

Research on Chrysomelidae 5

Edited by

Pierre Jolivet, Jorge Santiago-Blay & Michael Schmitt



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Cover photo: A male *Timarcha tenebricosa* (Fabricius, 1775), photo taken in Southern France, Département Aude, Domaine de Perry, 13.08.2015, by Michael Schmitt, identified by Pierre Jolivet.

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Michael Schmitt, Gabriele Uhl

Pierre H.A. Jolivet, the *spiritus rector* of leaf beetle research, with a list of his publications

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Since more than half a century, Pierre Hippolyte Auguste Jolivet has been the inspiring head of the community of leaf beetle researchers (Fig. 1). He promoted research on Chrysomelidae not only by his nearly 500 publications (see list below), but even more so by his personal input to the international and European symposia on leaf beetles, and especially by the six volumes he co-edited (nos. 274, 316, 338, 339, 340, 445 of the list below) and the three he (co-)authored (nos. 329, 347, 389).

Besides his numerous papers and books on leaf beetles, he has also published on ants, especially ant-plant interactions, on parasites of insects, and on broader topics, such as evolution. In 2005, Pierre initiated the project of a series of volumes, edited by him and the two of us, for which we agreed on the title *Research on Chrysomelidae* (RoC). The first two volumes appeared with Brill Academic Publishers, the following volumes as special issues of *ZooKeys* with Pensoft. Now, Pierre has decided to resign from his post as senior editor, and the two of us decided to dedicate the present volume 5 of RoC to honour him.

Pierre Jolivet was born on October 12, 1922, two o'clock in the morning, as he reports in his autobiography (Jolivet 2006, no. 421), in Avranches (Manche department, Lower Normandy). He entered the University of Rennes in 1941, where he studied zoology and botany. He received his bachelor in 1943 with a thesis (Diplôme d'Etudes

Supérieures) on the biology of the species of *Timarcha*. These beetles fascinated him through the whole of his scientific life, from his student times through his excursions to Brno (Czech Republic) in the 1950s until one of his most recent papers (no. 485). Finally, his autobiography (no. 421) has the title “Mémoires Entomologiques – Paramémoires d’un timarchophile”.

He received the degree of a “Docteur ès Sciences Naturelles” on April 04, 1954 from the Sorbonne, at that time the only university in Paris. There, he produced a thesis in two volumes (nos. 153, 158) on the hind wing morphology, especially venation of Chrysomelidae. In addition, he has studied and depicted the male copulatory organs of representatives of all subfamilies (except Bruchinae). This publication provides an invaluable treasure of basic morphological knowledge, the more because Pierre Jolivet dissected not only specimens of very common species but also of taxa difficult to obtain for students in Europe, e.g. Australian Sagrinae or American Aulacoscelidinae. He had completed the empirical work at the Musée Royal des Sciences Naturelles of Brussels (Belgium), but was supervised by Pierre Grassé at the Sorbonne. In those days in France, one had to produce two theses to obtain the doctoral degree. Pierre Jolivet handed in his second thesis on the leaf beetles of the Balearic Islands (no. 119), also a fundamental contribution to science, in this case to faunistics. No surprise, a considerable section of this second thesis treats extensively the endemic *Timarcha* species, *T. balearica*.

In 1954, Pierre Jolivet undertook the first of his numerous journeys to tropical and exotic areas outside Europe. He travelled through the then Belgian Congo with some detours to Kenya and Uganda, where he studied and collected, of course, leaf beetles. Back in Brussels, he began a series of joint projects with Jean Théodoridès – with whom he had collaborated on leaf beetles before – on gregarines, documented in 15 original papers. These parasites had been recognised as a separate taxon by Pierre Grassé in 1953 in his famous *Traité de Zoologie*.

With a four months expedition to Iran on behalf of the World Health Organisation began Pierre Jolivet’s “United Nations epoch”. His main duty was the scientific supervision of malaria control activities. He worked as a member of several Malaria Advisor Teams for the UN in many countries, e.g. Taiwan, The Philippines, Ethiopia, Sudan, Algeria, Vietnam, and the Cap Verdes, with teaching activities at universities in New Guinea and in Morocco, until his retirement in 1985. In between, he found his wife Madeleine (Mayon), and they married on March 24, 1962. They have two daughters and one son. She accompanied him on many of his trips, and since 1984 it was a familiar sight to see the couple on the occasion of our regular symposia on Chrysomelidae: 1984 in Hamburg (Germany), 1988 in Vancouver (Canada), 1992 in Beijing (China), 1996 in Florence (Italy), 2000 in Iguassu (Brazil), 2004 in Bonn (Germany), 2008 in Durban (South Africa), and 2010 in Budapest (Hungary). From time to time, the two of them also joined the meetings of the German coleopterists at Beutelsbach (near Stuttgart, Germany). Only the last two of our regular symposia had to take place without Pierre and Madeleine Jolivet – the 8th International Symposium on Chrysomelidae in Daegu (South Korea) in 2012, and the 2nd European Symposium on the Chrysomelidae in York (UK).

Out of Pierre's countless contributions to the understanding of life and evolution of leaf beetles, there is one to be emphasised especially. Together with Joao Vasconcellos-Neto he discovered, described, and named in 1988 a ring defence behaviour of larvae, which they called "cycloalexy" (nos. 276, 319, 477). This newly coined term has made its way into dictionaries of entomology and will always be connected with the name of its discoverers.

Pierre suffered increasingly from health problems in his legs and, since about 2012, did not dare to travel abroad any longer. This year, he decided to step down from the Board of Editors of *Research on Chrysomelidae*. He had initiated this series in 2007, after the three of us had successfully co-operated as editors of the 800 pages volume *New Developments in the Biology of Chrysomelidae*. We shall do our best to make Pierre's project live on.

We, editors, many authors, and publishers of *Research on Chrysomelidae* are grateful for Pierre's permanent intellectual stimulation, his helpful input, and his friendship. We wish Pierre and Madeleine all the best, especially a healthy body and mind, and hope that the present issue of *Research on Chrysomelidae* as well as the ones to follow will help to keep up the bond between us, the community of leaf beetle enthusiasts, and Pierre Jolivet, our *spiritus rector*.

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Figure 1. Pierre Jolivet, attending the 50th coleopterists' meeting in Beutelsbach (near Stuttgart, Germany) on October 27, 2007.

Publications by Pierre Jolivet

1942

1. Hybridation probable de deux Chrysomèles: *C. polita* X *C. menthastri*. Bulletin de la Société Entomologique de France 47(9): 141.

1943

2. Note sur deux Orthoptères rares pour le département de la Manche. Bulletin de la Société linnéenne de Normandie 9(3): 34–35.
3. Sur un coléoptère nouveau pour le département de la Manche: *Chrysomela hyperici* Forst. Bulletin de la Société linnéenne de Normandie 9(3): 60–62.
4. Sur un curieux tropisme de *Steropus madidus* Fabricius. Bulletin de la Société linnéenne de Normandie 9(3): 83–87.

5. *Chrysomela menthastri* et ses variations dans le département de la Manche. Notices, mémoires et documents / Société d'Agriculture, d'Archéologie et d'Histoire Naturelle du Département de la Manche 44: 69–77.
6. Capture de *Stenelmis canaliculatus* et *Anthaxia manca*. Bulletin de la Société Entomologique de France 45(7): 99.
7. Sur un cas de «phorésie» observé chez deux espèces du genre *Timarcha*. Bulletin de la Société linnéenne de Normandie 9 (3): 107–108.
8. *Platyarthrus hoffmanseggii* Br., isopode myrmécophile dans le département de la Manche. Bulletin de la Société linnéenne de Normandie 9(3): 136–137.
9. Capture d'un Triton rare pour la faune normande: *Triton (Molge) marmorata* Latr. Bulletin de la Société linnéenne de Normandie 9(3): 138–140.
10. Tableau dichotomique pour la détermination des espèces et variétés françaises du genre *Timarcha* Latreille. Miscellanea Entomologica 41(7): 67–72.
11. Jolivet P, Charles Roux: Sur la présence en Bretagne de *Microcystis (Clathrocystis) aeruginosa* Kutz. Bulletin de la Société Scientifique de la Bretagne 47(3–4): 166–168.
12. Frémy P, Jolivet P: Capture en très grande abondance près de Saint-Lô de *Scapholeberis mucronata*. (O.F. Müller) (Cladocères Daphniides). Bulletin de la Société linnéenne de Normandie 9(3): 47.

1944

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14. De l'hydrotropisme positif de *Steropus madidus*. Miscellanea Entomologica 41(7):102–106.

1945

15. Notice biographique sur l'abbé Frémy (1880–1944). Bulletin de la Société Botanique de France 92(4–6): 72–73.
16. Esquisses biogéographiques sur le genre *Timarcha* Latr. Bulletin de la Société linnéenne de Normandie 9 (4): 32–41.
17. Sur la présence d'*Araschnia levana* (Lep. *Nymphalidae*) dans l'ouest de la France. Bulletin de la Société linnéenne de Normandie 9(4):45–46.
18. Contribution à l'étude des parasites du genre *Timarcha* Latr. Miscellanea Entomologica 42(1): 1–4.
19. A propos du DDT. Miscellanea Entomologica 42(1):13–14.
20. Deux cas de phorésie chez les *Timarcha* (Col. Chrys.). L'Entomologiste 1(8–9): 141.

1946

21. Nouveaux cas de phorésie chez les Chrysomélides. L'Entomologiste 2(1): 35.
22. Captures de Puces et de Diptères. L'Entomologiste 2(4):160.

23. La Vie et l'Oeuvre de l'Abbé Frémy (1880–1944). Notices, mémoires et documents / Société d'Agriculture, d'Archéologie et d'Histoire Naturelle du Département de la Manche 55: 1–18.
24. Nouvelle station française et nouvel hôte du Ver *Gordius aquaticus*. *Miscellanea Entomologica* 42(2): 139–140.
25. Quelques remarques sur l'autohémorrhée chez les *Timarcha* (Col. Chrys.). *Miscellanea Entomologica* 43(4):29–30.
26. A propos des variations du Doryphore (*Leptinotarsa decemlineata* Say). *Miscellanea Entomologica* 43(4): 31–33.
27. Sur une larve inédite vivant en parasite dans le sang de *Timarcha tenebricosa* F. *Miscellanea Entomologica* 43(4): 33–35.
28. Une méthode simple et pratique pour préparer les Grégaires et autres parasites des Insectes. *Miscellanea Entomologica* 43 (4): 35–36.
29. Sur plusieurs cas de brachélytrie dysplasique dans une population de *Melasoma tremulae* F. *Miscellanea Entomologica* 43(4): 36–38.
30. Le réflexe d'enfouissement chez *Leptinotarsa* and *Timarcha* (Col. Chrys.). *Miscellanea Entomologica* 43(4): 38–39.
31. Les parasites des Chrysomélides français (1^o liste). *Miscellanea Entomologica* 43(7):87–92.
32. A propos d'une curieuse anomalie élytrale chez une femelle de *Timarcha tenebricosa* F. *Miscellanea Entomologica* 43(10): 133–134.

1947

33. Notes additives et correctives sur la répartition géographique du genre *Timarcha* Latr. *Bulletin de la Société linnéenne de Normandie* 9(5):33–34.
34. Le criquet migrateur en Normandie. *Bulletin de la Société linnéenne de Normandie* 9(5): 134.
35. Une méthode pratique pour la conservation des chenilles: le montage à la gélatine. *Revue Française de Lépidoptérologie* 11(4): 91–94.
36. Les parasites des Chrysomélides français (2^{me} liste). *Miscellanea Entomologica* 44(8):108–109.
37. Capture de *Locusta migratoria*, phase grégaire, dans la Manche. *L'Entomologiste* 3(3): 144.

1948

38. Introduction à la Biologie des *Timarcha*. *Miscellanea Entomologica* 45(1): 1–32.
39. Les Orsodacnidae de la faune française. *Miscellanea Entomologica* 45(3–4): 33–46.
40. Les parasites des Chrysomélides français. (3^{me} liste). *Miscellanea Entomologica* 45(5): 52–54.
41. Introduction à l'étude des Gordiacés, Vers parasites d'Insectes. *Miscellanea Entomologica* 45(9): 83–90.

42. Le rôle des Chrysomélides en pathologie végétale. *Miscellanea Entomologica* 45(10): 97–99.
43. La conservation de la couleur chez les Cassididae (Col. Chrys.). *L'Entomologiste* 4(3–4): 140–143.
44. Addenda à la liste des travaux de l'Abbé P. Frémy. Notices, mémoires et documents / Société d'Agriculture, d'Archéologie et d'Histoire Naturelle du Département de la Manche 57: 18.
45. Une «fleur d'eau» à Beuvrigny. Notices, mémoires et documents / Société d'Agriculture, d'Archéologie et d'Histoire Naturelle du Département de la Manche 57: 17.
46. Quelques données récentes sur la biologie des *Timarcha* Latr. (Col. Chrys.). *Miscellanea Entomologica* 45(10): 100–102.
47. Contribution à l'étude des *Americanotimarcha* n. subg. (Col. Chrys.). *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 24(43): 1–2.
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49. Les parasites des Chrysomélides français (4me liste). *Miscellanea Entomologica* 45(10): 109–111.
50. Victor Laboissière (1875–1942). *Miscellanea Entomologica* 45(11): 103–108.
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1949

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53. Les hybrides d'espèces chez les *Chrysolina* Motsch. *L'Entomologiste* 5(3–4): 77–80.
54. Les Chrysomélides qui changent de couleur. *L'Entomologiste* 5(5–6): 190–191.
55. Contribution à l'étude des *Iscadida* Chevrolat (Col. Chrys.). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique* 25(40): 1–19.

1950

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57. *Bechynieia spinosa*, nov. gen., nov. sp. (Col. Chrys.). *Bulletin et Annales de la Société Royale Entomologique de Belgique* 86(1–2): 36–39.
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59. Un Braconide nouveau pour la faune belge. *Bulletin et Annales de la Société Royale Entomologique de Belgique* 86(9–10): 203–204.
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61. Fluctuations dans une population de Blattes et de Gryllons. *L'Entomologiste* 6(4–5): 139.

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63. *Elytrophæra melas* n. sp. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 26(43): 1–4.
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66. Jolivet P, Théodoridès, J. Découverte d'une espèce nouvelle de *Timarcha* (Col. Chrys.) sur la plage de Banyuls-sur-Mer (Pyrénées Orientales). Bulletin de la Société Entomologique de France 55(8): 119–120.
67. Contribution à l'étude des *Microtheca* Stal (Col. Chrys.) (1re note). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 26(48): 1–27.
68. Rectifications de nomenclature chez les Chrysomelidae (1re note). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 26(56): 1–4.

1951

69. Contribution à l'étude du genre *Gastrophysa* Chevrolat (Col. Chrys.) (1re note). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 27(9): 1–11.
70. Quelques points de nomenclature restés longtemps litigieux chez les Chrysomélides. L'Entomologiste 7(1): 36–37.
71. Contribution à l'étude du genre *Gastrophysa* Chevrolat (Col. Chrys.) (2me note). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 27(13): 1–12.
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74. Contribution à l'étude du genre *Gastrophysa* Chevrolat (Col. Chrys.). (3me note). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 27(21): 1–47.
75. Les parasites des Coléoptères français (5me liste). Miscellanea Entomologica 46(1): 3–5.
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77. Pariades anormales chez les Chrysomélides (Col.). Miscellanea Entomologica 46(1): 7.
78. Contribution à l'étude des *Microtheca* Stal (Col. Chrys.). (2me note). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 27(38): 1–7.
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81. Variations géographiques chez deux espèces du genre *Chrysolina* Motschulsky Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 27(51): 1–7.
82. Contribution à l'étude des Coléoptères Chrysomeloidea de la région Indo-Australienne (1^o note). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 27(52): 1–7.
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85. Rectifications de nomenclature. Bulletin et Annales de la Société Royale Entomologique de Belgique 87(9–10): 194.
86. Un nouveau *Stenoplatys* Baly du Congo belge (Col. Galerucidae). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 27(58): 1–4.
87. Jolivet P, Théodoridès, J.: Capture accidentelle d'une Casside exotique à Banyuls. Vie et Milieu 2(2): 200.
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89. Megalopodidae (Col. Chrys.). Exploration du Parc National de l'Upemba, Mission G.F. De Witte 4(2): 13–14.
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1952

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101. Les Chrysomèles rares de la Belgique III. Les Haemonia. Naturalistes Belges 33(5–6): 92–97.
102. Contribution à l'étude des Coléoptères Chrysoméloidea de la région Indo-Australienne. 3me note). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique 28(28): 1–4.
103. A propos d'un endophyte de *Chrysocarabus auronitens* F. Bulletin et Annales de la Société Royale Entomologique de Belgique 88(3–4): 67–68.
104. A propos de l'écologie de *Chrysolina menthastri* Suffr. (Col. Chrys.). Vie et Milieu 2(4): 470–472.
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107. Un *Hydrothassa* nouveau pour la faune française. Vie et Milieu 2(4): 532.
108. Jolivet P, Théodoridès, J.: Capture de *Chrysolina* (Col. Chrys.) du Midi de la France. Vie et Milieu 2(4): 533.
109. Captures de Myrmécophiles. Bulletin et Annales de la Société Royale Entomologique de Belgique 88(5–6): 117.
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Together with 30 years of Symposia on Chrysomelidae! Memories and personal reflections on what we know more about leaf beetles

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Introduction

Certainly, Carabidae, Curculionidae and Chrysomelidae are the beetle families that are most studied and the most inspiring for scientific papers. Those three families are also among the most numerous and present the most colorful beetles. Publications go from simple articles in the past to sophisticated papers using cladistics, molecular biology and statistics, in pure research or, for leaf-beetles or weevils, in agriculture. Thousands of papers are published each year on Chrysomelidae. Probably the actual described number of Chrysomelidae, estimated last century as 35.000 species, reaches 45.000 and there probably exist 55.000 to 60.000 species around the world. Canopy species are among the least known, true also for minute species living in litter or mosses

Coleoptera can easily exceed 1 to 2 million species and, in the past (in the Mesozoic, but mostly in Cenozoic), they must have been much more numerous. Only Curculionidae and perhaps Staphylinidae can surpass the number of Leaf-Beetles. Curculionidae are present everywhere, even in the sub-Antarctic islands and in Greenland, where Chrysomelidae are missing, even if present there during the Pliocene. Still many

species of weevils remain to be described, among the endogenous, myrmecophilous, floricolous species. Symposia on Leaf Beetles, originally organized every four years, now perhaps every two years, together with International and European Congresses of Entomology, or independently, generally are published later in books, which tend actually and only very recently to be published electronically. Many international publishers were responsible for those books and we are indebted to many specialists and co-editors. There were also regular annual meetings of chrysomelid specialists in the United States, correlated with the Entomological Society of America meetings, grouping often part of the specialists from the previous symposia, the next one probably coinciding with the International Congress of Entomology in 2016. Annual meetings of chrysomelid workers were also held in Japan each year. One chrysomelid symposium was organized in Patiala, India, with 29 papers in March, 1989. Sporadic chrysomelid symposia are also held with French and Belgian workers in Paris or elsewhere, in Costa Rica, with Wills Flowers, as in 1995, etc. Regular meetings take place each year in Germany together with the meetings (58 actually) of German-speaking coleopterists. Many European chrysomelidologists attend it also. Those German meetings actually are held in Beutelsbach (Fig. 1), on a hill, in a charming country inn, with a big meeting room and all video facilities. There were also meetings on Chrysomelidae in Pretoria, Republic of South Africa, connected with the local Entomological Society, in Milano, Italy, in Uberlandia, in Brazil, in 2005, etc. The Academia Sinica in China has been and is an active centre of leaf beetle research under Shi-xiang Chen (Fig. 2) and



Figure 1. View of the venue of the meetings of the German-speaking coleopterists, Landgut Burg vicinity of Beutelsbach, 24.10.2009, southwest Germany (near Stuttgart, photo: M. Schmitt).



Figure 2. Prof. Shi-xiang Chen (5.11.1905 – 25.1.1988), from a booklet of the Chinese Academy of Sciences 1992.

his successors. The death of Chen in 1988 was a big loss for the chrysomelidologists, but new generations have taken up the torch.

So, progress of our knowledge on the Chrysomelidae, on taxonomy, distribution, physiology, biology has been relatively fast the last 30 years. A Newsletter, devoted to leaf beetles, *Chrysomela*, was founded in 1979 by Terry Seeno and Eric Smith. It is still alive, now entirely in colour, with a new editor, Caroline Chaboo, and that has been also a stimulant for all chrysomelid lovers.

The enormous Georg Frey Collection of beetles (originally housed on the Frey estate in Tutzing) is now in Basle Museum, Switzerland. The Frey Chrysomelidae were initiated in Munich by Jan Bechyné, and most of those beetles are authoritatively identified, but unfortunately a general collection, a former UN dream, has never been made assembling all world insect types. Those types are mainly in the primary museums in London, Paris, Berlin, Munich, Moscow, Basle, Washington, Honolulu, Canberra, Beijing, Brussels, Tervueren, Tokyo, Pretoria, Maracay, Sao Paulo, Rio de Janeiro, and several other big or smaller collections. Due to possible damage in the mail, saving collections staff time and to hastened receipt, museums now try to send excellent digital photographs instead of the specimens themselves. On the spot, examination, remains always possible. Jesús Gómez-Zurita for instance visited the National Museum of Prague (with Achard collections) to see the Bechyné *Timarcha* types in 1997. Which resulted many excellent papers on the genus, its classification, and many molecular biology studies.

