i> Miers ex Hook. & Arn., <i>Schinus</i> L.	Furth 1998	
	<i>Lithraea caustica</i> (Molina) Hook. & Arn.	Jerez 1995, 1999; Jolivet and Hawkeswood 1995	
	<i>Schinus latifolius</i> Engl.	Jerez 1995, 1999; Jolivet and Hawkeswood 1995	
	Schinus montanus Engl.	Jerez 1995, 1999; Jolivet and Hawkeswood 1995	
	<i>Schinus patagonicus</i> (Phil.) I.M. Johnst.	Jerez 1995, 1999	
	<i>Schinus polygamus</i> (Cav.) Cabrera	Jerez 1992, 1995, 1999; Jolivet and Hawkeswood 1995	
	<i>Schinus velutinus</i> (Turcz.) I.M. Johnst.	Jerez 1995; 1999	
<i>Procalus lenzi</i> (Harold)	<i>Lithraea caustica</i> (Molina) Hook. & Arn.	Grez 1988; Jerez 1992	
	Schinus polygamus (Cav.) Cabrera	Jerez 1992	
<i>Procalus malaisei</i> Bechyné	<i>Lithraea caustica</i> (Molina) Hook. & Arn.	Etchegarray and Fuentes 1980; Fuentes et al. 1987; Poiani 1989; Grez 1988; Jerez 1992	
Procalus mutans (Blanchard)	<i>Lithraea caustica</i> (Molina) Hook. & Arn.	Jerez 1992	
	Schinus montanus Engl.	Jerez 1992	
<i>Procalus reduplicatus</i> Bechyné	<i>Lithraea caustica</i> (Molina) Hook. & Arn.	Jerez 1992	
Procalus silvai Jerez	<i>Schinus patagonicus</i> (Phil.) I.M. Johnst.	Jerez 1995	
Procalus viridis (Philippi & Philippi)	<i>Lithraea caustica</i> (Molina) Hook. & Arn.	Fuentes et al. 1987; Poiani 1989	
	Schinus latifolius Engl.	Krauss 1962, 1963; Jerez 1985, 1988, 1992; Poiani 1989	
	Schinus montanus Engl.	Jerez 1992	
	<i>Schinus polygamus</i> (Cav.) Cabrera	Philippi and Philippi 1864; Jerez 1985, 1992; Poiani 1989	

Takizawa 1997). Immature stages are known for only *P. affinis* (Gröndal) (Fig. 7; Takizawa 1978; Furth and Lee 2000), *P. dalmani* Baly (Furth and Lee 2000), and *P. lutea* (Olivier) (Fig. 8; Takizawa 1978; Jolivet and Hawkeswood 1995; Kimoto and Takizawa 1997; Lee 1999; Furth and Lee 2000). With adults at ~2 cm long, *P. lutea*, the golden leaf beetle, is reputedly the largest flea beetle in the world (Fig. 8; Furth 1999).

Here, we review the biology of *Podontia* and other *Blepharida*-group genera and provide the first natural history account of *Podontia congregata* Baly, 1865. An endemic to the southern Western Ghats and adjoining areas, *P. congregata* is the largest flea beetle in southern India, ranging from 11.5 to 14.7 mm in length. Our study is based on both field and laboratory observations.

Natural History of Podontia Dalman, 1824

The biology for most *Podontia* species is unknown; however, host data on *P. affinis*, *P. lutea*, and *P. quatuordecimpunctata* (Linnaeus) indicate that these species severely defoliate anacardiaceous trees. For example, *P. affinis* (kedongdong spring-beetle) ranges from Indonesia to China and is a pest in Indonesia, where its larvae attack the foliage of *Spondias dulcis* Forster (Anacardiaceae; =*S. cytherea* Sonn., ambarella or kedong-dong tree; Daulmerie 1994; Morton 1987). Female *P. affinis* live about 3 months, lay loose groups of eggs on the undersides of leaves and coat them with some substance (Kalshoven 1951). The larvae are parasitised by an encyrtid wasp, *Ooencyrtus podontiae* (Gahan) (Table 2; Gahan 1922; Kalshoven 1951).

The golden leaf beetle, *P. lutea* is large sized (~2 cm, Fig. 8) and its attractive coloration promotes its use in cheap Lucite jewelry. The limited available data indicates biology like other *Blepharida*-group members (Hsu 1934a, b; Lee 1999; Furth and Lee 2000). This beetle is a pest of the anacardiaceous shrub, *Toxicodendron vernicifluum* (Stokes) F. Barkley (=*Rhus verniciflua* Stokes) which is the source of the lacquer used in Asian furniture manufacturing (Li and Wang 1984a, b). The coccinellid beetle, *Aiolocaria mirabilis* (Motschulsky), has been studied as a biocontrol agent (Li and Wang 1984a, b).

Podontia quatuordecimpunctata is the best-known *Podontia* species because both adults and larvae defoliate the tree *S. dulcis*. This tree, commonly known as the mak-ok, hog plum, or golden apple tree, is cultivated for its edible fruits in Indonesia, Malaysia, India, Thailand, and the Caribbean (Figs 11–15; Table 1 and references therein). Pramanik and Basu (1973) first described the *P. quatuordecimpunctata* life cycle (See also Singh and Misra 1989). Like *P. affinis*, this species' pest status has led to the use of a vernacular name, "kadondong beetle" (alternate spelling "kedongdong"; Corbett and Yusope 1921), which resembles that for *P. affinis* (Morton 1987). The colorful orange-pink adults are active from June to October, and form pairs that copulate multiple times (Fig. 12). [Additional images of live stages can be viewed at: http://greeneyesth.multiply. com/photos/album/33/Podontia_quatuordecimpunctata]. Females oviposit 20–60 eggs in clusters on the leaf surface; eggs are bright yellow, naked and are arranged in multiple

layers, usually two. Hatching occurs within 7–8 days and the yellow-brown larval instars feed gregariously and prefer younger leaves (Singh and Misra 1989). Barlow (1900) indicated that all five larval stages retain a fecal coat (Figs 13–14), possibly mimicing bird droppings (Barlow 1900; Stebbing 1914; Baksha 1997). The final instar descends the plant, enters the soil, and forms an earthen cell in which it pupates. The yellow-brown pupae last 14–29 days. Adults hibernate in soil or under leaves. Insect (e.g., Fig. 15), nematode, and fungal enemies are documented (Table 2; Singh and Misra 1989). Foliar sprays of cypermethrin (Baksha 1997), metathion (Sardar and Mondal 1983), and carbaryl (Singh and Misra 1989) have been recommended as effective controls.

Natural history of other Blepharida-group genera

Asiophrida Medvedev comprises 20 species in three subgenera (Medvedev 1999; Zhang and Yang, 2008; Mohammedsaid 2004). One of us (KDP) recently discovered populations of *Asiophrida marmorea* (Wiedemann) on one known host, *Garuga pinnata* Roxb. (Burseraceae; Table 1) at Vellanikkara, Kerala, southern India (Fig. 1). Larvae are naked, not retaining fecal coverings; field study is underway.

The biology of *Blepharida*, with 55 species, is currently the best known among *Blepharida*-group genera. Life cycle data have been published for *Blepharida rhois* (Forster) (as *B. dorothea* Mignot) (Frost 1972). *Blepharida evanida* (Baly) is reported as a source of arrow poison used by Kalahari San Bushmen (Lewin 1912, 1923). Furth (1982, 1985) summarized the biology of *B. sacra* (Weise), the sacred sumac flea beetle. Generally, *Blepharida* adults lay clusters of eggs on branches and cover them with fecal material. The slug-like larvae retain soft feces, or long fecal threads or pellets under drier conditions. The prepupal and pupal phases are underground in earthen cells and can last over 7 months. Eggs are parasitized by the eulophid wasp, *Tetrastichus* sp., while larvae are attacked by the fly parasitoid, *Meigenia mutabilis* Fallen (Diptera: Tachninidae; Furth 1985).

Crimissa cruralis Stål, the red cashew beetle, is a major pest of cultivated cashew in Brazil, *Anacardium occidentale* L. (Fig. 4; Pereira et al. 1975; Bastos 1975, 1977a; Bastos and Vieira 1977a, b; Bastos et al. 1979). Eggs are deposited on the trees, larvae eat from leaves, and adults rasp and leave characteristic lesions on leaf surfaces (Pereira et al. 1975). Pupation is underground in soil-based cocoons near the base of the trunk (Santos 1972; Bastos 1977b; Santos and Vieira 1977; Sales and Pereira 1978). Morphology of the immature stages is apparently undescribed. Various chemicals (Bastos 1975; Bastos and Vieira 1977a, b; Bastos et al. 1979) and cashew gum exudates (Marques et al. 1992) have been tested to control this pest.

The nine known species of *Diamphidia* are distributed along the eastern coast from Ethiopia to South Africa and into Namibia (Fig. 5; Baly 1865; Heikertinger and Csiki 1940). Several species of *Diamphidia* are implicated as sources of the Kalahari San arrow poison (Lewin 1923; Roodt 1993; Neuwinger 1996). *Diamphidia* biology is similar to that of other *Blepharida*-group members with the exception that most spe-

Species	Life stage	Enemy	Source
Podontia	Egg, larva	Coleoptera: Coccinellidae: <i>Aiolocaria</i> Crotch sp.	Li and Wang 1984a, b; Cox 1994, 1996
<i>Podontia affinis</i> (Gröndal)	Not indicated	Hymenoptera: Encyrtidae: <i>Ooencyrtus podontiae</i> (Gahan)	Gahan 1922
	Egg	Hymenoptera: Encyrtidae: <i>Ooencyrtus podontiae</i> (Gahan)	Kalshoven 1951
	Not indicated	Nematoda: Mermithidae: <i>Mermis</i> Dujardin sp.	Daulmerie 1994
	Not indicated	Sphaeriales: Hypocreaceae: <i>Cephalosporium</i> Corda sp.	Daulmerie 1994
<i>Podontia congregata</i> Baly	Egg	Hymenoptera: Encyrtidae: <i>Ooencyrtus keralensis</i> Hayat & Prathapan	Hayat and Prathapan 2010
	Larva	Heteroptera: Pentatomidae: <i>Eucanthecona parva</i> (Distant)	This paper (Figs 22, 23)
Podontia lutea (Olivier)	Egg, larva	Coleoptera: Coccinellidae: <i>Aiolocaria mirabilis</i> (Motschulsky)	Li and Wang 1984a, b
		Fungi: Laboulbeniales: <i>Laboulbenia podontiae</i> Thaxter	Thaxter 1914
Podontia	Adult	Arachnida: Lynx spider	Deka and Kalita 2003, 2004
<i>quatuordecimpunctata</i> (Linnaeus)	Adult	Aves: <i>Corvus splendens</i> Vieillot; <i>Acridotheres tristis</i> (L.)	Deka and Kalita 2003, 2004
	Egg, larva	Mantodea	Deka and Kalita 2003, 2004
	Egg	Hymenoptera: Braconidae: <i>Apanteles</i> Foerster, <i>Meteorus</i> Haliday; Trichogrammatidae: <i>Trichogramma</i> Westwood	Deka and Kalita 2003, 2004
	Egg	Hymenoptera: Chalcididae	Corbett and Yusope 1921
	Egg	Hymenoptera: Eulophidae: <i>Pediobius</i> Walker sp.	Baksha 1977
	Egg	Hymenoptera: Encyrtidae: <i>Ooencyrtus corbetti</i> Ferr.	Corbett and Miller 1933; Singh and Misra 1989; Baksha 1997
	Larva	Heteroptera: Pentatomidae	This paper (Fig. 15)
	Larva	Nematoda: Mermithidae: <i>Mermis</i> Dujardin sp.	Singh and Misra 1989; Daulmerie 1994; Baksha 1997
	Larva	Fungi: Laboulbeniales: <i>Laboulbenia podontiae</i> Thaxter	Thaxter 1914
	Larva	Fungi: Sphaeriales: Hypocreaceae: <i>Cephalosporium</i> Corda sp.	Singh and Misra 1989; Daulmerie 1994; Baksha 1997

Table 2. Documented enemies of *Podontia* species.



Figures 1–10. Habitus of adults of *Blepharida*-group genera, size <2 cm long. 1. *Asiophrida marmorea* (Wiedemann) (photo by C.-w. Shin). 2. *Blepharida rhois* (Forster) (photo by C.-w. Shin). 3. *Blepharida vittata* Baly (photo by C.-w. Shin). 4. *Crimissa cruralis* Stål (Photo by M. Tavares). 5. *Diamphidia femoralis* Gerstaecker (photo by C.S. Chaboo). 6. *Ophrida spectabilis* (Baly) (photo by C.-w. Shin). 7. *Podontia affinis* (Gröndal) (photo by C.-w. Shin). 8. *Podontia lutea* (Olivier) (photo by C.-F. Lee). 9. *Podontia rufocastanea* Baly (photo by C.-w. Shin). 10. *Polyclada flexuosa* Baly (photo by C.S. Chaboo).



Figures 11–15. *Podontia quatuordecimpunctata* on the host tree, *Spondias dulcis Forster* (Anacardiaceae; mak-ok, ambarella, kedongdong) in Thailand **11** Host plant **12** The colorful adult, ~ 2 cm long **13** A larva completely covered by feces **14** Larva, partially covered by feces **15** A juvenile pentatomid bug (Heteroptera: Pentatomidae) attacking a fecal-covered larva, with the beak inserted through the fecal cover. (Photos by S. Damrongsiri).

cies have woody hosts in Burseraceae (*Commiphora* Jacq.) or Anacardiaceae (*Sclerocarya* Hochst.) (Table 1; Chaboo et al. 2007).

The austral-oriental genus Ophrida Chapuis consists of four or five species (Medvedev 1999; Zhang and Yang 2008). Immature biology is known for Ophrida scaphoides (Baly) (Kimoto and Takizawa 1997), O. spectabilis (Baly) (Bilun 1998a; Park and Lee 2001; Lee and Cheng 2007), and O. xanthospilota (Baly) (Bai and Zhang 1990; Zhang and Yang 2008). There appears to be one generation per year, with eggs overwintering in slits of host twigs (Park and Lee 2001) or on host trunks (Bilun 1998a, b). The three larval instars are gregarious and retain fecal coverings. Mature larvae descend the plant and construct earthen cocoons underground, at about 20 cm deep; pupation takes about two months (Bilun 1998a). Ophrida spectabilis specializes on Rhus Linnaeus (Park and Lee 2001) and is a pest of R. chinensis Mill. (Bilun 1998a; Yang et al. 1997) and R. punjabensis J. L. Stewart (Wang et al. 1998). R. chinensis, or Chinese sumac, is the source of gallnuts (or nutgalls); these "nuts" are extruded tannins that harden and are used in traditional Chinese medicine (Bilun 1998a, b). The plant's medical value has led to the development of chemical and biocontrol measures that include egg and larval removal from the host (Bilun 1998b), powder applications containing Beauveria bassiana (Bals.-Criv.) Vuill. (Fungi: Clavicipitaceae) (Yang et al. 1997; Wu et al. 1999), and propagation of an egg-parasitoid wasp, Trichogramma Westwood (Hymenoptera: Trichogrammatidae; Yang et al. 1997; Bilun 1998a, b; Wang et al. 1998). In China, O. xanthospilota is a pest of the anacard Cotinus coggygria Scop. (Bai and Zhang 1990).

The 12 species of *Polyclada* Chevrolat are distributed along east Africa, from South Africa to the Arabian Peninsula (Heikertinger and Csiki 1940; Bryant 1942; Chaboo in review). Oddly, some species are also reported from Senegal, which suggests a wider distribution of species, misidentifications, or possibly an inaccurate application of generic concepts. So far as is known, all larvae retain feces (Chaboo et al. 2007). Late 4th instar larvae of some species are dug up, crushed, and their hemolymph is applied to hunting arrows by the San (Bushmen) in Namibia and Botswana (Neuwinger and Scherer 1976; Roodt 1993; Chaboo et al. 2007; Chaboo 2011).

The South American genus *Procalus* Clark comprises nine species that are associated with Anacardiaceae (Table 1; Jerez 1992, 1995, 1999). Two species are significant defoliators of economically important plants in the sub-Andean "matorral" habitat (Mediterranean shrubland) (Fuentes et al. 1987). In Hawaii, *P. mutans* (Blanchard) was introduced as a biocontrol agent for Christmas berry, the weed *Schinus terebinthifolius* Raddi (Anacardiaceae) (Krauss 1962, 1963). Viviane Jerez has described the biology of *P. artigasi* Jerez (Jerez 2003), *P. mutans* (Jerez 1999, 2003), *P. ortizi* Jerez (Jerez 2003), *P. mutans* (Jerez 1999, 2003), *P. ortizi* Jerez (Jerez 2003), *P. viridis* (Philippi and Philippi) (Jerez 1985, 1988), and *P. silvai* Jerez (Jerez 1995, 2003). Adults become active in early spring; by late spring (October) the females attach groups of cylindrical eggs to leaves and cover them with a secretion. The life cycle includes three larval instars. Third instar larvae construct underground cocoons of sand grains and overwinter for up to nine months. Cocoons are

found about 3 cm underground at the base of the host plant. Larvae of *P. viridis* and *P. mutans* retain fecal shields (Jerez 1985, 1999). Mermithid nematodes are known to be larval parasites (Jerez and Centella 1996).

Immature stages of *Euplectroscelis* Crotch, *Furthia* Medvedev, *Neoblepharella* (Medvedev) [=*Blepharella* Medvedev, which was previously occupied as a genus of tachinid flies (Özdikmen 2008)], and *Notozona* Chevrolat are unknown (Medvedev 1999).

Materials and Methods

One of us (KDP) studied natural populations of *Podontia congregata* on its host tree, *Garcinia gummi-gutta*, under field conditions during several visits in 2008–2010 in Vallamkulam, Pathanamthitta, Kerala, India. We also reared beetles in cages for laboratory observations. We examined beetle specimens obtained from the Department of Entomology, College of Horticulture, Mudigere, India (see Fig. 16).

Cage-reared beetle populations were maintained under ambient conditions at Vellayani, Trivandrum, Kerala, India. Individuals from these cage-reared populations were introduced onto field plants of the host for observations. Although *P. congregata* is absent in Vellayani, the host tree grows naturally on the banks of Vellayani Lake.

Habitat 1. India: Kerala State: Pathanamthitta District, Vallamkulum (76°36'18.4" E, 9°22'29.5" N; 12 - 20 m above msl). This is a typical urbanized village in Kerala, where the majority of the agricultural holdings are below 0.5 ha. Homestead farming, a hallmark of the settlement pattern in Kerala, comprises a diverse assortment of crop trees (e.g., *G. gummi-gutta*), shrubs and herbs, which enhances biodiversity conservation in this densely populated village. This rather hot and humid locality is endowed with a few rivulets to the extent that rice fields can remain submerged during the rainy season. Mature *G. gummi-gutta* trees are common on the banks of paddy fields and rivulets.

Habitat 2. India: Kerala State: Trivandrum District, Vellayani (76°59'8.3" E, 8°25'47.5" N; 18 m above msl). This is a watershed bordered by small hillocks that drain into Vellayani Lake, which is the second largest freshwater lake in Kerala. Banana and vegetable cultivation dominate the low-lying paddy fields, while a coconut-based cropping system is practiced on the hillocks. Perhaps because it is not preferred for culinary purposes in southern Kerala, *G. gummi-gutta* is generally uncommon in southern Kerala homesteads and particularly so in Trivandrum. A local preference for dried tamarind fruit (Fabaceae: *Tamarindus indica* Linnaeus) may explain the low abundance of the host plant here.

Habitat 3. India: Kerala State: Alappuzha District: Pandanad (76°35'0.7" E, 9°19'15.1" N; 12 m above msl), located ~8 km south of Vallamkulam. This is an urbanized village similar to Habitat 1.

Habitat 4. India: Kerala State: Trivandrum District: Ponmudi (77° 06' 43.7" E, 8° 45' 19.9" N; 872 m above msl), a hill station, near the southern end of the Western Ghats mountains. A century ago Ponmudi was covered with pristine wet ever green



Figure 16. The Western Ghats Mountains in south India with the localities Vellayani (1), Pomudi (2), Pandanad (3), Vallamkulam (4), Conoor (5), Meppadi (6), Mudigere (7) and Karwar (8) where *Podontia congregata* has been recorded in the present study and in Maulik (1926).

forests and is a hot spot of biodiversity in peninsular India. However, agricultural plantations, tourism, and commercial tree felling has altered the landscape significantly.

Laboratory conditions. Laboratory culture of Podontia congregata was started at Vellayani from nearly half a dozen adults and several larvae collected at Vallamkulam. Adults were confined in a cage of 30 cm³. We offered food and oviposition sites by supplying branches of the host plant, with the cut end placed in water in a glass bottle. Leaves with eggs were transferred to Petri dishes. Larvae were reared on branches in cages or plastic containers, as well as in Petri dishes. Wet soil was provided for pupation. Rearing was carried out at an ambient temperature of about $22-32^{\circ}$ C. About two dozen laboratory reared adults and larvae were introduced onto a naturally growing *G. gummi-gutta* tree at Vellayani during October–December, 2008, and the different life stages were observed.

Natural history of the host plant. Garcinia gummi-gutta (Figs 17–19) grows well in the high rainfall areas of the southern Western Ghats Mountains, India. This medium-sized tree (Fig. 17), locally known as *kodampuli*, is found naturally along banks of rivers, lakes and inundated paddy fields, and is common in Kerala's homestead gardens, as the fruits (Fig. 19) are used in various ways (Manomohandas et al. 2001). The rind is sun-dried for 3–5 days and smoked, and is used as a prized condiment, for curing fish, and as medicine for humans and cattle (Gupta 2002). The acidic pulp covering the seeds is also edible. The thick fleshy rind of ripe fruits is a rich source of hydroxy citric acid (HCA); its derivatives are unique metabolic regulators of obesity (George 2005). Other uses include coagulating rubber latex and polishing gold and silver (Manomohandas et al. 2001). The wood is used as firewood but not valued as timber (Verghese 1991; Geetha 1994; Manomohandas et al. 2001). The tree yields a translucent yellow resin, which does not form an emulsion with water. It is soluble in turpentine and gives a yellow varnish (Sastri 1956).

Study of fecal coat formation. Nine laboratory-reared second and third instar larvae were washed under a very light stream of tap water and lightly brushed with a soft camel-hair brush to remove the fecal cover. Larvae thus cleaned were observed for the formation of a new fecal cover. The fecal thread was removed from the live animal and immersed in water on a slide for microscopic examination.

Tables 1 and 2. For host plants of the *Blepharida*-group taxa (Table 1) we incorporated many little-known articles from Indian journals and assembled host records from an extensive primary literature to collate a list that could be most valuable to the widest community of users. We assembled data on enemies for *Podontia* only, to aid agriculturists dealing with the defoliating effects of these species in Asia. We suspect that there may be obscure agricultural records for other *Blepharida*-group taxa where they are pests (e.g., *Crimissa* is a pest of cashew in Brazil) but such a literature survey will need collaborators involved at the local level.

Specimens. The identity of *P. congregata* was determined by examining the holotype deposited in the Natural History Museum, London, UK, with four labels: Type HT, Baly coll., *Podontia congregata* Baly, examined K. Prathapan, 2005. Specimen vouch-



Figures 17–19. The host plant, *Garcinia gummi-gutta* (L.) N. Robson (Clusiaceae; kodampuli) in India. 17. Tree. 18. Flower. 19. Fruit. (Photos by D. Prathapan).

ers of our study are deposited in the Travancore Insect Collection, Kerala Agricultural University, Vellayani, India, and in the Snow Entomology Collection (SEMC), University of Kansas, Lawrence, U.S.A. (Voucher codes IMcsc00385–IMcsc00390). Vouchers of the bug predator, *Eucanthecona parva* (Distant) (Heteroptera: Pentatomidae), are deposited in the University of Agricultural Sciences, Bangalore, India, and in SEMC. Vouchers of *Ooencyrtus* are deposited in the Aligarh Muslim University, India, and in SEMC. Plant vouchers are deposited in the Calicut University Herbarium, Calicut, India (Accession no. 6394).