Symposia history

The first symposium on Chrysomelidae Alticinae (Scherer 1982), was held in Munich (Fig. 3), mid- August 1980. It brought together 12 specialists, and curiously this sym-



Figure 3. "The First Chrysomela Photo", showing the participants of the "First International Alticinae Workers' Symposium", Munich, August 1980: Walter Steinhausen, Manfred Doeberl, Bohumila Bechyné, Gerhard Scherer, Carmen Segarra, David Furth, Carlo Leonardi, Terry Seeno, Mauro Daccordi, Serge Doguet, Carmelèn Petitpierre, Eduard Petitpierre. From *Chrysomela* Newsletter 38/39 (2000, photo probably by Eric Smith).

posium has not been counted as Symposium on Chrysomelidae no. 1. That could be, if I can say so, Symposium no. 0. It brought together some of our leaders as Bohumila Bechyné, representing her husband Jan, who had died on 9th of March, 1973. Jan was a big describer of leaf beetles, a *Timarcha* lover, and, in some way, a pioneer in recent chrysomelid taxonomy. Most of those participants are still active actually. Some, as Gerhard Scherer and the Bechynés, have passed away. Good old times when in 1980 started *Chrysomela* story, with a general review of the taxonomy of the alticinae. *Chrysomela* newsletter (actually # 54) started with 74 entomologists, and, despite more than twenty deaths (Enrique Balcells, Michio Chûjô, the Bechynés, Roy A. Crowson, J. Gordon Edwards, Dieter Erber, Nicole Berti, Michel Bergeal, Serge Iablokoff-Khnzorian, Shinzaku Kimoto, René Paulian, Sandro Ruffo, Igor Lopatin, Gerhard Scherer, Ray Smith, Niilo Virkki, John Wilcox, Krishna Kumar Verma, Yu Peiyu, Laurent LeSage and perhaps few others) the subscriptions actually reach 276!

The so-called First International Symposium on the Chrysomelidae (Fig. 4) was organized, in August 20–25, 1984, by David Furth, in Hamburg, Germany, together with the 17th International Congress of Entomology. A paper on the phylogeny of Chrysomelidae by Sicien H. Chen was presented. It's really funny how the classification of the subfamilies evolved since Jacoby established in his time the first solid and long-time valid classification after Chapuis. Interesting papers on classification of Donaciinae by Ingolf Askevold, of Alticinae by David Furth, of Criocerinae by Michael Schmitt, of all the subfamilies by Kunio Suzuki, as well as on change of colour after death among Paropsini by Brian Selman were presented together with 22 other



Figure 4. Group photo of the First International Symposium on the Chrysomelidae, Hamburg 1984 (from left): Arthur J. Gilbert, Ingolf Askevold, David Furth, Eric Smith, Pierre Jolivet, Niilo Virkki, Michael Schmitt, Hans Kroker (hidden), Carmen Segarra, Klaus Hemmann, Krishna K. Verma, Eduard Petitpierre, Hans Silfverberg, Walter Steinhausen, J. Watt, Horst Kippenberg, Felix Breden, Gustav Adolf Lohse, Brian Selman, Dieter Erber. From *Chrysomela Newsletter* 12 (1984).

interesting papers. The symposium was published (Furth and Seeno, editors) in 1985. As part of most of these Congress Symposia, there were organized field excursions, with the authorization to collect some local insects. In 1988, the first volume on the Biology of the Chrysomelidae was published (JPH 1988).

It is with the Second International Symposium on the Chrysomelidae (8–9 July 1988, Furth and Seeno 1988), in Vancouver, Canada, that cycloalexy was borne. That was a joint idea of Joao Vasconcellos-Neto and myself, and *Coelomera*, *Chelymorphe* and *Platyphora* behaviour in Brazil gave us the idea. This symposium with 23 partici-



Figures 5, 6. **5** (left) Al Samuelson, Vancouver 10.07.1988 (photo: M. Schmitt) **6** (right). G. Kuschel, Vancouver 9.07.1988 (photo: M. Schmitt).

pants was held during two days, and Brian Farrell talked about leaf beetle community structure in Amazonian forest and Al Samuelson (Fig. 5) about pollen feeding in Alticinae. Some common interactions were done with the curculionidologists, namely with Willy Kuschel (Fig. 6) about soft wing structure. Dan Janzen made a brief appearance between two planes. He gave a bright talk on biodiversity, on his reforestation project in Costa Rica, asked for money and complained about the cost of our Conference: 6 million dollars. He was wearing leather boots, a hat on his head and was dressed as a true “Indiana Jones”. According to Ross Arnett, this was typical attire. I stopped him on his way to the airport, and the answer to my question: what about myrmecophytes? was “I will not do anything on ants before the coming 25 years!”

The Third International Symposium on the Chrysomelidae (Furth 1994) was held in Beijing (Fig. 7), in July 1992, organized by David Furth and Yu Peiyu, in a big convention centre. It was very enjoyable with an all-day collecting excursion near the Great Wall, where we captured interesting Chrysomelinae, and a local Beijing field trip to Yuan Park where we collected beetles, and had a lot of scientific communications. At the end, Dr. Yu Peiyu organized an unforgettable classical roasted duck dinner. Petitpierre exposed his ideas on phylogenetic relationships among Chrysomelidae subfamilies. At that time, the Chrysomelidae remained all in the same family. No Megalopodidae, no Orsodacnidae, no Spilopyrinae, but still survived then the Megascelidinae.



Figure 7. Group photo of the Third International Symposium on the Chrysomelidae, Beijing, 4 July, 1992, in front of the Academia Sinica (from left): Shu-yong Wang, Peter Verdyck, Shizuo Fujiyama, Eduard Petitpierre, Hans Silfverberg, Lech Borowiec, David Furth, Pei-yu Yu, Kunio Suzuki, Ting Hsiao, Michael Schmitt, Pierre Jolivet, Jacques Pasteels, Al Samuelson (photo: M. Schmitt).

The Fourth International Symposium on the Chrysomelidae was held as part of the XX International Congress of Entomology (ICE) in Florence, Italy from 25-31 August 1996. The symposium was organized by David Furth and Maurizio Biondi, and many entomologists from the whole planet attended. That was still at the end of the 30 "glorious years", and people had more money and still high level of security. The symposium was published in Italy, in Torino, by M. Biondi, M. Daccordi and D. G. Furth (editors) in 1998. Many formal presentations were done on various topics. Michael Schmitt showed photos from the previous two symposia. The excursion was to the Apuanian Mountains (Fig. 8), to find a new *Timarcha* from Mauro Daccordi. Some participants were lost and part of us did not see the famous *Timarcha apuana*. Michael Cox was there with his wife. Timarchologists and amateurs were all in search of *Timarcha*. Only one was captured! I like Italian cuisine and I enjoyed every evening spaghetti meat sauce (pasta Bolognese). The lunch with sandwiches on the spot was, on the contrary, not very attractive.



Figure 8. Part of the excursion group, after the Fourth International Symposium on the Chrysomelidae, Florence (Italy), 1 September, 1996 (from left): Michael Schmitt, Mauro Daccordi, Ron Beenen, Kunio Suzuki, Alessandro Bramanti, Maurizio Biondi, Roberto Bramanti, Károly Vig, Jörg Perner (photo: M. Schmitt).

The Fifth International Symposium on Chrysomelidae from August 25-27, 2000, was held in Iguassu Falls, Brazil (Fig. 9), a beautiful spot which I had visited



Figure 9. Fifth International Symposium on the Chrysomelidae, the participants of the after-congress excursion, Iguassu (Brazil), photo from Jolivet (2006).

already twice before. The symposium was organized by David Furth and Joao Vasconcellos-Neto. Many interesting papers were presented. The field trip was done in the Cabeza de Cachorro reserve, in the state of Paraná. During the trip, news arrived that it was suddenly forbidden to collect insects. The Proceedings of this Symposium were edited by David Furth as a book with Pensoft *Special Topics in Leaf Beetle Biology*, printed in 2003.

The Sixth International Symposium on the Chrysomelidae (Fig. 10) was held at the Museum Alexander Koenig, Bonn, Germany on 7th of May, 2004, with 22 participants from 10 countries. The 2004 ICE in Brisbane would not accept a symposium on only the Chrysomelidae. This meeting replaced the failure of the Prague Conference. It was organized by Michael Schmitt and connected with the Symposium on Tropical Biology. We had a joint dinner (Fig. 11) at a brew-pub, and we saw Beethoven house, the next day. As usual, interesting talks were held in a room near the former parliament of Germany, close to a historical giraffe. On Saturday, 8th of May, an excursion was made near Koblenz for collecting, but in the rain. Proceedings of the Sixth International Symposium were published by Michael Schmitt as a special issue of *Bonner zoologische Beiträge* in 2006 (vol. 54/-4).

Some kind of Symposium (6a) or a virtual Symposium on Chrysomelidae, without any number, was held in Brisbane, Australia with the International Congress of Entomology on 16–21 August 2004 and attended by Chris Reid who wrote a review for *Chrysomela* (Reid 2004). John Lawrence was present and co-organizer. 26 papers on



Figure 10. Sixth International Symposium on the Chrysomelidae, Bonn (Germany), 7 May, 2004, group photo in the great hall of the Zoologisches Forschungsmuseum Alexander Koenig, Bonn (from): Eva Sprecher-Übersax, David Furth, Jaap Winkelman, Horst Kippenberg, Wolfgang Freund, Helmut Bolz, Jürgen Gross, Thomas Wagner, Susanne Düngelhoef, Lasse Hubweber, Maurizio Biondi, Michael Schmitt, Károly Vig, Jolanta Swietojanska, Lech Borowiec, Matthias Schöller, Mauro Daccordi, Elisabeth Geiser, Gudrun Fuss, Ron Beenen, Fredric Vencl, Pierre Jolivet (photo: M. Jolivet).



Figure 11. In the brew-pub, 7 May, 2004: Horst Kippenberg, Mauro Daccordi, Maurizio Biondi, Susanne Düngelhoef, Elisabeth Geiser (photo: M. Schmitt).

Chrysomelidae were presented. A formal dinner, rather expensive, though very spartan (in my table they brought food for 5 people when we were 6), closed the meetings. In 2004, Caroline Chaboo took over the newsletter *Chrysomela*, formerly edited and published by Terry Seeno.

The real Seventh International Symposium on the Chrysomelidae was held on July 9 in Durban, South Africa in connection with the 23rd International Congress of Entomology (July 6–12, 2008). We had a big hall of more than 2500 seats for 20 people. It was co-organized by Michael Schmitt and Beth Grobbelaar. We talked about many aspects of leaf beetle biology, and I spoke on New Caledonia where I had made 6 visits



Figure 12. During the 23rd International Congress of Entomology, Durban (South Africa), 9 July, 2008: David Furth, Pierre Jolivet, Madeleine (Mayon) Jolivet (photo: M. Schmitt).

for collecting Chrysomelidae (Fig. 12). Andrew Moldenke, the Clytrine specialist, was present, but did not talk about leaf beetles (Fig. 13).

It is the volume 2 of *Research on Chrysomelidae* (Brill publisher, 2009) which contains the proceedings of 7th International Symposium on Chrysomelidae.

At this period started the new series of books *Research on Chrysomelidae* co-edited by P. Jolivet, J. Santiago-Blay and M. Schmitt with Brill. Later on Pensoft took over, and actually four volumes have been printed, the present one is the fifth, a sixth is in preparation.



Figure 13. In the Great Hall of the Durban International Convention Centre, 9 July, 2008 (from left): Hugh D.C. Heron, Károly Vig, Michael Schmitt, Eric Smith, Eduard Petitpierre, Elizabeth Grobbelaar, Thomas Wagner, David Furth, Pierre Jolivet, Gaylord Desurmont, Gunter Maywald, Andrew Moldenke (photo: M. Schmitt).

One Symposium on Chrysomelidae, the First European (but perhaps the 7a), was held in Hungary (Fig. 14), on Buda side of Budapest and organized by Károly Vig and Michael Schmitt. A beautiful evening boat trip, with an excellent dinner and adapted music, along the blue Danube, closed the 9th European Congress (August 22 to 27, 2010). Here, Eduard Petitpierre talked about chromosomal evolution. Many very interesting papers were presented including one by the Japanese rising star Yoko Matsumura (Fig. 15).

Two Turkish colleagues (Ali Gök and Ismail Sen) were present, and at the European dinner, in an inn nearby, Mauro Daccordi and Carlo Leonardi appeared coming from nowhere (Fig. 16).

Caroline Chaboo with her family was there also. She gave a very interesting tortoise beetle talk. Michael Schmitt succeeded to have the virtual 7th symposium published through L. Penev in *Research on Chrysomelidae*, volume 3, by Pensoft, Sofia.

The official Eighth International Symposium on the Chrysomelidae was held in Daegu (Fig. 17), South Korea, on 23rd of August, 2012, in conjunction with the 24th International Congress of Entomology. That was the first Congress that I missed, and I hesitated very much, pain in my knees were responsible for my absence. I have worked in Korea during 3 years before and I knew the place, where I once collected beetles and



Figure 14. The First European Symposium on the Chrysomelidae, Budapest (Hungary), 23 August, 2010: Eduard Petitpierre, Carmelèn Petitpierre, Pierre Jolivet, Madeleine Jolivet (photo: M. Schmitt).



Figure 15. The First European Symposium on the Chrysomelidae, Budapest (Hungary), 23 August, 2010: Yoko Matsumura (photo: M. Schmitt).



Figure 16. Budapest (Hungary), 23 August, 2010, joint dinner (from left: Michael Schmitt, Gabor Pszodai, Eduard Petitpierre, Carmelèn Petitpierre, Caroline Chaboo's mother-in-law, Caroline Chaboo, her daughter Teresa and her husband Fernando, (Caroline's father-in-law), Carlo Leonardi, Pierre Jolivet, Madeleine Jolivet, Elisabeth Geiser (photo: M. Schmitt).



Figure 17. A Korean dinner, after the 8th International Symposium on the Chrysomelidae, Daegu (South Korea), 23 August, 2012 (from left): Si Qin Ge, Jun-zhi Cui, Nicole Kalberer-Simmen, Antje Burse, Michael Schmitt, Choru Shin, Haruki Suenaga, Mai Bing, Jong Eun Lee, David Furth (photo: M. Schmitt).

organized aerial sprays. We used at that time the US base as a hotel, but that was many years ago. The proceedings of this meeting were printed within volume 4 of Research on Chrysomelidae, within ZooKeys, Pensoft, a normally electronic publication but which can be printed into a book. This 8th Symposium was organized by Michael Schmitt and Jong Eun Lee. Many first class papers were presented including one with the Chinese rising star of Chrysomelidae Si Qin Ge. David Furth was there with the Mexican Alticinae, Donald Windsor, Michael Schmitt, and some others presented well documented papers on various topics. The text of all those communications was available free of charge, but printing of this virtual book remains quite expensive. A success, this symposium, which precedes two more in the future, one in York, UK, in August 2014, perhaps also virtual, with the 10th European Congress of Entomology, and the 25th International Congress of Entomology, in September 2016, in Orlando, Florida, coordinated with the Entomological Society of America and a few other groups.

The Chrysomelidae International Symposia were always held in connection with the International Congresses of Entomology every 4 years and in between with the European Congresses of Entomology, also every four years, with few exceptions. Generally, the organizer was David Furth with a local chrysomelidologist. Actually Michael Schmitt, for the last four Chrysomelidae Symposia, took over the organization of those meetings.

Progress in Chrysomelidology

Numerous were the discoveries made during those last 30 years. Let us quote some of them: metafemoral spring of flea beetles and jumping by David Furth (1988, Furth and Suzuki 1994, 1998), and Michael Schmitt (2004); meioformulae of Leaf Beetles by Petitpierre (1997, 1999, 2011), Virkki (1985, 1988, 1989) and others; larvae research, by Steinhausen (1985, 1994, 1995, 1996) and others; chemical defense by Jacques Pasteels (Pasteels and Hartmann 2004, Pasteels and Rowell-Rahier 1989, Pasteels et al. 1986, 1988, 1989, 1994, 1996, 2004); cycloalexy, by Vasconcellos-Neto and Jolivet (1989, 1994); fossils by Santiago-Blay (1994; Santiago-Blay and Craig 1999, Santiago-Blay et al. 1996, 2004), followed by many others; mimicry by Balsbaugh (1988, Balsbaugh and Fauske 1991) and many others; zoogeography by Verma (Verma and Jolivet 2004, 2006), Scherer (1988), Daccordi (1994, 1996, 2000, 2003a, b, c), and many more; egg bursters by Cox (1988, 1994); structure of ovaries and viviparity by Christian Bontems (1988, Bontemps and Lee 2008); Criocerinae biology, by Fredric Vencel (Vencel and Morton 1998, 1999, Vencel and Nishida 2008, Vencel et al. 2004), M. Schmitt (1988), Yoko Matsumura (Matsumura and Akimoto 2009, Matsumura and Suzuki 2008, Matsumura and Yoshizawa 2010, 2012, Matsumura et al. 2010, 2012); African fauna of Alticinae by Maurizio Biondi (1989, 1999, 2001a, b, Biondi and D'Alessandro 2008, 2010a, b, 2012); Australian fauna by Mauro Daccordi (2000, 2003a, b, c, Daccordi and DeLittle 2003), Chris Reid (1989, 1991a, b, 1992, 2003, 2006, Reid and Beatson 2010a, b); colour and changes of colour by Jean-Pol Vigneron (Vigneron et al. 2007); biology of Tortoise Beetles by Fredric Vencel (Vencel and Allen

2006, Vencl and Srygley 2013, Vencl et al. 2004, 2013), Caroline Chaboo (2001, 2002, 2004, 2007, Chaboo and Nguyen 2004, Chaboo et al. 2014), Don Windsor (1987, Windsor and Choe 1994, Windsor et al. 2013) etc.; Chinese and Far East fauna, by Shi-xiang Chen (1985, Chen and Zia 1984a, b, Chen et al. 1985), Shinsaku Kimoto (1984, 1988, 2005), Mohamed Mohamedsaid (1990, 1991, 1992, 1993a, b, 1994, 1995, 1999, 2004, 2009, Mohamedsaid and Constant 2007, Mohamedsaid and Takizawa 2008), Haruo Takizawa (2007); Taiwan and Japanese fauna by Shinsaku Kimoto, Haruo Takizawa (Kimoto and Takizawa 1997), Jong Eun Lee (1991, 1993, Cho and Lee 2005, Park et al. 2012), and others; biology and taxonomy of Aulacoscelidinae by Don Windsor (Windsor et al. 1999), Jorge Santiago-Blay (2004), and others and its behaviour on cycads (*Zamia*); biology of *Oreina* by Martine Rahier (Rowell-Rahier and Pasteels 1994), and so many other papers. Larvae of Aulacoscelidinae are known, but, as for the Orsodacninae, we still are not sure where the larvae develop and on which plant. Attraction by cycads does not seem to be only pharmacology. We do not know anything about the development of the larvae of Australian Sagrinae, some with free pupae, others with pupation inside the stem. Pupation inside the stem seems sometimes the rule for Spilopyrinae (in New Caledonia at least). DNA barcodes were used to recognize the host-plants eaten by leaf beetles (Australian Chrysomelinae) from their gut contents and showing their evolutionary implications for insect-host plants interactions (Jurado-Rivera et al. 2009).

Terry Seeno and John A. Wilcox contributed to the clarification of the classification in 1982, as well as later on Kunio Suzuki (1996). Since then many new species and genera were described, mostly among Eumolpinae, Chrysomelinae, Alticinae, Galerucinae, and others. Host-plants of the group tend to be known more and more, and practically it has been deciphered for most of the Holarctic. In the tropics, we have many references, but still a lot of observations are requested. Too many missing data remain in Brazil, Africa and Australia (as for Sagrinae). Also many species, chiefly among Eumolpinae, can be rather polyphagous, when Chrysomelinae are mostly stenophagous. There are even in the tropics extremely rare cases of carnivory among *Diabrotica* (Mafra-Neto and Jolivet 1994). Clytrinae, some Eumolpinae and Cryptocephalinae can be myrmecophilous in East Africa within *Acacia* domatia. It is a field, myrmecophily, where research should be deepened, mainly in the tropics. Surprises can be expected. We know very little about Neotropical Clytrinae biology. According to William Eberhard (1996), female Chrysomelidae probably show also a cryptic selection of the male.

In South Africa, several beetles copy superficially the *Timarcha*. Beth Grobbelaar is going to clarify all the *Iscadida* mysteries (egg laying, food-plants, distribution). A very peculiar biology for a false timarchoid adapted to dryness and to a Mediterranean-type climate. More should be discovered about the biology of the South African timarchoids.

Problems arise also on the holes on elytra of certain leaf beetles sometimes in connection with glands or sensitive detection cells.

Books on Chrysomelidae

Outside the publications of the International symposia on Leaf Beetles, books were regularly published on the topic in the Netherlands, France, Germany, Russia, Poland, USA, sometimes in correlation, sometimes independently of the symposia (Fig. 18).

There are also the "festschrift" books (e.g., Borowiec and Furth 2007, Konstantinov et al. 2005, Pakaluk and Slipinski 1995), the monographs, etc. There are two "sacred" species groups among the chrysomelids: *Leptinotarsa decemlineata*, the Colorado Potato Beetle, and *Timarcha* spp., the bloody nose beetles, on which there are hundreds of publications. I am not including here the books or booklets on the Colorado Potato Beetle, the worshippers being, in the past, separated during the Congresses from the "real" chrysomelidologists, as for Ferro and Voss booklet (1985). Bruchidologists have traditionally, sadly, met the same fate. In both cases, it is more agricultural entomology. *Diabrotica virgifera*, sadly famous in the US, has actually invaded Europe and becomes also the subject of many books and articles.

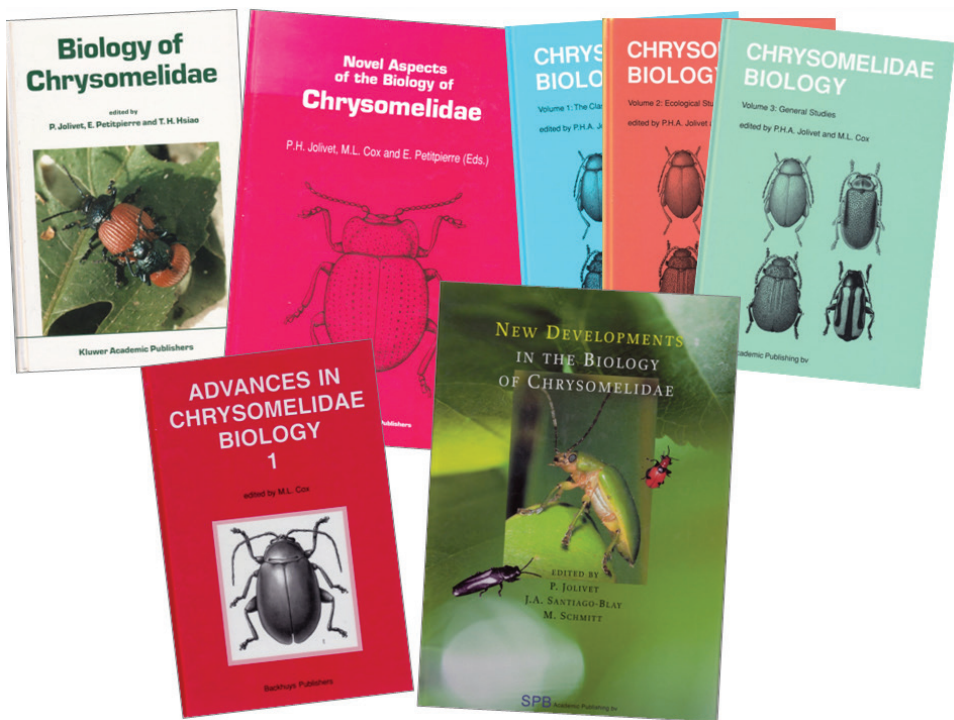


Figure 18. "The Books" on Chrysomelidae, except the proceedings volumes of the International Symposia: Jolivet P, Petitpierre E, Hsiao TH (Eds.) 1988, Jolivet PH, Cox ML, Petitpierre E (Eds.) 1994, Jolivet JHA, Cox ML (Eds.) 1996 (3 vols.), Cox ML (Ed) 1999, Jolivet P, Santiago-Blay JA, Schmitt M (Eds.) 2004.

Conclusions

Many discoveries were made the last 30 years in the field of Chrysomelidology. Since Chapuis, Jacoby and others in the past, and more recently since Chen (1964), there has been some evolution in the placement of subfamilies. The passing of Chen, Crowson, Bechyné, Chûjô, Balsbaugh, Edwards, Wilcox, Iablokoff, Lopatin, Ruffo, Kimoto, Kaszab, Erber, Monró, Scherer, Verma, Yu Peiyu, LeSage and so many others, were a great loss for chrysomelid taxonomy and biology. New stars appear, either in taxonomy or in biology, using new techniques. Some just pass as quick as a flash. Others remain faithful to the topic and the relief is ready. We owe to Roy Crowson many discoveries on the Chrysomelidae, including the perception of Spilopyrinae and of the peculiar *Eupales*, the study of Sagrinae, and the researches on some Galerucinae, and others INBio begun by Dan Janzen in La Selva, Costa Rica and STRI in Panama (Windsor, Flowers, Vencel, etc.) were also important centres of research on leaf beetles.

Some changes in taxonomy have also been proposed, based on simple morphology. Cladistics and molecular biology inspired some others (Hsiao, Farrell, Duckett, Gomez-Zurita, Reid and many others). On some big changes, I do not fully agree, mostly on the breaking of the family Chrysomelidae and the merging of Alticinae and Galerucinae, of Cassidinae and Hispinae. They are intermediary taxa. One subfamily has really merged with Eumolpinae: Megascelidinae (Jolivet 1957-1959) and one is probably correctly separated from Eumolpinae, the Spilopyrinae (Reid 2000). Those are, however, primitive Eumolpinae, but with different genitalia and behaviour. It was a feeling of Crowson and confirmed by Reid. Synetinae are an aberrant group, well characterized, and that makes for Chrysomelidae 19 subfamilies, at least for me. Recent new classifications separated Chrysomelidae and other supposedly closely related families(?) (Orsodacnidae and Megalopodidae). There are splitters for families as they exist also for species. Chrysomelidae are related also to Bruchidae, often now classified into Chrysomelidae, despite the opposition of some famous bruchidologists, as John Kingsolver (1995), Krishna K. Verma (Verma and Saxena 1996), etc. Here, splitters become mergers, but this is a personal decision, a free act. However, in agricultural journals, we find Bruchidae or Bruchinae according to the secret feelings of the authors of the papers and their convictions. *Rhaebus* and *Eubaptus* are transitional between bruchids and sagrines, as there exist also transitional genera between Cassidinae and Hispinae and between Alticinae and Galerucinae. Synetinae however seem to remain completely isolated.

I am very sorry if I forget some of our chrysomelidologist friends and their publications. This is not intentional. There were many in the past and a lot during those last 30 years, from many countries and continents. I am not sure to have them all in my list. Please forgive me, many being faunas and not in direct connection with the symposia. Sometimes those local faunas are in the language of the country.

It is certain that some areas need more investigation, as Madagascar for instance, and that there remain many biological problems to be solved or to be discovered. The fauna is near to be well investigated in Europe, in the US, in Japan, Australia and in

China. Still Indonesia, tropical America, India, Malaysia, Vietnam, tropical Africa, New Guinea can bring us some novelties, but deforestation reduces the number of species and genera, and many will disappear before being described. Few will persist as fossils in the tropics. Millions of Insects have existed in the past and will remain unknown forever.

Orsodacninae are distributed all along the Holarctic area and Aulacoscelidinae are restricted to the Neotropics. We do not know for sure where and on which plants the larvae develop. Archaic Australian Sagrinae are also practically unstudied regarding biology and development. They come to light, but are rarely discovered near a possible host plant. Eight symposia on Chrysomelidae have been held. Many new things have been found but some problems remain unsolved.

De Gruyter treatise of Zoology (Leschen and Beutel 2014) has put up to date the classification of the group. No doubt that our successors refine the system and perhaps will come back to a more reasonable grouping.

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Revision of the Afrotropical genus *Notomela* Jacoby, 1899 with description of *N. joliveti* sp. n. from Principe Island (Coleoptera, Chrysomelidae, Galerucinae, Alticini)

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Abstract

The Afrotropical flea beetle genus *Notomela* Jacoby, 1899 is reviewed. *Notomela joliveti* **sp.n.** from Principe Island is described. The following new synonymies are established: *N. cyanipennis* Jacoby, 1899 = *N. viridipennis* Bryant, 1941, **syn. n.** = *N. cyanipennis macrosoma* Bechyné, 1959, **syn. n.** In addition, the new combination is established: *Notomela fulvofasciata* Jacoby, 1903 is transferred to *Amphimela* [*A. fulvofasciata* (Jacoby, 1903), **comb. n.**]. Micrographs of male and female genitalia, scanning electron micrographs of some diagnostic morphological characters, a key to identification, and distributional data for all species of *Notomela*, are provided.

Keywords

Coleoptera, Chrysomelidae, Afrotropical region, *Notomela*, new species, new synonymy, new combination, taxonomy, faunistics

Introduction

Notomela Jacoby, 1899 is an endemic flea beetle genus occurring in Sub-Saharan Africa (Biondi and D'Alessandro 2012). Prior to this study, four species and one subspecies were attributed to it: *N. cyanipennis* Jacoby, 1899 and *N. fulvofasciata* Jacoby,

1903 from Western Africa; *N. fulvicollis* Bryant, 1931 from Kwazulu-Natal and *N. viridipennis* Bryant, 1941 from Uganda; *N. cyanipennis macrosoma* Bechyné, 1959, from Democratic Republic of Congo.

In this paper, a taxonomical review of the known species and the description of a new species, *Notomela jolivet* sp. n., from Principe Island are reported.

Materials and methods

Material examined consisted of dried pinned specimens preserved in the institutions listed below.

Specimens were examined, measured and dissected using WILD MZ12.5 and LEICA M205C binocular microscopes. Photomicrographs were taken using a Leica DFC500 camera and the Zerene Stacker version 1.04. Scanning electron micrographs were taken using a HITACHI TM-1000. Geographical coordinates of the localities are reported in degrees, minutes and, possibly, seconds (DMD-WGS84 format); coordinates and geographical information included in square brackets were added by the authors and follow those available at web sources. The terminology used follows: Döberl (1986), Furth and Suzuki (1994) and Suzuki (1988) for the spermatheca; Furth and Suzuki (1998) for the metafemoral spring.

Abbreviations. Morphology - LAED: length of median lobe of aedeagus; LAN: length of antennae; LB: total length of body; LE: length of elytra; LP: length of pronotum; LSPc: length of spermathecal capsule; WE: width of elytra; WP: width of pronotum.

Collections and depositories:

BAQ	Collection M. Biondi, Department of Health, Life and Environmental Sciences, University of L'Aquila, Italy;
BMNH	The Natural History Museum, London, United Kingdom;
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium;
MSNG	Museo Civico di Storia Naturale 'Giacomo Doria', Genova, Italy;
NHMB	Naturhistorisches Museum, Basel, Switzerland;
RMCA	Musée Royal de l'Afrique Centrale, Tervuren, Belgium.

Taxonomy

Notomela Jacoby, 1899: 357

Notomela Jacoby: Scherer (1961: 277); Biondi and D'Alessandro (2010: 411; 2012: 61)

Type species. *Notomela cyanipennis* Jacoby, 1899: 357, designation by monotypy (Type locality: "Cameroons").

Morphological remarks. Based on newly examined material, morphological characteristics of *Neodera* are revised and updated with respect to the original description (Jacoby 1899). Body (Figs 1–3) thickset, sub-cylindrical or elliptical, strongly convex. Head (Figs 4–5) with vertex and frons distinctly punctated; frontal tubercles sub-quadrate, clearly distant from each other; frontal carina not raised; genae short. Antennae moderately elongate, about as long as from 1/3 to half body length.

Pronotum (Figs 8, 10, 12) moderately transverse (WP/LP > 1.5 but ≤ 1.8), anteriorly slightly wider than posteriorly, without antebasal furrow; lateral margins bordered, with dentiform and curved anterior angles, not visible in dorsal view; posterior margin very finely bordered, slightly sinuous.

Elytral punctation (Figs 9, 11, 13) partially irregular, arranged in simple or double rows, with submarginal stria of distinctly and deeply impressed punctures laterally, delimiting wide and distinctly raised lateral band (Biondi and D'Alessandro 2012, p. 112, Fig. 220); interstriae flat and very finely punctulated. Hind femora moderately enlarged; hind tibiae dorsally channeled in distal half, with short apical spur; tarsal claws appendiculate.

Ventral surface sub-smooth, with sparsely and finely impressed punctation, denser on abdominal sternites; procoxal cavities posteriorly closed, with narrow intercoxal process; metasternum about as long as first abdominal sternite; elytral epipleura wide, weakly obliquely downward, laterally just visible, with very sparsely punctulated, almost smooth, surface.

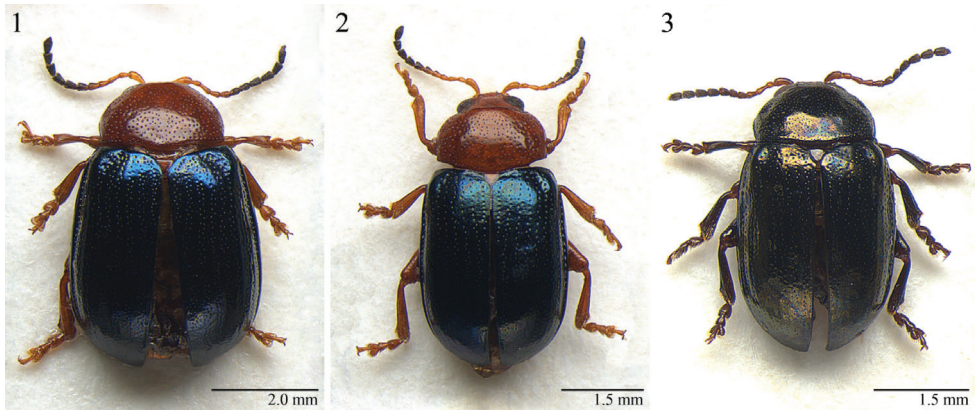
Metafemoral spring (Fig. 6) showing several similarities with the *Blepharida* morpho-group (Furth 1982) and characterized by: rather straight dorsal lobe with a distinct extended arm which projects far beyond apex of ventral lobe; ventral lobe with large, obtuse basal angle; dorsal edge of ventral lobe without any sclerotized recurve flange (Furth and Suzuki 1998). However it should be made quite clear that the irregular tissue attached to the dorsal margin of the ventral lobe is the “cuticular sheet”, an irregular sheet of connective tissue by which the primary tibial extensor muscle is inserted onto the dorsal edge of the ventral lobe (Furth 1982).

Spermatheca (Figs 7A, B) of form A (Furth and Suzuki 1998) with basal and distal parts very elongate, not separate from each other; ductus uncoiled but with 2 or 3 evident curves.

Vaginal palpi (Fig. 7D) wide and short; tignum (Fig. 7C) clearly T shaped.

Distribution. Cameroun, Democratic Republic of the Congo, Equatorial Guinea (Fernando Poo Island), São Tomé and Príncipe, Ivory Coast, Liberia, Nigeria, Ethiopia, Kenya, Republic of South Africa (Limpopo, North-West Province, Gauteng, Kwa-zulu-Natal, Eastern Cape Province), Rwanda and Uganda (Fig. 17).

Notes. *Notomela* can be placed next to *Amphimela* Chapuis, 1875, genus wide-spread in Sub-Saharan Africa, Madagascar, Australian, Eastern Palaearctic and Oriental regions. *Notomela* shares with *Amphimela* the same pronotal shape, head with wide interantennal space, frontal carina not raised, metafemoral spring (personal data) and spermathecal type. However, these two genera are easily distinguishable by the: presence of a submarginal elytral stria of distinctly and deeply impressed punctures



Figures 1–3. Habitus. *Notomela cyanipennis* Jacoby, male (1) *N. fulvicollis* Bryant, male (2) *N. joliveti* sp. n., male (3).

laterally, delimiting wide and distinctly raised lateral band in *Notomela*, absent in *Amphimela*; frontal tubercles clearly delimited and raised in *Notomela*, absent or just visible in *Amphimela*; pronotal punctuation laterally more strongly and densely impressed, uniformly impressed in *Amphimela*; elytral punctuation partially irregular in *Notomela*, regular in *Amphimela*.

Ecological data. Host plants reported for this flea beetle genus in southern Africa (*N. fulvicollis* Bryant) are *Citrus* and *Zanthoxylum* [= *Xanthoxylum*; = *Fagara*] (Rutaceae) (Jolivet and Hawkeswood 1995). Based on the distributional data, *Notomela* species seem to be associated mainly with tropical and temperate lowland and montane forest ecosystems.

Notomela cyanipennis Jacoby, 1899

Notomela cyanipennis Jacoby, 1899: 357; Bechyné 1960: 32; Scherer 1969: 371
 = *Notomela viridipennis* Bryant, 1941: 212; Bechyné 1955: 559 syn. n.
 = *Notomela cyanipennis macrosoma* Bechyné, 1959: 35 syn. n.

Type material examined. Lectotype designation. (*N. cyanipennis*): Cameroons, W. Afr., ♂ (Biondi M. des.) (BMNH). Holotype ♂ (*N. viridipennis*): Uganda, Madi [= 3°19'N, 31°46'E], v.1927, G.D.H. Carpenter (BMNH). Holotype ♂ (*N. cyanipennis macrosoma*): Stanleyville [= Kisangani 00°31'N, 25°12'E], 31.iii.1928 (IRSNB). **Further material studied.** IVORY COAST: Bingerville [5°21'N, 3°54'E], 1-6.ii.1964, J. Decelle leg., 1 specimen (NHMB); LIBERIA: Monrovia [6°18'48"N 10°48'05"E], Coll. Chapuis (BMNH), 1 specimen; NIGERIA: Southern Nigeria, Lagos, Ussher, Fry Collection, 1 specimen (IRSNB); CAMEROUN: Southern Cameroun, Ekok [2°44'32"N 14°25'13"E], xi, A. Mayne leg., 2 specimens (BMNH); Fernando Poo [=

Bioko Island 3°30'N, 8°42'E], 1 specimen (NHBM); DEMOCRATIC REPUBLIC OF CONGO: Stanleyville, 31.iii.1928 [= Kisangani 00°31'N, 25°12'E], 8 specimens (RMCA); Kivu, Kavimvira [3°21'10"S, 29°09'18"E] (Uvira), xii. 1954, G. Marlier leg., "à la lumière", 3 specimens (RMCA), 7 specimens (BMNH); ditto, ii-iii.1955, 1 specimen (BMNH); RWANDA: Rusumo, Ibanda Makera [2°22'56"S, 30°46'33"E], x.1993, T. Wagner leg., "galeriewald lichtfang", 1 specimen (BAQ); Kigali Province, Kicukiro District [2°00'37"S, 30°07'04"E], xi.1972, F. Cuypers leg., 1500 m, 1 specimen (RMCA); ETHIOPIA: 60 km N of Yabelo [5°26'39"N 38°05'56"E], Sidamo Province [= Oromia Province], vi.1994, J. Werner leg., 1 ♂ (BAQ);

Notes. Bryant (1941) described the species *N. viridipennis* from Uganda, however the examination of the holotype and other material attributed to this taxon allow us to consider *N. viridipennis* only as a chromatic form of *C. cyanipennis*, more frequent in the eastern area of its distribution. In addition, also *N. cyanipennis macrosoma* Bechyné shows no significant diagnostic character if compared to the typical form.

Distribution. Ivory Coast, Nigeria, Cameroun, Democratic Republic of the Congo, Rwanda, Uganda and Ethiopia (Fig. 17). Afro-Intertropical chorotype (AIT) (Biondi and D'Alessandro 2006).

Ecological data. Host plant is unknown. This species seems to be associated mainly with tropical lowland and montane humid forest ecosystems, more rarely with grassland and savannah environments.

Notomela fulvicollis Bryant, 1931

Notomela fulvicollis Bryant, 1931: 255; Bechyné 1960: 32.

Type material examined. Lectotype designation: Durban, Natal, 27-10.22 / feeding on *Fagara capensis* / Ser. No. 1378 [29°51'29"S, 31°01'09"E], ♂ (M. Biondi des.) (BMNH). **Further material studied.** REPUBLIC OF SOUTH AFRICA: Limpopo, Modimolle [24°42'S, 28°24'22"E], 30.xii.2008, M. Snižek leg., 2 specimens (BAQ); North-West Province, Transvaal, road to Potchefstroom, 20 km N of Potchefstroom [26°32'S, 27°00'E], 1500 m, 8.xi.1993, M. Bologna leg., 1 specimen (BAQ); Gauteng, Pretoria [25°43'S, 28°17'E], xi.1928, N.K. Munro leg., feeding on leaves of *Xanthoxylon capensis*, 3 specimens (BMNH); Transvaal, Potchefstroom [26°42'52"S, 27°05'49"E], xii.1952, F. Zumpt leg., 1 specimen (BAQ); Kwazulu-Natal, Ntendeka Wilderness Area, Ngomi Forest, 27°51'S, 31°23'E, 24-27.xi.2006, P. Burlisch leg., 2 specimens (BAQ); Port Natal (= Durban 29°51'29"S, 31°01'09"E), 1 specimen (BMNH); Eastern Cape Province, Pondoland, Port St. Johns [31°37'43"S, 29°31'12"E], ix.1923, R.E. Turner leg., 1 specimen (BMNH).

Distribution. Eastern part of the Republic of South Africa: Limpopo, North-West Province, Gauteng, KwaZulu-Natal and Eastern Cape Province (Fig. 17). Bechyné (1960: 32) reported this species from the south of the Democratic Republic of the Congo (Congo belge: Elisabethville [= Lubumbashi 11°40'S, 27°28'E], i.1939, H.J.

Bredo), but this record needs further confirmation. Southern-Eastern African chorotype (SEA) (Biondi and D'Alessandro 2006).

Ecological data. Specie reported by Bryant (1931) as feeding on leaves of *Zanthoxylum* (reported as *Fagara capense* (Thunb.) Harv. (Rutaceae) in South East Africa. Preferred ecosystems seem to be warm temperate forest and tropical lowland shrubland.

Notomela fulvofasciata Jacoby, 1903

Notomela fulvofasciata Jacoby, 1903: 308

Amphimela fulvofasciata (Jacoby, 1903), comb. n.

Type material examined. Holotype ♂: Cameroons, West Africa, Conrad (BMNH).

Notes. This species described from West Africa is really to attribute to the genus *Amphimela* Chapuis. Therefore we proposed the new combination above.

Notomela jolivet sp. n.