Results

Eggs of *P. congregata* are deposited in masses (Fig. 20), usually laid in two layers at Vellayani, egg masses were observed in the field on both abaxial and adaxial surfaces of leaves. In the laboratory, the egg masses comprise 4–20 eggs, and were attached mostly on the adaxial surface. Each orange-yellow egg is oriented vertically. Eggs measure 1.82–1.92 mm long and 0.94–1.03 mm wide. About 6–7 days after oviposition, the egg coloration changes to grey brown just before hatching.

The neonate larva (Fig. 21) is lemon yellow with a dark head. Young larvae feed by scraping on the adaxial surface of the lamina (Fig. 21). Older larvae feed by cutting the leaf lamina while positioning themselves on the abaxial side of the leaf. Older larvae were observed singly on leaves, indicating a solitary nature (Figs 22–24). Larvae that are old enough to cut the leaf tend to remain on the abaxial side of the leaf. The larva with its fecal coat resembles bird droppings (Figs 22–23). The larval period varied from 18–25 days.

The larval fecal coat is formed with feces being excreted as a single thread, which is then transversely folded over the back to cover the dorsum of each larva (Fig. 25). Convulsive movements of the dorsum move it forward. The fecal thread is extruded with a glue-like, transparent material that binds the particles together (Fig. 25). When the fecal coats were removed, larvae took about 6–8.5 hours to refurbish a new coat. The coat color depends on the maturity of the leaf eaten by the larva; larvae feeding on tender leaves have a light colored, wet fecal cover, while those feeding on mature leaves have a rather dark green, apparently drier fecal coat.

Formation of pupae (Figs 27–29) was observed in the laboratory. Full fed final instar larvae shed the fecal coat and remained motionless for about 1–2 days and then assumed a C-shape with concave venter. Prior to pupation, they wriggle on wet soil that was provided in the rearing cage, creating a small depression on the surface and then gathering soil particles from around the body and manipulating these with the legs and mouthparts to form a layer covering the body. Ultimately this layer becomes an earthen cocoon roughly globular in shape (Figs 27–28). The larva never dug into soil, but always constructed the cocoon on the surface.

The adult emerged through a nearly circular exit hole. Construction of the cocoon to adult emergence took 21–24 days. The total life cycle was completed in 49–53 days. Adults (Fig. 30) lived in captivity for about 3–4 months. They feed by cutting the leaf lamina. Adults feign death and fall down (= thanatosis) or reluctantly jump when disturbed. Laboratory-reared adults released on naturally growing host plants at Vellayani were found to be less mobile. Some adults remained on the same branch for weeks and oviposited. The color pattern of adults appears to mimic bird droppings. Like larvae, adults too preferred to remain on the abaxial side of leaves.

At Vallamkulam, the insect was active throughout the year except during the dry summer months. Adult and larval presence was noticed after the onset of monsoon rains in May-June in 2008, and larvae were observed until early January 2009. Neither larvae nor adults were observed during the harsh, dry, summer months. Vellayani received the first summer rain of 9.8 mm on 13 March in 2009, and a single newly emerged adult was noticed on 15 March in the field. Two third instar larvae were observed on 11 April indicating sustenance and possible establishment of *P. congregata* at Vellayani where it was newly introduced. Six adults and several larvae were noticed on this tree during the last week of May, 2009. Two adults and three final instar larvae could be spotted after thorough checking of 14 host trees on 14 April at two spots in Vallamkulam. This indicates a similar seasonality and pre-monsoon buildup of the



Figures 20-30. Life stages of *Podontia congregata* Baly in India. 20. Egg mass. 21. Gregarious instar I larva scraping leaf. 22. Instar II covered with green fecal pellets, being attacked by a juvenile predatory bug, *Eucanthecona parva* (Distant) (Heteroptera: Pentatomidae: Asopini). 23. Instar III larva with incomplete fecal cover and under attack by the juvenile bugs. 24. Mature larva with long fecal strands. 25. Fecal strand, immersed in water. 26. Mature larva, prior to construction of pupation chamber. 27. Pupation chamber. 28. Prepupa within pupation chamber. 29. Pupa. 30. Adult and chewing damage on leaf. (Beetle adult < 2 cm long; Photos by D. Prathapan, N. Anith).

population in both the localities. Interestingly, the introduced *P. congregata* at Vellayani was confined to the single tree on which it was introduced, till the last quarter of 2009. There are 11 other host trees in its vicinity, with the nearest one at a distance of 19 m. Grown-up larvae were observed during December, 2009 on a second tree about 22 m

away from the tree on which the beetle was first introduced. This indicates extremely slow dispersal of the insect.

At Vellayani, in 2010, the host trees put forth new flushes during the harsh summer, and all stages of the insect were active throughout the summer, without a break in activity. Diapause in *P. congregata* is probably correlated with flushing of the host tree rather than the harsh dry summer. However, the entire population mysteriously disappeared in May, indicating a probable local extinction of the species.

Nymphs of a pentatomid, *Eucanthecona parva* (Distant) (Heteroptera), were observed feeding on the larvae of *P. congregata*. A parasitoid was reared from the beetle eggs at Vellayani and is described as a new species, *Ooencyrtus keralensis* Hayat and Prathapan (Hymenoptera: Encyrtidae; Hayat and Prathapan 2010).

Discussion

The occurrence of *Podontia congregata* at Vallamkulam and Pandanad extends its range beyond the Western Ghats Mountains to the southwest plains. The absence of *P. congregata* at Vellayani in Trivandrum District, in spite of the presence of the host plant, is curious. Vellayani is only at a linear distance of about 37 km away from Ponmudi, the nearest locality where *P. congregata* was collected. There is no significant difference in altitude, vegetation, or climate between Vellayani and Pandanad or Vallamkulam, except that the rainfall is low at Vellayani (average annual rainfall of about 1833 mm) compared to Vallamkulam (average annual rainfall recorded at Thiruvalla, about 4 km north of Vallamkulam, is 2912 mm) (M. C. Kiran, pers. comm.). Low rainfall, low abundance of the host plant population, competition or poor rate of dispersal could probably explain its past absence in Vellayani.

Members of the Blepharida-group have been reported on many plant families (Table 1), but some records are questionable as they are singleton reports lacking further confirmation. For example, Stebbing's (1914) report of Podontia quatuordecimpunctata on Ficus elastica Roxb. ex Hornem is that of adult feeding; this may be accidental, as is common in flea beetles, and does not necessarily indicate true trophic relationships. Anacardiaceae and Burseraceae are the unequivocally proven host plant families of Blepharida-group species. This has been confirmed by multiple observations and reports of natural history. These two plant families are closely related; Anacardiaceae, Burseraceae, and Sapindaceae belong to the Order Sapindales of Malvids, but Clusiaceae is phylogenetically distant from Malvids, being situated within the Order Malpighiales of Fabids (Judd et al. 2008). Our novel discovery of a Clusiaceae as host for a Blepharida-group taxon is intriguing. Other chrysomelid genera on Clusiaceae include Nodina Motschulsky, Homoschema Blake, and Megistops Boheman (Jolivet and Hawkeswood 1995). There is also a report of larvae of an unnamed beetle defoliating Garcinia gummi-gutta from India (Anonymous 2003), which is probably P. congregata. Despite being phylogenetically distant, it is possible that G. gummi-gutta is chemically similar to Anacardiaceae and Burseraceae and it produces resinous gum like most

Anacardiaceae. Interestingly, a similar pattern of host selection exists with leafhoppers (Hemiptera: Cicadellidae); Anacardiaceae are common host plants of Oriental Idiocerinae leafhoppers with ten species documented on mango, *Mangifera indica* L., alone (Viraktamath and Viraktamath 1985). Two species of the idiocerine genus *Busoniomimus* Maldonado Capriles occur in India (Viraktamath and Murphy 1980; Viraktamath and Viraktamath 1985); *Busoniomimus mudigarensis* (Viraktamath) feeds on *Buchanania angustifolia* Roxb. (Anacardiaceae) in south India (Viraktamath and Murphy 1980). The second species, *Busoniomimus manjunathi* Viraktamath and Viraktamath, feeds on mango (Viraktamath and Viraktamath 1985) and *G. gummi-gutta* in Kerala (Mathew et al. 2002; KDP personal observations), showing a similar host plant selection to *P. congregata*.

At least three *Podontia* species are regarded as serious pests— *P. affinis* on *S. dulcis* in Indonesia, *P. lutea* on *T. vernicifluum* in China, and *P. quatuordecimpunctata* on *Spondias* spp. At this time, *P. congregata* is a minor pest of *G. gummi-gutta*, causing damage of little economic significance. The large size and fecundity of these species may contribute to their defoliating impacts. Documenting natural enemies as in Table 2 may be useful in finding biocontrol agents.

Species in six *Blepharida*-group genera are now documented with fecal retention— *Blepharida* (Becerra et al. 2001), *Diamphidia* and *Polyclada* (Chaboo et al. 2007), *Ophrida* (Lee and Cheng 2007), and *Podontia* (Barlow 1900; Corbett and Yusope 1921; Pramanik and Basu 1973; Takizawa 1978; Singh and Misra 1989). Both Pramanik and Basu (1973) and Singh and Misra (1989) mention an exudate covering the feces of *Podontia quatuordecimpunctata*. No such exudate was observed in *P. congregata*. Cast exuvial skins are retained in the larval fecal covering of *P. lutea* and *Blepharida nigrotesselata* Baly, but such inclusions have not been reported in other *Blepharida*group species (Paterson 1943; Takizawa 1978). Among chrysomelids that retain a fecal covering, exuvial skin inclusions in larval and pupal fecal shields is a widespread and significant structural feature only in Cassidinae (Chaboo 2007 and citations therein). The gum-like substance covering the fecal thread, revealed through microscopic examination, probably acts as a binding material to create a single, unbroken thread that forms the fecal shield (Fig. 25).

Larvae may reduce enemy attack in several ways. Larvae which are large enough to feed by cutting the lamina position themselves on the abaxial side of the leaf and thus probably evade pouring rains as well as secure some cover from natural enemies. Young larvae prefer to feed on young, tender leaves. Older larvae feed on both light green tender leaves as well as tougher, darker green mature leaves. Fecal cover of larvae feeding on tender leaves is light green while that of those feeding on tougher mature leaves is dark green-grey, which may enhance any background camouflage effect. The fecal coats may further act as physical barriers against some predators and parasitoids. However, bugs may be specialist predators by virtue of their propensity to insert their beaks into the vulnerable ventro-lateral area of the body not covered by the fecal coat (Figs 15, 23). Host specific parasitoids, like *Ooencyrtus podontiae*, are also known to attack *Podontia affinis* (Gahan 1922). Pupation within hard earthen cocoons is widespread among flea beetles and may reduce vulnerability to predators and parasites. Bose (1953) reported leaf inclusions in these cocoons. Such constructions may minimize desiccation, particularly in the drier habitats where many *Blepharida*-group species occur. Most pupation is underground which further enhances protection, but surface pupation occurs in *P. congregata*. Reports for *P. quatuordecimpunctata* are contradictory, indicating underground pupation (Corbett and Yusope 1921; Pramanik and Basu 1973; Sardar and Mondal 1983; Singh and Misra 1989; Baksha 1997; Deka and Kalita 1999) and surface pupation (Bose 1953; Singh and Misra1989; Baksha 1997).

Podontia adults escape by thanatosis, whereby they fall from the foliage, remain motionless and thus disappear into the undergrowth. This defensive tactic is a wide-spread escape response among Chrysomelidae. Larvae appear to use an "anal extremity" to adhere to leaves (Pramanik and Basu 1973); this may be referring to the adhesive anal disc of the pygopods in some chrysomelids which acts as a holdfast organ, minimizing the risk of falling off hosts (Gustafson and Chaboo 2009).

Chrysomelids are well known for their chemical defenses (e.g., Pasteels et al. 1989, 1994) and *Blepharida*-group species have intimate ecological and evolutionary relationships with their host plants, and which appear to be chiefly driven by a chemical arms race based on host secondary metabolites (e.g., Becerra 2003). *Blepharida*-group species present two different strategies of chemical defense: (1) the sequestration of host plant chemicals for incorporation into their fecal defenses, and (2) an apparent synthesis of toxins by the beetle itself like in southern African taxa. As an example of the first strategy, chemical analyses of the feces of *B. rhois* larvae (Morton 1997; Vencl and Morton 1998, 1999) revealed a mix of fatty acids, tannins, and phytol derived from its host plant, *Rhus glabra* Linnaeus, which function as deterrents to ant attack. As an example of the second strategy, diamphotoxin, a relatively small hemolytic and neurotoxic protein, has been isolated from larvae of *D. nigroornata*, one of the beetles used by southern African Kalahari San as a source of their arrow poisons (Koch 1958; Mebs et al. 1982; Woollard et al. 1984). It is unclear if this protein occurs in other species of *Diamphidia*, *Polyclada*, and *Blepharida* which are also suspected sources of arrow poison.

The monophyly of the *Blepharida*-group is supported by characters from host plants, beetle morphology, and behavior of all life stages (Takizawa 1978; Furth and Lee 2000; Chaboo et al. 2007). Takizawa's (2005) *Podontia*-group was based on eggs being deposited in rows; however Hsu (1934b) illustrates eggs of *P. lutea* clustered at the apex of a leaf. Farrell (1998) identified the relationship *Podontia* + (*Orthocrepsis* + *Nisotra*) based on = 18S ribosomal sequence (entire). Becerra (2004a, and subsequent studies) has focused on *Blepharida* and its co-evolutionary association with *Bursera*, but the similar host plant choices of *Blepharida*-group species suggest that Becerra's coevolutionary model may be extrapolated to the entire *Blepharida*-group.

The host plant choices of *Blepharida*-group species are interesting to agriculturists, foresters, anthropologists, and chemists. In Brazil, India and Thailand, the pest species on economically important plants attract agricultural interests. In China, forestry officials are concerned about damage to forests and trees used in traditional medicine.

Southern African species are the source of the San's indigenous arrow poisons. The *Blepharida*-group is a model for research on diverse questions.

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References

- Ahmad T (1939) Plant hosts and immature stages of some chrysomelids from Dehra Dun. Indian Journal of Entomology 1: 1–109.
- Anonymous (2003) Camboge Package of Practices. Spice India (October): 27-29.
- Bai JT, Zhang XD (1990) Studies on bionomics of Ophrida xanthospilota. Forest Pest and Disease 1: 5–7.
- Baksha MW (1997) Biology, ecology and control of amra defoliator, *Podontia quatuordecim-punctata* Linn. (Chrysomelidae: Coleoptera) in Bangladesh. Bangladesh Journal of Forest Science 26: 43–46.
- Baly JS (1865) Descriptions of new genera and species of Galerucidae. Annals and Magazine of Natural History: Zoology, Botany, and Geology 5: 403–410.
- Barlow E (1900) Notes on insect pests from the Entomological Section, Indian Museum. Indian Museum Notes 4: 56–78.
- Bastos JAM (1975) Estudos preliminares para o controle de larva do besouro vermelho do cajueiro, *Crimissa cruralis* Stål, com inseticidas orgânicos sintéticos em laboratório. Fitossanidade 1: 84–86.

- Bastos JAM (1977a) Açãao de contacto de alguns inseticides orgânicos sintéticos sobre a forma adulta do besouro vermelho do cajuiero, *Crimissa cruralis* Stål, 1858. Ciencia Agronomica, Fortaleza 7: 71–74.
- Bastos JAM (1977b) Preliminary information on the life-span of the adult of the red cashew beetle, *Crimissa cruralis* Stål. Fitossanidade 2: 17–18.
- Bastos JAM, Lopes LO, Mota APB, Mesquita ALM (1979) Control of the adult form of the red cashew beetle, *Crimissa cruralis* Stål with synthetic organic insecticides. Fitossanidade 3: 50–51.
- Bastos JAM, Vieira FV (1977a) Control of the larva of the red cashew beetle, *Crimissa cruralis* Stål, with synthetic organic insecticides in the laboratory. Fitossanidade 2: 7–9.
- Bastos JAM, Vieira FV (1977b) Systemic action of monocrotophos against the larva of the red cashew beetle, *Crimissa cruralis* Stål. Fitossanidade 2: 30–31.
- Becerra JX (1994) Squirt-gun defense in *Bursera* and the chrysomelid counterploy. Ecology 75: 1991–1996. doi: 10.2307/1941603
- Becerra JX (1997) Insects on plants: macroevolutionary chemical trends in host use. Science 276: 253–256. doi: 10.1126/science.276.5310.253
- Becerra JX (2003) Synchronous coadaptation in an ancient case of herbivory. Proceedings of the National Academy of Sciences 100: 12804–12807. doi: 10.1073/pnas.2133013100
- Becerra JX (2004a) Ecology and evolution of New World *Blepharida*. In: Jolivet P, Santiago-Blay J, Schmitt M (Eds) New Developments in Biology of the Chrysomelidae. SPB Academic Publishing by, The Hague, 137–143.
- Becerra JX (2004b) Molecular systematics of *Blepharida* beetles (Chrysomelidae: Alticinae) and relatives. Molecular Phylogentics and Evolution 30: 107–117. doi: 10.1016/S1055-7903(03)00158-1
- Becerra JX (2007) The impact of herbivore-plant coevolution on plant community structure. Proceedings of the National Academy of Sciences 104: 7483–7488. doi: 10.1073/ pnas.0608253104
- Becerra JX, Noge K, Venable DL (2009) Macroevolutionary chemical escalation in an ancient plant-herbivore arms race. Proceedings of the National Academy of Sciences 106: 18062– 18066. doi: 10.1073/pnas.0904456106
- Becerra JX, Venable DL (1990) Rapid-terpene bath and "squirt-gun" defense in *Bursera* schlechtendlii and the counterploy of chrysomelid beetles. Biotropica 22: 320–323. doi: 10.2307/2388545
- Becerra JX, Venable DL (1999) Macroevolution of insect-plant associations: the relevance of host biogeography to host affiliation. Proceedings of the National Academy of Sciences 96: 12626–12631. doi: 10.1073/pnas.96.22.12626
- Becerra JX, Venable DL, Evans PH, Bowers WS (2001) Interactions between chemical and mechanical defenses in the plant genus *Bursera* and their implications for herbivores. American Zoologist 41: 865–876. doi: 10.1668/0003-1569(2001)041[0865:IBCAMD]2.0.CO;2
- Beeson CFC (1919) The food plants of Indian forest insects. Part III. Indian Forester 45: 312–323.
- Beeson CFC (1941) The ecology and control of the forest insects of India and the neighboring countries. Forest Research Institute, Dehra Dun, 1006 pp.

- Bilun Y (1998a) A study on the biological characteristics of the sumac flea beetle *Ophrida spectabilis* Baly. Journal of Southwest Forestry College 18: 291–294.
- Bilun Y (1998b) The control of the sumac flea beetle *Ophrida spectabilis* Baly. Journal of Southwest Forestry College 18: 295–298.
- Bose M (1953) Notes on life-histories of some common beetles. Agra University Journal of Research, Part II Science 2: 309–317.
- Bryant GE (1942) New species of *Polyclada* from Africa. Proceedings of the Royal Entomological Society London, ser. B 11: 161–162.
- Brunner S, Scaramutta CLC, Otero AR (1975) Catlogo de los Insectos que atacan a las plantas económicas de Cuba. Academa de Ciencias de Cuba. Instituto de Zoología, Habana, Cuba, 399 pp.
- Chaboo CS (2007) Biology and phylogeny of Cassidinae Gyllenhal (tortoise and leaf-mining beetles) (Coleoptera: Chrysomelidae). Bulletin of the American Museum of Natural History 305: 1–250. doi: 10.1206/0003-0090(2007)305[1:BAPOTC]2.0.CO;2
- Chaboo CS (2011) Defensive behaviors in leaf beetles: From the unusual to the weird. In: Vivanco J, Weir T (Eds) Chemical Biology of the Tropics. Springer Verlag, Berlin, 59–69. doi: 10.1007/978-3-642-19080-3_4
- Chaboo CS (In review) New records of *Diamphidia* Gerstaecker 1855 and *Polyclada* Chevrolat 1840 in the Republic of Mozambique (Chrysomelidae: Galerucinae *s.l.*). The Coleopterists Bulletin.
- Chaboo CS, Grobbelaar E, Larsen A (2007) Fecal ecology in leaf beetles: novel records in the African arrow-poison beetles, *Diamphidia* Gerstaecker and *Polyclada* Chevrolat (Chrysomelidae: Galerucinae). The Coleopterists Bulletin 61: 297–309. doi: 10.1649/0010-065X(2007)61[297:FEILBN]2.0.CO;2
- Chujo M (1935) Studies on the Chrysomelidae in the Japanese Empire (VIII). Subfamily Halticinae (3). Transactions of the Natural History Society of Formosa 25: 459–476.
- Corbett GH, Miller NCF (1933) A list of insects with their parasites and predators in Malaya. Science Serial Department Agriculture, S.S. & F.M.S., 13, 15 pp.
- Corbett GH, Yusope M (1921) Preliminary notes on the "Kadongong" beetle, *Podontia* 14-punctata Linn. Agricultural Bulletin of the Federated Malay States 9: 192–200.
- Cox ML (1994) The Hymenoptera and Diptera parasitoids of Chrysomelidae. In: Jolivet PH, Cox ML, Petitpierre E (Eds) Novel aspects of the biology of Chrysomelidae. Series Entomologica 50. Kluwer Academic Publishers, Dordrecht, 419–468. doi: 10.1007/978-94-011-1781-4_35
- Cox ML (1996) Insect predators of Chrysomelidae. In: Jolivet PHA, Cox ML (Eds) Chrysomelidae biology: Ecological studies. SPB Academic Publishers, Amsterdam, 23–91.
- Daulmerie S (1994) Investigations on golden apples (*Spondias cyatherea*) production with particular reference to post-harvest technology and processing. Miscellaneous Publications Series. Inter-American Institute for Cooperation on Agriculture, Port of Spain, 116 pp.
- Deka S, Kalita J (1999) Biology of *Podontia quatuordecimpunctata* L. a defoliator of *Spondias pinnata* (Koem) Kurz in Assam. Journal of Assam Science Society 40: 19–24.

- Deka S, Kalita J (2002a) Assessment of foliage loss caused by *Podontia quatuordecimpunctata* (Coleoptera Chrysomelidae) - a defoliator of *Spondias pinnata* in Assam. Journal of Ecobiology 14: 3–8.
- Deka S, Kalita J (2002b) Distribution pattern of *Podontia quatuordecimpunctata* (Insecta) under natural conditions. Journal of Ecobiology 14: 189–194.
- Deka S, Kalita J (2002c) Seasonal incidence of *Podontia quatuordecimpunctata* (Coleoptera) on hog plum (*Spondias pinnata*, Anacardiaceae) in Assam. Journal of Ecotoxicology and Environmental Monitoring 12: 201–204.
- Deka S, Kalita J (2002d) Field biology of ambara defoliator, *Podontia quatuordecimpunctata* L. (Coleoptera, Chrysomelidae) in Assam. Journal of Applied Zoological Researches 13: 176–178.
- Deka S, Kalita J (2003) Natural enemies of Ambara defoliator, *Podontia quatuordecimpunctata* L. in Guwahati, Assam. Insect Environment 9: 72–73.
- Deka S, Kalita J (2004) Natural enemies of Ambara defoliator, *Podontia quatuordecimpunctata* L. in Guwahati, Assam. Insect Environment 9: 159–160.
- Etchegarry JM, Fuentes ER (1980) Insectos defoliadores asociados a siete especies arbustivas del matorral. Anales del Museo de Historia Natural de Valparaíso 13: 159–166.
- Evans PH, Becerra JX, Venable DL, Bowers WS (2000) Chemical analysis of squirt-gun defense in *Bursera* and counterdefense by chrysomelid beetles. Journal of Chemical Ecology 26: 745– 754. doi: 10.1023/A:1005436523770
- Farrell BD (1998) "Inordinate Fondness" explained: why are there so many beetles? Science 281: 555–559. doi: 10.1126/science.281.5376.555
- Fletcher TB (1920) Annotated list of Indian crop-pests. In: Fletcher TB (Ed) Report of the Proceedings of the Third Entomological Meeting, Pusa, 3–15 February, 1919 Volume 1. Superintendent of Government Printing, Culcutta, 33–314.
- Fletcher TB (1921) Annotated list of Indian crop-pests. Pusa Agricultural Research Institute Bulletin No. 100. Superintendent of Government Printing, Culcutta, 246 pp.
- Frost SW (1972) Notes on *Blepharida dorothea* Mignot (Coleoptera: Chrysomelidae). Entomological News 83: 45–47.
- Frost SW (1973) Hosts and eggs of *Blepharida dorothea* (Coleoptera: Chrysomelidae). Florida Entomologist 56: 120–122. doi: 10.2307/3493236
- Flowers RW, Janzen DH (1997) Feeding records of Costa Rican Leaf Beetles (Coleoptera: Chrysomelidae). Florida Entomologist 80: 334–366. doi: 10.2307/3495768
- Fuentes ER, Poiani A, Molina JD (1987) Shrub defoliation in the Chilean matorral: what is its significance. Revista Chilena de Historia Natural 60: 276–283.
- Furth DG (1982) Blepharida biology, as demonstrated by the sacred sumac flea beetle (B. sacra Weise). Spixiana, Supplement 7: 43–52.
- Furth DG (1985) The natural history of a sumac tree, with an emphasis on the entomofauna. Transactions of the Connecticut Academy of Arts and Sciences 46: 137–234.
- Furth DG (1992) The New World *Blepharida* group, with a key to genera and description of a new species (Coleoptera: Chrysomelidae). Journal of New York Entomological Society 100: 399–414.
- Furth DG (1998) New World *Blepharida* Chevrolat 1836 (Coleoptera: Chrysomelidae: Alticinae). Memoirs of the Entomological Society of Washington 21: 1–109.