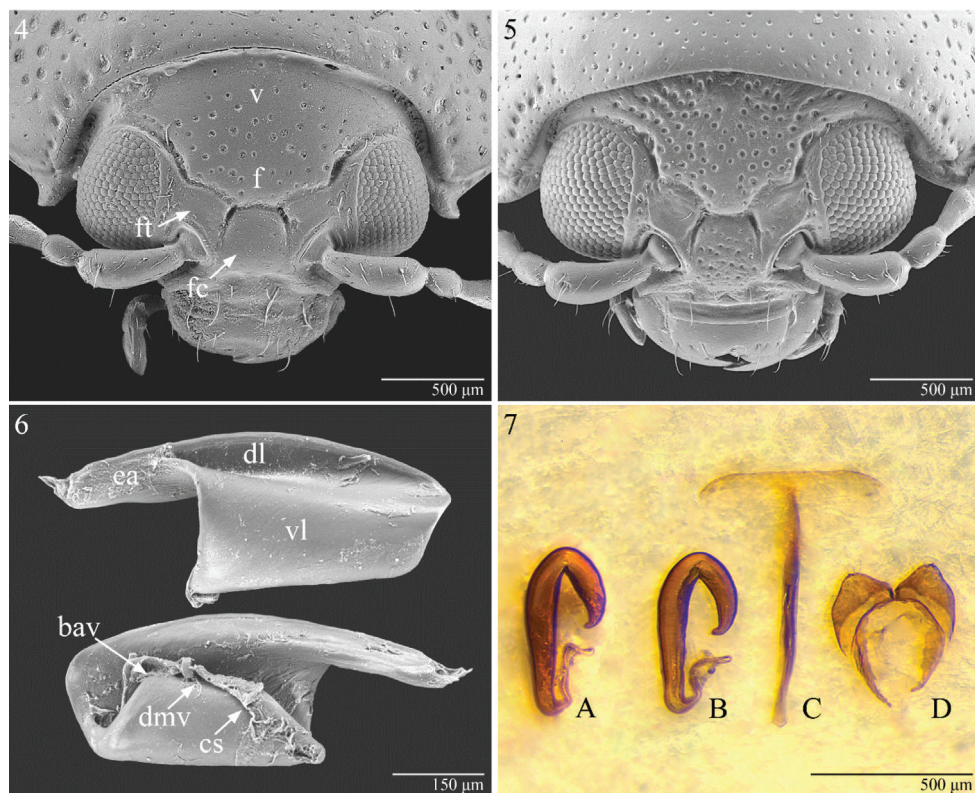
<http://zoobank.org/103F908A-AB0A-4F6E-AD61-A52C2FBB72B8>

Type series. Holotype ♂: “Is. Principe, Roca Inf. D. Henrique, iv.1901, L. Fea” [São Tomé and Principe: Principe Island, Infante Dom Enrique 1°34'02"N, 7°24'52"E] (MSNG). Paratypes (2 ♂♂): same locality, date and collector of the holotype (MSNG, BAQ).

Diagnosis. *Notomela jolivet* sp. n. is the smallest species of the genus (LB ♂ = 3.90–4.20 mm). This new species is easily distinguishable from both *N. cyanipennis* and *N. fulvicollis* for having: dorsal integuments unicolor (Fig. 3); head with densely and strongly punctated vertex and frons (Fig. 5); pronotum with weak but evident depressions on surface near anterior angles and base (Fig. 12); median lobe of aedeagus comparatively longer and less thickset (LE/LAED < 2.50) in ventral view and less curved, almost straight, in lateral view (Fig. 16).

Description. Holotype ♂. Dorsal integument (Fig. 3) entirely dark green black with evident metallic reflection. Body elliptical elongate (LB = 4.20 mm), clearly convex. Maximum pronotal width at distal third (WP = 1.98 mm); maximum elytral width at basal fifth (WE = 2.56 mm).

Frons and vertex (Fig. 5) subrugose, clearly punctate on microreticulate surface shagreened; frontal tubercles distant from each other, sub-quadrate, clearly delimited, with almost smooth surface; frontal grooves distally deep, particularly along ocular margin; interantennal space wide, distinctly wider than length of first antennomere; frontal carina large, not raised; clypeus short, sub-triangular; labrum sub-trapezoidal, brownish, with six setiferous punctures; palpi dark brown; eye sub-elliptical, normally sized; antennae filiform, about as long as half body length (LAN = 2.20 mm; LAN/LB = 0.52), with

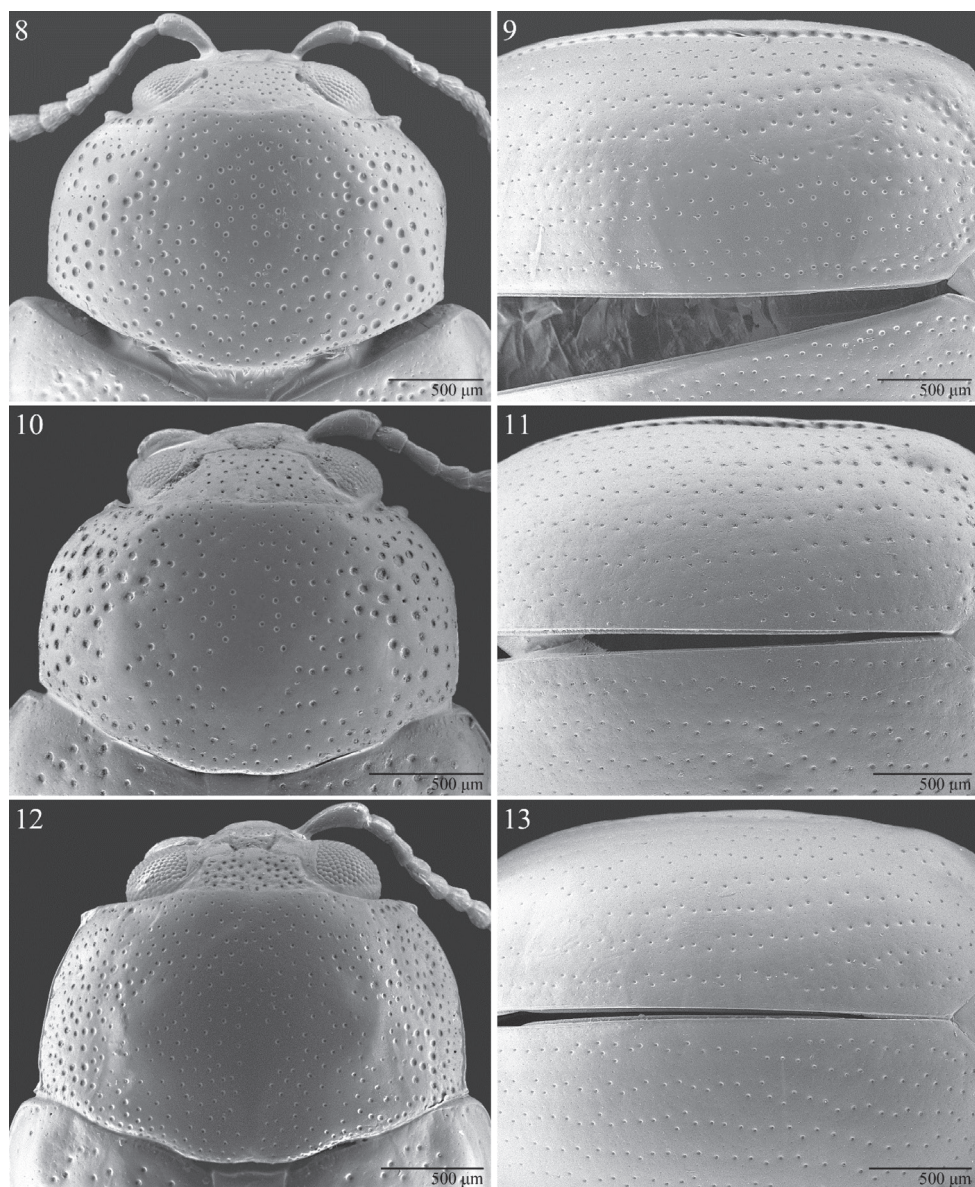


Figures 4–7. Head of *Notomela fulvicollis* Bryant (4); f = frons; fc = frontal carina; ft = frontal tubercle; v = vertex. Ditto, *N. joliveti* sp.n. (5) Metafemoral spring of *N. fulvicollis* Bryant (6); bay = basal angle of ventral lobe; dm = dorsal margin of ventral lobe; ea = extended arm of dorsal lobe; cs = cuticular sheet; vl = ventral lobe. Female genitalia (7); spermatheca of *N. cyanipennis* Jacoby (A); spermatheca (B), tignum (C), and vaginal palpi (D) of *N. fulvicollis* Bryant.

antennomeres 1–5 brownish and 6–11 gradually darker; length of each antennomere proportional to numerical sequence 26:14:18:14:15:16:15:16:18:18:25 (right antenna).

Pronotum (Fig. 12) sub-rectangular, strongly transverse (LP = 1.16 mm; WP/LP = 1.71), laterally clearly rounded forward and basally narrower than elytra; pronotal surface laterally and basally weakly depressed; basal margin very finely bordered, evenly arcuate; lateral margin distinctly bordered, with small anterior setiferous pore; punctation finely and sparsely impressed on disc, more strongly and densely impressed on sides; surface sub-smooth. Scutellum large, sub-triangular, reddish-brown; surface almost smooth, just with very sparse and fine punctulation.

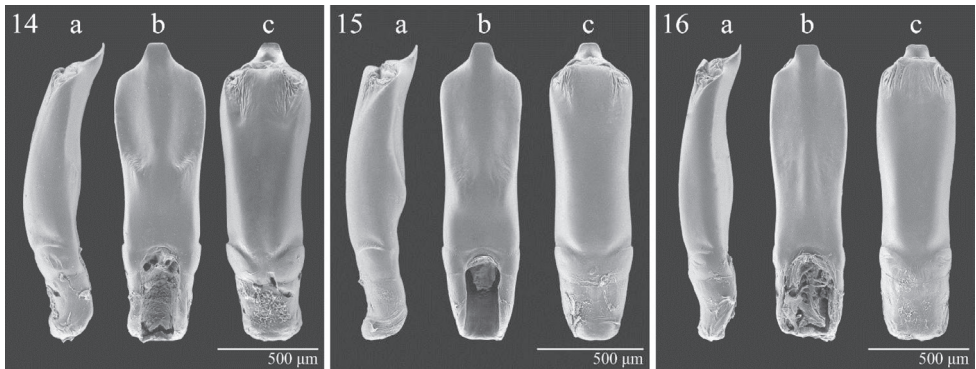
Elytra elongate (LE = 3.56 mm; LE/LP = 3.07), covering entire pygidium, laterally sub-parallel, very weakly arcuate, apically jointly rounded; punctures small but clearly impressed (Fig. 13), arranged in 9 semi-regular rows (+ 1 short scutellar row); first row in epipleural area very strongly impressed; interstriae flat with smooth and



Figures 8–13. Pronotum and elytra. *Notomela cyanipennis* Jacoby (**8, 9**). *N. fulvicollis* Bryant (**10, 11**). *N. joliveti* sp. n. (**12, 13**).

sparsely punctulated surface; humeral callus clearly prominent; macropterous meta-thoracic wings.

Leg strongly blackened, with partially reddish tarsi and femoro-tibial joints; hind tibia straight with no dentate external margin; apical spur of hind tibia short, reddish. First anterior and middle tarsomeres clearly dilated (Fig. 3).



Figures 14–16. Median lobe of aedeagus in lateral (a), ventral (b) and dorsal (c) view. *Notomela cyanipennis* Jacoby (14). *N. fulvicollis* Bryant (15). *N. joliveti* sp.n. (16).

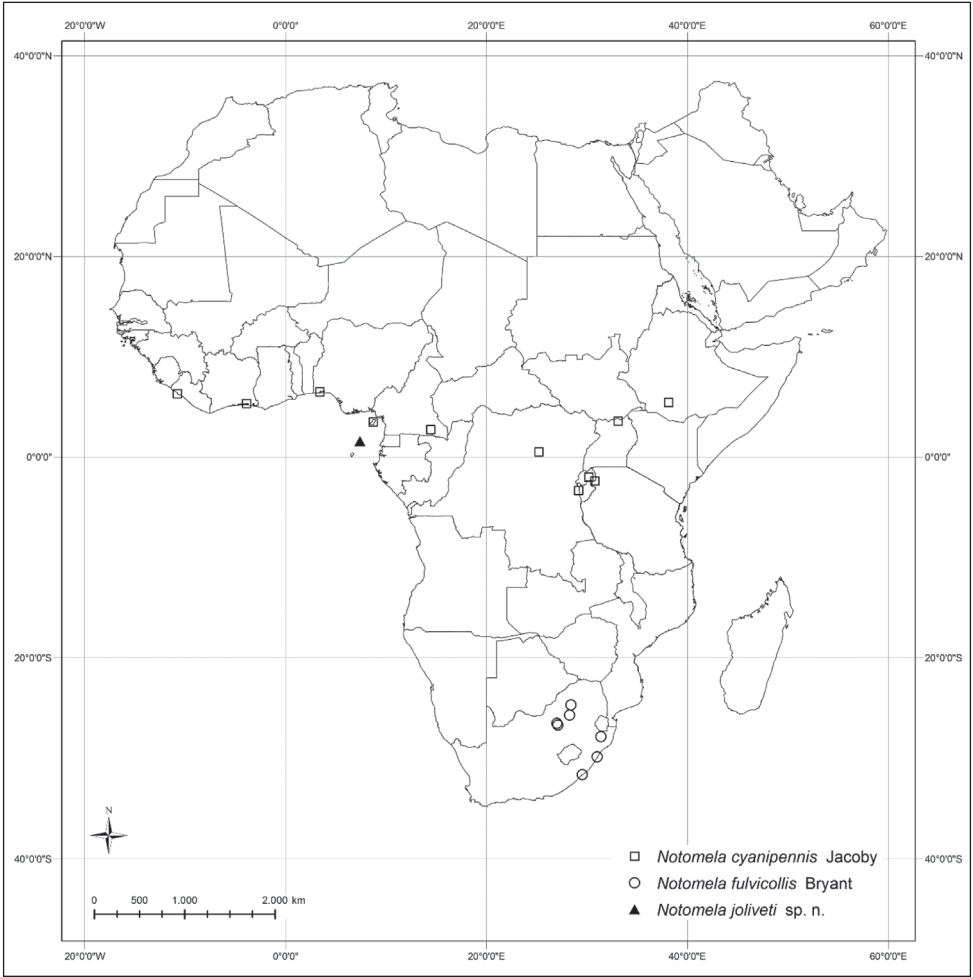


Figure 17. *Notomela* Jacoby species distribution.

Ventral surface blackish, partially reddish, with dense and rather uniformly distributed yellow pubescence; last abdominal sternite with a clear preapical depression with strongly punctated surface.

Median lobe of aedeagus (Fig. 16) thickset (LAED = 1.45 mm; LE/LAED = 2.45), in ventral view, smooth, laterally larger in distal half and distinctly narrowed in basal half; apex widely truncate, sub-trapezoidal; ventral sulcus weakly impressed in basal half, with evident longitudinal wide median carina basally and distally clearly expanded; dorsal sulcus obliterate; dorsal ligula well-developed, apically sub-rectangular; median lobe in lateral view almost straight, just slightly sinuate in distal half with apex bent in ventral direction.

Variation. ♂ (n = 2): LE = 3.28 and 3.28 mm; WE = 2.32 and 2.60 mm; LP = 1.04 and 1.12 mm; WP = 1.76 and 1.92 mm; LAN = 1.88 and 2.00 mm; LAED = 1.45 and 1.45 mm; LB = 3.95 and 4.00 mm; LE/LP = 3.15 and 2.93; WE/WP = 1.32 and 1.35; WP/LP = 1.69 and 1.71; LE/LAED = 2.26 and 2.26; LAN/LB = 0.48 and 0.50.

Paratypes (two males) very similar in shape, sculpture and color to the holotype; one paratype not completely mature. Female unknown.

Etymology. With great pleasure we name the new species after our friend Pierre Jolivet, the “Great Old Man” of all the chrysomelid workers around the world.

Distribution. São Tomé and Príncipe: Príncipe Island (Eastern Cape Province) (Fig. 17).

Ecological notes. Host plant is unknown. Species probably associated with forest ecosystems.

Key to species

- 1 Dorsal integuments bicolor with reddish pronotum and blue or green elytra. Head with vertex and frons more sparsely and weakly punctated (Fig. 4). Pronotal surface without evident depressions (Figs 8, 10). Body size larger (generally LE+LP \geq 4.80). Antennae comparatively shorter in male (LB/LAN \leq 0.47). Median lobe of aedeagus (Figs 14–15) shorter and more thickset (LE/LAED \geq 2.50) in ventral view and slightly curved in lateral view..... 2
- Dorsal integuments unicolor dark green. Head with more densely and strongly punctated vertex and frons (Fig. 5). Pronotal surface with weak but evident depressions near anterior angles and pronotal base (Fig. 12). Body size smaller (LE+LP < 4.80 mm). Antennae comparatively longer in male (LB/LAN > 0.47). Median lobe of aedeagus (Fig. 16) longer and less thickset (LE/LAED < 2.50) in ventral view and almost straight in lateral view. Female unknown *N. joliveti* sp. n.
- 2 Elytral punctation strongly impressed, generally partially arranged in double rows (Fig. 9). Elytra blue or green (f. *viridipennis*) with vivid metallic reflections. Pronotal punctation more densely strongly impressed on disc (Fig. 8). Body larger (generally LE+LP > 5.10 mm). Median lobe of aedeagus (Fig. 14) longer (LAED

- > 1.40 mm), in ventral view wider in distal half, with ventral sulcus laterally more deeply impressed; in lateral view with a distinct median hump on ventral side. Spermatheca in Fig. 7A (LSPc = 0.49 mm).....***N. cyanipennis* Jacoby**
- Elytral punctation more weakly impressed, generally partially arranged in singular rows (Fig. 11). Elytra dark blue with weak metallic reflections. Pronotal punctation more sparsely and finely impressed on disc (Fig. 10). Body smaller (generally LE+LP ≤ 5.10 mm). Median lobe of aedeagus (Fig. 15) shorter (LAED ≤ 1.40 mm) in ventral view narrower in distal half, with ventral sulcus laterally less deeply impressed; in lateral view with a just visible median hump on ventral side. Spermatheca in Fig. 7B (LSPc = 0.49 mm)....***N. fulvicollis* Bryant**

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We are grateful to all colleagues and friends who enabled us to study material in their respective institutions: Wouter Dekoninck (IRSNB), Marc De Meier (RMCA), Michael Geiser (BMNH), Roberto Poggi (MSNG) and Eva Sprecher (NHMB).

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Revision of “*Phyllobrotica*” from Taiwan with description of *Jolibrotica* gen. n. (Coleoptera, Chrysomelidae, Galerucinae)

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Abstract

All Taiwanese species formerly classified the genus *Phyllobrotica* Chevrolat, 1836 are revised. *Jolibrotica* Lee & Bezděk, **gen. n.**, is described for *Phyllobrotica sauteri* (Chûjô, 1935) (Taiwan, China: Guangxi) and *P. chujoi* Kimoto, 1969 (Taiwan). *Phyllobrotica shirozui* Kimoto, 1969 is transferred to the genus *Haplosomoides*. All species are redescribed and their diagnostic characters illustrated.

Keywords

Jolibrotica gen. n., *Haplosomoides*, Verbenaceae, taxonomic revision, Palearctic Region, new genus

Introduction

Luperus sauteri Chûjô was described in 1935 and named in honor of Hans Sauter. Later Chûjô (1963) described another species in honor of this German entomologist, *Phyllobrotica sauteri* Chûjô. Kimoto (1969) transferred the older species to *Phyllobrotica* and proposed a new replacement name, *P. chujoi* Kimoto, 1969 for more recent species due to homonymy. A third Taiwanese *Phyllobrotica* species, *P. shirozui* Kimoto, 1969 was described by him in the same paper.

Currently, the genus *Phyllobrotica* Chevrolat, 1836 is composed of 12 species from the Palaearctic, 2 from the Oriental, and 17 from the Nearctic Region (Bezděk 2010). However, the three Taiwanese species differ from *Phyllobrotica* in important characteristics. One of these, *P. shirozui* Kimoto, 1969, actually belongs to *Haplosomoides* Duvivier, 1890. The two remaining species, *Phyllobrotica sauteri* (Chûjô, 1935) and *P. chujoi* Kimoto, 1969, need to be classified in a new genus, *Jolibrotica* gen. n., described here in.

Based on reduced elytral epipleurae the genus *Jolibrotica* gen. n. should be classified in the section Phyllobrotices of Luperina (Luperini). This section was proposed by Chapuis (1875) exclusively for genera with reduced epipleurae. Wilcox (1965) stated that the section Phyllobrotices was poorly and tentatively defined. Surprisingly, Wilcox (1973) combined the sections Phyllobrotices and Mimastrites, the latter containing genera with well developed epipleurae, which made the definition of the section Phyllobrotices even more ambivalent. The same arrangement was used in the generic list of Seeno and Wilcox (1982). It is also necessary to note that there is a lack of modern phylogenetic studies on Luperini system. The arrangement of various sections within Luperini should be revised in the future.

Both species of *Jolibrotica* gen. n. were previously placed in *Phyllobrotica* based on the reduced epipleurae. However, the genus *Phyllobrotica* is completely different from any species from Taiwan (see Diagnosis below). *Jolibrotica* gen. n. is known from Taiwan and several females tentatively assigned to *J. sauteri* were collected also in continental China (Guangxi).

The Taiwan Chrysomelid Research Team (TCRT) was founded in 2005 and is composed of 10 members. Most of them amateurs interested in making an inventory of all species of Chrysomelidae in Taiwan. Specimens of the new genus have been extensively surveyed and studied, and host plants recorded. Diagnostic characters were assessed and the status of all species was evaluated based on a series of more than 400 specimens. Most of them were collected by the TCRT and others belonged to the historic collection of TARI.

Materials and methods

To prepare drawings of the adult reproductive systems, the abdomens of adults were separated and boiled in a 10% KOH solution, cleared in distilled water, and then mounted on microscope slides in glycerin for observation. Specimens were examined and drawings were made using a Leica M165 stereomicroscope. Microscope slides were examined and illustrated using a Nikon ECLIPSE 50i microscope. Body parts were then stored in glycerin tubes with the dry mounted specimens.

Host plants are recorded by observing adult feeding behavior in the field.

Specimens examined are deposited at the following institutes and museums.

BMNH The Natural History Museum, London, UK [Michael Geiser];

NHM Hungarian Natural History Museum, Budapest, Hungary [Ottó Merkl];

- JBCB** Jan Bezděk collection, Brno, Czech Republic;
KUEC Faculty of Agriculture, Kyushu University, Fukuoka, Japan [Osamu Tadauchi];
KMNH Kitakyushu Museum of Natural History, Kitakyushu, Japan [Yûsuke Minoshima];
NMPC National Museum, Prague, Czech Republic [Jiří Hájek];
SDEI Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany [Stephan Blank];
TARI Taiwan Agricultural Research Institute, Taichung, Taiwan

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

Taxonomy

Jolibrotica gen. n.

<http://zoobank.org/A2B1F043-F232-49A4-A565-9556016BA172>

Type species. *Luperus* (*Luperus*) *sauteri* Chûjô, 1935

Description. Coloration: dorsum lustrous, black or metallic blue-green. Antennae black. Legs metallic, black, or brown. Ventral side metallic or black. Body length 3.2–4.3 mm.

Head. Labrum trapezoidal, transverse, with four pores in transverse row bearing pale seta, anterior margin straight. Anterior part of head very short, almost impunctate and glabrous, several setae on anterior margin of clypeus and along lateral margins of nasal keel. Nasal keel narrow, sharp. Interantennal space very narrow, cca 0.5 as wide as transverse diameter of antennal insertion. Frontal tubercles transverse, subtriangular, slightly elevated, lustrous, glabrous, impunctate, anterior tips not separated by nasal keel. Vertex with distinct shallow impression in middle just behind frontal tubercles, with several larger punctures at each side just behind frontal tubercles bearing very long pale setae, rest of vertex impunctate or with indistinct fine punctuation and glabrous. Antennae slender, 0.80–1.00 as long as body, all antennomeres dull, covered with dense setae, antennomere II as long as wide, antennomere III three times as long as antennomere II, antennomeres III–VII ca 2.8–3.0 as long as wide.

Pronotum 1.30–1.60 times as broad as long, widest in anterior quarter, parallel anteriorly, convergent posteriorly, anterior margin straight, posterior margin rounded. Disc covered with fine punctures. Posterior half of disc with wide shallow transverse impression. Anterior margin unbordered in middle, laterally with indistinct fine border, lateral and posterior margins bordered. Anterior and posterior margins with dense short setae, lateral margins with sparse setae. Anterior angles moderately

swollen, rectangular, posterior angles obtuseangulate, all angles with setigerous pore bearing long pale seta.

Scutellum subtriangular, impunctate, glabrous, with rounded apex.

Elytra ca 1.90–2.10 times as long as wide, almost glabrous (with almost indistinct very scarce short pale setae on humeri, lateral margins and apical slopes), widest at apical quarter, densely covered with fine small confused punctures. Humeral calli well developed. Epipleura extremely narrow, visible only in anterior third of elytra, towards apex more or less only indicated. Macropterous.

Ventral surface lustrous, sparsely covered with fine punctures and pale setae. Anterior coxal cavities opened posteriorly. Prosternal process not visible between procoxae. Abdomen simple, posterior margin of last ventrite with two short incisions, surface behind posterior margin subtriangularly impressed.

Legs slender. All tibiae with fine apical spine in both sexes. Protarsomeres I slender, ca 0.75 times as long as II and III combined. Metatarsomeres I slender, ca as long as II and III combined. Claws appendiculate.

Penis (Figs 9, 10, 25, 26) extremely elongate, without lateral processes, weakly curved at lateral view; internal sac with at least one elongate sclerite.

Females. Antennae distinctly more slender than in males. Protarsomeres I same as in males. Posterior margin of last ventrite entire. Gonocoxae (Figs 11, 27) slender, well separated from each other, narrowly connected at middle; each gonocoxa with seven setae from apical 1/6 to apex. Ventrite VIII (Figs 12, 26) well sclerotized; apical margin widely rounded, with dense setae along outer margin. Spermatheca very characteristic, spermathecal receptaculum (Fig. 13, 29) extremely swollen; pump extremely slender and curved; sclerotized spermathecal duct short and wide, hardly separated from receptaculum.

Diagnosis. *Jolibrotica* gen. n. can be differentiated from *Phyllobrotica* as follows: body black or metallic; interantennal space very narrow, cca 0.5 as wide as transverse diameter of antennal insertion; vertex with several larger punctures at each side just behind frontal tubercles bearing very long pale setae; antennae 0.80–1.00 as long as body; antennomere II as long as wide, antennomere III three times as long as II; male abdominal ventrites not modified; all tibiae with fine apical spine in both sexes; body length 3.2–4.3 mm. Same characters in *Phyllobrotica*: body coloration always partly orange; interantennal space wider, ca as wide as transverse diameter of antennal insertion; vertex completely glabrous except one setigerous pore behind each eye; antennae distinctly shorter than body; antennomere II ca twice as long as wide, antennomere III 1.5 times as long as II; male abdominal ventrites strongly modified; all tibiae in both sexes without apical spines; body length more than 5.0 mm.

Based on Wilcox (1973) and Seenó and Wilcox (1982), the section Phyllobroticites includes the following Asiatic genera: *Euliroetis* Ogloblin, 1936; *Japonitata* Strand, 1935; *Hoplasoma* Jacoby, 1884 (= *Hapломela* Chen, 1942); *Hemygascelis* Jacoby, 1896; *Konbirella* Duvivier, 1892; *Mimastra* Baly, 1865 (? = *Neoatysa* Abdullah & Qureshi, 1968); *Trichomimastra* Weise, 1922; *Haplosomoides* Duvivier, 1890; *Sosibiella* Jacoby, 1896. All these genera (except *Konbirella*) can be easily distinguished from *Jolibrotica*

gen. n. by tibiae lacking apical spines. Additional distinguishing characters can be described as follows: *Euliroetis* has the male abdomen strongly modified and penis bifurcate (abdomen not modified in male and penis extremely elongate, not bifurcate in *Jolibrotica* gen. n.), *Japonitata* has elytra bearing distinct carinae and impressions (elytra even in *Jolibrotica* gen. n.), *Hoplasoma* has bifurcate claws (claws appendiculate in *Jolibrotica* gen. n.), *Hemygascelis* has the male abdomen strongly modified and pronotum much longer than wide (abdomen simple and pronotum transverse in *Jolibrotica* gen. n.), *Mimastra* has epipleurae that are wide in the basal quarter, than suddenly narrowed and visible towards apex (epipleurae extremely narrow, visible only in anterior third of elytra in *Jolibrotica* gen. n.), *Trichomimastra* has the elytra densely pubescent (almost glabrous in *Jolibrotica* gen. n.), *Haplosomoides* is larger and the body is completely or predominantly yellow (body smaller and completely black or metallic in *Jolibrotica* gen. n.), and, finally, *Sosibiella* has wide epipleurae. *Konbiarella* and *Jolibrotica* gen. n. apparently are the only genera in Phyllobroticites with apical spurs on all tibiae. *Konbiarella* differs by possessing antennae that are 1.3 times longer than the body and the pronotum is longer than wide (antennae shorter, 0.80–1.00 as long as body and pronotum transverse in *Jolibrotica* gen. n.).

Recently, three additional genera were described and probably belong to Phyllobroticites although it is not specified in the description. From *Jolibrotica* gen. n. they can be separated as follows: *Pubibrotica* Medvedev, 2002 has tibiae lacking apical spines and elytra densely pubescent; *Mimastrosoma* Medvedev, 2004 is much larger, predominantly pale and the aedeagus is bifurcate; *Hirtomimastra* Medvedev, 2009 has elongate metatarsus I, body pale and elytra densely pubescent.

Distribution. Taiwan, China: Guanxi.

Etymology. Composed from Jolivet and *Phyllobrotica* to honor Pierre Jolivet, who promoted leaf beetle research more than any other person in recent history.

Jolibrotica sauteri (Chûjô, 1935), comb. n.

Luperus (*Luperus*) *sauteri* Chûjô, 1935: 162.

Luperus sauteri: Chûjô 1962: 238.

Phyllobrotica sauteri: Kimoto 1969: 38; Wilcox 1973: 474; Kimoto 1989: 252; Kimoto and Chu 1996: 72; Kimoto and Takizawa 1997: 303, 377; Beenen 2010: 487.

Type locality. Taiwan: New Taipei City, Tinschungchi [頂雙溪] (= Chosokei), 25°01'27"N, 121°52'22"E, 50 m.

Type material examined. Lectotype male (TARI), pinned, here designated to fix the concept of *Luperus* (*Luperus*) *sauteri* Chûjô and to ensure the universal and consistent interpretation of the same, labeled: "Chosokei [= Tinschungchi, New Taipei City] (Form) / H Sauter, 1914 [p, w] // COTYPE [p, circle label with yellow letters] // *Luperus* / *sauteri* / CHÛJÔ [h] / DET. M. CHUJO [p, b] // No. 1356 [p, w] // **Lectotypus** / *Luperus sauteri* ♂ / Chûjô, 1935/ des. C.-F. Lee, 2015 [p, r]". Paralectotypes:

1♀ (TARI): “Chosokei (Form) / H Sauter, 1914 [p, w] // COTYPE [p, circle label with yellow letters] // *Luperus / sauteri* / CHÛJô [h] / DET. M. CHUJO [p, b] // No. 1355 [p, w]”; 1♂, 1♀ (SDEI): “Chosokei (Form) / H Sauter, 1914 [p, w] // Syntypus [p, r] // *Luperus / sauteri* / CHÛJô [h] / DET. M. CHUJO [p, b] // DEI Müncheberg / Col – 05057 and 05058”; 1♂ (SDEI): “Taihoku-Dist. / Maruyama [= Yuanshan, Taipei City] XII.1912 [p, w] // Syntypus [p, r] // *Luperus / sauteri* / CHÛJô [h] / DET. M. CHUJO [p, b] // DEI Müncheberg / Col – 05056”. Each paralectotype has a type label: “**Paralectotypus** [p] / *Luperus sauteri* ♂ [or ♀] [p] / ChÛjô, 1935 [p] / des. C.-F. Lee, 2015 [p, pink label]”

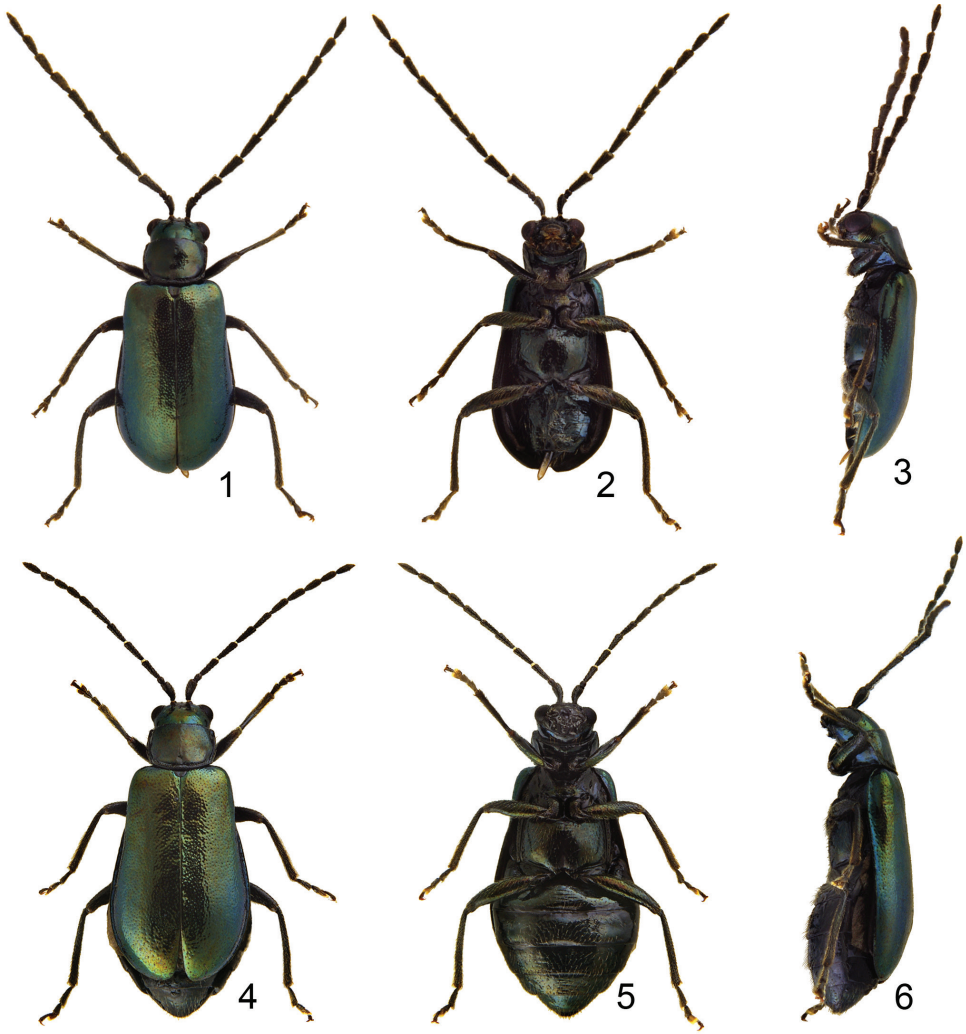
Additional specimens examined (n = 181). **TAIWAN. Chiayi:** 1♂, 1♀, Lachitashan, 19.III.2009, leg. H. Lee (TARI); 2♀♀, Tutzuhu trail, 1.VI.2014, leg. W.-C. Liao (TARI); **Hsinchu:** 1♂, 1♀, Litungshan, 26.II.2009, leg. S.-F. Yu (TARI); 4♂♂, 15.III.2009, leg. M.-H. Tsou (TARI); 2♂♂, 3♀♀, same locality, 13.III.2009, leg. M.-H. Tsou (TARI); 1♂, Lupi, 4.IV.2009, leg. M.-H. Tsou (TARI); 1♀, Talu logging trail, 24.VI.2009, leg. Y.-F. Hsu (TARI); **Hualien:** 14♂♂, 8♀, coastal range SE of Fuli, 12.–16.XI.2008, leg. L. Dembický (BMNH, 2♂♂, 1♀ JBCB); **Ilan:** 1♀, Chiaosi, 7.XII.2008, leg. H.-J. Chen (TARI); 1♀, Fushan Botanical Park, 14.II.2009, leg. M.-H. Tsou (TARI); 3♂♂, 2♀♀, same locality, 20.III.2009, leg. C.-F. Lee (TARI); 1♂, Hsinliao, 19.I.2010, leg. S.-F. Yu (TARI); 1♀, Mingchi, 27.IV.2008, leg. M.-H. Tsou (TARI); 1♀, Fushan Chihwuyan, 20.III.2009, leg. C.-F. Lee (JBCB); **Kaoshiung:** 3♂♂, Chungchihkuan, 16–17.IV.2012, leg. L.-P. Hsu (TARI); 1♂, 2♀♀, Chunyunshan, 1.III.2009, leg. U. Ong (TARI, 1♀ JBCB); 3♂♂, 24.III.2009, leg. C.-F. Lee (TARI); 1♂, 5♀♀, Shihshan logging trail, 24.III.2009, M.-H. Tsou (TARI); 1♂, 8♀♀, Tengchih, 2–5.VI.2008, leg. C.-F. Lee (TARI, 1♂, 1♀ JBCB); 2♂♂, 4♀♀, same locality, 26.V.2009, leg. C.-F. Lee (TARI); 1♀, same locality, 4.VIII.2012, leg. J.-C. Chen (TARI); 1♂, Tona trail, 3.II.2013, leg. B.-X. Guo (TARI); 1♀, same locality, 3.II.2013, leg. W.-C. Liao (TARI); 1♂, 2♀♀, same locality, 9.XI.2013, leg. W.-C. Liao (TARI); **Keelung:** 1♀, Lungkang trail, 5.IV.2011, leg. H. Lee (TARI); 1♀, Tawulunshan, 21.III.2009, leg. H.-J. Chen (TARI); **Nantou:** 1♂, 2♀♀, Lushan, 7.III.2009, leg. U. Ong (TARI); 3♂♂, Meifeng, 19–21.IV.1983, leg. K. C. Chou & S. P. Huang (TARI); 1♂, Peitungyanshan, 14.V.2014, leg. C.-F. Lee (TARI); 4♂♂, 2♀♀, Tatachia, 9.VI.2009, leg. C.-F. Lee (TARI); 1♂, Tsuifeng, 23.V.1982, leg. L. Y. Chou (TARI); 1♂, Tungpu, 20–24.VI.1983, leg. K. C. Chou & C. Y. Wong (TARI); 2♀♀, same locality, 16–20.IV.1984, leg. K. C. Chou & C. H. Yung (TARI); 1♀, Tunyuan, 10.III.2010, leg. Y.-F. Hsu (TARI); 13♂♂, 12♀♀, Wushe, 19–22.IV.1983, leg. K. C. Chou & S. P. Huang (TARI); **Pingtung:** 2♀♀, Lilungshan, 23.XII.2009, leg. J.-C. Chen (TARI); 2♀♀, Peitawushan, 17.II.2010, leg. M.-H. Tsou (TARI); 1♂, same locality, 19.II.2014, leg. Y.-T. Chung (TARI); 1♀, Tahanshan, 6.II.2008, leg. S.-F. Yu (TARI); 1♂, 3.III.2008, leg. C.-F. Lee (TARI); 1♀, same locality, 25.V.2008, leg. C.-F. Lee (TARI); 1♂, same locality, 21.III.2009, leg. M.-H. Tsou (TARI); 1♀, same locality, 5.IV.2009, leg. C.-F. Lee (TARI); 1♀, 6.IV.2013, leg. W.-C. Liao (TARI); 1♂, same locality, 19.II.2014, leg. Y.-T. Chung (TARI); **Taichung:** 2♂♂, Kukuan, 19.III.2014, leg. C.-F. Lee (TARI); 1♀, Tahsuehshan, 24.IV.2012, leg.

C.-F. Lee (TARI); 3♂♂, 5♀♀, Wushihkeng, 19.III.2008, leg. C.-F. Lee (TARI, 1♂ JBCB); **Taipei**: 1♀, Fushan, 2.III.2012, leg. H.-J. Chen (TARI); 1♂, Hsiaoyukeng, 29.III.2008, leg. M.-H. Tsou (TARI); 1♂, 5♀♀, Sukanshui, 24.XII.2006, leg. S.-F. Yu (TARI); 1♀, Tanshui, 9.IV.2008, leg. W.-T. Liu (TARI); 3♀♀, same locality, 19.IV.2009, leg. H.-T. Cheng (TARI); 2♀♀, Wulai, 3.XII.2006, leg. M.-H. Tsou (TARI); 1♀, same locality, 22.XII.2006, leg. H.-J. Chen (TARI); 3♂♂, 3♀♀, same locality, 28.II.2007, leg. C.-F. Lee (TARI, 1♂ JBCB); 1♂, same locality, 22.II.2008, leg. H.-J. Chen (TARI); 3♂♂, same locality, 2.I.2010, leg. H. Lee (TARI); 1♂, same locality, 21.II.2010, leg. Y.-L. Lin (TARI); 1♀, same locality, 17.III.2010, leg. H.-J. Chen (TARI); 1♀, same locality, 17.III.2010, leg. C.-F. Lee (TARI); 1♂, 2♀♀, Yangmingshan, 15.III.1998, leg. C.-F. Lee (TARI); 1♀, same locality, 3.V.2009, leg. M.-H. Tsou (TARI); **Taitung**: 2♀♀, Lichia, 15–16.VII.2014, leg. Y.-T. Chung (TARI); 1♀, Liyuan, 19.IV.2014, leg. W.-C. Huang (TARI); **Taoyuan**: 1♀, Fuhsing, 6.V.1983, leg. K. C. Chou & C. C. Pan (TARI); 2♂♂, Hsuehwunao, 2–3.IV.2011, leg. M.-H. Tsou (TARI); 1♀, same locality, 10.IV.2011, leg. M.-H. Tsou (TARI); 1♂, Lalashan, 2.IV.2009, leg. C.-F. Lee (TARI); 3♀♀, Paling, 3–5.V.1983, leg. K. C. Chou & C. C. Pan (TARI). **CHINA. Guangxi**: 5♀♀, Longsheng Hot Spring, 25°53.6'N 110°12.4'E, 360 m, 11.–14.IV.2013, M. Fikáček, J. Hájek & J. Růžicka leg. (NMPC).

Diagnosis. *Jolibrotica sauteri* is characterized by its metallic blue or green color and extremely elongate penis.

Males. Length 3.3–3.8 mm, width 1.4–1.6 mm. Color metallic green or blue (Figs 1–3); antenna and legs black. Eyes small, distance between eyes 3.0 times wider than diameter of eye. Antenna (Fig. 7) filiform and long, as long as body, ratio of length of antennomeres III to XI about 1.0 : 1.0 : 1.0 : 1.0 : 1.0 : 1.0 : 1.0 : 1.0 : 1.3; ratio of length to width from antennomere III to XI about 2.6 : 2.7 : 2.6 : 2.6 : 2.6 : 2.6 : 2.0 : 2.0 : 4.0. Pronotum quadrilateral; 1.43–1.48 times wider than long; widened anteriorly; disc moderately depressed behind middle. Elytra elongate, 1.73–1.78 times longer than wide; widest at apical 1/3. First tarsomeres normal. Abdominal ventrites without modification, ventrite V with apical margin truncate. Penis (Figs 9, 10) extremely elongate, about 8.8 times longer than wide; parallel-sided, slightly wider in basal third; tectum membranous; ventral surface with longitudinal median area membranous; extremely slender and slightly curved in lateral view; internal sac with one longitudinal sclerite, apically pointed and with base truncate.