- Furth DG (1999) Searching for sumacs and flea beetles: from African poison arrows to Mexican poison ivy. Entomological News 110: 183.
- Furth DG (2004) Fun with flea beetle feces. Chrysomela Newsletter 43: 10.
- Furth DG, Lee JE (2000) Similarity of the *Blepharida*-group genera using larval and adult characters (Coleoptera: Chrysomelidae: Alticinae). Journal of the New York Entomological Society 108: 26–51. doi: 10.1664/0028-7199(2000)108[0026:SOTBGG]2.0.CO;2
- Furth DG, Young DA (1988) Relationships of herbivore feeding and plant flavanoids (Coleoptera: Chrysomelidae and Anacardiaceae: *Rhus*). Oecologia 74: 496–500. doi: 10.1007/ BF00380045
- Gahan AB (1922) Report on a small collection of parasitic Hymenoptera from Java and Sumatra. Treubia 3: 47–52.
- Geetha CK (1994) Kodampuli (*Garcinia cambogia*) An under exploited crop in the Kerala Homesteads. Spice India (April): 9–10.
- George ST (2005) Exploitation of Malabar tamarind in humid tropics. In: Rajamony L (Ed) Winter school on "Trade oriented exploitation of horticulture in humid tropics - Opportunities and challenges". 1–21 December, 2005, College of Agriculture, Kerala Agricultural University, Vellayani, 82–86.
- Gressitt JL, Kimoto S (1963) The Chrysomelidae (Coleopt.) of China and Korea. Part II. Pacific Insects Monograph 1B: 893–939.
- Grez AA (1988) *Procalus lenzi* y *Procalus malaisei* (Coleoptera: Chrysomelidae): dos especialistas del matorral. Revista chilena Entomología 16: 65–67.
- Gupta VK (2002) The wealth of India. A dictionary of Indian raw materials and Industrial Products. First Supplement Series (raw materials). National Institute of Science Communication and Information Resources, New Delhi, 351 pp.
- Gustafson G, Chaboo CS (2009) Ambulatory use of abdominal ampullae in larvae of *Labi*domera clivicollis (Kirby) (Coleoptera: Chrysomelidae: Chrysomelinae). The Coleopterists Bulletin 63: 357–363. doi: 10.1649/1162.1
- Hayat M, Prathapan KD (2010) A new species of *Ooencyrtus* (Hymenoptera: Encyrtidae), parasitoid in the eggs of *Podontia congregata* (Coleoptera: Chrysomelidae) from India. Oriental Insects 44: 35–39.
- Heikertinger F, Csiki E (1940) Partes 166 et 169. Chrysomelidae: Halticinae, Volumen 25. In: Schenkling S (Ed) Coleopterorum Catalogus. Dr. W. Junk, Publisher, Gravenhage, 635 pp.
- Hossain MA, Taj HFE, Ahad MA, Ara R (2004) Biology and food consumption of hog plum leaf beetle, *Podontia quatodecimpunctata* L. Journal of Subtropical Agricultural Research and Development 2: 45–50.
- Howlader MA (1993) Growth, development, and survival of *Podontia quaturdecempunctata* (Coleoptera: Chrysomelidae) larvae on different parts of host plant. Bangladesh Journal of Zoology 21: 1–7.
- Hsu KT (1934a) The methods for controlling some important harmful insects of Chekiang. Entomology and Phytopathology (Hangchow, China) 2: 222–228.
- Hsu KT (1934b) Notes on a trip to Yenchow. Entomology and Phytopathology (Hangchow, China) 2: 276–283.

Husain M, Ahmad M (1977) Notes on chrysomelid beetles (Coleoptera) of the Bangladesh Agricultural University area, Mymensingh. Bangladesh Journal of Zoology 5: 71–75.

International Plant Names Index (2011) http://www.ipni.org (accessed 5. VIII. 2011).

- Jerez VR (1985) Posición taxonómica y redescripción de *Procalus viridis* (Philippi y Philippi, 1864) (Coleoptera-Chrysomelidae). Boletín de la Sociedad de Biología de Concepción 56: 43–47.
- Jerez V (1988) Ciclo de vida y biología de *Procalus viridis* (Phil. Y Phil., 1864) (Coleoptera: Chrysomelidae). Comunicaciones del Museo Regional de Concepción 2: 7–11.
- Jerez V (1992) Revisión taxonómica del género *Procalus* Clark, 1865 (Chrysomelidae: Alticinae). Gayana Zoología 56: 109–125.
- Jerez V (1995) *Procalus silvai* n. sp. descripción e interacción con *Schinus patagonicus* (Chrysomelidae: Alticinae). Gayana Zoológica 59: 161–165.
- Jerez V (1999) Biology and ecology of *Procalus* Clark, 1865, endemic to the Andino-Patagonian region (Alticinae). In: Cox ML (Ed) Advances in Chrysomelidae Biology 1. Backhuys Publishers, Leiden, 545–555.
- Jerez V (2003) Interspecific differentiation in eggs and first instar larvae in the genus *Procalus* Clark 1865 (Chrysomelidae: Alticinae). In: Furth DG (Ed) Special topics in leaf beetle biology. Proceedings of the fifth International Symposium on the Chrysomelidae, 25–27 August 2000, Iguassu Falls, Brazil, XXI International Congress of Entomology. Pensoft, Sofia-Moscow, 147–153.
- Jerez V, Centella C (1996) Primer registro de nematodos Mermithidae, parásitos de *Procalus mutans* y *Procalus reduplicatus* (Chrysomeldiae: Alticinae). Acta entomología Chilena 20: 107–110.
- Jolivet P, Hawkeswood TJ (1995) Host-plants of Chrysomelidae of the world: an essay about the relationships between the leaf-beetles and their food plants. Backhuys Publishers, Leiden, 281 pp.
- Jolivet P, Verma KK (2002) Biology of leaf beetles. Intercept Limited, Andover, 313 pp.
- Judd SW, Campbell CS, Kellog EA, Stevens PF, Donoghue MJ (2008) Plant systematics: a phylogenetic approach (3rd edition). Sinauer Associates, Inc., Sunderland, USA, 611 pp.
- Kalshoven LGE (1951) Pests of crops of Indonesia. Ichtiar Baru-W. Van Hoeve, Jakarta, 701 pp.
- Kimoto S, Takizawa H (1997) Leaf beetles (Chrysomelidae) of Taiwan. Tokai University Press, Tokyo, 581 pp.
- Koch C (1958) Preliminary notes on the coleopterological aspect of the arrow poison of the bushmen. Pamphlet of the South African Biological Society 20: 49–54.
- Krauss NLH (1962) Biological control investigations on insect, snail and weed pests in tropical America. Proceedings of the Hawaiian Entomological Society 18: 131–133.
- Krauss NLH (1963) Biological control investigations of Christmas berry (*Schinus terebinthifolius*) and *Emex* (*Emex* spp.). Proceedings of the Hawaiian Entomological Society 18: 281–287.
- Lee JE (1999) Taxonomic study of the larvae of the genus *Blepharida* (Coleoptera: Chrysomelidae: Alticinae) from Vietnam. Korean Journal of Entomology 29: 203–207.
- Lee CF, Cheng HT (2007) The Chrysomelidae of Taiwan Vol. 1. Sishou-Hills Insect Observation Network Press, Taipei, 199 pp.
- Lewin L (1912) *Blepharida evanida*, cin neuer Pfeilgiftkafer. Archiv fur experimentelle Pathologie und Pharmakologie 69: 60–66.

Lewin L (1923) Die Pfeilgifte. Verlag von Johann Ambrosius Barth, Leipzig, 517 pp.

- Li LH, Wang W (1984a) A preliminary study on *Aiolocaria mirabilis* an important natural enemy of *Podontia lutea*. Forest Science and Technology Linye Keji Tongxun 10: 22–25.
- Li LH, Wang W (1984b) A preliminary study on *Aiolocaria mirabilis*, a natural enemy of *Podontia lutea*. Natural Enemies of Insects Kunchong Tiandi 6: 230–235.
- Manomohandas TP, Anith KN, Gopakumar S, Jayaranja M (2001) Kodampuli a fruit for all reasons. Agroforestry Today 13: 7–8.
- Marques MR, Albuquerque LMB, Xavier-Filho J (1992) Antimicrobial and insecticidal activities of cashew tree gum exudate. Annals of Applied Biology 121: 371–377. doi: 10.1111/ j.1744-7348.1992.tb03450.x
- Mathew G, Mohandas K (1989) Insects associated with some forest trees in two types of natural forests in the Western Ghats, Kerala (India). Entomon 14: 325–333.
- Mathew MP, Bhaskar H, Ushakumari R, Thomas J (2002) A new leafhopper pest on Malabar tamarind *Garcinia cambogia* Desr. Insect Environment 8: 136–137.
- Maulik S (1926) Coleoptera. Chrysomelidae (Chrysomelinae and Halticinae). In: Shipley AE (Ed) The fauna of British India including Ceylon and Burma. Taylor and Francis, London, 442 pp.
- Maxwell-Lefroy H (1909) Indian insect life. Thacker, Spink and Co, Calcutta, 786 pp.
- Mebs D, Brüning F, Neuwinger HD (1982) Preliminary studies on the chemical properties of the toxic principal from *Diamphidia nigroornata* larvae, a source of bushman arrow poison. Journal of Ethnopharmacology 6: 1–11. doi: 10.1016/0378-8741(82)90068-X
- Medvedev LN (1999) A revision of the group Blepharidiini (Chrysomelidae: Alticinae) from the Oriental region. Russian Entomological Journal 8: 175–184.
- Medvedev LN, Dap DT (1982) Host plants of Chrysomelidae of Vietnam. In: Medvedev L (Ed) Insect Fauna of Vietnam. Nauka, Moscow, 84–97.
- Mignot EC (1971) Review of *Blepharida* Chevrolat (Chrysomelidae, Alticinae) of America north of Mexico. The Coleopterists Bulletin 25: 9–16.
- Mohamedsaid MS (1989) Flea beetles of the genus *Podontia* from Peninsular Malaysia (Chrysomelidae: Alticinae). Malayan Nature Journal 42: 277–285.
- Mohamedsaid MS (2004) Catalogue of the Malaysian Chrysomelidae (Insecta: Coleoptera). Pensoft Publishers, Sofia, 239 pp.
- Morton J (1987) Fruits of warm climates. Julia F. Morton, Miami, 505 pp.
- Morton TC (1997) Sequestration of host-plant-chemistry into frass-based defenses of Chrysomelidae: Lema trilineata, Neolema sexpunctata (Criocerinae), Plagiometriona clavata (Cassidinae) and Blepharida rhois (Alticinae). PhD Thesis. Pennsylvania, USA: Pennsylvania State University, State College.
- Morton TC, Vencl FV (1998) Larval leaf beetles form a defense from recycled host plant chemicals discharged in fecal wastes. Journal of Chemical Ecology 24: 765–786. doi: 10.1023/A:1022382931766
- Neuwinger HD (1996) African ethnobotany: poisons and drugs: chemistry, pharmacology, toxicology. Chapman & Hall, London, 941 pp.
- Neuwinger HD, Scherer G (1976) Die Larven-Pfeilgift der Buschmänner. Biologie in unserer Zeit 6: 75–82. doi: 10.1002/biuz.19760060303

- Newbold T, Meregalli M, Colonelli E, Barclay M, Elbanna S, Fandud NA, Flegg F, Fouad R, Gilbert F, Hall V, Hancock C, Ismail M, Osamy S, Saberi I, Semida F, Zalat S (2007) Redescription of a weevil *Paramecops sinaitus* (Coleoptera: Curculionidae: Molytinae) from the Sinai and an ecological study of its interaction with the Sinai milkweed *Asclepias sinaica* (Gentianales: Asclepiadaceae). European Journal of Entomology 104: 505–515.
- Noge K, Becerra JX (2009) Germacrene D, a common sesquiterpene in the genus *Bursera* (Burseraceae). Molecules 14: 5289–5297. doi: 10.3390/molecules14125289
- Nonaka K (1996) Ethnoentomology of the Central Kalahari San. African Study Monographs Suppl. 22: 29–46.
- Özdikmen H (2008) Substitute names for some preoccupied leaf beetles genus group names described by L. N. Medvedev (Coleoptera: Chrysomelidae). Munis Entomology and Zoology 3: 643–647.
- Park JY, Lee JE (2001) Biology and immature stages of *Ophrida spectabilis* (Baly) from Korea (Coleoptera: Chrysomelidae: Alticinae). Korean Journal of Entomology 31: 257–260.
- Pasteels JM, Rowell-Rahier M, Braekman JC, Daloze D, Duffey S (1989) Evolution of exocrine chemical defense in leaf beetles (Coleoptera: Chrysomelidae). Experientia 45: 295–302. doi: 10.1007/BF01951815
- Pasteels JM, Rowell-Rahier M, Braekman JC, Daloze D (1994) Chemical defence in adult leaf beetles updated. In: Jolivet PH, Cox ML, Petitpierre E (Eds) Novel aspects of the biology of Chrysomelidae. Series Entomologica 50. Kluwer Academic Publishers, Dordrecht, 289–301. doi: 10.1007/978-94-011-1781-4_22
- Paterson NF (1943) Early stages of two species of Halticinae (Chrysomelidae, Coleoptera). Journal of the Entomological Society of South Africa 6: 29–36.
- Peterson A (1953) Larvae of insects. Coleoptera, Diptera, Neuroptera, Siphonaptera, Mecoptera, Trichoptera Part II. Edwards Brothers Inc., Columbus, OH, 416 pp.
- Pereira L, de Andrade JM, da Silva CCA (1975) Measurements of the eggs of the red cashew beetle, *Crimissa cruralis* Stål (Col., Chrysomelidae). Fitossanidade 1: 72–74.
- Philippi RA, Philippi F (1864) Beschreibung einiger neuen Chilenischen Käfer. Stettiner Entomologische Zeitung 25: 313–406.
- Poiani A (1989) Interacciones entre *Procalus* (Coleoptera, Chrysomelidae) y *Lithrea caustica* (Sapindales, Anacardiaceae). Un caso de monofagia en el matorral de Chile central. Orsis 4: 99–112.
- Pramanik LM, Basu AC (1973) Biology of *Podontia 14-punctata* Linnaeus (Chrysomelidae: Coleoptera), a defoliator pest of hogplum in West Bengal. Indian Journal of Entomology 35: 339–340.
- Riley CV (1874) The jumping sumach beetle *Blepharida rhois* (Forst.) (Ord. Coleoptera; Fam. Chrysomelidae). Sixth annual report on the noxious, beneficial and other insects of the State of Missouri 118–121.
- Roodt V (1993) The Shell field guide to the common trees of the Okavango Delta and Moremi Game Reserve. Shell Oil, Botswana, 110 pp.
- Sales FM, Pereira L (1978) Ecological site of the pupa of the cashew red beetle, *Crimissa cruralis* Stål, 1858. Fitossanidade 2: 71–74.

- Sales FJM, Carlos-Filho F, Pinto GL (1981) Estudo comparativo do consumo foliar do besouro vermelho do cajueiro. Fitossanidade 5: 31–37.
- Santos JHR (1972) Determinação do período larva madura a adulto recém emergido, em *Crimissa* sp. Ciência Agronomica Fortaleza 2: 27–28.
- Santos JHR, Vieira FV (1977) Habitos do Crimissa cruralis Stål, 1858. Fitossanidade 2: 31–32.
- Sardar MA, Mondal A (1983) Bio-ecology and chemical control of *Podontia 14-punctata* (Linn.) on hogplum. Indian Journal of Agricultural Sciences 53: 745–748.
- Sastri BN (Ed) (1956) The wealth of India a dictionary of Indian raw materials and industrical products. Raw Materials vol. 4: F-G. National Institute of Science Communication and Information Resources. Council of Scientific and Industrial Research, New Delhi, 287+viii pp.
- Scherer G (1969) Die Alticinae des indischen Subkontinentes (Coleoptera Chrysomelidae). Pacific Insects Monograph 22: 1–251.
- Scherer G (1973) Ecological and historic zoogeographic influences on concepts of the genus as demonstrated in certain Chrysomelidae (Coleoptera). Zoologica Scripta 2: 171–177. doi: 10.1111/j.1463-6409.1974.tb00749.x
- Shaw EM, Woolley PL, Rae FA (1963) Bushman arrow poisons. Cimbebasia 7: 2-41.
- Singh P, Misra RM (1989) Bionomics of the ambara defoliator *Podontia 14- punctata* Linn. (Coleoptera: Chrysomelidae). Indian Forester 115: 910–915.
- Stebbing EP (1914) Indian forest insects of economic importance. Eyre and Spottiswoode Ltd., London, 648 pp.
- Susainathan P (1923) Some important pests of the Malay Peninsula. In: Fletcher B (Ed) Proceedings of the Fifth Entomological Meeting. Superintendent Govt. Printing, Calcutta, India, 28–33.
- Swartz (1808) Chrys. Soriculata. In: Schönherr CJ. Synonymia Insectorum, oder: Versuch einer Synonymie Aller bisher bekannten Insecten, nach Fabricii Systema Eleutheratorum &c. geordnet. Erster Band. Eleutherata oder Käfer. Zweiter Theil. Spercheus *Cryptocephalus*. Stockholm, X, 246.
- Takizawa H (1978) Notes on Taiwanese chrysomelid larvae, V. Entomological Review of Japan 31: 75–84.
- Takizawa H (2003) Checklist of Chrysomelidae in West Indies (Coleoptera). Hispaniolana N.S. 2. Museo Nacional de Historia Natural, Santo Domingo, 125 pp.
- Takizawa H (2005) Supra-generic subdivisions of the subfamily Alticinae based on larval characters, with descriptions of larvae of Hispaniolan species (Coleoptera: Chrysomelidae). Insecta Matsumurana 62: 187–206.
- Tandon PL, Verghese A (1985) World list of insect, mite and other pests of mango. Technical Document No. 5. Indian Institute of Horticultural Research, Bangalore, 21 pp.
- Thaxter R (1914) Laboulbeniales parasitic on Chrysomelidae. Proceedings of the American Academy of Arts and Sciences 50: 15–50. doi: 10.2307/20025507
- Vencl FV, Morton TC (1998) The shield defense of the sumac flea beetle, *Blepharida rhois* (Chrysomelidae: Alticinae). Chemoecology 8: 25–32. doi: 10.1007/PL00001800
- Vencl FV, Morton TC (1999) Shield defenses of larval Chrysomelidae: ecological and phylogenetic aspects. In: Cox ML (Ed) Advances in Chrysomelidae Biology. Backhuys Publishers, Leiden, The Netherlands, 140–163.

Verghese J (1991) Garcinia cambogia (Desr.) - Kodampuli. Indian Spices 28: 19-20.

- Viraktamath CA, Murphy DH (1980) Description of two new species with notes on some Oriental Idiocerinae (Homoptera: Cicadellidae). Journal of Entomological Research 4: 83–90.
- Viraktamath S, Viraktamath CA (1985) New species of *Busoniomimus* and *Idioscopus* (Homoptera: Cicadellidae: Idiocerinae) breeding on mango in south India. Entomon 10: 305–311.
- Wang BQ, Ai XR, Chen ZJ, He YF, Song TW (1998) Biology of *Ophrida spectabilis* (Baly) and its control. Entomological Knowledge 35: 26–29.
- Wolcott GN (1936) Insectae Borquenses with a host plant index. Journal of Agriculture of the University of Puerto Rico 20: 1–627.
- Woollard JMR, Fuhrman FA, Mosher HS (1984) The Bushman arrow poison toxin, Diamphidia toxin: isolation from pupae of *Diamphidia nigro-ornata*. Toxicon 22: 937–946. doi: 10.1016/0041-0101(84)90185-5
- Wu MN, Gou Y, Lin L, Yang SZ (1999) Study on the control technique of *Ophrida spectabilis* (Baly). Entomological Knowledge 36: 329–332.
- Yang S, Lin L, Gou Y, Wu M (1997) A preliminary study on the control of *Rhus chinensis* pest, *Ophrida spectabilis* with *Beauveria bassiana*. Chinese Journal of Biological Control 13: 132–134.
- Yunus A, Hua TH (1980) List of economic pests, host plants, parasites and predators in West Malaysia (1920–1978). Bulletin No. 153. Ministry of Agriculture, Kuala Lampur, Malaysia, 538 pp.
- Zhang LJ, Yang XK (2008) Description of the immature stages of *Ophrida xanthospilota* (Baly) (Coleoptera: Chrysomelidae) from China. Proceedings of the Entomological Society of Washington 11: 693–700. doi: 10.4289/07-041.1
- Zhao SH (1985) A preliminary observation of the biology of *Ophrida xanthospilota* (Baly) (In Chinese). Plant Protection 11: 15–16.

RESEARCH ARTICLE



Types of geographical distribution of leaf beetles (Chrysomelidae) in Central Europe^{*}

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Abstract

A comparison of the geographical distribution patterns of 647 species of Chrysomelidae in Central Europe revealed 13 types of distribution: (1) widely distributed, (2) southern, (3) southeastern, (4) southwestern, (5) northern, (6) eastern, (7) south east quarter, (8) south west quarter, (9) fragmented, (10) montane, (11) subalpine & alpine, (12) scattered, (13) unusual, and irregular patterns produced by insufficient data. Some of these distributions are trivial (e. g. northern, eastern, etc., alpine) but others are surprising. Some cannot be explained, e. g. the remarkable gaps in the distribution of *Chrysolina limbata* (Fabricius, 1775) and in *Aphthona nonstriata* (Goeze, 1777). Although our 63.000 records are necessarily tentative, we found that the distribution maps from these data reflect in many cases the common knowledge on the occurrence of leaf beetles in specific areas.

Keywords

Insecta, Coleoptera, Chrysomelidae, zoogeography, grid maps, faunistics, Central Europe

Introduction

Distribution data of organisms are necessary for basic research, as they provide insights into their potential ecological interactions and the colonisation of a given area. Moreover, comparing distribution patterns, morphological and/or physiological traits can inspire hypotheses on how ecological adaptations and phylogenetic constraints become

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possible. Such data are also a prerequisite for sound decisions in nature conservation and an integral contribution to applied sciences.