Females. Length 3.6–3.9 mm, width 1.8–1.9 mm. Similar to male (Figs 4–6); antenna relatively shorter and slender than male (Fig. 8), about 0.8 times as long as body, ratio of length of antennomeres III to XI about 1.0 : 1.0 : 1.0 : 1.0 : 1.0 : 0.9 : 0.9 : 0.8 : 1.2; ratio of length to width from antennomere III to XI about 3.3 : 3.3 : 3.3 : 3.3 : 2.9 : 2.8 : 2.5 : 3.2. Apical margin of ventrite V truncate. Gonocoxae (Fig. 11) slender, well separated from each other, combined together from apical 2/5 to 3/5; each gonocoxa with seven setae from apical 1/6 to apex. Ventrite VIII (Fig. 12) well sclerotized; apical margin widely rounded, with several long setae near lateral margins, and several long and short setae mixed along apical margin. Spermathecal



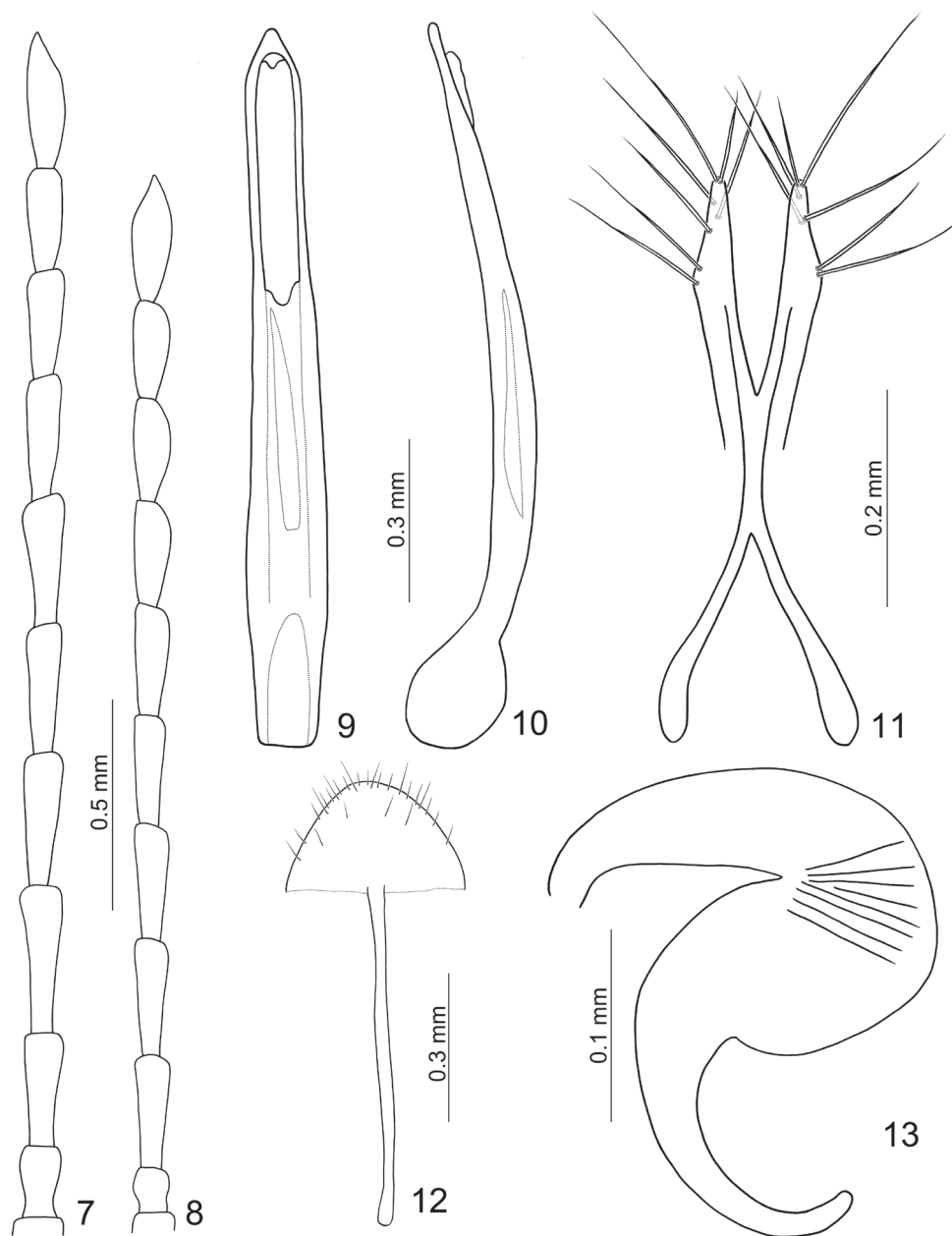
Figures 1–6. Habitus of *Jolibrotica sauteri*. **1** Male, dorsal view **2** ditto, ventral view **3** ditto, lateral view **4** Female, dorsal view **5** ditto, ventral view **6** ditto, lateral view.

receptaculum (Fig. 13) extremely swollen; pump extremely slender and curved; sclerotized spermathecal duct short and wide.

Distribution. Taiwan, China: Guangxi. *Jolibrotica sauteri* is more widespread (Fig. 14) than *J. chujoi* (Fig. 15). In Taiwan, most adults appear below 1500 m elevation and are active during winter.

Host plant. *Callicarpa formosana* Rolfe var. *formosana* Rolfe (Verbenaceae).

Comments. Four females collected in Guangxi are tentatively assigned to *Jolibrotica sauteri*. No difference were observed between females from Guangxi and Taiwan.



Figures 7–13. *Jolibrotica sauteri*. **7** Antenna male **8** Antenna, female **9** Penis, dorsal view **10** Penis, lateral view **11** Gonocoxae **12** Ventrite VIII **13** Spermatheca.

The shapes of spermatheca and ventrite VIII of females from Guangxi slightly differ from Taiwan specimens, but such slight differences may be infraspecific. The gonocoxae from both populations are identical.



Figures 14–16. Distribution maps, solid line: 1000 m, broken line: 2000 m. **14** *Jolibrotica sauteri* **15** *J. chujoi* **16** *Haplosomoides shirozui*.

***Jolibrotica chujoi* (Kimoto, 1969), comb. n.**

Phyllobrotica sauteri Chûjô, 1963: 395.

Phyllobrotica chujoi Kimoto, 1969: 38 (replacement name); Wilcox 1973: 471; Kimoto 1989: 252; Kimoto 1991: 12; Kimoto and Chu 1996: 72; Kimoto and Takizawa 1997: 303, 377; Beenen 2010: 487.

Type locality. Taiwan: Kaoshiung city, Chiasien [甲仙] (= Kosempo), 23°06'52"N, 120°37'53"E, 500 m.

Type material examined. Holotype ♂ (HNHM), labeled: “Kosempo [= Chiasien, in Kaoshiung] / 980. [p, w] // Formosa / Sauter [p, w] // Holotype [h, r] // Holotypus [p, red letters] / *Phyllobrotica* / *sauteri* / Chujo [h, w, with red border] // *Phyllobrotica* / *sauteri* CHÛJÔ [h] / Det. M. CHUJO, 1961 [p, w]”.

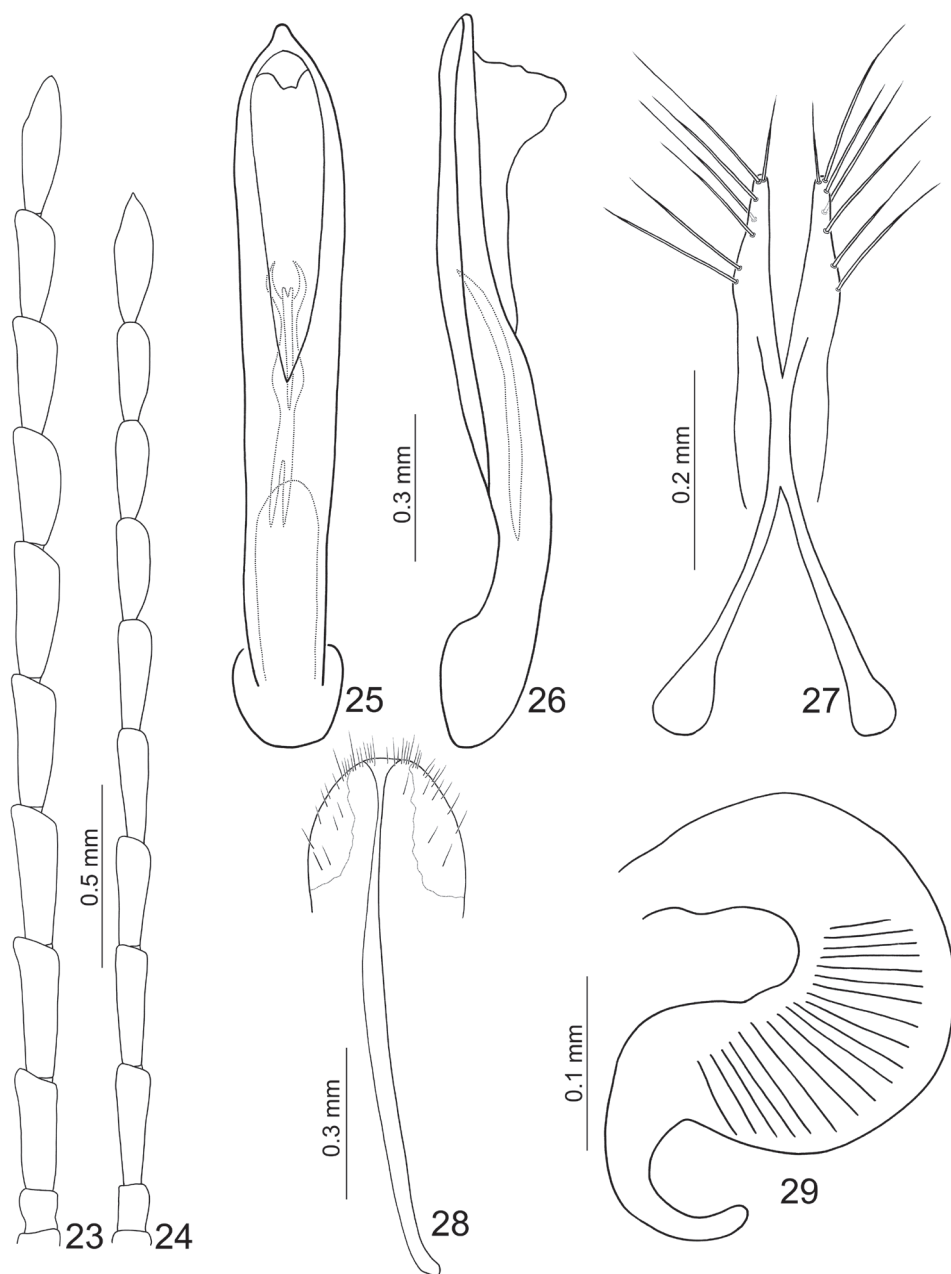
Additional specimens examined (n = 21). **TAIWAN. Kaoshiung:** 1♀, Tengchih, 4.VII.2011, leg. M.-H. Tsou (TARI); 1♀, same locality, 8.VI.2013, leg. W.-C. Liao (TARI); **Pingtung:** 1♂, Kenting, 22–26.III.1982, leg. T. Lin & S. C. Lin (TARI); 3♂♂, 2♀♀, Nanjenhu, 31.III.2011, leg. J.-C. Chen (TARI, 1♂, 1♀ JBCB); 1♂, Peitawushan, 8.V.2014, leg. J.-C. Chen (TARI); 1♀, same locality, 3.VI.2014, leg. Y.-T. Chung (TARI); 3♂♂, Sheding Park, 9.IV.2012, leg. Y.-C. Lan & W.-N. Lu (TARI, 1♂ JBCB); 1♀, Sheting, 5.V.2010, leg. J.-C. Chen (JBCB); 1♂, Wutai, 22.III.2010, leg. J.-C. Chen (TARI); 2♂♂, 3♀♀, same locality, 23.VI.2014, leg. J.-C. Chen (TARI); 1♂, 8–15 km NE of Hengchung, 15.–20.VI.2008, leg. F. & L. Kantner (JBCB).

Diagnosis. *Jolibrotica chujoi* is similar to *J. sauteri* but differs by its shiny black color and wider penis.



Figures 17–22. Habitus of *Jolibrotica chujoi*. **17** Male, dorsal view **18** ditto, ventral view **19** ditto, lateral view **20** Female, dorsal view **21** ditto, ventral view **22** ditto, lateral view.

Males. Length 3.2–3.8 mm, width 1.2 mm. Color blackish brown (Figs 17–19). Eyes small, distance between eyes 4.3 times wider than diameter of eye. Antenna (Fig. 23) filiform and long, as long as body size, ratio of length of antennomeres III to XI about 1.0 : 1.2 : 1.2 : 1.1 : 1.1 : 1.0 : 0.9 : 0.9 : 1.1; ratio of length to width from antennomere III to XI about 2.8 : 3.1 : 3.1 : 3.0 : 3.0 : 2.7 : 2.8 : 2.7 : 3.6. Pronotum quadrilateral; 1.47–1.54 times wider than long; widened anteriorly; disc moderately depressed behind middle. Elytra elongate, 1.66–1.69 times longer than wide; wid-



Figures 23–29. *Jolibrotica chujoi*. **23** Antenna male **24** Antenna, female **25** Penis, dorsal view **26** Penis, lateral view **27** Gonocoxae **28** Ventrite VIII **29** Spermatheca.

est at apical 1/3. First tarsomeres normal. Abdominal ventrites without modification, ventrite V with apical margin truncate. Penis (Figs 25, 26) elongate, about 6.8 times longer than wide, apex rounded with small distinct tip, widest at apical 1/10, towards

base gradually narrowed; tectum membranous; ventral surface with longitudinal median area membranous; extremely slender and slightly curved behind middle at lateral view; internal sac with one longitudinal sclerite, apex forming inwards forked processes, base deeply bifurcate.

Females. Length 4.1–4.3 mm, width 2.1–2.2 mm. Similar to male (Figs 20–22); antenna relatively slender than in male (Fig. 24), about 0.9 times as long as body, ratio of length of antennomeres III to XI about 1.0 : 1.0 : 0.9 : 0.9 : 0.9 : 0.8 : 0.8 : 0.8 : 1.1; ratio of length to width from antennomere III to XI about 3.6 : 3.6 : 3.2 : 3.2 : 3.2 : 3.0 : 3.0 : 2.9 : 3.3. Apical margin of ventrite V truncate. Gonocoxae (Fig. 27) slender, well separated from each other, combined together from apical 2/5 to 3/5; each gonocoxa with seven setae from apical 1/6 to apex. Ventrite VIII (Fig. 28) only laterally sclerotized; apical margin widely rounded, with several long setae near lateral margins, and several long and dense setae mixed along apical margin. Spermathecal receptaculum (Fig. 29) extremely swollen; pump extremely slender and curved; sclerotized spermathecal duct short and wide.

Distribution. Endemic to southern Taiwan below 1500 m elevation (Fig. 15).

Host plant. *Callicarpa kochiana* Makino (Verbenaceae).

Haplosomoides shirozui (Kimoto, 1969), comb. n.

Phyllobrotica shirozui Kimoto, 1969: 37; Wilcox 1973: 474; Kimoto 1989: 252; Kimoto 1991: 12; Takizawa et al. 1995: 12; Kimoto and Chu 1996: 72; Kimoto and Takizawa 1997: 303, 378; Beenen 2010: 487.

Type locality. Taiwan: Chiayi county, Fenchihu [奮起湖], 23°30'22"N, 120°42'01"E, 1500 m.

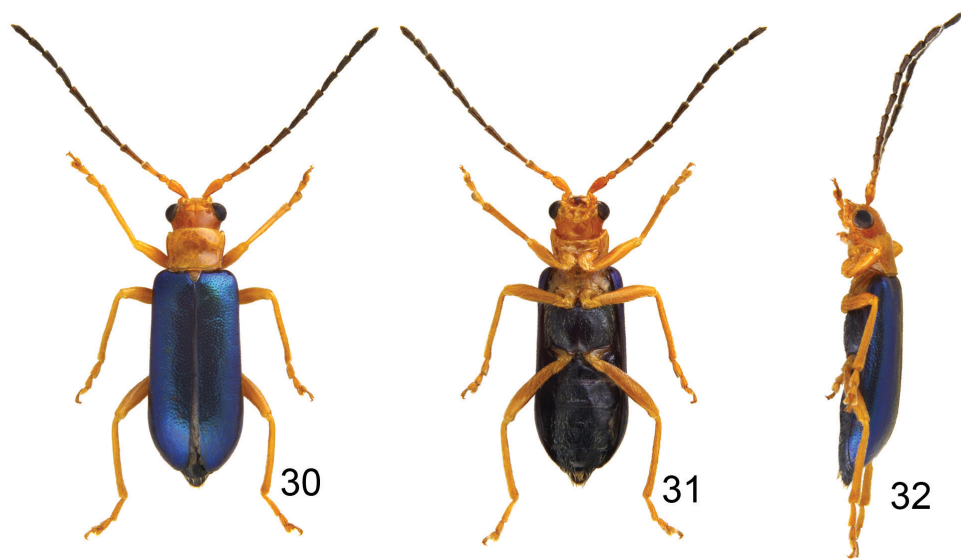
Type material examined. Holotype ♂ (KUEC), labeled: "(Taiwan) / Fenchihu, 1400m / Chiayi Hsien [p, w] // 12.IV.[h]1965[p] / T. Shirôzu [p, w] // Host: [p] / 食草標本 No. 6 [h, w] // Japan-U. S. / Co-op. Sci. / Programme [p, y] // *Phyllobrotica* / *shirozui* / Kimoto, n. sp, [h, w] // HOLOTYPE [p, r]". Paratypes: 1♀ (KMNH): "(Taiwan) / Fenchihu, 1400m / Chiayi Hsien [p, w] // 12.IV[h]. 1965[p] / T. Shirôzu [p, w] // Host: [p] / 食草標本 No. 6 [h, w] // Japan-U. S. / Co-op. Sci. / Programme [p, y] // *Phyllobrotica* / *shirozui* / Kimoto, n. sp, [h, w] // PARATOPOTYPE [p, b]"; 1♂ (KMNH), same but without "Host: [p] / 食草標本 No. 6 [h, w]"; 1 ex., (KMNH): "(Taiwan) / Sungkang / Nantou Hsien [p, w] // 10.VI[h].1965[p] / T. Shirôzu [p, w] // *Phyllobrotica* / *shirozui* / Kimoto, n. sp, [h, w] // PARATOPOTYPE [p, b]"; 2♀♀ (KMNH): "(Taiwan) / Sungkang / Nantou Hsien [p, w] // 31. [h] V.1965[p] / T. Shirôzu [p, w] // *Phyllobrotica* / *shirozui* / Kimoto, n. sp, [h, w] // PARATYPE [p, b]"; 2♂♂ (KMNH): "(Taiwan) / Sungkang / Nantou Hsien [p, w] // 10. VI. [h]1965[p] / T. Shirôzu [p, w] // *Phyllobrotica* / *shirozui* / Kimoto, n. sp, [h, w] // PARATYPE [p, b]"; 1♂ (KMNH), same but with "PARATOPOTYPE [p, b]"; 1♀ (KMNH): "(Taiwan) / Sungkang / Nantou Hsien [p, w] // 29[h]. vi. 1965[p]

/ T. Yamasaki [p, w] // Japan-U. S. / Co-op. Sci. / Programme [p, y] // *Phyllobrotica shirozui* / Kimoto, n. sp, [h, w] // PARATYPE [p, b]”; 1♀ (KMNH): “(Taiwan) / Sungkang, 2000m / --Tsifeng, 2300m / Nantou Hsien [p, w] // 29[h]. vi. 1965[p] / S. Kimoto [p, w] // Japan-U. S. / Co-op. Sci. / Programme [p, y] // *Phyllobrotica shirozui* / Kimoto, n. sp, [h, w] // PARATYPE [p, b]”.

Additional specimens examined (n = 247). **TAIWAN. Chiayi:** 1♂, Fenchihu, 25.V.2013, leg. W.-C. Liao (TARI); 2♂♂, Laichitashan, 19.III.2009, leg. H. Lee (TARI); **Hualien:** 1♂, 1♀, Tayuling, 9–16.VI.1980, leg. K. S. Lin & B. H. Chen (TARI); **Hsinchu:** 2♂♂, 3♀♀, Kuanwu, 1.V.2010, leg. M.-H. Tsou (TARI); **Kaoshiung:** 1♂, 1♀, Chungchihkuan, 17.IV.2012, leg. L.-P. Hsu (TARI); 2♂♂, 4♀♀, Erhchituan, 8.III.2013, leg. B.-X. Guo (TARI); 1♂, Shanping, 22.III.2014, leg. W.-C. Liao (TARI); 5♂♂, 4♀♀, Shihshan logging trail, 24.III.2009, leg. M.-H. Tsou (TARI); 3♂♂, 3♀♀, same data, S.-F. Yu leg. (JBCB); 13♂♂, 9♀♀, Tengchih, 2–5.VI.2008, leg. C.-F. Lee (TARI); 1♂, 2♀♀, Tona logging trail, 12.III.2013, leg. B.-X. Guo (TARI); **Nantou:** 1♀, Fenghuanshan, 9.III.2014, leg. J.-C. Chen (TARI); 1♂, 1♀, Meifeng, 10.V.1979, leg. K. C. Chou (TARI); 2♀♀, same locality, 17–22.VI.1979 (TARI); 1♂, 1♀, same locality, 20–22.VI.1979, leg. K. S. Lin & B. H. Chen (TARI); 1♀, same locality, 22–29.VI.1979 (TARI); 1♀, same locality, 27–29.VI.1979, leg. K. S. Lin & L. Y. Chou (TARI); 1♀, same locality, 2–4.VI.1980, leg. L. Y. Chou & C. C. Chen (TARI); 1♂, 2♀♀, same locality, 8.VI.1980, leg. K. S. Lin & B. H. Chen (TARI); 37♂♂, 43♀♀, same locality, 7–9.V.1981, leg. K. S. Lin & S. C. Lin (TARI); 6♂♂, 7♀♀, same locality, 24–26.VI.1981, leg. K. S. Lin & W. S. Tang (TARI); 4♂♂, 11♀♀, same locality, 22.V.1982, leg. L. Y. Chou (TARI); 4♀♀, same locality, 15.VII.1982, leg. S. C. Lin & C. N. Lin (TARI); 7♂♂, 6♀♀, same locality, 19–21.IV.1983, leg. K. C. Chou & S. P. Huang; 2♂♂, 1♀, same locality, 8–11.V.1984, leg. K. C. Chou & C. C. Pan (TARI); 2♀♀, Tatachia, 9.VI.2009, leg. C.-F. Lee (TARI); 3♂♂, 6♀♀, Tunyuan, 27.IV.2014, leg. M.-H. Tsou (TARI); **Pingtung:** 7♂♂, 4♀♀, Lilungshan, 8.III.2014, leg. J.-C. Chen (TARI); 1♂, Peitawushan, 17.II.2010, leg. S.-F. Yu (TARI); 2♂♂, same locality, 8.IV.2013, leg. Y.-T. Chung (TARI); 6♂♂, 1♀, same locality, 19.II.2014, leg. Y.-T. Chung (TARI); 3♂♂, 2♀♀, same locality, 22.IV.2014, leg. Y.-T. Chung (TARI); 1♂, 1♀, same locality, 8.V.2014, leg. Y.-T. Chung (TARI); 1♀, Tahanshan, 6.IV.2013, leg. W.-C. Liao (TARI); **Taichung:** 2♀♀, Anmashan, 7.VI.2010, leg. C.-F. Lee (TARI); 1♀, Wuling, 27–29.VI.1979, leg. K. S. Lin & L. Y. Chou (TARI); **Tainan:** 1♂, Meiling, 24.III.2011, leg. U. Ong (TARI); **Taitung:** 1♂, Liyuan, 29.III.2011, leg. C.-F. Lee (TARI).