In the autumn of 1987, a group of 18 amateur and professional coleopterists working on leaf beetles decided to co-operate in continuing the faunistics project of Adolf Horion (12.07.1888 – 28.05.1977). He had published a series of 12 volumes on the geographic distribution of beetles in Central Europe between 1941 and 1974 but could not complete his project of treating all coleopteran families. As they considered it necessary to compile the available data on the zoogeography of Chrysomelidae, the 18 enthusiasts formed a working group on leaf beetle faunistics (CHRYFAUN) (those whose names and last names are given in Italics left the group in the meantime): Ulf Arnold (Schöneiche, Germany), Wolfgang Bäse (Rheindorf, Germany), Ron Beenen (Nieuwegein, The Netherlands), Bozidar Drovenik (Ljubljana, Slovenia), Manfred Döberl (Abensberg, Germany), Dieter Erber (24.02.1933 - 28.02.2004, Giessen, Germany), Frank Fritzlar (Jena, Germany), Elisabeth Geiser (Salzburg, Austria), Uwe Heinig (Berlin, Germany), Horst Kippenberg (Herzogenaurach, Germany), Michael Langer (Niederwiesa, Germany), Winrich Mertens (Freiburg im Breisgau, Germany), "Theo" Michael Schmitt (now in Greifswald, Germany), Matthias Schöller (Berlin, Germany), Dieter Siede (now in Retterath, Germany), Walter Steinhausen (München, Germany), and Andrzej Warchałowski (Wroclaw, Poland).

We built a database with entries either based on voucher specimens or on reliable literature data. 'Reliable' was defined as records with geographic coordinates down to one minute. There is hardly a consensus among zoogeographers how to circumscribe "Central Europe" in scientific terms. Horion (1951, p. III) defined Central Europe "sensu stricto" as comprising Germany, Austria and Czechoslovakia. Political borders are definitively irrelevant for the target organisms but indeed they are relevant for human researchers. In addition, decisions in nature conservation regularly require an evaluation of the rareness and the ecological importance of certain species in a given political area. How rare or special a species in a target area is can only be asserted if distribution data are available for the area of concern and for a wider geographic frame. Thus, we apply a broader concept of Central Europe and focus on a rectangular area comprising 12 countries: Belgium, The Netherlands, Luxembourg, Switzerland, Liechtenstein, Germany, Poland, Austria, Czech Republic, Slovakia, Hungary, and Slovenia. This rectangle lies between 2° and 25°E and 45° and 55°N.

There are numerous ways to visualise geographic distributions, partly due to the fact that there are several possibilities to project the earth surface on a plane map (see, e.g. Snyder 1987). Horion (1965) marked $10^{\circ} \times 10^{\circ}$ grid cells with pencil crosses for selected species. Beenen and Winkelman (2002) use a Universal Transverse Mercator (UTM) grid for the Netherlands and plot open and solid circles to indicate records from before and after 1950. In another publication, Beenen et al. (2005) use spots of different diameter for the same purpose. In 1998, Beenen had reported on five different patterns of distribution of Galerucinae in The Netherlands (a: evenly dispersed, b: restricted to sandy soil and limestone, c: restricted to sandy areas with Pleistocene soil and to limestone areas, d: restricted to marshes, e: near the borders of The Netherlands) and presented also maps with an UTM grid. The UTM grid was also used by Silfverberg (1987) in his in-

vestigation on the distribution of Chrysomelidae in Finland. Warchałowski (1985) gives the geographical distribution by homogeneous blackening of certain areas of the maps. Gruev and Tomov (2007) plotted individual records on 10 km UTM grid cells for Bulgaria. Besides these maps, also tables of different spatial resolution were used to publish information on geographic distribution of beetles, e. g. by Gruev and Döberl (2005) for the flea beetles (Alticinae) of the Palaearctic subregion, within which they differentiated 13 areas; Köhler and Klausnitzer (1998) for the beetles of Germany in 18 areas; or by Lundberg and Gustafsson (1995) for the beetles of Sweden subdivided in 30 provinces.

We decided to present our results finally as grid maps with fields of size 30° east to west and 20° north to south. This provides the opportunity to include records of which we do not have precise geographic data but know definitely to which grid cell they belong. Our rectangle contains 1380 cells in total, 1291 include land, at least partly, and 1126 grid cells lie at least partly over a focus country. The grid cells differ somewhat in size. Their N-S extension is 37.12 km, but the length of their E-W axis and consequently their surface area varies, e.g. between 31.80 km (= 1180.42 km²) at 55°N, 35.77 km (= 1327.78 km²) at 50°N, or 39.21 km (= 1456.59 km²) at 45°N.

The members of the working group chose the larger grid cell size as compared to that used in Great Britain (10×10 km, Cox 1992) because it allows for the inclusion of more records which could not be georeferenced but only assigned to a grid cell. An approach similar to ours is followed by the Bruchidae/Chrysomelidae Recording Scheme in Great Britain (Cox 1992, 2007). However, their grid cells are 10 km-squares, which means that the spatial resolution is approximately twelve times higher than ours. On the other hand, the area we treat is about five times larger than the UK. This might in part compensate for the coarse resolution in CHRYFAUN.

There are 787 species of Chrysomelidae (s. l., i. e. including 66 bruchids) in checklists, but we have data for only 647 species in 63,136 records for 737 grid cells (57 % of 1291, or 65 % of 1126). Here, we present a progress report on the project "faunistics of Central European seed and leaf beetles". We hope to show that already at the present state some scientifically interesting results have been attained.

Material and methods

Records were taken into the CHRYFAUN database from (1) the notes of Adolf Horion, forwarded by Dieter Siede, (2) the collections of Zoologisches Forschungsmuseum Alexander Koenig – ZFMK, Bonn (Germany) and Zoologisches Institut und Museum of Ernst-Moritz-Arndt-Universität – EMAU, Greifswald (Germany), and (3) the private collections of Ron Beenen, Manfred Döberl, Uwe Heinig, Horst Kippenberg, "Theo" Michael Schmitt, Matthias Schoeller, Dieter Siede (see above for locations), and Klaus Renner (Bielefeld, Germany). Literature data were taken from the reports published in Fragmenta faunistica 1932-1998 (Adamczewski, Bartoszynski, Bartowska, Bielawski, Brischke, Burakowski, Ciszkiewicz, Enderlein, Glazek, Goljan, Kapuscinski, Karpinski, Karpowicz, Kinel, Krzeminski, Kulczinski, Nunberg, Maczynski, Makolski, Markowski, Mazurowa, Mroczkowski, Ogloblina, Pawlowski, Pisarski, Podoski, Popek, Raabe, Stobiecki, Szymczakowski, Tenenbaum, Wasowska, Wegrzecki, Wierzbicki), Mitteilungen der Arbeitsgemeinschaft rheinischer Koleopterologen (Baumann, Böhme, Brenner, Eisinger, Franzen, Höhner, Junker, Katschak, Koch, Köhler, Matern, Müller, Siede, Stüben, Stumpf, Wagner, Wenzel, Wunderle), Mitteilungen des Entomologischen Vereins Stuttgart (Bense, Braun, Bretzendorfer, Büche, Dynort, Frank, Gladitsch, Hemmann, Kless, Knapp, Konzelmann, Kostenbader, Krell, Lange, Malzacher, Maus, Reibnitz, Rheinheimer, Roppel, Ulbrich, Weber, Wolf-Schwenninger, Ziegler), Geiser (2001), Gürlich (1992), Gürlich et al. (1995), and Vig (1996). Since our data will be accessible through GBIF-D in the near future, we do not list the above sources in detail. They can be seen on each individual entry of a record in the database.

"Record" means a single collection act for a species, as documented on the label(s) on the pin(s) of the voucher specimen(s), or the equivalent information in a publication. We used only such data which allowed for relating a record to a certain grid cell, and which offered a time specification of "before 1900", "between 1899 and 1950", and "after 1949", or more exact. If there were several specimens on a single pin or a series of several specimens with exactly the same label data, we opened only one "record" and entered the number of specimens in a "remarks" field. The geographical coordinates of the localities were entered exact to the minute when possible. Where we could only assign a locality to a certain grid cell of $20' \times 30'$, we used the centre of the grid cell as a dummy in generating distribution maps. In such a record, the assignment of coordinates to the locality was labelled "artificial" in the database.

Our database CHRYFAUN was developed by the first author and was housed at ZFMK until 2009. Since then, the master database is ministered by the first author at EMAU, copies are distributed among the members of the working group. The database software CHRYFAUN is programmed by Hicosoft (Joachim Hilgers, Düsseldorf, Germany) on a MS Visual FoxPro[®] platform. Distribution maps are produced using DMAP[®] (by Alan Morton, Penrhynoch, Aberystwyth, Ceredigion, UK).

In the maps produced, grid cells in light yellow indicate those for which we have data. Consequently, we can only speculate on blank areas. As even most common species are not necessarily reported for all covered grid cells, we plot the distribution of the species of interest using red diamonds against the sampled records of all species of the same genus (or a genus with similarly looking species, in case of monotypic genera). The rationale behind this procedure is that collectors would hardly look for a single species and discard specimens of the remaining species of the same genus. Also, we hope to avoid confusing occurrence gaps with report gaps.

Maps were generated for all of the 647 species under study. Of these, 115 were discarded because they were based on less than 10 records. The other maps were compared by eye according to superficial similarity. The maps could be grouped to certain easily circumscribable types, and there were only few intermediates. Afterwards, the types were described as detailed and objective as possible. For this purpose, also the frequency maps of all species were considered. This allowed us to assign each species unequivocally to one of the distribution types.

Results

Frequency of records

The 63,136 records for the 647 target species are not distributed equally over the 737 grid cells of which we have data at all. Fig. 1 shows the frequencies of records plotted on the grid cells. Only for 77 grid cells we have more than 200 records, and only 30 grid cells would allow – cautious - statements for more than 400 species. When scaled differently, it turns out that for 254 grid cells less than 11 records are in our database.

The highest number of records lie in areas (brown squares) where either amateur coleopterists clubs (Rhineland, Baden-Württemberg) or individual collectors (e.g., The Netherlands: Utrecht, Germany: Berlin) are very active, or at touristically and faunistically attractive sites, e. g. Lake Neusiedl in Austria and Hungary.

Species for which we have less than 10 records in the database (114) were only included in the calculations if the records coincide with the zoogeographic information given by Mohr (1966), Koch (1992), or Köhler and Klausnitzer (1998). (See Fig. 1)



Figure 1. Frequency distribution map, based on 63,136 records of 647 species over 737 grid cells of 20 × 30 geographic minutes. Blank areas mean no records.

Widely distributed: Oulema melanopus (Linnaeus, 1758)

Ninety seven (97) species in our database are reported from all German federal states (Saarland as the smallest state - 2568.7 km² - only facultatively) and additionally from at least four other Central European countries.

Not surprisingly, as an example of a "common" species we present the distribution data of the Cereal Leaf Beetle, *Oulema melanopus* (Linnaeus, 1758), a major crop pest in Central Europe. This species is reported of 209 grid cells, all species of the genus from 315. Records are lacking especially for the Czech Republic and for Slovakia. Very frequently taxonomists did (and still do) not discriminate *O. melanopus* from *O. duftschmidi* (Redtenbacher, 1874). Therefore, we plot additionally the records reported under this latter name on the map.

We present this map in spite of the difficult species identification because there is no other species in the database represented by more records. Thus, these records give the clearest picture of a "widespread" species that is deemed to be "common everywhere" in the literature and illustrates the importance of accurate identifications. (See Fig. 2)

Southern distribution: Altica helianthemi (Allard, 1859)

The distribution of 103 species has a northern border between 50°N and 53°N approximately parallel to the latitude. As an example we present the map of the flea beetle *Altica helianthemi* (Allard, 1859). This species is reported from 34 grid cells, all species of the genus from 255.

Thirty seven (37) of our 50 records have been either originally identified or later verified by experts on Central European flea beetles (Manfred Döberl, Uwe Heinig, Karl-Heinz Mohr, Dieter Siede). Therefore, we chose this species as an example although it belongs to a group of species in the genus *Altica* which are extraordinarily difficult to discriminate. The records of *Altica helianthemi* fit best to our definition of a "southern" distribution. Most other species have single records lying outside the "southern" domain so that only the overwhelming majority of records show a "southern" pattern. (See Fig. 3)

South-Eastern distribution: Chrysochus asclepiadeus (Pallas, 1773)

Fifty two (52) species had their northern boundary between 51°N and 55°N, stretching from South-West to North-East. As an example we present the map of *Chrysochus asclepiadeus* (Pallas, 1776). This species is reported from 41 grid cells. Since this is the only species of its genus, we plot the records against those of the genus *Chrysolina* (assuming that collectors of *Chrysolina*-species most probably will in the field also take *Chrysochus asclepiadeus*, due to the similar appearance), species of the genus *Chrysolina* are reported from 483 grid cells. (See Fig. 4)



Figure 2. Distribution map of *Oulema melanopus/duftschmidi*, based on 775 records for "*Oulema melanopus*", 109 for "*Oulema duftschmidi*" and 1836 for the genus *Oulema*.



Figure 3. Distribution map of *Altica helianthemi*, based on 50 records for the species and 1113 for the genus *Altica*.

South-Western Distribution: Timarcha tenebricosa (Fabricius, 1775)

Twelve species are found only in the south-western part of the study area. Their range extended north between 50° and 54°, while the boundary stretches from North-West to South-East. *Timarcha tenebricosa* is presented as a representative of this type. This species is reported from 46 grid cells, all species of the genus from 141. *Timarcha-tenebricosa*-individuals are the largest leaf beetles in our area. Therefore, we expect that it has not been overlooked so that the pattern of our map shows the real north-eastern boundary of distribution. (See Fig. 5)

Northern Distribution: Galerucella grisescens (Joannis, 1865)

Eight of the listed species are distributed north of 49°N or the abundance of which decreases remarkably between 53°N and 49°N. An example of these species is *Galeru-cella grisescens* (Joannis, 1865). This species is reported from 38 grid cells, all species of the genus from 245. All 68 records of *Galerucella grisescens* lay north of 49°N, all but one even north of 50°. In the other "northern" species, a certain proportion of records comes from south of 49°N, e.g. 13 of 186 in *Mantura chrysanthemi* (Koch, 1803), or 20 of 103 in *Phyllotreta armoraciae* (Koch, 1803) (most of these southern records lay north of 48° anyway). (See Fig. 6)

Eastern Distribution: Aphthona nigriscutis Foudras, 1860

Of the 647 species analysed, 16 had a western distribution boundary between 10°E and 14°E. As an example we present the distribution map of *Aphthona nigriscutis* Foudras, 1860. This species is reported from 16 grid cells, all species of the genus from 308. Of the 22 records for this species, 6 lay west of 12°E, and of these, 4 are in grid cell 4256 which covers the Vinschgau in South Tyrol. (See Fig. 7)

Southeast-quarter Distribution: Crioceris quinquepunctata (Scopoli, 1763)

52 species occurred only in areas south of 51°N and east of 10°E. The Five-spotted Asparagus Beetle *Crioceris quinquepunctata* (Scopoli, 1763) is given as an example of this type. This species is reported from 20 grid cells, all species of the genus from 175. As the westernmost record represents a single specimen from an *Asparagus*-plantation in Lower Franconia near Würzburg, the natural western boundary of this species lies supposedly more eastern. (See Fig. 8)



Figure 4. Distribution map of *Chrysochus asclepiadeus*, based on 77 records for the species and 4814 for the genus *Chrysolina*.



Figure 5. Distribution map of *Timarcha tenebricosa*, based on 127 records for the species and 432 for the genus *Timarcha*.



Figure 6. Distribution map of *Galerucella grisescens*, based on 68 records for the species and 1099 for the genus *Galerucella*.



Figure 7. Distribution map of *Aphthona nigriscutis*, based on 22 records for the species and 1761 for the genus *Aphthona*.
Southwest-quarter Distribution: Bruchidius varius (Olivier, 1795)

Only five species were reported exclusively from areas south of 51°N and west of 10°E. One of them is the seed beetle *Bruchidius varius* (Olivier, 1795) which is given as the example in Fig. 9, it is reported from 16 grid cells, all species of the genus from 70. Possibly this species is not confined to the southwestern area, as indicated by the single record from northern Hungary. (See Fig. 9)

Fragmented Distribution: Aphthona nonstriata (Goeze, 1777)

Of the studied species, 37 showed a surprising distribution pattern. These species are reported from all over Central Europe, but have a remarkable gap, in most cases in Central Germany, Southeast Germany and/or the Alpine region. These gaps cannot plausibly be explained by selective collecting, as congeneric species are reported from these gaps. An example of such a pattern is *Aphthona nonstriata* (Goeze, 1777). This species is reported from 91 grid cells, all species of the genus from 308. The distribution gap in Central Germany is obvious, but also other areas from which congeneric species are reported but not *A. nonstriata* can be recognised, e. g. in South Germany, in Austria and in Hungary. The example of *Aphthona nonstriata* is especially striking because the gaps cover areas which have been extensively studied by numerous flea beetle specialists. (See Fig. 10)

Montane Distribution: Oreina alpestris (Schummel, 1844)

Eighteen (18) species are distributed in montane areas, i. e. between 200 m and 1500 m a. s. l. As an example we present the distribution map of *Oreina alpestris* (Schummel, 1844) which is found in The Vosges, Black Forest, around the European Alps, in the Harz and the Erz Mountains, and in the Carpathians. This species is reported from 77 grid cells, all species of this genus from 176. It is obvious that all *Oreina*-species are distributed in a similar way. (See Fig. 11)

Alpine Distribution: Lilioceris tibialis (Villa, 1838)

Distributions restricted to alpine areas, i. e. regions comprising peaks of more than 1500 m a. s. l., were characteristic of 28 species. The example chosen here is *Lilioceris tibialis* (Villa, 1838). This species is reported from 24 grid cells, all species of this genus from 218. Seemingly, the frequencies of *Lilioceris*-spp. decrease towards North, but when generating a frequency map of the 619 records, it turns out that there are grid cells with more than 20 records in the surroundings of Berlin, and even from the east-ern part of the island of Rügen there are five findings. (See Fig. 12)



Figure 8. Distribution map of *Crioceris quinquepunctata*, based on 70 records for the species and 762 for the genus *Crioceris*.



Figure 9. Distribution map of *Bruchidius varius*, based on 40 records for the species and 281 for the genus *Bruchidius*.



Figure 10. Distribution map of *Aphthona nonstriata*, based on 197 records for the species and 1761 for the genus *Aphthona*.



Figure 11. Distribution map of *Oreina alpestris*, based on 171 records for the species and 1587 for the genus *Oreina*.

Scattered Distribution: Chaetocnema aerosa (Letzner, 1846)

As "scattered" we define a pattern of few (less than 25) records which are seemingly distributed at random over the map. This is the case in 53 species, *Chaetocnema aerosa* (Letzner, 1846), the example chosen to represent this "pattern". This species is reported from 17 grid cells, all species of this genus from 226. This distribution pattern is possibly characteristic for a "rare" species, i. e. one with very low abundances. (See Fig. 13)

Unusual Distribution: Chrysolina limbata (Fabricius, 1775)

Fifty (50) species show a distribution with a marked pattern, which can, however, not plausibly be explained by referring to known patterns. In *Chrysolina limbata* (Fabricius, 1775), some of the marked grid cells are situated around Berlin and in the area of Lake Neusiedl (Austria), the first is residence of several amateur collectors, the second a favoured touristic site, which could explain why beetles of this species were collected right there. But most other records are not correlated with known factors (climate, phytogeography of food plants, collecting activities, orography etc.) pertaining to the probability that a beetle individual gets collected. Similar facts apply for the other 49 cases. *Chrysolina limbata* is reported from 24 grid cells, all species of this genus from 476. (See Fig. 14)



Figure 12. Distribution map of *Lilioceris tibialis*, based on 36 records for the species and 619 for the genus *Lilioceris*.



Figure 13. Distribution map of *Chaetocnema aerosa*, based on 21 records for the species and 2097 for all species of the genus.



Figure 14. Distribution map of *Chrysolina limbata*, based on 47 records for the species and 4814 records for all species of the genus *Chrysolina*.

Proportions of distribution types

The types of geographic distributions we distinguish are represented by remarkably different numbers of species, which is shown in Fig. 15.



Figure 15. Relative frequency of distribution types of Chrysomelidae in Central Europe.

Discussion

A first, and unexpected, result of the present study was that the distribution patterns of those 532 species of which we have more than 10 records in our file are not all different or all similar but can easily be grouped into eleven distinct types (widely distributed, southern, south-eastern, south-western, northern, eastern, south-east quarter, southwest quarter, fragmented, montane, and alpine, plus two less distinct forms: irregular and scattered). As it is normal for patterns in nature, there are cases in which the geographical limits are less sharp than the circumscription of the "types" could suggest. But even in these cases, the frequency maps allow for clear assignment of a species pattern to a distribution type, which means that only few records from the edge of a presumed distribution area lie beyond the defining borders.

A second and also remarkable result is that the eleven rather distinct types correspond to zoogeographic patterns described in literature, e.g. in de Lattin (1967). Since we have so few records from Poland and hardly any from France, we refrain from applying de Lattin's terms which imply a historical zoogeographical interpretation. Our "South-East quarter"-type probably corresponds to de Lattin's term "pannonian", our "South-West quarter"-type possibly corresponds to de Lattin's "atlantomediterranean", but we find the adoption of these interpretations premature, in spite of the suggestive resemblances. The patterns of certain species, however, differ from the descriptions given in regional catalogues as, e.g., Köhler and Klausnitzer (1998) and Mohr (1966).

Although in numerous cases it is tempting to regard our results as true reflections of real distribution patterns, several caveats must be considered:

(1) As our target area comprises 1291 or at least 1126 grid cells, and we aim at judging on the geographical distribution of 647 species (or ideally 787), it is entirely clear that 63.000 records are definitely too few to allow for justified conclusions. A rough estimate shows that for coverage of 100 records per grid cell and species we would need more than 83 million records. Even if we assume that not all species occur in all grid cells and that less than 100 records would be sufficient, more than 10 million records is a sound estimate for a database meeting all our desires.

(2) Collecting activity of private and professional entomologists is strongly influenced – and was so even more in the past – by political borders and (restricted) freedom to travel. This factor can easily lead to erroneous conclusions on beetle distribution in Central Europe.

(3) An unknown but possibly considerable number of specimens in private and museum collections may be incorrectly determined. This applies more to museum collections than to private ones, since museum curators and collection managers are normally not taxonomic experts of all the taxa they are responsible for. Thus, as many museum specimens come from donations of uncertain taxonomic reliability, or from samples from student projects in the field etc., there are countless causes of mis-identification. These could be detected by the taxonomic specialists in our group in a limited number of cases only. In case of a doubtful record voucher specimens were revised when it was possible. Despite to our effort, a certain degree of uncertainty remains.

(4) There is some arbitrariness in the assignment of a "distribution type". Although we tried to define these types as clear as possible, we had to cope with cases in which all records but one or extremely few fit into one of our types, and in which we decided to ignore these "aberrant" records (as e.g., with *Bruchidius varius*, see Fig. 9). It can, however, well be that a more complete set of records will prove these decisions wrong, as the "aberrant" records might be indications of a wider or differently shaped distribution.

(5) Similar as above, additional records may lead to a distribution type different from the one we assigned. This was already the case when 9656 additional records were entered into the database after one of us (T.R.) had completed his diploma thesis in 2008 ("Historisch-zoogeographische Analyse der rezenten Verbreitung der Blattkäfer (Coleoptera: Chrysomelidae) in Mitteleuropa", Rheinische Friedrich-Wilhelms-Universität Bonn, Germany). We found 97 instead of 90 species "widely" distributed, 103 instead of 116 "southern", 52 instead of 51 "south-eastern", 37 instead of 36 "fragmented", 18 instead of 16 "montane", and 53 instead of 52 "scattered".

(6) Data density varies extremely with respect to species and areas, as can be seen from Fig. 1. Private and museum collections (which are normally composed of several private collections over time) contain specimens according to individual biases and different scientific purposes. One example are the seed beetles which were regarded a

separate family, Bruchidae, and consequently ignored by most leaf beetle enthusiasts. Thus, they are notoriously underrepresented in our data. Another aspect is the low motivation of amateur collectors to collect, mount, label and report "common" species. This is the only plausible explanation for the incompleteness of the records for *Oulema melanopus/duftschmidi* (see Fig. 2) and other species which we would expect from all grid cells. But even the extremely dense data yielded by the Oxfordshire Biological Recording Scheme for Oxfordshire show coverage of only about 14 % of all the 2 × 2 km grid cells of the map by records for *Oulema melanopus* (Campbell 1980). The 1992 progress report of the "Bruchidae/Chrysomelidae Recording Scheme" for Great Britain was based on 1800 of its 3033 10-km-squares of which only 563 (Cox 1992) or 780 (Cox 2007) listed "*Oulema melanopus*". This shows that also there a "common" and "widespread" species is by far not recorded from all areas where it is supposedly present.

Remark on taxonomy and nomenclature of Oulema melanopus/duftschmidi/ rufocyanea.

Berti (1989) published her decision to split the traditionally accepted species Oulema melanopus (Linnaeus, 1758) into two, based on her investigation of more than 570 specimens labelled Oulema melanopus of the collection of the Muséum National d'Histoire Naturelle (MNHN) at Paris. As she found that the oldest available name for the "new" species is Oulema duftschmidi (Redtenbacher, 1874) and no type specimen could be found, she designated a neotype, kept at MNHN. Cox (1995) stated that the "new" species has to bear the name Oulema rufocyanea (Suffrian, 1847), since he held the opinion that O.duftschmidi and O.rufocyanea are synonyms. An up to now unpublished molecular study (Susanne Dobler, University of Hamburg, pers.comm. 2009) revealed that all tested specimens of O.rufocyanea were conspecific with O.duftschmidi, thus corroborating Cox' statement. Consequently, the correct name of the "new" species should indeed be O.rufocyanea. Petitpierre (2000) and Warchałowski (2010), however, listed three similar Oulema-species for the Fauna Iberica or for the Palaearctic region, respectively, O.duftschmidi, O.melanopus, and O.rufocyanea. This could mean that there is a third species which must not bear the name O.rufocyanea as long as this name has to be applied to the species named O.duftschmidi by Berti. As there are three specimens of the Oulema-melanopus-complex (one from Spain, two from West-Germany) in Dieter Siede's collection (Retterath, Germany) with male genitalia corresponding to neither alternative depicted in Berti (1989), we leave the question open as to the number of species in the Oulema-melanopus-complex and which have to be the correct names for them.

For the purpose of the present paper the only relevant aspect of the records labelled "*Oulema melanopus*" is the fact that one would expect to find this "species" in literally all grid cells if our database were as complete as it should be.

Despite these limitations, of which most have been discussed by Geiser (2001b, 2005) already, a great proportion of our results is in line with those found in related

scientific literature. However, we must keep in mind that "literature data" arose from collecting activities of individual entomologists and are thus prone to be influenced by the same factors as our data. Other findings, however, may provide more relevant corroborations of our results. The available distribution maps of host plants (Bundesamt für Naturschutz) in Germany are in accordance with the geographical distribution of their guests produced from our data. It turns out that no leaf beetle record is present in a grid cell in Germany in which its food plant is not present. The distribution of certain specialists coincide exactly with the occurrence of their food plant, e. g. the flea beetle *Psylliodes marcida* (Illiger, 1807) and its food plant *Cakile maritima* Scopoli, 1772. Especially interesting is a gap of ca. 300 km in the distribution of *Artemisia campestris* Linnaeus, 1753, the food plant of *Galeruca interrupta* Illiger, 1802. The distribution of records of this beetle species shows exactly such a gap in the same area as the gap in its food plant. It is also worth mentioning that just those species turned out to occur in montane areas or in the alpine regions, respectively, that are characterised as restricted to these areas by countless experienced field entomologists.

The fact that so many species (34.8 %) are distributed in the southern part of our study area (Fig. 15) is congruent with the general decline in species richness from South(-West) to North(-East)and, as, e.g., demonstrated by the zoogeographic data reported in De Lattin (1967, pp. 420ff.) for Rhopalocera in Palatia and other Lepidoptera in the Western Palaearctic. Here, more than 50 % of the species are assigned to a southern (Mediterranean) type of geographical distribution. Silfverberg (1985) mentioned a parallel decline in Finland, which is evident from the 76 grid maps he published in 1987 on species of the subfamilies Donaciinae, Criocerinae, Orsodacninae, Synetinae, Zeugophorinae, Clytrinae and Cryptocephalinae.

The distribution data of most species fit remarkably well to the faunistic literature. For some cases, however, we have no plausible explanation at hand, other cases differ from published statements. Köhler and Klausnitzer (1998) state that *Chrysomela cuprea* Fabricius, 1775 should not occur in the German federal state of Mecklenburg-Vorpommern, from where we have records; or differing from their table we have data for *Psylliodes sophiae* Heikertinger, 1914 also from Bavaria and from Lake Neusiedl. Other than Mohr (1966), we found *Altica brevicollis* Foudras, 1816 also from northern parts of Germany, *Crioceris quatuordecimpunctata* (Scopoli, 1763) also from Schleswig-Holstein and Hessia, *Cryptocephalus nitidus* (Linnaeus, 1758) also in Northern Italy and Slovenia, and *Dibolia depressiuscula* Letzner, 1847 – which is said to occur in whole Central Europe – only south-west of a line from Bonn to Frankfurt an der Oder. Since we do not expect a bias in the selectivity of the collectors of our data especially in these conflicting cases, we are confident that they do not represent "noise" but provide a rewarding basis for future research.

As stated above, more data are needed. However, except for few special cases, no additional collecting in the field is necessary. Our experience in the course of the present study is that private and museum collections harbour enough data to backfill our database up to the intended amount. Thus, we are confident that we can retrieve this buried treasure of knowledge with joint effort.

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References

- Beenen R (1998) Patterns in the distribution of Galerucinae in the Netherlands (Contribution EIS - Nederland 87). In: Biondi M, Daccordi M, Furth DG (Eds) Proceedings of the Fourth International Symposium on the Chrysomelidae. Atti di Museo regionale di Science naturale di Torino, 7–16.
- Beenen R, Winkelman J (2002) Aantekeningen over Chrysomelidae (Coleoptera) in Nederland6. Entomologische Berichten Amsterdam 62: 135–137.
- Beenen R, Winkelman J, van Nunen F (2005) Aantekeningen over Chrysomelidae (Coleoptera) in Nederland 7. Entomologische Berichten 65: 128–131.
- Berti N (1989) Contribution à la faune de France. L'identité d'Oulema (O.) melanopus (L.). Bulletin de la Société Entomologique de France 94: 47–57.
- Bundesamt für Naturschutz http://www.floraweb.de/pflanzenarten/artensteckbriefe.html [last accessed 23.10.2011]
- De Lattin G (1967) Grundriss der Zoogeographie. VEB Gustav Fischer, Jena, 602 pp.
- Campbell JM (1980) An atlas of Oxfordshire Coleoptera, Chrysomelidae. Occasional Papers No. 13. Oxfordshire Museums, Woodstock, Oxon., VII+100 pp.
- Cox ML (1992) Progress report on the Bruchidae/Chrysomelidae recording scheme. Coleopterist 1: 18–24.
- Cox ML (1995) Identification of the *Oulema 'melanopus'* species group (Chrysomelidae). Coleopterist 4: 33–36.
- Cox ML (2007) Atlas of the Seed and Leaf Beetles of Britain and Ireland. Pisces Publications, Newbury, VII + 336 pp.
- Geiser E (2001a) Die Käfer des Landes Salzburg. Faunistische Bestandserfassung und tiergeographische Interpretation. Monographs on Coleoptera (Wien) vol. 2: 1–706.
- Geiser E (2001b) Risiken und Nebenwirkungen einer umfangreichen entomologischen Datenbank. Entomologica Austriaca 4: 15–18.
- Geiser E (2005) Die entscheidenden Faktoren für den langfristigen Erfolg einer tiergeografischen Datenbank - am Beispiel der ZOBODAT (früher: ZOODAT). Linzer biologische Beiträge - Verhandlungen 18. SIEEC, Linz 2003 37: 49–69.
- Gruev B, Döberl M (2005) General Distribution of the Flea Beetles in the Palaearctic Subregion (Coleoptera, Chrysomelidae: Alticinae). Supplement. Pensoft, Sofia Moscow, 239 pp.
- Gruev B, Tomov V (2007) A Distributional Atlas and Catalogue of the Leaf Beetles of Bulgaria (Zoocartographia Balcanica 3). Pensoft, Sofia Moscow, VI+350 pp.

- Gürlich S (1992) Die Blattkäfer (Coleoptera: Chrysomelidae) des Niederelbegebietes und Schleswig-Holsteins. Verhandlungen des Vereins für naturwissenschaftliche Heimatforschung zu Hamburg 40: 1–78.
- Gürlich S, Suikat R, Ziegler W (1995) Katalog der Käfer Schleswig-Holsteins und des Niederelbegebietes. Verhandlungen des Vereins für naturwissenschaftliche Heimatforschung zu Hamburg 41: 1–111.
- Horion A (1941) Faunistik der deutschen Käfer, Band 1. Hans Goecke Verlag, Krefeld, 464 pp.
- Horion A (1951) Verzeichnis der Käfer Mitteleuropas (Deutschland, Österreich, Tschechoslowakei) mit kurzen faunistischen Angaben. Alfred Kernen Verlag, Stuttgart, 536 pp.
- Horion A (1965) Faunistik der mitteleuropäischen Käfer, Band 10. Klostermann, Frankfurt am Main, XV+335 pp.
- Horion A (1974) Faunistik der mitteleuropäischen Käfer, Band 12. Verlagsdruckerei Ph. C. W. Schmidt, Neustadt an der Aisch, 228 pp.
- Koch K (1992) Die Käfer Mitteleuropas, Ökologie, Band 3. Goecke & Evers, Krefeld, 389 pp.
- Köhler F, Klausnitzer B (Eds) (1998) Entomofauna Germanica Verzeichnis der Käfer Deutschlands. Entomologische Nachrichten und Berichte Beiheft 4: 1–185.
- Lundberg S, Gustafsson R (1995) Catalogus Coleopterorum Sueciae (without pagination). Naturhistoriska Riksmuseet & Entomologiska Föreningen: Stockholm, [1+217 pp.]
- Mohr K-H (1966) 88. Familie: Chrysomelidae. In: Freude H, Harde KW and Lohse GA (eds.) Die Käfer Mitteleuropas Band 9. Goecke & Evers, Krefeld, 95–299.
- Petitpierre E (2000) Coleoptera Chrysomelidae I. Fauna Iberica 13. Museo Nacional de Ciencias Naturales: Consejo Superior de Investigaciones Científicas, Madrid, 521 pp. + 6 pls.
- Silfverberg H (1985) Mapping the Chrysomelidae of Finland. Entomography 3: 503
- Silfverberg H (1987) Mapping the finnish Chrysomelidae (Coleoptera) I. Notulae entomologicae 67: 5–16.
- Snyder JP (1987) Map Projections: A Working Manual. Geological Survey (U.S.) Professional Paper 1395 [IX + 385 pp. + 1 plate], available online under http://pubs.er.usgs.gov/publication/pp1395.
- Vig K (1996) A nyugat-magyarországi-peremvideék levélbogaár faunájának alapvetése (Coleoptera: Chrysomelidae sensu lato). Praenorica Folia historico-naturalia 3: 1–178.
- Warchałowski A (1985) Chrysomelidae stonkowate (Insecta: Coleoptera). Czesc 1 (Donaciinae, Orsodacninae, Synetinae, Zeugophorinae i Criocerinae). Fauna Polski - Fauna Poloniae Tom 10. Panstwowe Wydawnictwo Naukowe, Warszawa, 273 pp.
- Warchałowski A (2010) The Palaearctic Chrysomelidae. Identification Keys. Natura optima dux foundation, Warszawa, 2 vols. 1212 pp., 102 plates.

Appendix I

List of species, assigned to the distribution types.

Species of which we have less than 10 records (116): Altica ampelophaga (Guérin-Meneville, 1858), A. cornivora Kral, 1969, A. ericeti (Allard, 1859), A. longicollis (Allard, 1860), Aphthona aeneomicans Allard, 1875, A. beckeri Jacobson, 1895, A. czwallinae Weise, 1888, A. delicatula Foudras, 1860, A. erichsoni (Zetterstedt, 1838), A. illigeri Bedel, 1898, Argopus bicolor Fischer, 1824, A. nigritarsis (Gebler, 1823), Batophila fallax Weise, 1888, Bruchidius bimaculatus (Olivier, 1795), B. dispar (Gyllenhal, 1833), B. lividimanus (Gyllenhal, 1833), B. nanus (Germar, 1824), B. pauper (Boheman, 1829), B. seminaries (Linnaeus, 1767), Bruchus ervi Frölich, 1799, B. griseomaculatus Gyllenhal, 1833, B. lentis Frölich, 1799, B. pisorum (Linnaeus, 1758), B. sibiricus Germar, 1824, B. signaticornis Gyllenhal, 1833, B. venustus Fahraeus, 1839, Callosobruchus chinensis (Linnaeus, 1758), Cassida aurora Weise, 1907, C. bergeali Bordy, 1995, C. lineola Creutzer, 1799, C. seladonia Gyllenhal, 1827, Chaetocnema subcoerulea (Kutschera, 1864), Chrysolina americana (Linnaeus, 1758), Ch. fimbrialis (Kuester, 1845), Ch. globipennis (Suffrian, 1851), Ch. grossa (Fabricius, 1792), Ch. morio (Krynitskii, 1832), Ch. purpurascens (Germar, 1817), Ch. quadrigemina (Suffrian, 1851), Ch. reitteri (Weise, 1884), Ch. schneideri (Weise, 1882), Cryptocephalus bohemius Drapiez, 1819, C. carinthiacus Suffrian, 1848, C. gamma Herrich-Schaeffer, 1829, C. loreyi Solier, 1836, C. macellus Suffrian, 1860, C. marginellus Olivier, 1791, C. octacosmus Bedel, 1891, C. octomaculatus Rossi, 1790, C. quadripunctatus Olivier, 1808, C. trimaculatus Rossi, 1790, C. turcicus Suffrian, 1847, C. villosulus Suffrian, 1847, Dibolia alpestris Mohr, 1981, Donacia brevitarsis Thomson, 1884, D. reticulata Gyllenhal, 1817, Euluperus xanthopus (Duftschmid, 1825), Galerucella sagittariae (Gyllenhal, 1813), Gonioctena flavicornis (Suffrian, 1851), G. kaufmanni (Miller, 1880), G. variabilis (Olivier, 1790), Hermaeophaga cicatrix (Illiger, 1807), Hydrothassa flavocincta (Brullé, 1832), Lilioceris schneideri (Weise, 1900), Longitarsus aeneicollis (Faldermann, 1837), L. albineus (Foudras, 1859), L. bertii Leonardi, 1973, L. callidus Warchałowski, 1967, L. celticus Leonardi, 1975, L. fuscoaeneus Redtenbacher, 1849, L. longipennis Kutschera, 1863, L. nigrocillus Motschulsky, 1849, L. obliteratus (Rosenhauer, 1847), L. pallidicornis Kutschera, 1863, L. pinguis Weise, 1888, L. rectilineatus (Foudras, 1860), L. strigicollis Wollaston, 1864, L. substriatus Kutschera, 1863, L. tristis Weise, 1888, L. weisei Guillebeau, 1895, Luperus carniolicus Kiesenwetter, 1861, L. flaviceps Apfelbeck, 1912, L. nigripes Kiesenwetter, 1861, Mantura ambigua (Kutschera, 1862), Minota alpina Biondi, 1986, M. carpathica Heikertinger, 1911, M. halmae (Apfelbeck, 1906), M. impuncticollis (Allard, 1860), Neocrepidodera basalis (Daniel, 1900), N. brevicollis (Daniel, 1904), N. crassicornis (Faldermann, 1837), N. impressa (Fabricius, 1801), N. interpunctata (Motschulsky, 1859), N. simplicipes (Kutschera, 1860), Oreina caerulea (Olivier, 1807), O. elongata (Suffrian, 1851), O. plagiata (Suffrian, 1861), O. tristis (Fabricius, 1792), Orestia aubei Allard, 1859, O. electra Gredler, 1868, Oulema septentrionis (Weise, 1880), Pachybrachis carpathicus Rey, 1883, P. pallidulus Suffrian, 1851, Phratora polaris (Schneider, 1886), Phyllotreta acutecarinata Heikertinger, 1941, Ph. consobrina (Curtis, 1837), Ph. hochetlingeri Fleischer, 1917, Ph. nigripes (Fabricius, 1775), Ph. variipennis (Boieldieu, 1859), Ph. ziegleri Lohse, 1980, Psylliodes frivaldszkyi Weise, 1888, Ps. pyritosa Kutschera, 1864, Sclerophaedon carpathicus (Weise, 1875), Timarcha gibba (Hagenbach, 1825), T.rugulosa Herrich-Schaeffer, 1838, Zeugophora turneri Power, 1863.

Widely distributed species (97): Altica lythri Aubé, 1843, A. oleracea (Linnaeus, 1758), Batophila rubi (Paykull, 1799), Bromius obscurus (Linnaeus, 1758), Cassida flaveola Thunberg, 1794, C. hemisphaerica Herbst, 1799, C. margaritacea Schaller, 1783, C. murraea Linnaeus, 1767, C. rubiginosa Müller, 1776, C. viridis Linnaeus, 1758, Chaetocnema aridula (Gyllenhal, 1827), Ch. hortensis (Geoffroy, 1785), Ch. picipes Stephens, 1831, Ch. sahlbergi (Gyllenhal, 1827), Chrysolina coerulans (Scriba, 1791), Ch. fastuosa (Scopoli, 1763), Ch. graminis (Linnaeus, 1758), Ch. haemoptera (Linnaeus, 1758), Ch. oricalcia (Müller, 1776), Ch. polita (Linnaeus, 1758), Ch. staphylaea (Linnaeus, 1758), Chrysomela collaris Linnaeus, 1758, Crepidodera aurata (Marsham, 1802), C. fulvicornis (Fabricius, 1792), C. plutus (Latreille, 1804), Crioceris asparagi (Linnaeus, 1758), C. duodecimpunctata (Linnaeus, 1758), Cryptocephalus coryli (Linnaeus, 1758), C. decemmaculatus (Linnaeus, 1758), C. flavipes Fabricius, 1781, C. fulvus (Goeze, 1777), C. labiatus (Linnaeus, 1761), C. nitidus (Linnaeus, 1758), C. pini (Linnaeus, 1758), C. pusillus Fabricius, 1777, C. rufipes (Goeze, 1777), Donacia aquatica (Linnaeus, 1758), D. cinerea Herbst, 1784, D. impressa Paykull, 1799, D. thalassina Germar, 1811, D. vulgaris Zschach, 1788, Galeruca pomonae (Scopoli, 1763), Galerucella calmariensis (Linnaeus, 1767), G. lineola (Fabricius, 1781), G. nymphaeae (Linnaeus, 1758), Gastrophysa polygoni (Linnaeus, 1758), G. viridula (De Geer, 1775), Gonioctena quinquepunctata (Fabricius, 1787), Hippuriphila modeeri (Linnaeus, 1761), Lema cyanella (Linnaeus, 1758), Leptinotarsa decemlineata (Say, 1824), Lilioceris lilii (Scopoli, 1763), Lochmaea crataegi (Forster, 1771), L. suturalis (Thomson, 1866), Longitarsus anchusae (Paykull 1799), L. atricillus (Linnaeus, 1761), L. brunneus (Duftschmid, 1825), L. dorsalis (Fabricius, 1781), L. exoletus (Linnaeus, 1758), L. ferrugineus (Foudras, 1869), L. jacobaeae Waterhouse, 1858, L. luridus (Scopoli, 1763), L. lycopi (Foudras, 1860), L. nasturtii (Fabricius, 1792), L. pratensis (Panzer, 1794), L. quadriguttatus (Pontoppidan, 1765), L. succineus (Foudras, 1860), L. tabidus (Fabricius, 1775), Luperus longicornis (Fabricius, 1761), Lythraria salicariae (Paykull, 1800), Neocrepidodera ferruginea (Scopoli, 1763), N. transversa (Marsham, 1802), Oulema melanopus (Linnaeus, 1758), Phaedon armoraciae (Linnaeus, 1758), Ph. cochleariae (Fabricius, 1792), Phratora laticollis (Suffrian, 1851), Ph. vitellinae (Linnaeus, 1758), Phyllotreta exclamationis (Thunberg, 1784), Ph. nemorum (Linnaeus, 1758), Ph. tetrastigma (Comolli, 1837), Ph. undulata Kutschera, 1860, Ph. vittula (Redtenbacher, 1849), Plagiosterna aenea (Linnaeus, 1758), Plateumaris affinis (Kunze, 1818), P. consimilis (Schrank, 1781), P. sericea (Linnaeus, 1761), Prasocuris phellandrii (Linnaeus, 1758), Psylliodes affinis (Paykull, 1799), Ps. chrysocephalus (Linnaeus, 1758), Ps. napi (Fabricius, 1792), Ps. picina (Marsham, 1802), Pyrrhalta viburni (Paykull, 1799), Sermylassa halensis (Linnaeus, 1767), Sphaeroderma testaceum (Fabricius, 1775), Zeugophora flavicollis (Marsham, 1802), Z. scutellaris Suffrian, 1840, Z. subspinosa (Fabricius, 1781).

Southern distribution (103): Altica helianthemi (Allard, 1859), A. tamaricis Schrank, 1785, Aphthona abdominalis (Duftschmid, 1825), A. atrovirens (Förster, 1849), A. cyparissiae (Koch, 1803), A. herbrigada (Curtis, 1837), A. pallida (Bach, 1856), A. pygmaea (Kutschera, 1861), A. venustula (Kutschera, 1861), Apteropeda orbiculata (Marsham, 1802), Calomicrus circumfusus (Marsham, 1802), C. pinicola (Duftschmid, 1825), Cassida panzeri Weise, 1907, Chaetocnema arida Foudras, 1860, Ch. obesa (Boieldieu, 1859), Ch. semicoerulea (Koch, 1803), Chrysolina cuprina (Duftschmid, 1825), Ch. hemisphaerica (Germar, 1817), Ch. herbacea (Duftschmid, 1825), Ch. hyperici (Forster, 1771), Ch. marginata (Linnaeus, 1758), Ch. rufa (Duftschmid, 1825), Chrysomela cuprea Fabricius, 1775, Ch. saliceti (Weise, 1884), Ch. vigintipunctata (Scopoli, 1763), Coptocephala rubicunda (Laicharting, 1781), Crepidodera aurea (Geoffroy, 1785), C. lamina (Bedel, 1901), C. nitidula (Linnaeus, 1758), Cryptocephalus biguttatus (Scopoli, 1763), C. frontalis Marsham, 1802, C. laetus Fabricius, 1792, C. primarius Harold, 1872, C. pygmaeus Fabricius, 1792, C. querceti Suffrian, 1848, C. quinquepunctatus (Scopoli, 1763), C. saliceti Zebe, 1855, C. schaefferi Schrank, 1789, C. sexpunctatus (Linnaeus, 1758), C. signatifrons Suffrian, 1847, C. variegatus Fabricius, 1781, C. vittatus Fabricius, 1775, Derocrepis rufipes (Linnaeus, 1758), Dibolia foersteri Bach, 1859, Donacia springeri Müller, 1916, Epitrix atropae Foudras, 1860, E. intermedia Foudras, 1860, Galeruca laticollis (Sahlberg, 1837), Galerucella tenella (Linnaeus, 1761), Gonioctena intermedia (Helliesen, 1913), G. linnaeana (Schrank, 1781), G. pallida (Linnaeus, 1758), G. viminalis (Linnaeus, 1758), Hermaeophaga mercurialis (Fabricius, 1792), Hispa atra Linnaeus, 1767, Hydrothassa glabra (Herbst, 1783), Labidostomis humeralis (Schneider, 1792), L. lucida (Germar, 1823), L. pallidipennis (Gebler, 1839), L. tridentata (Linnaeus, 1758), Lachnaia sexpunctata (Scopoli, 1763), Lilioceris merdigera (Linnaeus, 1758), Longitarsus absynthii Kutschera, 1862, L. echii (Koch, 1803), L. lateripunctatus (Rosenhauer, 1856), L. longiseta Weise, 1889, L. membranaceus (Foudras, 1860), L. minusculus (Foudras, 1860), L. nanus (Foudras, 1860), L. pellucidus (Foudras, 1860), L. pulmonariae Weise, 1893, L. scutellaris (Rey, 1873), Luperus flavipes (Linnaeus, 1767), Mantura mathewsi (Curtis, 1834), Neocrepidodera femorata (Gyllenhal, 1813), Ochrosis ventralis (Illiger, 1807), Oomorphus concolor (Sturm, 1807), Orsodacne cerasi (Linnaeus, 1758), Pachnephorus pilosus (Rossi, 1790), Pachybrachis hieroglyphicus (Laicharting, 1781), P. hippophaes Suffrian, 1848, P. picus Weise, 1882, P. sinuatus Mulsant, 1859, P. tesselatus (Olivier, 1791), Phaedon laevigatus (Duftschmid, 1825), Phratora tibialis (Suffrian, 1851), Ph. vulgatissima (Linnaeus, 1758), Phyllotreta christinae Heikertinger, 1941, Ph. ochripes (Curtis, 1837), Ph. procera (Redtenbacher, 1849), Ph. punctulata (Marsham, 1802), Plagiodera versicolora (Laicharting, 1781), Psylliodes chalcomera (Illiger, 1807), Ps. instabilis Foudras, 1860, Ps. isatidis Heikertinger, 1912, Ps. thlaspis Foudras, 1860, Smaragdina affinis (Illiger, 1794), S. flavicollis (Charpentier, 1825), Sphaeroderma rubidum (Graëlls, 1858), Timarcha goettingensis (Linnaeus, 1758), T. metallica (Laicharting, 1781), T. pratensis (Duftschmid, 1825), Zeugophora frontalis Suffrian, 1840.