Diagnosis. Although *Haplosomoides shirozui* resembles *H. changi* Lee, Bezděk & Staines, 2011 with the similarly peculiar shaped penis and absence of longitudinal ridge on the elytron, it can be easily recognized by its metallic blue elytra (pale in *H. changi*, see Lee et al 2011).

Males. Length 4.1–5.1 mm, width 1.4–1.7 mm. Color yellowish-brown (Figs 30–32); antenna blackish-brown, three or four basal antennomeres paler; elytron metallically blue; metathoracic and abdominal ventrites black. Eyes extremely small, distance between eyes 3.7 times wider than diameter of eye. Antenna (Fig. 33) filiform and

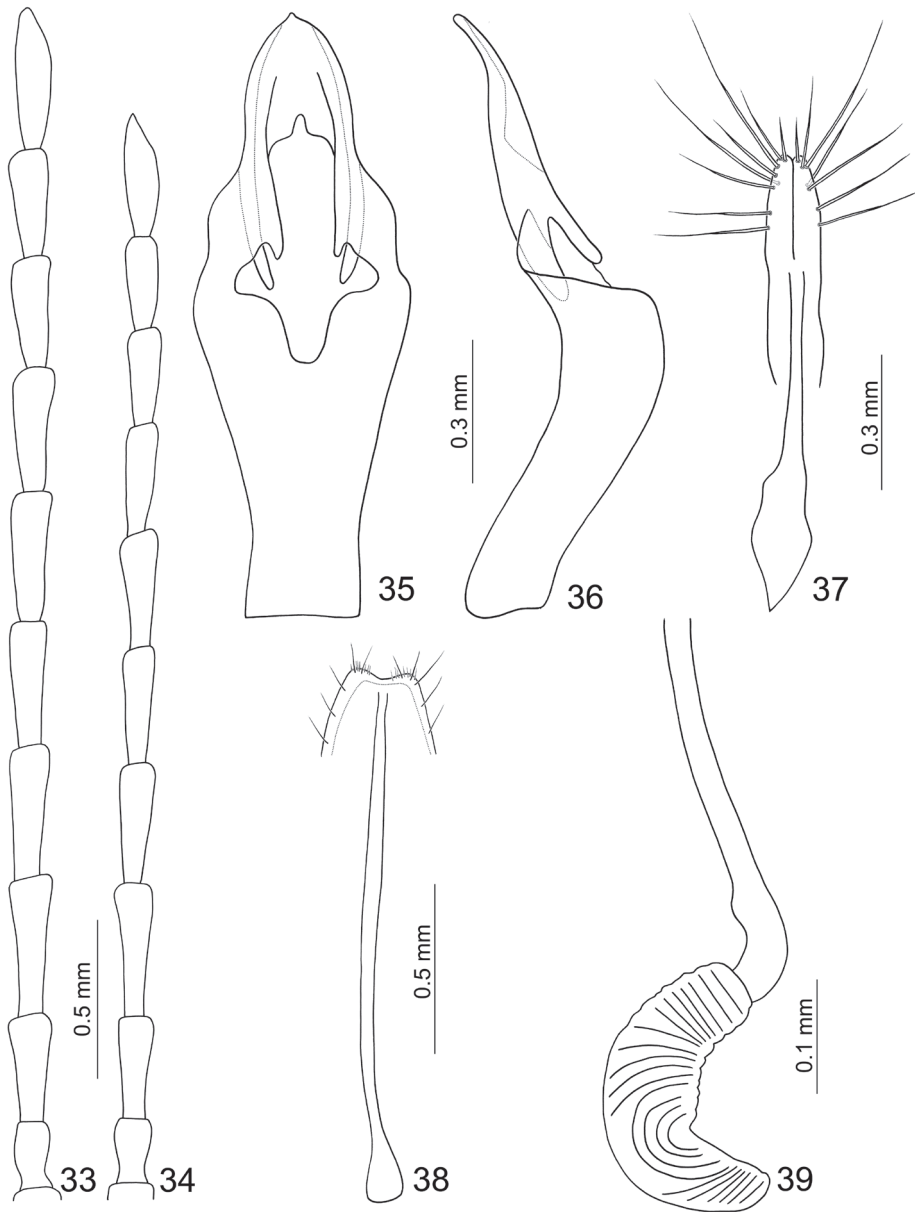


Figures 30–32. Habitus of *Haplosomoides shirozui*, male. **30** Dorsal view **31** Ventral view **32** Lateral view.

long, 0.9 times as long as body size, ratio of length of antennomeres III to XI about 1.0 : 1.3 : 1.3 : 1.2 : 1.2 : 1.2 : 1.0 : 1.0 : 1.3; ratio of length to width from antennomere III to XI about 2.6 : 3.3 : 3.4 : 3.2 : 3.3 : 3.1 : 2.8 : 2.7 : 3.9. Pronotum quadrilateral; 1.33–1.47 times wider than long; widened anteriorly; disc moderately depressed behind middle. Elytra elongate, 2.17–2.23 times longer than wide; parallel-sided. First tarsomeres normal. Abdominal ventrites without modification, ventrite V with apical margin truncate. Penis (Figs 35, 36) abruptly widened at middle, apex pointed, with median and wide groove from near apex to middle, central area membranous; ventral surface with longitudinal ridges close to lateral margin from apex to middle; moderately curved from lateral view.

Females. Length 5.7–5.9 mm, width 2.0–2.2 mm. Similar to male; ratio of length of antennomeres III to XI about 1.0 : 1.3 : 1.2 : 1.1 : 1.1 : 1.1 : 0.9 : 0.9 : 1.2; ratio of length to width from antennomere III to XI about 2.9 : 3.8 : 3.4 : 3.3 : 3.3 : 3.2 : 2.7 : 2.8 : 3.9 (Fig. 34). Apical margin of ventrite V widely rounded. Gonocoxae (Fig. 37) slender, extremely close to each other from apex to apical 1/4, each gonocoxa with seven to eight setae from apical 1/6 to apex; basally combined from base to apical 1/4. Ventrite VIII (Fig. 38) with lateral and apical margin strongly sclerotized; apical margin emarginate, with several long setae along lateral margins, and one cluster of short setae at antero-lateral angles. Spermathecal receptaculum (Fig. 39) as wide as pump; pump hardly separated from receptaculum, moderately curved; sclerotized spermathecal duct slender and extremely long.

Distribution. Endemic to Taiwan. Although not as widespread as *Jolibrotica sauteri*, it is abundant locally in mountains at elevations between 1000 and 2500 m, extending north to Hsinchu County.



Figures 33–39. *Haplosomoides shirozui*. **33** Antenna male **34** Antenna, female **35** Penis, dorsal view **36** Penis, lateral view **37** Gonocoxae **38** Ventrite VIII **39** Spermatheca.

Host plant. *Clerodendrum trichotomum* Thunb (Verbenaceae).

Discussion. *Phyllobrotica shirozui* is transferred to *Haplosomoides* based on male abdomen simple (strongly modified in *Phyllobrotica*), pronotum with wide transverse depression in posterior half (pronotum regularly convex in *Phyllobrotica*) and elytral

epipleura present (absent in *Phyllobrotica*). *Haplosomoides shirozui* belongs to *H. anamita* species group as defined by Lee et al (2011) and in the structure of aedeagus it is very close to *H. changi* Lee, Bezděk & Staines, 2011.

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Acronymolpus, a new genus of Eumolpinae, endemic to New Caledonia (Coleoptera, Chrysomelidae)

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Abstract

The genus *Acronymolpus* is proposed as new. It is represented by four new species, all of which are endemic to New Caledonia. Proposed are: *Acronymolpus joliveti* **sp. n.** (type species), *A. gressitti* **sp. n.**, *A. meteorus* **sp. n.**, and *A. turbo* **sp. n.**

Keywords

Chrysomelidae, Eumolpinae, Eumolpini, *Acronymolpus*, new genus with 4 new species, New Caledonia

Introduction

Acronymolpus, a new genus of Eumolpinae, is proposed herein. The four included species are new and are endemic to New Caledonia. This genus is unique among its allied Eumolpini, e.g. *Dematochroma* Baly, by having the metacoxae enlarged and nearly reaching the posterior margin of the first abdominal ventrite.

Specimens appear to be very rare in collections, with only seven individuals known to date. This study is based only on these specimens representing the four new species. The earliest examples were taken in 1963, then through later years to 2005.

Material and methods

Collections: **BPBM**, Bishop Museum, Honolulu, Hawaii; USA; **CXMNC**, Collection Xavier Montrouzier, Institut Agronomique néo-Calédonien, La Foa, New Caledonia, with a holotype from the latter to be deposited in the **MNHN**, Museum of Natural History, Paris, France.

Owing to the rarity of specimens, three of the species are left intact and not compromised by dissecting.

Measurements are taken from a calibrated ocular micrometer on a Leica MZ7 stereo microscope and are reported in mm and cmm, the latter = 1/100 of a mm. Abbreviations or brief names of selected body structures are: BL body length; BB body breadth; HB head breadth; IAS transverse breadth of interantennal space; AS transverse diameter of antennal socket; ORB transverse space of orbit between antennal socket and eye; IOS shortest transverse distance between eyes; EYE maximum diameter × breadth of eye; GENA distance between genal apex and lower eye margin; PNL pronotal length; PNB pronotal breadth.

Taxonomy

Tribe Eumolpini

Acronymolpus gen. n.

<http://zoobank.org/80C47612-8196-4FE4-B645-8BCDA9AE49FA>

Description. Proepisternal margin straight; pygidial groove present; metatibial apex entire, lacking emargination; claws appendiculate.

Body fusiform, stout, with elytra strongly narrowed from robust basal region to preapex. Head: frontal surfaces flattened; postantennal swellings ± subtriangular or oblique, not conspicuous; oblique suture present, shallow internally, deeper along upper eye margin; coronal suture deep along mid-vertex; eye subovate. Antenna slender, elongate and attaining apical 1/3 or more of elytron. Pronotum convex with anterolateral area strongly descended and appearing narrowed in dorsal view; base broadly and shallowly biconvex; posterior angle small, ± dentate; lateral margin convex and narrowed anteriorly; anterior angle slightly produced, subangulate; disc moderately to strongly punctate. Scutellum small, triangular, surface nearly smooth. Elytral punctures basically arranged in regular striae but the inner discal rows quite obliterated and confused on the basal half before they become organized into straight rows apically. Elytral epipleuron narrow to preapex and continued to apex as a thin thread. Wing normally developed.

Ventral surfaces: prosternum subquadrate, flattened; hypomeron ± smooth, impunctate; metasternum broadly and gently convex, ± smooth; first abdominal ventrite (Fig. 1C) not quite trisected by enlarged metacoxae on each side but on dissection with thin shelf-like extensions beneath metacoxae; intercoxal piece of forming an acute,

steeply inclined triangle anteriorad; remaining ventrites strongly narrowed posteriorly, collectively subtriangular in outline. Legs: femora subclavate; metacoxa enlarged; tibiae slender, subequal to femur length.

Type species. *Acronymolpus joliveti* sp. n.

Etymology. *acro* (height) + *nyma* (name) + *molpus* (for *Eumolpus*); masculine.

***Acronymolpus joliveti* sp. n.**

<http://zoobank.org/189F246C-8110-41AD-8878-1EDCAB384DA0>

Fig. 1A–E

Description (Holotype female). Body stout, fusiform, broadest across elytral humeral area, then strongly tapered to preapex. Body surfaces largely castaneous; elytron with inner interstices becoming paler orangish along apical half; antenna yellow- to orange-testaceous; legs castaneous. Dorsum glabrous; mesosternum and central part of abdominal ventrite 1 sparsely setose. Body length 3.3 mm; body breadth 2.2 mm.

Head: frontal surfaces smooth with hint of isodiametric sculpture; frons with a few large deep punctures mostly above middle; postantennal swellings \pm triangular, surfaces nearly smooth; oblique suture becoming a deep sharp sulcus along upper eye margin; vertex with a few large deep punctures on each side near beginning of deep coronal suture; interantennal space flat, about $2.6 \times$ as broad as transverse diameter of antennal socket; antennal socket and orbit with breadths subequal; interocular space about $1.4 \times$ as broad as maximum eye diameter; eye subovate, moderately narrowed below; gena slightly over $0.6 \times$ as deep as eye.

Antenna: slender, attaining apical $1/3$ of elytron; relative lengths of segments (cmm units = $1/100$ mm): $28 : 14 : 24 : 26 : 28 : 28 : 34 : 34 : 32 : 32 : 40$; segments 3–6 slender, very slightly broadened apically; 7–10 distinctly heavier than preceding; last gradually thickened to apical $1/3$, then narrowed to acute apex.

Prothorax: $0.57 \times$ as long as broad; lateral margin moderately and evenly convex from base to apex; disc moderately punctate; central punctures somewhat ovate and commonly $1\text{--}2 \times$ as large as interspaces; interspaces nearly smooth and shining with occasional micropunctures and nearly obsolete fine sculpture.

Elytron: smooth and shining; lateral margin beyond broad basal region strongly narrowed posteriorly to knob-like extremity at side of sutural apex; humerus weakly swollen, mostly smooth; discal punctures larger and deeper than pronotal ones and commonly $1\text{--}2 \times$ as large as interspaces; interspaces commonly \pm costate to subtuberculate.

Ventral surfaces: prosternum with surface dull-punctulate; hypomeron subshining, with obsolescent fine sculpture; metasternum broad, smooth-shining with fine sculpture, sparsely micropunctate; metacoxae nearly touching posterior margin of abdominal ventrite 1; relative lengths of abdominal ventrites (cmm): $48 : 10 : 10 : 12 : 20$; surfaces subshining, with fine sculpture; first ventrite with median part acutely triangular and strongly inclined between coxae; last ventrite lacking median impression before apex.

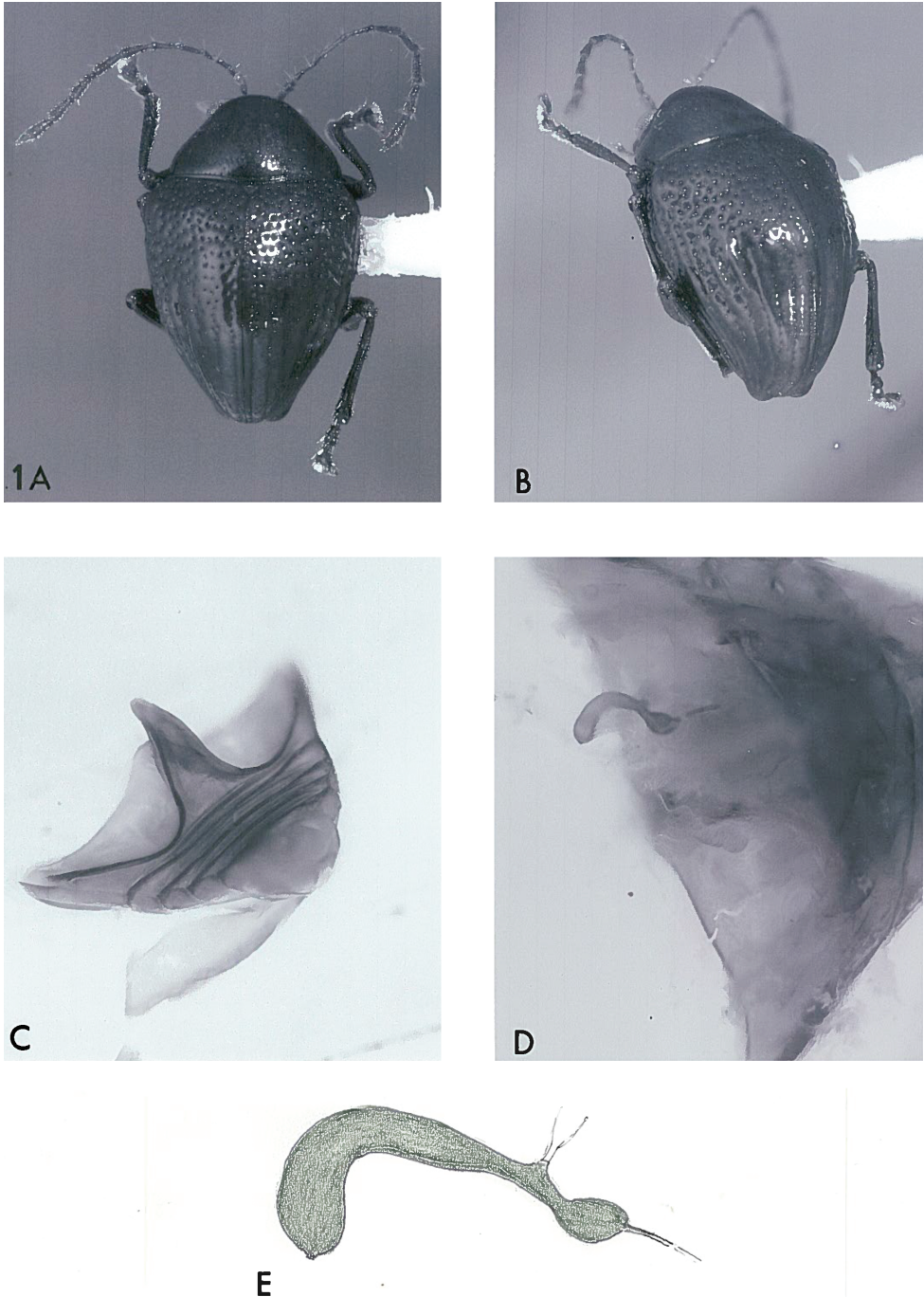


Figure 1. *Acronymolpus jolivetii* sp. n. **A** habitus view of holotype, body length 3.3 mm **B** apical oblique view of holotype, showing apical knob-like terminations **C** abdomen of paratype ♀, oblique ventral view showing elevated intercoxal process **D** abdomen of paratype ♀, showing position of spermatheca **E** spermatheca of paratype ♀, lateral view, length of main body 26 cmm.

Legs: slender; femora subclavate, smooth with obsolescent sculpture but sparsely punctulate; metatibia just as long as femur.

Measurements: BL 3.3 mm; BB 2.3 mm; HB 110 cmm; IAS 26 cmm; AS 8 cmm; ORB 8 cmm; IOS 58 cmm; EYE 41 × 31 cmm; GENA 26 cmm; PNB 176 cmm; PNL 102 cmm.

Paratype (Female). Fig. 1D–E. Essentially identical to holotype. Spermatheca J-shaped, slender, as figured. BL 3.2 mm; BB 2.15 mm.

Holotype ♀. NEW CALEDONIA: Vallée d'Amoa, 7.ii.1963, C.M. Yoshimoto to collector (BPBM HT16,842); Paratype ♀, Mt Panie trail, 550 m, 9.ii.1963, G. Kuschel coll. (BPBM).

Remarks. Near *A. turbo*, sp. n. in general stature, including the close proximity of the metacoxae to the apical margin of the first abdominal ventrite; both species also have ornamentation on the elytral preapex – knob-like in this species and briefly explanate in *A. turbo*. The name honors Prof. Pierre Jolivet of Paris, who has charted our knowledge of Chrysomelidae in general and of New Caledonia in particular.

***Acronymolpus turbo* sp. n.**

<http://zoobank.org/855A02E1-9776-4EAA-ABE4-46401516DF01>

Fig. 2A–B

Description (Holotype). Body robust, broadest across elytral posthumeral area, then strongly tapered to preapical region. Coloration reddish-piceous with paler yellowish apical elytral disc; antenna orange-testaceous. Dorsum glabrous. Body length 3.1 mm; body breadth 2.0 mm.

Head: frontal surfaces with general isodiametric sculpture; frons with several large, deep punctures above; oblique suture weak internally, becoming deeper along upper eye margin; vertex bearing several large punctures on each side of shallow coronal suture which ends near mid vertex; interantennal space rough, about 2.6 × as broad as transverse diameter of antennal socket; antennal socket and orbit subequal in breadth; interocular space about 1.3 × as broad as maximum diameter of eye; eye subovate, narrowed below; gena 0.5 × as deep as eye.

Antenna: slender, nearly reaching elytral apex; relative lengths of segments (cmm): 28 : 16 : 21 : 21 : 24 : 24 : 36 : 32 : 32 : 34 : 40; apical 2 segments heavier than preceding ones.