- South-Eastern (52): Bruchidius marginalis (Fabricius, 1776), Bruchus atomarius (Linnaeus, 1761), Cassida ferruginea Goeze, 1777, C. rufovirens Suffrian, 1844, C. sanguinolenta Müller, 1776, C. subferruginea (Schrank, 1776), C. subreticulata Suffrian, 1844, C. vibex Linnaeus, 1767, Chrysochus asclepiadeus (Pallas, 1773), Chrysolina geminata (Paykull, 1799), Ch. kuesteri (Helliesen, 1912), Ch. lichenis (Richter, 1820), Ch. sturmi (Westhoff, 1882), Ch. varians (Schaller, 1783), Chrysomela populi Linnaeus, 1758, Ch. tremulae Fabricius, 1783, Clytra laeviuscula Ratzeburg, 1837, C. quadripunctata (Linnaeus, 1758), Coptocephala unifasciata (Scopoli, 1763), Cryptocephalus aureolus Suffrian, 1847, C. bilineatus (Linnaeus, 1767), C. chrysopus Gmelin, 1788, C. cordiger (Linnaeus, 1758), C. elegantulus Gravenhorst, 1807, C. exiguus Schneider, 1792, C. frenatus Laicharting, 1781, C. hypochaeridis (Linnaeus, 1758), C. marginatus Fabricius, 1781, C. moraei (Linnaeus, 1758), C. octopunctatus (Scopoli, 1763), C. violaceus Laicharting, 1781, C. vittula Suffrian, 1848, Dibolia depressiuscula Letzner, 1847, D. femoralis Redtenbacher, 1849, D. rugulosa Redtenbacher, 1849, Galeruca tanaceti (Linnaeus, 1758), Labidostomis longimana (Linnaeus, 1761), Longitarsus apicalis (Beck, 1817), L. ballotae (Marsham, 1802), L. foudrasi Weise, 1893, L. melanocephalus (De Geer, 1775), L. nigrofasciatus (Goeze, 1777), L. obliteratus (Rosenhauer, 1847), L. salviae Gruev, 1975, Mantura obtusata (Gyllenhal, 1813), Minota obesa (Waltl, 1839), Oulema gallaeciana (Heyden, 1870), Phyllotreta diademata Foudras, 1860, Ph. nodicornis (Marsham, 1802), Podagrica fuscicornis (Linnaeus, 1767), Smaragdina aurita (Linnaeus, 1767), S. salicina (Scopoli, 1763).
- South-Western (12): Apteropeda globosa (Illiger, 1794), A. splendida Allard, 1860, Bruchus rufipes Herbst, 1783, Cryptocephalus ocellatus Drapiez, 1819, Dibolia cryptocephala (Koch, 1803), Donacia bicolora Zschach, 1788, D. simplex Fabricius, 1775, Longitarsus aeruginosus (Foudras, 1860), L. ganglbaueri Heikertinger, 1912, L. rubiginosus (Foudras, 1860), Mniophila muscorum (Koch, 1803), Timarcha tenebricosa (Fabricius, 1775).
- Northern (8): Galerucella grisescens (Joannis, 1865), Hydrothassa hannoverana (Fabricius, 1775), Longitarsus plantagomaritimus Dollman, 1912, Mantura chrysanthemi (Koch, 1803), Phaedon concinnus Stephens, 1831, Phyllotreta armoraciae (Koch, 1803), Psylliodes crambicola Lohse, 1954, Ps. marcida (Illiger, 1807).

- Eastern (16): Aphthona nigriscutis Foudras, 1860, A. placida (Kutschera, 1854), Cassida berolinensis Suffrian, 1844, Chrysolina analis (Linnaeus, 1767), Ch. marcasitica (Germar, 1824), Ch. umbratilis (Weise, 1887), Colaphus sophiae (Schaller, 1783), Crioceris quatuordecimpunctata (Scopoli, 1763), Cryptocephalus distinguendus Schneider, 1792, C. quadripunctatus Olivier, 1808, C. virens Suffrian, 1847, Dibolia schillingi (Letzner, 1847), Galeruca dahli (Joannis, 1865), Luperus saxonicus (Gmelin, 1790), Phyllotreta scheuchi Heikertinger, 1941, Psylliodes hyoscyami (Linnaeus, 1758).
- South-East quarter (52): Altica carduorum Guérin-Meneville, 1858, Aphthona flava Guillebeau, 1895, A. franzi Heikertinger, 1944, A. lacertosa (Rosenhauer, 1847), A. semicyanea Allard, 1859, A. stussineri Weise, 1888, Argopus ahrensi (Germar, 1817), Cassida atrata Fabricius, 1787, C. inquinata Brullé, 1832, Chaetocnema arenacea (Allard, 1860), Ch. chlorophana (Duftschmid, 1825), Ch. conducta (Motschulsky, 1838), Ch. major (Jacquelin-Duval, 1852), Chrysolina carpathica (Fuss, 1856), Ch. chalcites (Germar, 1824), Ch. globosa (Panzer, 1805), Ch. olivieri (Bedel, 1892), Ch. rossia (Illiger, 1802), Ch. rufoaenea (Suffrian, 1851), Coptocephala chalybaea (Germar, 1824), C. scopolina (Linnaeus, 1767), Crioceris quinquepunctata (Scopoli, 1763), Cryptocephalus apicalis Gebler, 1830, C. connexus Olivier, 1807, C. imperialis Laicharting, 1781, C. laevicollis Gebler, 1830, C. quatuordecimmaculatus Schneider, 1792, Entomoscelis adonidis (Pallas, 1771), E. sacra (Linnaeus, 1758), Exosoma lusitanica (Linnaeus, 1767), Galeruca rufa Germar, 1824, Gonioctena fornicata (Brüggemann, 1873), G. gobanzi (Reitter, 1902), Labidostomis cyanicornis (Germar, 1817), Lachnaia italica (Weise, 1882), Longitarsus cerinthes (Schrank, 1798), L. languidus Kutschera, 1863, L. linnaei (Duftschmid, 1825), L. medvedevi Shapiro, 1956, L. minimus Kutschera, 1864, L. monticola Kutschera, 1863, L. pallidicornis Kutschera, 1863, Neocrepidodera brevicollis (J. Daniel, 1904), Pachnephorus tesselatus (Duftschmid, 1825), P. villosus (Duftschmid, 1825), Phyllobrotica adusta (Creutzer, 1799), Phyllotreta ganglbaueri Heikertinger, 1909, Podagrica menetriesi (Faldermann, 1837), Psylliodes attenuata (Koch, 1803), Ps. brisouti Bedel, 1898, Ps. gibbosa Allard, 1860, Tituboea macropus (Illiger, 1800).
- South-West quarter (5): Bruchidius varius (Olivier, 1795), Batophila aerata (Marsham, 1802), Longitarsus brisouti Heikertinger, 1912, Mantura horioni Heikertinger, 1940, and Podagrica fuscipes (Fabricius, 1775).
- Fragmented (37): Agelastica alni (Linnaeus, 1758), Altica aenescens (Weise, 1888), A. palustris (Weise, 1888), A. quercetorum Foudras, 1860, Aphthona nonstriata (Goeze, 1777), Bruchus loti Paykull, 1800, Cassida denticollis Suffrian, 1844, C. nebulosa Linnaeus, 1758, C. nobilis Linnaeus, 1758, C. prasina Illiger, 1798, C. sanguinosa Suffrian, 1844, C. stigmatica Suffrian, 1844, C. vittata Villiers, 1789, Chaetocnema concinna (Marsham, 1802), Ch. mannheimeri (Gyllenhal, 1827), Cheilotoma musciformis (Goeze, 1777), Chrysolina sanguinolenta (Linnaeus, 1758), Cryptocepha-

lus bipunctatus (Linnaeus, 1758), C. janthinus Germar, 1824, C. parvulus Müller, 1776, Dibolia occultans (Koch, 1803), Donacia clavipes Fabricius, 1793, D. crassipes Fabricius, 1775, D. marginata Hoppe, 1795, D. sparganii Ahrens, 1810, Epitrix pubescens (Koch, 1803), Galerucella aquatica (Fourcroy, 1785), Galerucella pusilla (Duftschmid, 1825), Longitarsus holsaticus (Linnaeus, 1758), L. kutscherae (Rye, 1872), Phyllotretaq atra (Fabricius, 1775), Ph. cruciferae (Goeze, 1777), Ph. ochripes (Curtis, 1837), Ph. striolata (Fabricius, 1803), Plateumaris rustica (Kunze, 1818), Psylliodes cuprea (Koch, 1803), Ps. dulcamarae (Koch, 1803).

- Montane (18): Aphthona ovata Foudras, 1860, Calomicrus gularis (Gredler, 1857), Chaetocnema angustula (Rosenhauer, 1847), Chrysolina aurichalcea (Mannerheim, 1825), Cryptocephalus nitidulus Fabricius, 1787, Longitarsus helvolus Kutschera, 1863, Luperus viridipennis Germar, 1824, L. xanthopoda (Schrank, 1781), Oreina alpestris (Schummel, 1844), O. bifrons (Fabricius, 1792), O. cacaliae (Schrank, 1785), O. intricata (Germar, 1824), O. speciosa (Linnaeus, 1767), O. speciosissima (Scopoli, 1763), Psylliodes glabra (Duftschmid, 1825), Ps. toelgi Heikertinger, 1914, Ps. vindobonensis Heikertinger, 1914, Sclerophaedon carniolicus (Germar, 1824).
- Alpine (28): Chrysolina globosa (Panzer, 1805), Ch. latecincta (Demaison, 1896), Ch. relucens (Rosenhauer, 1847), Cryptocephalus albolineatus Suffrian, 1847, C. strigosus Germar, 1823, Gonioctena holdhausi (Leeder, 1950), Lilioceris tibialis (Villa, 1838), Longitarsus rubellus (Foudras, 1860), Neocrepidodera cyanescens (Duftschmid, 1825), N. cyanipennis (Kutschera, 1860), N. melanostoma (Redtenbacher, 1849), N. norica (Weise, 1860), N. obirensis (Ganglbauer, 1897), N. periolerii (Kutschera, 1860), N. rhaetica (Kutschera, 1860), Oreina frigida (Weise, 1883), O. gloriosa (Fabricius, 1781), O. liturata (Scopoli, 1763), O. melanocephala (Duftschmid, 1825), O. virgulata (Germar, 1824), O. viridis (Duftschmid, 1825), O. vittigera (Suffrian, 1851), Orestia alpina (Germar, 1824), Phaedon segnis Wesie, 1884, Psylliodes aerea Foudras, 1860, Ps. picipes Redtenbacher, 1849, Ps. rambouseki Heikertinger, 1909, Ps. subaenea Kutschera, 1864.
- Scattered (53): Acanthoscelides obtectus (Say, 1831), Altica brevicollis Foudras, 1860, Aphthona atrocaerulea (Stephens, 1831), A. euphorbiae (Schrank, 1781), A. lutescens (Gyllenhal, 1813), A. violacea (Koch, 1803), Bruchidius cisti (Fabricius, 1775), B. villosus (Fabricius, 1792), Bruchus affinis Frölich, 1799, B. brachialis Fahraeus, 1839, B. luteicornis Illiger, 1794, B. rufimanus Boheman, 1833, Cassida azurea Fabricius, 1801, C. canaliculata Laicharting, 1781, C. fastuosa Schaller, 1783, C. pannonica Suffrian, 1844, Chaetocnema aerosa (Letzner, 1846), Ch. confusa (Boheman, 1851), Chrysolina brunsvicensis (Gravenhorst, 1807), Ch. cerealis (Linnaeus, 1767), Cryptocephalus caerulaescens Sahlberg, 1839, C. ochroleucus Stephens, 1834, C. pallifrons Gyllenhal, 1813, C. populi Suffrian, 1848, C. punctiger Paykull, 1799, C. quadripustulatus Gyllenhal, 1813, Dibolia cyanoglossi (Koch, 1803), Donacia antiqua Kunze, 1818, D. brevicornis Ahrens, 1810, Donacia dentata Hoppe, 1795,

D. malinowskyi Ahrens, 1810, D. tomentosa Ahrens, 1810, D. versicolorea (Brahm, 1790), Longitarsus agilis (Rye, 1868), L. curtus (Allard, 1860), L. fulgens (Foudras, 1860), L. gracilis Kutschera, 1864, L. niger (Koch, 1803), L. nigerrimus (Gyllenhal, 1827), L. ochroleucus (Marsham, 1802), L. reichei (Allard, 1860), L. symphyti Heikertinger, 1912, Macroplea appendiculata (Panzer, 1794), Mantura rustica (Linnaeus, 1767), Neocrepidodera motschulskii Konstantinov, 1991, N. nigritula (Gyllenhal, 1813), Oulema erichsonii (Suffrian, 1841), Phratora atrovirens (Cornelius, 1857), Phyllotreta dilatata Thomson, 1866, Ph. flexuosa (Illiger, 1794), Psylliodes laticollis Kutschera, 1864, Ps. luteola (Müller, 1776), Xanthogaleruca luteola (Müller, 1776).

Unusual (50): Altica carinthiaca (Weise, 1888), A. impressicollis (Reiche, 1862), Chaetocnema compressa (Letzner, 1847), Ch. procerula (Rosenhauer, 1856), Ch. tibialis (Illiger, 1807), Chrysolina carnifex (Fabricius, 1792), Ch. fuliginosa (Olivier, 1807), Ch. gypsophilae (Küster, 1845), Ch. limbata (Fabricius, 1775), Chrysomela lapponica (Linnaeus, 1758), Cryptocephalus cyanipes Suffrian, 1847, C. elongatus Germar, 1824, C. sericeus (Linnaeus, 1758), Dibolia timida (Illiger, 1807), Donacia obscura Gyllenhal, 1813, D. semicuprea Panzer, 1796, Galeruca interrupta Illiger, 1802, G. melanocephala Ponza, 1805, Gonioctena decemnotata (Marsham, 1802), G. interposita (Franz & Palmén, 1950), G. olivacea (Forster, 1771), Lochmaea caprea (Linnaeus, 1758), Longitarsus australis (Mulsant & Rey, 1802), L. lewisii (Baly, 1874), L. noricus Leonardi, 1976, L. parvulus (Paykull, 1799), L. suturellus (Duftschmid, 1825), Luperus luperus (Sulzer, 1776), Macroplea mutica (Fabricius, 1792), Orsodacne lineola (Panzer, 1896), Oulema duftschmidi (Redtenbacher, 1874), O. rufocyanea (Suffrian, 1847), O. tristis (Herbst, 1786), Pachybrachis fimbriolatus Suffrian, 1848, Phaedon pyritosus (Rossi, 1792), Phyllotreta astrachanica Lopatin, 1977, Ph. austriaca Heikertinger, 1909, Plateumaris bracata (Scopoli, 1772), P. discolor (Panzer, 1795), Podagrica malvae (Illiger, 1807), Prasocuris junci (Brahm, 1790), P. marginella (Linnaeus, 1758), Psylliodes cucullata (Illiger, 1807), Ps. cupreata (Duftschmid, 1825), Ps. reitteri Weise, 1888, Ps. sophiae Heikertinger, 1914, Smaragdina diversipes Letzner, 1839, S. xanthaspis (Germar, 1824), Spermophagus calystegiae (Lukjanov & Ter-Minassian, 1957), S. sericeus (Fourcroy, 1785).

REVIEW ARTICLE



On whose shoulders we stand – the pioneering entomological discoveries of Károly Sajó^{*}

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Abstract

The excellence of Károly Sajó as a researcher into Hungary's natural history has been undeservedly neglected. Yet he did lasting work, especially in entomology, and a number of his discoveries and initiatives were before their time.

Born in 1851 in Győr, he received his secondary education there and went to Pest University. He taught in a grammar school in 1877–88 before spending seven years as an entomologist at the National Phylloxera Experimental Station, later the Royal Hungarian State Entomological Station. Pensioned off at his own request in 1895, he moved to Őrszentmiklós, where he continued making entomological observations on his own farm and wrote the bulk of his published materials: almost 500 longer or shorter notes, articles and books, mainly on entomological subjects.

Sajó was among the first in the world to publish in 1896 a study of how the weather affects living organisms, entitled *Living Barometers*. His *Sleep in Insects*, which appeared in the same year, described his discovery, from 1895 observations of the red turnip beetle, *Entomoscelis adonidis* (Pallas, 1771), of aestivation in insects – in present-day terms diapause.

It was a great loss to universal entomology when Sajó ceased publishing about 25 years before his death. His unpublished notes, with his library and correspondence, were destroyed in the World War II. His surviving insect collection is now kept in the Hungarian Natural History Museum, Budapest.

Keywords

Károly Sajó, history of entomology, diapause, Chrysomelidae, Hungary, Germany

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A brief account of Károly Sajó's life

The main events in the life of Károly Sajó (Figure 1.) are known from a laconic biography that appeared after his death (Szent-Iványi 1941). The writings and objects he left behind were destroyed in the World War II. The same fate befell many document collections (for instance those of the Hungarian Entomological Society) in which details of his life might otherwise have been found. However, his articles and books have survived, as true reflections of the fruitful life he led.

Károly Sajó (originally Schemiz) was born in Győr on 20 June 1851. His father, Károly Schemiz had been born in Sasvár-Morvaőr (Nyitra County, now Šaštín-Stráže in Slovakia, Schoßberg-Strascha in German). Károly Schemiz the elder graduated in medicine in Vienna in 1835 and began to practise as a physician in Győr, where he died aged 53 on 4 February 1865. Contemporary comments delineated a man of noble thoughts, humanity, and many parts (Kramoliny 1865).

The son was educated at Győr Gymnasium and the Pest University, where he obtained a teaching degree in natural science, and then withdrew for three years to educate himself, gain specialist knowledge, and learn languages. He then taught at Royal Catholic High Gymnasium in Ungvár (now Uzhhorod, Ukraine) (Blanár 1913). There are plenty of publications from that period to show that he was already engaged in scientific work. In 1888, he was invited to join Géza Horváth at the National Phylloxera Experimental Station. There and in its successor institution, the Royal Hungarian State Entomological Station, he spent seven years as an entomologist (Howard 1930). However, he was retired at his own request in 1895 due to deafness caused by scarlet fever, and retired to his wife's family estates at Kisszentmiklós (later Őrszentmiklós, now quarter of Őrbottyán), where he spent the rest of his life on scientific studies and observations. His last scientific publication appeared in 1914.

Sajó belonged to numerous learned societies, including the Hungarian Entomological Society, the Royal Hungarian Natural History Society and the Association of Economic Entomologists, as well as the Kaiserlich-königliche zoologisch-botanische Gesellschaft in Vienna and the Verein für schlesische Insektenkunde in Breslau. The yearbooks of the last show that his latest works were regularly reported at general meetings.

The wife he chose at the age of 22 was Ilona Kvassay, to whom he had family ties. They had three sons. After his first wife's death, he was remarried to his sister-inlaw, Júlia Kvassay. Both wives were sisters to the celebrated hydrological engineer Jenő Kvassay. He outlived all three of his sons. One of them, Elemér Sajó, became a talented hydrological engineer, who superintended the regulation of the Soroksár branch of the Danube and installation there of the Kvassay Lock to his own design (Filotás 2005). Elemér's three sons and their descendants bore the surname Kvassay-Sajó.

Károly Sajó died at Őrszentmiklós on 9 February 1939. His death went largely unnoticed, although this quiet, scholarly man had gained Hungary more international renown than most of his scientist compatriots. His reputation abroad is exemplified by the fact that his likeness appeared among those of the best-known scientific writers in a feature in a German illustrated paper in the early years of the century. He (along with Raoul Francé, who always declared he was Hungarian and whom fate drove to Hungary to die) was pictured larger, at the centre of the page. How sad, indeed tragic it is that Károly Sajó, the veteran leader of German life science, should have been silenced for his style, so bold and progressive in spirit, and most of his writings neglected (Szilády 1941, Balás and Sáringer 1982, Bognár 2001). However, his years at Örszentmiklós are



Figure 1. Károly Sajó (1851–1939).

still remembered in the place-name Sajó tanya (now quarter of Őrbottyán, Pest county, Hungary; http://www.historicgarden.net).

Károly Sajó's entomological writings: general works

Though Károly Sajó's father had an excellent knowledge of German, Sajó knew not a word of it until he was seven. He taught himself Western languages. A remarkable knowledge of French and English is apparent in his letters, and his books and articles were enhanced by use of the best literary German. One of the main sources of his success and popularity was the way he, amidst writers debased by journalese and scientific jargon, would use the language of Goethe and Schiller (Szilády 1941).

The bulk in Sajó's scientific writings appeared after his retirement. In the last two years before he retired, he wrote 15 articles totalling 46 pages; in the first two years after, he wrote 64 pieces totalling 282 pages. His active writing period stretched from 1872 to 1914, during which he wrote almost 500 longer or shorter contributions, brochures, reviews and books on subjects to do with entomology, general biology, agriculture, horticulture, and plant and nature protection (Balás and Sáringer 1982).

Researchers writing about insects at the turn of the 19th and 20th centuries still practised descriptive and systematic entomology at once. Sajó dealt primarily with applied entomology. He and Géza Horváth were among the first to study insects (whether pests or not) in the context of their environment and relations with other organisms and the first to encourage their readers to do likewise. He thought it was most important to note the smallest piece of biological data, for instance the ratio of males to females in the material collected, or the dates of first and last appearance of the species. His was probably the first study of insect phenology in detail. He applied these observations on his own farm and garden (Figure 2.), and his writings and advices were of much benefit to farmers at home and abroad. Naturally, the name of Károly Sajó appears alongside those of Géza Horváth and József Jablonowski as members of the Association of Economic Entomologists established in 1889. A succession of his articles about applied entomology appeared in the Hungarian and German press, as the forerunners of the new trend. It was a strange coincidence that he should have been in 1914 that he stopped publishing after three decades, just as a new scientific endeavour appeared in Europe in April that year, the *Zeitschrift für Angewandte Entomologie*. (At the same time, the seventh volume of the *Journal of Economic Entomology* was appearing in the United States.)

His works on horticultural entomology continue to be important sources that provide a sound basis for further research. He was the first to give accurate information on many horticultural and agricultural pests, including the cherry fruit fly, and several pests of asparagus and roses (Sajó 1895b, 1896a, 1901, 1902a, 1902b, 1902c, 1902d, 1902e, 1902f, 1903, 1904). Sajó's years at the Royal Hungarian State Entomological Station and its predecessor coincided with the first outbreak of Moroccan locust, *Dociostaurus maroccanus* (Thunberg, 1815) in the Carpathian Basin, in 1888–90, and his works of that period provide the best account of its discovery and the practical measures taken to control it (Sajó 1889, 1890a, 1891a) (Figure 3.). His articles are particularly valuable even today for an emphasis on ecological and biocoenological aspects that was well ahead of its time.

Sadly, his writings have still to be explored in full. His communications appeared in 13 periodicals at home and 12 abroad, mainly in German. He was a senior staff member for 18 years, from 1895 to 1913, of Prometheus, the main German-language journal of popular natural history, published in Berlin, where 169 pieces, including some of his most important studies, appeared. Also published in Germany were three of his four books. He wrote the most successful about honey bees (Unsere Honigbiene; Sajó 1909, 1914, 1923a) and about ants (Krieg und Frieden im Ameisenstaat; Sajó 1905a, 1908, 1923b) (Figure 4.); these appeared in almost 30 editions and 300,000 copies in Germany between 1905 and 1923. His ant monograph also appeared in Hungarian in a translation by Ede Früchtl (Sajó no date), and his bee work twice in Czech, through the cooperation of A. Muťovský and J. Kebrle (Sajó 1919). A major work of applied entomology by him that appeared in 1910 (Sajó 1910a) (Figure 5.) also contained much cultural information connected with scarabaeoids and meloids, including a remarkably interesting idea that was cited in many later publications (Schimitschek 1968, Hogue 1983, Kevan 1985, Scholtz 2008): "That the association between the dung ball of scarabaeids and wheels might be not so far fetched is documented by the vision of Ezekiel in the Bible (Ezekiel 1: 1–28). In his vision the prophet Ezekiel describes four cherub angels that resemble scarab beetles in several aspects including the metallic appearance, four wings with two different pairs, spines at the anterior limb pair, cleft feet, the back and forth movement, and the carrying of a wheel that is round in every direction. The idea that cherubim might represent scarab beetles originated from the Hungarian zoologist Sajó (1910) and was re-



Figure 2. The house in the Nyáras district of Őrszentmiklós in 1891. This is where Sajó set up his laboratory.

fined by the American cultural entomologist Hogue (1983). The interesting aspect of this hypothesis is that the so-called Ezekiel's Wheel, which is often depicted as two wheels interlaced at right angles and carried by the cherubim, might be the transformed description of the dung pill. Thus, the association of a scarab dung ball with a wheel might not be a foreign thought of Middle Eastern ancient people" (quoted from Scholtz 2008).

The first edition of his fourth book, *Blätter aus der Lebensgeschichte der Naturwesen* (Sajó 1911a) contained a collection of his papers. Subsequent editions are also known (Sajó 1911b, 1922). It was to be the first of a ten-volume collection of articles, but the other volumes never appeared, due to the First World War and the economic crisis that ensued.

Sajó kept up a very lively correspondence with specialists and institutions abroad. He was sending three or four letters or packets a day in the 1920s and early 1930s. These connections and writings of his did much to make the entomology of the sandy puszta of the Great Hungarian Plain known abroad (Sajó 1880a, 1882, 1883). He noted down observations with daily regularity. He himself stated that for many years, hardly a day went by without discovering something new or solving some old conundrum. It is a huge loss to universal entomology that he should have ceased his writing a quarter of a century before he died. For a long time, World War II Őrszentmiklós was a war zone, and his home and laboratory, his library of 3000 volumes, his unpublished notes, and all his correspondence were destroyed. All that remained of his library was a handful of volumes that his heirs presented to the Hungarian Museum



Figure 3. Front cover of Sajó's book on the first outbreak of Moroccan locust, *Dociostaurus maroccanus* (Thunberg, 1815) in the Carpathian Basin, in 1888–90.

of Natural Sciences, Budapest after his death.

The question arises: why should a man whose life had been imbued with research and research findings suddenly and irrevocably have laid down his pen? Two possible reasons were advanced by Szilády (1941). One was advancing years, the other a change of editor at Prometheus. Editor Otto Nicolaus Witt had great praise for Sajó's writings in a letter of 18 April 1913: "I had to read several thousand pages, but there was only one man whose writings it was always a joy to take up, for I knew that I could always find new knowledge and stimulation in them" (cited in Szilády 1941). Sajó received even greater recognition from his readers, in the form of letters, congratulations and requests for advice. When Witt died and the new editor began to delay publishing his writings, Sajó became permanently disillusioned.

Sajó's foresight was shown in 1894, when he was among the first to write about the role of insects in spreading disease (Sajó 1894a, 1894b, 1895a, 1898a, 1910b), predicting that *Anopheles*-mosquitoes would be found to spread malaria, and the African *Glossinia*-flies and the Kolumbács fly, *Simulium colombaschense* (Scopoli, 1780) several other diseases. This pioneering article appeared in *Prometheus*, whose editor drew readers' attention in a footnote to the fact that it was the first article in the field to appear in Europe. It was cited in French papers also. Sajó wrote in the study that insects *"are not just the loving postmen of flowers,"* but *"heralds of the scythe of Death."* His prediction became crystal-clear not long afterwards, as he noted that *"a very important and interesting field is opening up for bacteriologists."*

Sajó dealt in his works with the connection between the weather and the behaviour of living organisms (Sajó 1896c, 1896d, 1896e, 1896f, 1897a, 1899). Although Sajó was not the first to recognize this, his name is associated with a deterministic approach to that connection, i. e. in the strong wind that precedes a storm, insects will rise up into the air and so produce a mass spread over longer distances, which is advantageous to the species (Sziráki 1985). For completeness's sake it should be mentioned that the first detailed description of the phenomenon was made by South (1885),

although his account was confined to the noctuid moth *Autographa gamma* (Linnaeus, 1758), whereas Sajó generalized it.

His report (Sajó 1896b), written in most enjoyable Hungarian prose, met with scarcely any reaction in Hungary, where contemporaries simply did not concern themselves with matters of a theoretical nature. For instance, Sajó's discoveries about aestivation - covered later - were ignored for half a century. The next Hungarian entomologist to deal substantively with diapause was Gyula Sáringer, in conjunction with Tibor Jermy, from the 1950s onwards. On the other hand, the German versions of his papers were widely noticed in Europe and overseas. This is well exemplified in an article in the American Naturalist (Webster 1902): "Relative to the concluding point in this paper, viz., the influence of wind and thunderstorms combined on insect diffusion, I beg to



Figure 4. Cover of Sajó's Krieg und Frieden im Ameisenstaat.

call attention to a most interesting series of papers contributed to Prometheus, a German scientific journal much like our Scientific American, by Prof. Karl Sajó, of Budapest, Hungary. Professor Sajó says that it is known that before thunderstorms the crayfish come out of the water into the grass on the banks of the river or lake; many fishes act as if they were insane, and many birds and mammalia become irritated and angry. Even the micro-organisms are subject to similar changes; for instance, before thunderstorms in late fall, the wine fermentation can reach so great a violence as to cause the fermenting juice to suddenly run out of the vats. The greater the change in the atmosphere, the greater the unrest of the living being ...' Continuing, Professor Sajó calls particular attention to the 'great unrest and activity that takes place in the insect world just in the sultry hours preceding a thunderstorm, and to the fact that insects in the air at the time the storm bursts are driven like chaff to great distances, - perhaps into other countries, across rivers, lakes, and mountains; not only the species that fly but many that do not fly may thus be transported to new homes.' And again, 'Many Aphides creep to the crowns of the plants, then drop themselves at the proper moment into the violent current of the storm. A number of these insects land in places where there is no food supply for them and they die. A part of them reach places where their species is already established,



Figure 5. Front page of Sajó's Aus dem Leben der Käfer.

and fare no better. Part are thrown into the water, sometimes in oceans, and perish. A proportionally small number arrive at such places as may be called really favorable for their diffusion, viz., where the species has never established itself before, or, having done so, died out before the arrival of newcomers, and, therefore, natural enemies had not preceded them. Such individuals as are thus thrown into favorable places have a chance to multiply into large, populous colonies within a short space of time, and continue until their enemies find them out, or they become over-populous and devour all of their food supply, resulting in what to them is famine.' There is probably not an American entomologist who has not encountered illustrations similar to those enumerated by the writer of the above, and, while we may not have wholesale introductions of new things among us, there is no doubt that localities are often first

colonized by certain kinds of insects in this manner, whereas the wind or the thunderstorm acting separately would not bring about such a condition of affairs. I have stated that, in applying trap lights or lanterns, or edible baits like sweetened sour beer, we, as a rule, secure males and spent females, but the influence of weather conditions that usually precede a thunderstorm (that is, a close, sultry condition) has the effect of bringing out both sexes, -a result due, so far as can now be determined, to some subtile action on their sexual life. As Professor Sajó so aptly illustrates this point, I will quote him again quite fully: 'What influence the weather has, especially on the activity sexual life, must be known to every zoologist; even man is not an exception from these "living barometers." Not only children, not only the female sex, but the sick ones experience the influence of the weather on the functions, especially on the nervous system; and everybody without exception are thus influenced, though not all may be aware of the fact. The same causes that in many produce unrest and irritation render others dizzy, stupid, or sleepy, according to the temperament of the individual.' The effect of electricity on the nervous systems of insects, especially as relative to their love affairs, would constitute an interesting study, and one that ought to be carried out; but even as it is, we can see that the thunderstorm, in conjunction with the wind, may accomplish in the diffusion of insects that which neither element alone would bring about."

Sajó's articles on the subject appeared mainly in German-language journals, and although most later references were made not to the original papers (for example Sajó 1897a) but to references in Uvarov's *Insect and Climate* (Uvarov 1931), it is heartening to find several exceptions (Wellington 1946, Edwards 1961, Flitters 1963).

Burgeoning pathogens and insect pests caused increasing problems as agricultural production spread and intensified. How could these be contained without doing damage to the environment? Sajó recognized what a blessing the natural enemies of the pests represented to plant protection and was among the first to propose employing them (Sajó 1902g).

Károly Sajó's investigations into leaf-beetles

Sajó's outlook on nature was decisive also in his researches into the life history of leafbeetles. Although he broke ground with his discoveries about the life history of many harmful leaf-beetle species, his most important findings concerned the aestivation of *Entomoscelis adonidis* (Pallas, 1771), which he published in Hungarian (Sajó 1896g) and in German (Sajó 1896h, 1896i). He returned to the matter some years later, in the light of other findings (Sajó 1900a, 1900b, 1911c).

In 1895, Sajó began to investigate on his own estate at Őrszentmiklós the life history of *Entomoscelis adonidis* (Pallas, 1771) and its larva, the so-called "black caterpillar", which was a formidable pest of seed rape in Central and Southern Hungary in the 19th century. He recalled a letter that a farmer by name of Friedrich Rovara had sent to the Royal Hungarian State Entomological Station in the 1880s, stating that he had found developed examples of *Entomoscelis adonidis* (Pallas, 1771) in the soil. The staff had probably thought the communication was mistaken and taken no action. Not so Sajó, who placed specimens in an insectarium, where they did indeed disappear into the soil at the end of May and reappear only in October. Sajó established that this was a perfect case of aestivation, and managed to find the reason for it (Sajó 1896j). Although the phenomenon appeared at that time to be unique, Sajó was sure it must occur in some other species as well. This was soon confirmed: W. Kolbe (1899) augmented Sajó's finding by discovering aestivation in two other leaf-beetle species: *Gonioctena viminalis* (Linnaeus, 1758) and *Chrysolina sanguinolenta* (Linnaeus, 1758). Sajó went on to experiment with other leaf-beetles, but without clearly confirming aestivation among them.

The discovery was a milestone as the first experimental observation of the phenomenon known today as aestivation. He also confirmed hibernation in a number of insects (Sajó 1896e, 1896f). The biological explanation for diapause he could not yet give, of course. He proposed a process of self-purification from metabolic intoxication in the insects (see also Bodenheimer 1952).

Sajó, as an out-and-out practical man, dealt mainly with the leaf-beetle pests in agriculture and horticulture. He presented the life history of *Oulema melanopus* (Linnaeus, 1758), and how to defend against it in several publications (Sajó 1890b, 1890c, 1893a, 1893b, 1894c). He was the first scientist in this country to investigate beetles inhabiting asparagus, notably the *Crioceris* spp. (Sajó 1895b, 1897b, 1902d, 1902f).

He also presented in shorter papers the life history of *Xanthogaleruca luteola* (O. F. Müller, 1766) and *Gonioctena fornicata* (Brüggemann, 1873), in Sajó 1888 and 1892 respectively, along with the damage they did and how to protect against it.

While working on protection against phylloxera, Sajó lit on damage done by the Western Grape Root-Worm, Bromius obscurus obscurus (Linnaeus, 1758). He was occupied for some time with its life history and range of food plants (Sajó 1891b, 1896k, 1898b), and with the taxonomic problems it raised. When dealing with the latter, he noticed that of the two morphologically differentiable taxa ("Eumolpus obscurus" and "Eumolpus vitis"), "Eumolpus obscurus" never occurred on grape vines, even though the investigations had extended to wine regions throughout the Carpathian Basin. He collected "Eumolpus obscurus" solely from Epilobum species, mainly in hilly and mountainous habitats and beside streams. He emphasized repeatedly that "Eumolpus obscurus" and "Eumolpus vitis" are two separate species, although they were being treated as one at that time. He stressed that life history and length of development needed to be considered when distinguishing the species. He raised the question again in a lecture delivered to the Zoological Department of the Royal Hungarian Natural History Society on 13 April 1893 (Sajó 1893c). He drew a parallel with the species pair Entomoscelis adonidis (Pallas, 1771) and Entomoscelis sacra (Linnaeus, 1758), because he did not think it was justified to amalgamate two species simply because there existed transitional forms between them. He showed that the habitats, food plants and time of appearance of the two species differed markedly.

In 1896, an analysis of the *Eumolpus* species by Émile E. A. Topsent appeared in the *Bulletin de la Société d' Etüde des Sciences naturelles de Reims*. Sajó quickly put up an opposing view (Sajó 1897c): Topsent's hypothesis, that *"Eumolpus vitis"* and *"Eumolpus obscurus"* are one and the same, and that the difference in colour is due to the food plant from which each may chance to be taken, was shown to be without the support of facts or even an investigation.

Surprisingly, this problem has still not been solved. According to many authors (Kaszab 1962, Mohr 1966, Gruev 1992, Gruev and Tomov 1984, 1998, Jelínek 1993, Vig 2002) the *villosulus* (Schrank 1781) variation (= *vitis* auct. nec. Fabricius 1775) is a separate subspecies, and the taxonomic structure is *Bromius obscurus obscurus* (Linnaeus, 1758) and *Bromius obscurus villosulus* (Schrank, 1781). More recently the view has spread that the distinction is unjustified (Warchałowski 2003, Moseyko and Sprecher-Uebersax 2010), although I am not familiar with the actual evidence for saying so.

Károly Sajó's work on taxonomy

Károly Sajó had wide interests, but his prime focus was on applied entomology; his work in classic taxonomy is modest. His main concerns were the Hymenoptera and Hemiptera, and among the beetles of Coccinellidae.

In the Örszentmiklós district, he collected four specimens of a sphecid wasp that he described as a new species named *Oxybelus treforti* (Sajó, 1884). (This is now classified as the subspecies *Oxybelus argentatus treforti* Sajó, 1884; see Bohart and Menke 1976). Although he was the first to collect a specimen of *Oxybelus aurantiacus*, he conceded the right of describing it to Sándor Mocsáry (Mocsáry 1883). He was also the first to discover the macropterous forms of the Hemiptera *Blissus doridae* Ferrari, 1874 and a *Plinthisus hungaricus* Horváth, 1875 (now a synonym of *Plinthisus longicollis* Fieber, 1861) (Sajó 1880b, 1880c, 1880d, 1880e).

In line with his period, that paid great attention to describe aberrations and variations (Weise 1882), he also described numerous ladybird variations (Sajó 1880f, 1881), which count now as synonyms or invalid categories (Leman 1922, Kovář 2007).

Sajó possessed a huge collection of insects, from which he sent significant amounts abroad, in an attempt to relieve his financial problems after the First World War and during the Great Depression (personal communication of Alfred C. Kinsey, cited by Balás and Sáringer 1982). There is confirmation of this in the Scientific Notes and News column of the 12 June 1925 number of *Science* (Kinsey 1925): *"The death of Dr. Karl Sajó of Hungary was reported during the year of 1924. I have a characteristic letter from Professor Sajó, dated April 23, and I am delighted to be able to make this correction. Dr. Sajó has been rendering a good service to American entomologists by offering Hungarian insects for sale, and I hope that this mistaken report has not interfered with his work."*

Not long ago, about a thousand beetle specimens originating from Hungary were found in the collection of the Sam Noble Oklahoma Museum of Natural History, part of the University of Oklahoma (email letter from Katrina Menard, collections manager of recent invertebrates). Based on the collecting labels, some of these were collected in 1909–11 in the district of Őrszentmiklós, and many specimens also bear the name Károly Sajó. There can be no doubt that they formed one of the consignments he sent to the United States.

Shortly after Sajó's death, his insect collection was presented by his family to the Hungarian Natural History Museum in Budapest, where it can still be studied. One item from it was a specimen of *Adapsilia coarcata* Waga, 1842 (Pyrgotidae), which added a new species and a new family of flies to the fauna of Hungary (Soós 1943). Indeed Sajó collected between May and September the only specimens of the family yet found in Europe. Árpád Soós, a celebrated dipterist, found specimens from Sajó, collected at Őrszentmiklós, in the Thalhammer Collection in Kalocsa. There also the labelling shows that János Thalhammer received these from Sajó.

Sajó was concerned with problems of classifying insects and the proliferation of synonyms (Sajó 1900c). He criticized the habit of awarding different specific names within a genus based only on differences of form. He also disapproved of those who published specific descriptions in little-known, small-circulation periodicals, which he believed was partly responsible for this proliferation of synonyms.

Károly Sajó's nature protection work and the beginnings of nature protection in Hungary

The earliest initiatives in Hungary for protection of the environment date back to the early 19th century, although these relied on the personal activity of a few individuals

and did not take any institutionalized form. In 1841, János Salamon Petényi, an eminent zoologist, was almost the first to warn that the buffalo of the Carpathian Basin were dying out and so were the beavers (Petényi 1847)¹. At a meeting of the Royal Hungarian Natural History Society in 1866, János Kreisch called for protection of the Tatra marmot, Marmota marmota latirostris Kratochvil, 1961. Such isolated initiatives had little success, for they lacked a scientific backing. More effective legislative assistance in protecting the environment came with the game laws (IV/1872 and XX/1883). These defined close seasons and listed the species that could be hunted. Those seen as beneficial (from the hunting and other economic points of view) were given protection and those seen as detrimental could be shot "at any time", but debates around the concepts of benefit and detriment caused further uncertainty. Apart from the game laws, there appeared in 1888 a ministry order (32.042/1888. FIK) giving protection on crown land to Pallas's sand grouse, Syrrhaptes paradoxus (Pallas, 1773), a species found normally on the Asian steppes, and seeking to encourage its presence. This was done purely on grounds of natural value, regardless of benefit or detriment, which was to be gauged by subsequent research. This makes the 1888 order the first action by the state to have an express purpose of nature protection.

The social and economic efforts towards a nature protection movement in Hungary had succes at the turn of the 19th and 20th centuries thanks to the presence of a social demand and basis for it. This receptive milieu gave support to a concept of nature protection that had been proposed on a specialist level, with Károly Sajó playing a formulating part in it. Even in his early writings, he was listing animal and plant species that were in danger of extinction. In 1905 he was outlining the main steps to require to "rescue the treasures of virgin nature" (Sajó 1905b). Here two underlying ideas appear: that all living organisms should be preserved in their original environment, and that the cause of nature protection had to be furthered through legislation. He made a specific proposal: that there should be purchased out of the annual state budget "national protected areas" that are "interesting and excellent for their fauna or their flora or their geological features, or even their natural beauty." He also described in detail how protected areas in various parts of the country might be chosen from state-owned estates, and their preservation be placed in the hands of nature protection guards drawn mainly from the forestries. He issued an appeal to Hungarian society in the meantime, before the "national protected areas" were designated, for scientists and others with a feeling of responsibility for nature at least to refrain from shooting rarer mammals and birds, and made bold and frank criticisms of them, primarily for the responsibility they bore for the irreversible damage and destruction wrought by procrastinating over the protection of the country's natural assets: "Let it not be science, not men of science who destroy the treasures of nature, but only those who still have no notion

¹ However, Petényi's appeal for the European buffalo, *Bison bonasus* (Linnaeus, 1758) came too late: the last specimen in Hungary was killed in 1762 on the Plaj heights in Borgó, although a note at the time puts the extermination of the last specimen later, in 1814, on the Udvarhely side the Madaras Hargita. The beaver fared no better: the last specimen was shot a few years later near Ács, in 1854.

of what marvellous, multifarious masterpieces cover the surface of our globe: masterpieces whose effects are irretrievable, for the crude works of man cannot even approach the delicacies of the organic and inorganic realm. For we scientists of the last century have indeed been at fault! At fault in not striving with enough energy the veto of science whenever we saw a wave of total destruction overwhelm in a few years works that had taken Mother Nature millions of years to produce, and allowing destruction to plumb the depths" (Sajó 1905b).

Sajó considered that the species of plains and hills and watery habitats were in the greatest danger. He devoted a separate article to the exceptional importance of primary forests (Sajó 1905c). He intended an important role in the operation of nature protection to be played by professional societies, especially in the natural sciences. He assigned to them above all the role of enlightenment and propaganda, in the hope that their actions would also encourage various private initiatives (Lukács 1976).

Sajó settled near Őrszentmiklós in the period after the phylloxera epidemic. He was appalled to notice the extent to which viticulture on sandy soil had been at the expense of the original plant cover and the beetle community associated with it (Sajó 1893d), and so he established a reservation on five cadastral *hold* (3 hectares) of his estate. This to the author's knowledge was the first territory in Hungary to be set aside for purposes of nature protection, on which Sajó gave ecological stability priority over farming. In that respect he was the first active Hungarian practitioner of nature protection. He was the first to ask how the damage from pests and diseases could be reduced without damaging the environment. Following the example of the famous *Pozsony Garden* of the Jesuit János Lippay (Lippay 1664), he established several noble exotic and indigenous tree and shrub species on the alkaline dunes (Sajó 1896l, 1902h). The marked out wider than usual roads on his estate and would not allow the verges to be mown, so as to protect the plant and insect life living there. Unfortunately, this nature protection area, unique in Hungary and even in Europe, was neglected after this death.

However, it was not so much by his personal example as through his writings that he furthered the cause of nature protection at home and elsewhere in Europe. He spoke out against the damage caused by habitual hunting, inordinate collecting, and unplanned afforestation. His articles spoke of the national parks that already existed in North America and Africa and of the initial efforts at nature protection by European nations.

Károly Sajó's writings also contributed to the conceptual foundations for nature protection and for political decision-making in Germany (Genath 2005). Based on Sajó's contributions to *Prometheus* and on personal experiences of natural destruction, Wilhelm Wetekamp argued in the Prussian provincial assembly in 1898 that a network of national parks based on those in North America should be set up (Piechocki 1998). Wetekamp's speech prompted Agriculture Minister Hugo Conwentz to commission him to survey the Prussian forests, and his report (Conwentz 1900) can be considered the first nature protection inventory (Sajó 1900d). The initial steps were being taken in Europe as well ...

In 1905, the year in which Sajó's famous study of the "treasures of all nature" appeared, the subject of nature protection was regularly discussed at meetings of the Zoological and Botanical Department of the Royal Hungarian Natural History Society. There were several debates within the society, culminating in a request to the board

that it should seek legislature on the protection of natural assets. The resulting proposal was backed also by the Hungarian Geographical Society and the National Forestry Association. Károly Kaán proposed to the Royal Hungarian Natural History Society in 1907 that an appeal be made to the agriculture minister on the subject of protecting "the primary forests, the spectacular museums of nature". Kaán's proposal provided the basis for a detail plan of action from the National Forestry Association and the Royal Hungarian Natural History Society, which emphasized measures to protect the oak woods of the plains and hills and the gallery forests along the Danube. Thereafter, the work of Agriculture Minister Ignác Darányi and of Károly Kaán led to the passage of the first nature protection legislation in 1909.

Epilogue

Károly Sajó inhabited and influenced at the turn of the 19th to the 20th century a world that was undergoing radical transformation. He was a pioneer in the true sense, whose many discoveries and innovative proposals, and whose whole outlook opened up new fields in applied entomology. Sadly, he never received the recognition he deserved in his own country, though he remained an out-and-out Hungarian entomologist, who gained great prestige for his country. In many cases his contemporaries failed to grasp his outstanding achievements and pioneering discernments, and recognition of their importance had to wait until the 1950s. Even today, his writings have not been fully charted, but most of those on the subject of plant protection are referenced fully in Balás and Sáringer (1984) and in the appropriate chapters of the six-volume manual edited by Tibor Jermy and Klára Balázs (1988–1996). His wide interests, his writings, his intellectual heritage and his outlook on life may well justify the conclusion reached by Nagy (1992): Károly Sajó was Hungary's Jean-Henri Fabre.

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References

Balás G, Sáringer Gy (1982) Kertészeti kártevők. [Horticultural Pests.] Akadémiai Kiadó, Budapest, 1069 pp. [in Hungarian]

- Blanár Ö (1913) Az ungvári királyi katolikus főgymnasium háromszázados története, 1613– 1913. [Three hundred years history of the Royal Catholic High Gymnasium in Ungvár, 1613–1913.] Az ungvári Gimnázium Értesítője, Ungvár, 365 pp. [in Hungarian]
- Bodenheimer FS (1952) Arrested development and arrested activity in insect life. Transactions of the IXth International Congress of Entomology, Volume I. The congress plenary sessions, communications at the sectional meetings, Amsterdam, 21–40.
- Bognár S (2001) Emlékezzünk a 150 éve született Sajó Károlyra (1851–1939)! [Remembering Károly Sajó, born 150 years ago.] 6. Tiszántúli Növényvédelmi Fórum. Előadások–Proceedings, Debreceni Egyetem, Debrecen, 121–124. [in Hungarian]
- Bohart RM, Menke AS (1976) Sphecid Wasps of the World: a Generic Revision. University of California Press, Berkeley CA, 600 pp.
- Conwentz WH (1900) Forstbotanisches Merkbuch für Westpreußen Nachweis der beachtenswerthen und zu schützenden urwüchsigen Bestände, Bäume und Bestände im Königreich Preußen. I. Provinz Westpreußen. Herausgegeben auf Veranlassung des preußischen Ministers für Landwirtschaft, Domänen und Forsten, Borntraeger, Berlin, 94 pp.
- Edwards DK (1961) Activity of two species of *Calliphora* (Diptera) during barometric pressure changes of natural magnitude. Canadian Journal of Zoology 39(5): 623–635.
- Filotás I (2005) Emlékbeszéd Kvassay Jenő és Sajó Elemér őrbottyáni sírjánál. [Memorial address at the Őrbottyán grave of Jenő Kvassay and Elemér Sajó.] Hidrológiai Tájékoztató 2005: 3–5. [in Hungarian]
- Flitters NE (1963) Observations on the effect of hurricane "Carla" on insect activity. International Journal of Biometeorology 6(2): 85–90.
- Genath P (2005) Es geht fast täglich auf den Brocken …! Der Arbeitsalltag der Ranger im Nationalpark Hochharz aus volkskundlicher Perspektive. Internationale Hochschulschriften, Bd. 453., Waxmann Verlag GmbH, Münster, 399 pp.
- Gruev B (1992) Geographical distribution of leaf beetle subfamilies Lamprosomatinae, Eumolpinae, Chrysomelinae, Alticinae, Hispinae and Cassidinae (Coleoptera, Chrysomelidae) on the Balkan Peninsula. Plovdiv University Press, Plovdiv, 512 pp.
- Gruev B, Tomov V (1984) Coleoptera, Chrysomelidae, 2. Fauna Bulgarica, 13, Aedibus Academie Scientiarum Bulgaricae, Sofia, 220 pp.
- Gruev B, Tomov V (1998) Coleoptera, Chrysomelidae. Catalogus Faunae Bulgaricae, 3., Pensoft Publishers, Sofia–Moscow, 160 pp.
- Hogue CL (1983) An entomological explanation of Ezekiel's wheels? Entomological News 94: 73–80.
- Howard L (1930) A history of applied entomology (somewhat anecdotal). Smithsonian Miscellaneous Collections 84. Smithsonian Institution, Washington, 564 pp.
- Jelínek J (1993) Check-list of Czechoslovak Insects IV (Coleoptera). Folia Heyrovskyana, Supplementum, Praha 1: 1–172.
- Jermy T, Balázs K (Eds) (1988–1996) A növényvédelmi állattan kézikönyve. [Handbook of plant protection zoology.] Akadémiai Kiadó, Budapest, 1. (1988) 443 pp., 2. (1989) 304 pp., 3. (1990) 673 pp., 4. (1993) 831 pp., 5. (1994) 376 pp., 6. (1996) 307 pp. [in Hungarian]

- Kaszab Z (1962) Levélbogarak–Chrysomelidae. Magyarország Állatvilága, IX: 6 (Fauna Hungariae 63.), Akadémiai Kiadó, Budapest, 416 pp.
- Kevan DK (1985) Soil zoology, then and now mostly then. Quaestiones Entomologicae 21(4): 371.7–472.
- Kinsey AC (1925) Dr. Alfred C. Kinsey of Indiana University writes... Science 61(1589): 607.
- Kolbe W (1899) Ueber das Eintreten eines Sommerschlafes bei Chrysomeliden. Zeitschrift für Entomologie. Herausgegeben vom Verein für schlesische Insektenkunde zu Breslau (Neue Folge) 24: 26–37.
- Kovář I (2007) Family Coccinellidae Latreille, 1807. In: Löbl I & Smetana A (Eds) Catalogue of Palaearctic Coleoptera, Vol. 4. Elateroidea, Derodontoidea, Bostrichoidea, Lymexyloidea, Cleroidea and Cucujoidea. Apollo Books, Stenstrup, Denmark, 568–631.
- Kramoliny I (1865) Emlékbeszéd Schemiz Károly orvostudor felett. [In remembrance of physician Károly Schemiz.] Győr, 15 pp. [in Hungarian]
- Leman GBC (1922) Hippodamia variegata Goeze. Description of some further new aberrations, and observations on ab. 3-punctata Haw. and ab. 9-punctata Haw. The Entomologist's Record and Journal of Variations 34(6): 101–105.
- Lippay J (1664) Posoni Kert. [Poson Garden.] Cosmerovius Máthé Császár urunk Ő Fölsége könyv-nyomtatójának bötüivel, Bécs, 143, 244, 303 pp. [in Hungarian] [reprint: Akadémiai Kiadó, Budapest, 690 pp. (1966)]
- Lukács D (1976) A magyar természetvédelem kezdetei: Sajó Károly úttörő munkássága. [The beginnings of nature protection in Hungary: Pioneer work by Károly Sajó.] Búvár 31(5): 215. [in Hungarian]
- Mocsáry S (1883) Hymenoptera nova Europaea et exotica. (Európai és másföldi új hártyaröpűek.) MTA Értekezések a természettudományok köréből 13(11): 1–72.
- Mohr KH (1966) Die Käfer Mitteleuropas. Band 9. Cerambycidae, Chrysomelidae. Goecke & Evers, Krefeld, 299 pp.
- Moseyko AG, Sprecher-Uebersax E (2010) Subfamily Eumolpinae Hope, 1840. In: Löbl I, Smetana A (Eds) Catalogue of Palaearctic Coleoptera, Vol. 6. Chrysomeloidea. Apollo Books, Stenstrup, Denmark, 619–643.
- Nagy B (1992) Centenary of the Hungarian Royal Entomology Station. Acta Phytopathologica et Entomologica Hungarica 27: 9–12.
- Petényi JS (1847) Petényi Salamon felszólítása a honunkból már végkép[p]en kipusztult bölények, és az elenyészés örvényében forgó hódok ügyében. [Contribution by Salamon Petényi on the matter of the buffalo irrevocably extinct in this country and the beaver in the throes of extinction.] A magyar orvosok és természetvizsgálók Kassa–Eperjessen tartott hetedik nagygyűlésének történeti vázlata és munkálatai. Pest, 215–218. [in Hungarian]
- Piechocki R (1998) 100 Jahre Nationalparkbewegung in Deutschland. Nationalpark 101(4): 24–28.
- Sajó K (1880a) Entomologische Bilder aus den ungarischen Flugsandsteppen I. Entomologische Nachrichten 6(18): 198–202.
- Sajó K (1880b) Die bisher unbekannte makroptere Form von *Blissus doriae* Ferr. Entomologische Nachrichten 6(21): 235–238.

- Sajó K (1880c) Unser Blissus doriae. Illustrierte Wochenschrift für Entomologie 2(29): 449-451.
- Sajó K (1880d) Die bisher unbekannte makroptere Form von *Plinthisus convexus* Fieb. (= *hun-garicus* Horv.). Entomologische Nachrichten 6(13–14): 141–142.
- Sajó K (1880e) Weitere Funde von makropteren Exemplaren des *Plinthisus convexus* Fieb. und die Larven dieser Art. Entomologische Nachrichten 6(21): 238–240.
- Sajó K (1880f) Beiträge zu Weise's Bestimmungs-Tabellen der europäischen Coccinelliden. Entomologische Monatsblätter 2(20): 159–160.
- Sajó K (1881) Acht neue Coccinelliden-Varietäten aus Central-Ungarn. Entomologische Nachrichten 7(19): 273–274.
- Sajó K (1882) Entomologische Bilder aus den ungarischen Flugsandsteppen II. (Sommerbild). Entomologische Nachrichten 8(1): 1–10.
- Sajó K (1883) Rovarászati képek a magyar alföld futóhomok-pusztáiról I–IV. [Entomological pictures on the drifting sand dunes of the Great Hungarian Plain I–IV.] Rovarászati Lapok 1(1): 6–8, 1(2): 20–24, 1(3): 37–40, 1(4): 56–61.
- Sajó K (1884) Eine neue *Oxybelis*-Art aus Central-Ungarn. Wiener Entomologische Zeitung 3(3): 87–88.
- Sajó K (1888) A szilfa-pusztító bogárról (*Galerucella xanthomela* Schrk.). [On *Galerucella xan-thomela* Schrk.] Természettudományi Közlöny 20(230): 406. [in Hungarian]
- Sajó K (1889) A péczel-maglódi sáska irtása. [Control of locusts in the vicinity of Péczel and Malód.] Természettudományi Közlöny 21(237): 206–211.
- Sajó K (1890a) A marokkói sáska Magyarországon. [The Moroccan locust in Hungary.] Természettudományi Közlöny 22(249): 225–256. [In Hungarian]
- Sajó K (1890b) A zabpusztító Lema melanopáról. [*Lema melanopa* as a pest of oat.] Természettudományi Közlöny 22(252): 442–443. [in Hungarian]
- Sajó K (1890c) Az árpa és zabvetést pusztító *Lema melanopa* nevű bogár a kukoriczán. [*Lema melanopa*, pest of barley and oat, on corn.] Természettudományi Közlöny 22(252): 444. [in Hungarian]
- Sajó K (1891a) A marokkói sáska Magyarországon az 1888, 1889 és 1890. években. [The Moroccan locust in Hungary in the years of 1888, 1889 and 1890.] A Magyar Királyi Rovartani Állomás Kiadványa 1(4): 1–80.
- Sajó K (1891b) Az *Eumolpus vitis* nevű szőlőrontó bogár. [*Eumolpus vitis* as pest of grape.] Borászati Lapok 23: 362–364. [in Hungarian]
- Sajó K (1892) A luczernapusztító bogárról, *Phytodecta fornicata* Brüggm. (*Gonioctena sexpunc-tata* Panz.) és az újabb rovarirtó anyagokról. [On *Phytodecta fornicata* Brüggm. (*Gonioctena sexpunctata* Panz.) and on the new insecticides.] Természettudományi Közlöny 24(274): 333–334. [in Hungarian]
- Sajó K (1893a) A vetés elfehéredése. Lema melanopus L. [Bleaching of the sowings Lema melanopus L.] Természettudományi Közlöny 25(281): 1–13. [in Hungarian]
- Sajó K (1893b) Das Getreidehähnchen (*Lema melanopus*). Zeitschrift für Pflanzenkrankheiten 3(3): 129–137.

- Sajó K (1893c) Néhány érdekes magyarországi rovarfaj. [Some interesting Hungarian insect species.] Természettudományi Közlöny 25(288): 437–438. [in Hungarian]
- Sajó K (1893d) Rovarfaunánk változásairól. [About changes in our insect fauna.] Természettudományi Közlöny 25(Pótfüzetek): 107–115. [in Hungarian]
- Sajó K (1894a) A rovarok és rokonaik, mint a betegségek terjesztői. [Insects and allies as vectors of diseases.] Természettudományi Közlöny 26(300): 401–412. [in Hungarian]
- Sajó K (1894b) Die Gliedertiere als Vermittler von Krankheiten. Prometheus 6: 81–84, 97–102.
- Sajó K (1894c) A vetésfehérítő bogár (*Lema melanopus* L.). [Cereal leaf beetle (*Lema melanopus* L.).] A Magyar Királyi Állami Rovartani Állomás Közleményei 1(10): 1–31., Földmívelésügyi Magyar Királyi Minisztérium kiadása, Budapest [in Hungarian]

Sajó K (1895a) A betegségek terjesztése. [The spread of disease.] Természettudományi Közlöny 27(310): 296–298. [in Hungarian]

- Sajó K (1895b) A spárgatermelés ellenségei. [Enemies of asparagus production.] Gyümölcskertész 5: 210, 221, 242. [in Hungarian]
- Sajó K (1896a) Ein bisher unbekannter Feind des Spargels. Illustrierte Wochenschrift für Entomologie 1: 597–598.
- Sajó K (1896b) Eleven barometrumok. [Living barometers.] Természettudományi Közlöny 28(327): 573–581. [in Hungarian]
- Sajó K (1896c) Lebende Barometer. Österreichisches landwirtschaftliches Wochenblatt 40: 313–315, 41: 321–322.
- Sajó K (1896d) Thierische Barometer. Österreichisches landwirtschaftliches Wochenblatt 44: 345–347.
- Sajó K (1896e) Kälte und Insektenleben. Illustrierte Wochenschrift für Entomologie 1(25): 394–397, 1(26): 405–407.
- Sajó K (1896f) Nochmals Kälte und Insektenleben. Illustrierte Wochenschrift für Entomologie 1(29): 457–461.
- Sajó K (1896g) A rovarok alvása. [Sleep in insects.] Természettudományi Közlöny 28(326): 546–548. [in Hungarian]
- Sajó K (1896h) Der Schlaf der Insekten. Prometheus 7: 817–819.
- Sajó K (1896i) Sommerschlaf eines Käfers. Illustrierte Wochenschrift für Entomologie 1(6): 87–89.
- Sajó K (1896j) Entomoscelis adonidis Pall. und E. sacra L. Illustrierte Wochenschrift f
 ür Entomologie 1(8): 117–120., 189.
- Sajó K (1896k) Der Weinstock-Fallkäfer (*Eumolpus vitis* F.) Illustrierte Wochenschrift für Entomologie 1(32): 501–506, 1(33): 517–525.
- Sajó K (1896l) Ueber Parkanlagen auf Flugsand. Wiener Illustrierte Garten-Zeitung 21(1): 4–13.
- Sajó K (1897a) Insektenreisen. Illustrierte Wochenschrift für Entomologie 2(15): 229–235, 2(16): 241–242, 2(17): 257–263.
- Sajó K (1897b) Egy eddig fel nem ismert spárgaellenség és a védekezés az összes spárgaellenség ellen. [A hitherto unknown pest of asparagus and protection against all asparagus pests.] Gyümölcskertész 7: 109–112. [in Hungarian]
- Sajó K (1897c) Weitere Mitteilungen über den Weinstock-Fallkäfer. Illustrierte Wochenschrift für Entomologie 2(9): 129–134.
- Sajó K (1898a) Az afrikai czecze-légy és a nagana-betegség. [The African tsetse fly and the nagana illnes.] Természettudományi Közlöny 30(347): 375–379. [in Hungarian]
- Sajó K (1898b) *Epilobium angustifolium* und *Eumolpus vitis*. Illustrierte Wochenschrift für Entomologie 3(20): 314.
- Sajó K (1899) Das Wandern der Insekten. Prometheus, 10(515): 737–741, 10(516): 758–761, 10(517): 770–772, 10(518): 785–789, 10(519): 802–806, 10(520): 817–821.
- Sajó K (1900a) A rovarok alvása és ébredése. [Sleep and awakening in insects.] A Természet 3(12): 4–5. [in Hungarian]
- Sajó K (1900b) Sommerschlaf im Kreise der Blattkäfer. Prometheus 11(566): 723–724.
- Sajó K (1900c) Wissenschaftliche Benennungen in der Naturgeschichte. Prometheus 11(547): 417–420, 11(548): 433–437.
- Sajó K (1900d) Német intézkedések az erdő természetes emlékkincsinek megvédésére. [German actions to protect the natural treasures of forest.] Erdészeti Lapok 39: 379–384. [in Hungarian]
- Sajó K (1901) Die Kirschfliege. Prometheus 12(614): 663-668.
- Sajó K (1902a) Die Kirschfliege, Spilographa cerasi. Pomologische Monatshefte 48: 155-157.
- Sajó K (1902b) Zur Bekämpfung der Kirschfliege. Wiener illustrierte Gartenzeitung 1902(3): 96–98.
- Sajó K (1902c) A cseresznyelégy. [The cherry fruit fly.] Gyümölcskertész 12: 33–34, 47–48. [in Hungarian]
- Sajó K (1902d) Die Spargelkäfer. Prometheus 13(635): 166-171.
- Sajó K (1902e) Die Spargelfliegen und der Spargelrost. Prometheus 13(650): 403-404.
- Sajó K (1902f) Die Bekämpfung der Spargelfeinde und einige Schlussbetrachtungen. Prometheus 13(656): 497–498, 13(657): 521–524.
- Sajó K (1902g) Die Bekämpfung der landwirtschaftlich schädlichen Insecten mittels ihrer natürlichen Feinde. Prometheus 13(667): 673–676, 13(668): 689–692.
- Sajó K (1902h) Bäume und Gesträuche welche für den dürrsten Flugsand geeignet sind. Prometheus 13(673): 769–773.
- Sajó K (1903) Zur Entwicklung der Kirschfliege. Prometheus 14(679): 33-34.
- Sajó K (1904) Nachträge zur Lebensweise der Kirschfliege. Prometheus 15: 119–120.
- Sajó K (1905a) Krieg und Frieden im Ameisenstaat. Kosmos, Gesellschaft der Naturfreunde, Stuttgart, 107 pp.
- Sajó K (1905b) Az őstermészet kincseinek megmentése. [Saving nature's treasures.] Természettudományi Közlöny 37(436): 705–739. [in Hungarian]
- Sajó K (1905c) Néhány szó az őserdőkről. [A few words about primary forests.] A Természet 8(13): 145–150. [in Hungarian]
- Sajó K (1908) Krieg und Frieden im Ameisenstaat. (16. Auflage) Franckh'sche Verlagshandlung, Stuttgart, 106 pp.
- Sajó K (1909) Unsere Honigbiene. Kosmos, Gesellschaft der Naturfreunde, Stuttgart, 108 pp.

- Sajó K (1910a) Aus dem Leben der Käfer: mit Rücksicht auf die Beziehungen der Kerfe zur menschlichen Kulturgeschichte. Verlag von Theodor Thomas, Leipzig, 89 pp.
- Sajó K (1910b) Betegségeket terjesztő rovarok irtása. II. A szúnyogok. [Control of disease vector insects II. Midges.] Természettudományi Közlöny 42(511): 593–619. [in Hungarian]
- Sajó K (1911a) Blätter aus der Lebensgeschichte der Naturwesen. Erster Band. Druck der Patria, privately published, Budapest, 256 pp.
- Sajó K (1911b) Blätter aus der Lebensgeschichte der Naturwesen. Friedländer R. & Sohn., Berlin, 256 pp.
- Sajó K (1911c) Sommerschlaf der Insekten. In Sajó K (Ed) Blätter aus der Lebensgeschichte der Naturwesen, 97–102.
- Sajó K (1914) Unsere Honigbiene. (8. Auflage) Franckh'sche Verlagshandlung, Stuttgart, 108 pp.
- Sajó K (1919) Včela medonosná a její chov, dle spisu Dra. Zemedělské knihkupectví A. Neubert, Praze, 61 pp. (in series: Rolníkova knihovna 9.)
- Sajó K (1922) Blätter aus der Lebensgeschichte der Naturwesen. C. Reissner, Dresden, 256 pp.
- Sajó K (1923a) Unsere Honigbiene. (27 Auflage) Franckh'sche Verlagshandlung, Stuttgart, 93 pp.
- Sajó K (1923b) Krieg und Frieden im Ameisenstaat. (24 Auflage) Franckh–Kosmos, Stuttgart, 91 pp.
- Sajó K (no date) Háború és béke a hangyaállamban. [War and peace in the ant colony.] Pallas Irodalmi és Nyomdai Rt., Budapest, 90 pp. [in Hungarian]
- Schimitschek E (1968) Insekten als Nahrung, in Brauchtum, Kult und Kultur. In: Helmcke JG, Starck D, Wermuth H (Eds) Kukenthal's Handbuch der Zoologie, 2. Ed, Walter de Gruyter & Co., Berlin, 4(2) [1/10]: 1–62.
- Scholtz G (2008) Scarab beetles at the interface of wheel invention in nature and culture? Contributions to Zoology 77(3): 139–148.
- Soós Á (1943) Új légycsalád a magyar faunában. [New Diptera-family in the Hungarian fauna.] Folia Entomologica Hungarica 8(1–4): 94–96.
- South R (1885) Insect migration. Entomologist's Monthly Magazine 21: 208–211.
- Szent-Iványi J (1941) Sajó Károly. [Károly Sajó.] Folia entomologica hungarica 6: 41–43.
- Szilády Z (1941) Sajó Károly emlékezete. [In memoriam Károly Sajó.] A Természet 37: 168– 170. [in Hungarian]
- Sziráki Gy (1985) Migráció és diszperzió mint az életmód része. [Migration and dispersion as parts of the manner of living.] Állattani Közlemények (1984) 71: 151–158. [in Hungarian]
- Uvarov BP (1931) Insects and Climate. Transactions of the Royal Entomological Society of London 79(1): 1–232. doi: 10.1111/j.1365-2311.1931.tb00696.x
- Vig K (2002) Beetle collection of the Savaria Museum, Szombathely I. The leaf beetle collection of Attila Podlussány. Praenorica Folia historico-naturalia 5: 1–171.
- Warchałowski A (2003) Chrysomelidae. The Leaf-beetles of Europe and the Mediterranean Area. Natura optima dux Foundation, Warszava, 600 pp. + LVI Tables
- Webster FM (1902) Winds and storms as agents in the diffusion of insects. The American Naturalist 36(430): 795–801. doi: 10.1086/278217

- Weise J (1882) Welche Coccinelliden-Varietäten sind zu benennen? Wiener Entomologische Zeitung 1(5): 115–117.
- Wellington WG (1946) The effects of variations in atmospheric pressure upon insects. Canadian Journal of Research 24d(2): 51–70. doi: 10.1139/cjr46d-006

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