Prothorax: 0.55 × as long as broad; lateral margin slightly narrowed basally to mid-point, then more convexly narrowed to acutely produced anterior angle; disc closely and confusedly punctate; punctures deep and commonly 3–4 × as large as raised inter-spaces; only the antebasal area narrowly impunctate.

Elytron: robust basally across humeral region, then strongly narrowed posteriorly to preapical area, marked by an apical explanate margin originating at preapex of 7th interstitial interval; humerus briefly pustulate and smooth, and slightly heavier than inner basal costae; disc densely punctate-subtuberculate on inner part of basal disc where



Figures 2–4. **2** *Acronymolpus turbo* sp. n. **A** habitus view of paratype, body length 3.0 mm **B** apical oblique view of paratype, showing apical explanate spoon-like terminations **3** *Acronymolpus gressitti* sp. n., habitus view of holotype, body length 2.35 mm **4** *Acronymolpus meteorus* sp. n. habitus view of holotype, body length 2.6 mm.

punctures are confused and about $1.5 \times$ as large as pronotal ones; elytral interstices generally swollen, with a hint of microsculpture but nearly smooth and shining.

Ventral surfaces: prosternum nearly flat, surface \pm rough and punctulate; hypomeron with fairly heavy isodiametric sculpture, surface impunctate; metasternum with slightly smoother sculpture, sparsely micropunctate; metacoxa nearly touching posterior margin of abdominal ventrite 1; relative lengths of ventrites (cmm): $40 : 6 : 6 : 10 : 18$; surfaces subshining with hint of sculpture and sparsely micropunctate; first ventrite strongly inclined between coxae, surface irregular slightly swollen medially on inclined part, median area apparently lacking setose patch; last ventrite lacking median impression before apex.

Legs: slender; femora weakly subclavate; metatibia linear, as long as femur.

Measurements: BL 3.1 mm; BB 2.1 mm; HB 104 cm; IAS 26 cm; AS 10 cm; ORB 10 cmm; IOS 52 cmm; EYE 40×34 cmm; GENA 20 cmm; PNL 92 cm; PNB 168 cmm.

Paratype. Essentially identical to holotype. BL 3.0 mm; BB 2.0 mm.

Holotype. NEW CALEDONIA: Sarramea, Col d'Amieu, 2-23.xii.2005, Cazères, Mille, and Kataoui collectors (CXMNC/MNHN); Paratype, same locality but 2-30.xi.2005, Cazerès, Mille, and Kataoui coll. (CXMNC).

Remarks. Differs further from its close relative, *A. jolivetii*, sp. n., by having closer discal puncturation of the pronotum. The name refers to the stout, \pm conical form of the elytra.

Acronymolpus gressitti sp. n.

<http://zoobank.org/CE9C4FE9-955F-4C56-A3B6-9D0E7D70CB5F>

Fig. 3

Description (Holotype). Body moderately robust, broadest across elytral humeral region then moderately narrowed to rounded apex. Body surfaces and appendages largely piceous; antennal segments 1-2 yellow, 3-4 brownish; tarsal pads yellowish. Dorsum glabrous, venter: metasternum and first abdominal ventrite each with group of elongate pale setae. Body length 2.35 mm; body breadth 1.4 mm.

Head: frontal surfaces largely smooth, with a hint of fine sculpture; upper frons with a few large, deep punctures; postantennal swellings \pm subquadratae; oblique suture becoming deep above eye; vertex with coronal suture deep, with surfaces on each side convexly swollen; interantennal space broad, flat, about $3 \times$ as broad as antennal socket; orbit slightly broader than antennal socket; interocular space with breadth subequal to maximum eye diameter; gena not quite $0.5 \times$ as deep as eye.

Antenna rather slender, attaining apical $1/3$ of elytron; relative lengths of segments (cmm): $18 : 12 : 18 : 18 : 20 : 17 : 20 : 20 : 20 : 20 : 30$; apical 5 segments distinctly heavier than preceding ones.

Prothorax $0.59 \times$ as broad as long; base broadly convex across middle; lateral margin moderately convex; disc uniformly convex and rather uniformly punctured, punctures \pm elliptical and commonly $1 \times$ as large as interspaces; interspaces smooth with hint of microsculpture.

Elytron smooth and shining; lateral margin moderately narrowed from post-humeral area to preapex; apex convex; humerus slightly produced, smooth; inner basal disc with punctures deep, and larger than pronotal ones.

Ventral surfaces: hypomeron subshining, with fine isodiametrical sculpture; metasternum with isodiametric sculpture; metacoxae enlarged and ending slightly before apical margin of ventrite 1; relative lengths of abdominal ventrites (cmm): 32 : 8 : 6 : 10 : 16; surfaces subshining, with moderate isodiametric sculpture; first abdominal ventrite moderately inclined between coxae; last ventrite with median impression before apex.

Legs: femora subclavate, surfaces with fine sculpture; metafemur and tibia subequal in length.

Measurements: BL 235 mm; BB 1.4 mm; HB 82 cmm; IAS 20 cmm; AS 6 cmm; ORB 7 cmm; IOS 36 cmm; EYE 34 × 26 cmm; GENA 16 cmm; PNL 70 cmm; PNB 118 cmm.

Holotype. NEW CALEDONIA: Mt Panie, 500 m, 3.iii.1981, on *Freycinetia*, J. L. Gressitt collector (BPBM 16,843).

Remarks. The less tapered body form of this species separates it from *A. meteorus*, sp. n., which is very strongly narrowed apically. This is the only specimen of the genus with any information on plant associates; in this case *Freycinetia*. The name honors the late J. Linsley Gressitt, who contributed greatly to entomology of the Pacific and beyond.

***Acronymolpus meteorus* sp. n.**

<http://zoobank.org/5B958AA0-981F-4706-821A-7A275152A777>

Fig. 4

Description (Holotype). Body subrobust with elytron strongly narrowed from humeral region to briefly rounded apex. Dorsal surfaces piceous; antenna with basal 3 segments orange-testaceous, remainder piceous; venter largely piceous but coxae and abdominal ventrites reddish testaceous; legs piceous. Dorsum glabrous; venter: metasternum with sparse adpressed pubescence. Body length 2.6 mm; body breadth 1.5 mm.

Head: frontal surfaces largely with fine, isodiametric sculpture; frons fairly closely punctulate above; postantennal swellings ± oblique, not conspicuous; oblique suture a fairly deep sulcus along upper eye margin; vertex below with several large punctures on each side, coronal suture deep at mid-vertex, then obsolete above; upper vertex with moderately large punctures centrally; interantennal space about 2.75 × as broad as transverse diameter of antennal socket, surface rough, punctate; antennal socket and orbit subequal in breadth; interantennal space slightly broader than maximum eye diameter (22 : 19); eye subovate; gena slightly over 0.4 × as deep as eye.

Antenna attaining apical 1/4 of elytron; relative lengths of segments (cmm): 24 : 12 : 16 : 18 : 24 : 30 : 26 : 24 : 24 : 26 : 36; apical 5 segments distinctly heavier than preceding ones.

Prothorax about 0.60 × as long as broad; lateral margin nearly straight basally before convexly narrowed anteriorly; disc closely and heavily punctate, central punctures commonly 3–4 × as broad as raised interstices.

Elytron broadest across humeral region, then subevenly narrowed to convex apex; humerus moderately produced, very briefly impunctate; basal discal punctures closely and confusedly punctate, punctures larger and rounder than the pronotal ones, and 3-4 × as large as interspaces; elytral interstices smooth-shining with hint of microsculpture.

Ventral surfaces: hypomeron impunctate but with heavy isodiametric sculpture; metasternum with finer microsculpture, obscurely punctulate; metacoxae enlarged and ending slightly before apical margin of abdominal ventrite 1; relative lengths of ventrites (cmm): 42 : 11 : 10 : 10 : 18; surfaces with moderate isodiametric sculpture; first ventrite moderately inclined between coxae; last ventrite with median impression apically.

Legs: femora nearly smooth, with fine microsculpture; metatibia as long as femur, straight, surface with duller microsculpture than femur.

Measurements: BL 2.6 mm; BB 1.4 mm; HB 90 cmm; IAS 22 cmm; AS 8 cmm; ORB 8 cmm; IOS 44 cmm; EYE 38 × 26 cmm; GENA 16 cmm; PNL 74 cmm; PNB 124 cmm.

Paratype. Essentially identical to holotype; body length 2.6 mm; body breath 1.5 mm.

Holotype. NEW CALEDONIA: Plateau de Dogny, 700 m, 1.ii.1963, N.L.H. Krauss collector (BPBM 16,844); Paratype, NEW CALEDONIA: Col d'Amieu, 500-600 m, 28.xii.1976, J.L Gressitt coll. (BPBM).

Remarks. The uniform piceous dorsal coloration along with the closely and deeply punctate dorsal surfaces mark this species. Differs from *A. gressitti*, sp. n. by the closer pronotal puncturation and the more narrowed elytral preapex. The name refers to the pitted surface of an iron meteorite.

Key to species of *Acronymolpus* gen. n. and the separation of this genus from other New Caledonia Eumolpini

- 1 First abdominal ventrite largely occupied by enlarged metacoxae; the metacoxae nearly reaching apical margin of the ventrite (Fig. 1C) *Acronymolpus* gen. n....2
- First abdominal ventrite not occupied by enlarged metacoxae; the metacoxae extending only little into basal part of the ventrite other **Eumolpini**
- 2 Elytron each with apex adorned with a rounded knob-like or explanate spoon-like extension; elytral humeral area especially robust; dorsal color reddish fuscous with elytra basally darker..... 3
- Elytron each normally and convexly rounded without adornments; humeral area broad but less robust; dorsal color piceous 4
- 3 Pronotal disc with punctures commonly 1-2 × as large as interspaces; each elytral apex with a short broad rounded tubercle (Fig. 1B); body length 3.2–3.3 mm..... *joliveti* sp. n.
- Pronotal disc with punctures commonly 3-4 × as large as interspaces; each elytral apex with short rounded costa at side (Fig. 2B); body length 3.0–3.1 mm..... *turbo* sp. n.

- 4 Pronotal disc not so closely or deeply punctate; punctures commonly 1–2 × as large as interspaces; interspaces between punctures ± shining and flattened to slightly swollen; body length 2.35 mm**gressitti sp. n.**
- Pronotal disc closely and deeply punctate; punctures commonly 3–4 × as large as interspaces; interspaces between punctures dull and strongly raised color; body length 2.6 mm**meteorus sp. n.**

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Elevation and temporal distributions of Chrysomelidae in southeast Brazil with emphasis on the Galerucinae

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Abstract

In this study we present an ecological pattern of elevation and temporal variations found in the Chrysomelidae in one of the highest mountains in southeastern Brazil. Monthly surveys using an entomological sweep-net were conducted between April 2011 and June 2012, at five different elevations (800 m, 1000 m, 1750 m, 2200 m and 2450 m). A total of 2318 individuals were collected, belonging to 91 species. The elevation and temporal patterns of distribution of Chrysomelidae were heavily dominated by the Galerucinae. This subfamily had the highest richness and abundance at intermediate altitudes and during the rainy season. Probably the food availability as well as abiotic factors this time of the year favor the development of Galerucinae. Also, most of the more abundant Galerucinae species showed broad elevation ranges but approximately 20% of these species were only collected on the mountaintop sites. We would expect these species to be ones most prone to extinction in a scenario of climate warming or even after local disturbances.

Keywords

Altitude, distribution patterns, leaf beetle, species richness, abundance, seasonality

Introduction

Chrysomelidae is the major component of tropical herbivore guilds and it can be easily collected (Basset et al. 1996, Farrell and Erwin 1988, Wagner 2000). Linzmeier and Ribeiro-Costa (2013) noted a similar trend of the abundance pattern of Chrysomelidae and Coleoptera as a whole when using a Malaise trap. They suggested that this result is probably related to the dominance of herbivorous families sampled. In several studies, using different methodologies, the subfamily Galerucinae represented approximately 80% of all collected Chrysomelidae (Flowers and Hanson 2003, Sánchez-Reyes et al. 2014). This is the largest subfamily within the Chrysomelidae (Chaboo 2007), with 13,000 described species in approximately 1,048 genera (Gillespie et al. 2008). This subfamily includes representatives of the former subfamily Alticinae and is currently divided into two tribes, Galerucini and Alticini (Reid 1995, 2000).

Chrysomelidae larvae and adults are, for the most part, phytophagous (Jolivet and Hawkeswood 1995), which means that this group has a strong relationship with its host plant (Marques and Oliveira 2004). Abiotic factors such as precipitation and temperature can influence Chrysomelidae composition and distribution. However, these factors directly affect vegetation composition and structure, which can be a major factor in determining the composition and abundance of phytophagous insects (Sánchez-Reyes et al. 2014).

In elevation gradients host plants are exposed to various environmental factors which rapidly change over short horizontal distances (Hodkinson 2005). These factors may also affect plant phenology, size, morphology, physiology and spatial configuration which will in turn affect the populations of insects that depend upon these plants (Kronfuss and Havranek 1999). Besides that, factors as temperature, humidity, precipitation, radiation input and wind speed can directly affect the distribution of insects along elevation gradient (see Hodkinson 2005 for details). Studies on elevation gradients have been of growing interest also because the rapid changes in temperatures over short distances can provide an interesting framework to study climate warming (e.g. Parkash et al. 2013, Menéndez et al. 2014).

Studies on Chrysomelidae found on mountains show different patterns of species composition, abundance and richness along elevation gradients (e.g. Carneiro et al. 1995, Flinte et al. 2009, Furth 2009, Flinte et al. 2011, Sánchez-Reyes et al. 2014) as already described for insects in general (Hodkinson 2005). Climatic variables as well as factors associated to host plants can drive Chrysomelidae spatial distribution in such habitats and also determine their occurrence during the year. According to Wolda (1978, 1980) insects in the tropics are more abundant in the rainy season. Indeed this is supported for studies on Chrysomelidae in Brazil, which commonly show abundance peaking in the warm and rainy months (Nogueira-de-Sá et al. 2004, Linzmeier and Ribeiro-Costa 2008, Flinte et al. 2009, Linzmeier and Ribeiro-Costa 2013).

This paper aims to describe the pattern of abundance and richness of Chrysomelidae at different altitudes and throughout the year in a tropical mountain rainforest in southeast Brazil, with emphasis on the Galerucinae, and also discussing the elevation range of species in this group.

Methods

Study site

The study was conducted at Itatiaia National Park (INP), which is located in the Serra da Mantiqueira, between the States of Rio de Janeiro, São Paulo and Minas Gerais (22°15' and 22°30'S; 44°30' and 44°45'W) (Fig. 1). The park covers an area of 28,155.97 ha with elevations extending from 600 m to 2791 m a.s.l. at its highest point, called *Pico das Agulhas Negras*, one of the highest peaks in Brazil. The vegetation is classified as Atlantic Rainforest and changes along the elevation: lower montane forest (below 500 m), montane forest (from 500 to 1500 m), high-montane forest (from 1500 to 2000 m), and the *campos de altitude* (more than 2000 m) (Ururahy et al. 1983). The *campos de altitude*, also known as paramos, is a set of grass- and shrub-dominated communities varying with topography, microclimate and soil resulting in several physiognomies (Vasconcelos 2011). According to the Köppen system, the climate of the region is classified as Cwb (mesothermal, mild summer and defined rainy season for areas above 1600 m elevation) and Cpb (mesothermal, mild summer, without strong dry season in lower elevations). Precipitation is intense, with annual values around 2600 mm in the upper part of the park and 1800 mm in the lower part. The driest period occurs between May and September, while the rainy season occurs between October and April, with rainfall peaking in January. In the dry season fire can occur especially in areas of *campos de altitude* often caused by anthropogenic disturbances (Tomzhinski et al. 2012).

Sampling procedures

Monthly samples were taken from April 2011 to June 2012 at five different elevations of INP: 800 m, 1000 m, 1750 m, 2200 m and 2450. The first two sampling sites were located within montane forest, the third one was in high-montane forest and the two highest ones were in *campos de altitude*. In September 2011 and January 2012 field work was not possible due to adverse weather conditions, resulting in a total of 13 sampling months. At each site individuals of Chrysomelidae were collected using a 38 cm sided triangular entomological sweep-net. The peripheral vegetation was swept top-down and bottom-up for 12 minutes along the main paths of the park trails by two persons, one on each side, at each elevation site, totaling one hour per person per sampling date. The same two persons were responsible for the sweeping every month to minimize variability due to collector effect. The contents of the sweep net of each site were placed in a plastic bag with cotton soaked with ethyl acetate, and each bag was labelled with the site and the sampling date. In the laboratory, the chrysomelids were first separated into subfamilies, then into unique categories of morphospecies (Derraik et al. 2002), mounted and counted. In favor of simplicity morphospecies will be referred to as species in this study. Other insects were preserved in 70% alcohol. The material is deposited in the scientific collections of the "Laboratório de Ecologia de Insetos" at the Federal University of Rio de Janeiro.

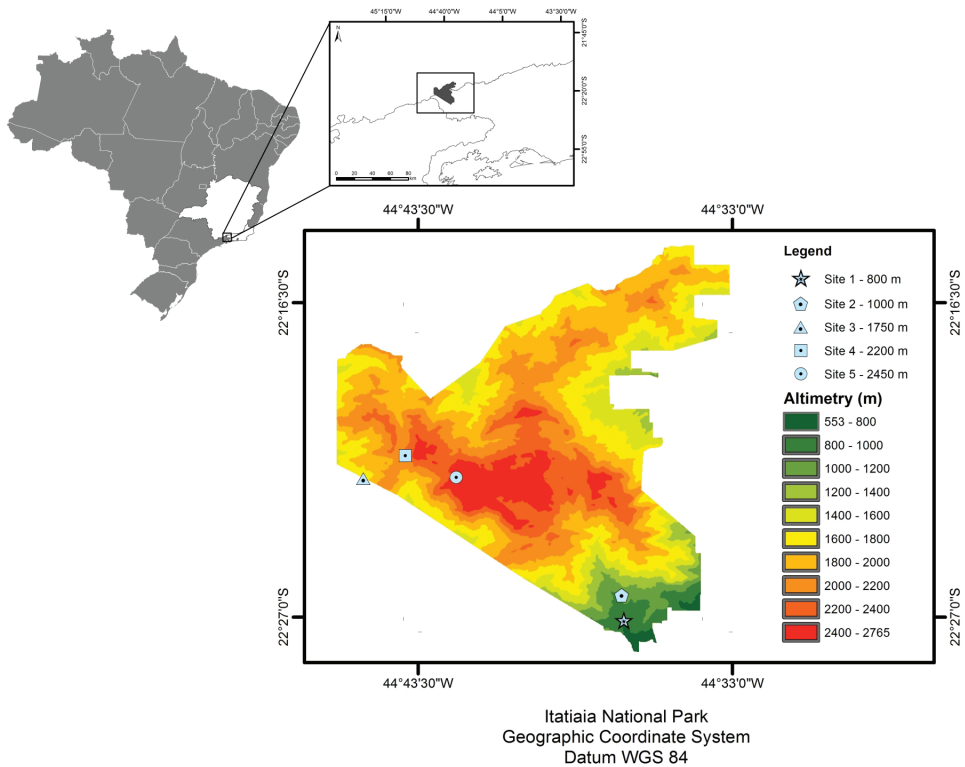


Figure 1. Location of Itatiaia National Park (IPN) in the State of Rio de Janeiro, Brazil, and location of sampling sites along study area (each site indicated by a different symbol).

Data analysis

To describe the general pattern of richness and abundance in Chrysomelidae and in each subfamily all samples were considered from all sites for the 13 months. The relative abundance of each subfamily of Chrysomelidae was based on the number of individuals in each taxon in all sites and all months, divided by the total abundance of the family. The equivalent was made to calculate relative richness.

Elevation patterns were assessed by summing up all 13 samples in each elevation site for the whole family and for the most abundant and rich subfamily in Chrysomelidae: Galerucinae. To calculate the similarity among Chrysomelidae fauna from the five sites the Bray-Curtis dissimilarity index was used, using the program STATISTICA 8.0, grouping all data of all sampling months for each site. The relative abundance of Galerucinae per elevation site was calculated for the 17 species with 10 or more individuals as: number of individuals of each species in one altitudinal site divided by the total number of individuals in all altitudes times 100.

Temporal distribution was evaluated for the Chrysomelidae species by considering all the species and individuals collected in all sites per month. The mean abundance of Galerucinae per season at each elevation site was also calculated. After testing for data

distribution normality (Shapiro-Wilk test), the Student's *t*-test was used to analyze the differences in number of individuals at each site for the wet and dry seasons, again in the program STATISTICA 8.0. Based on literature records (Tomzhinski et al. 2012), the cold and dry season was defined as April, May, June, July and August 2011; and hot and wet as October, November and December 2011, and February and March 2012. Finally, Shannon diversity index (*H'*) was used to calculate the diversity of the five sites and months, using the package "Vegan" of the software R (R Development Core Team 2012).

Results

Abundance and richness of Chrysomelidae

A total of 2,318 individuals belonging to 91 species of seven subfamilies of Chrysomelidae was obtained from sweep samples: Bruchinae, Cassidinae, Chrysomelinae, Criocerinae, Cryptocephalinae, Eumolpinae and Galerucinae (Table 1). The number of individuals per species ranged from one to 665. Galerucinae was the most abundant group, with 2,123 specimens, representing more than 90% of all individuals sampled, followed by Eumolpinae (4.9%) and Criocerinae (1.5%). Galerucinae was also the subfamily with the highest richness (53 species or 58.2% of all sampled species), followed by Cassidinae and Criocerinae (each with 9.9% of the total richness), and Eumolpinae (8.8%) (Table 1). Within the Galerucinae the tribe Alticini was much more abundant and had more species than the Galerucini, totaling 98.2% of the individuals and 69.8% of the species collected.

Elevation distribution

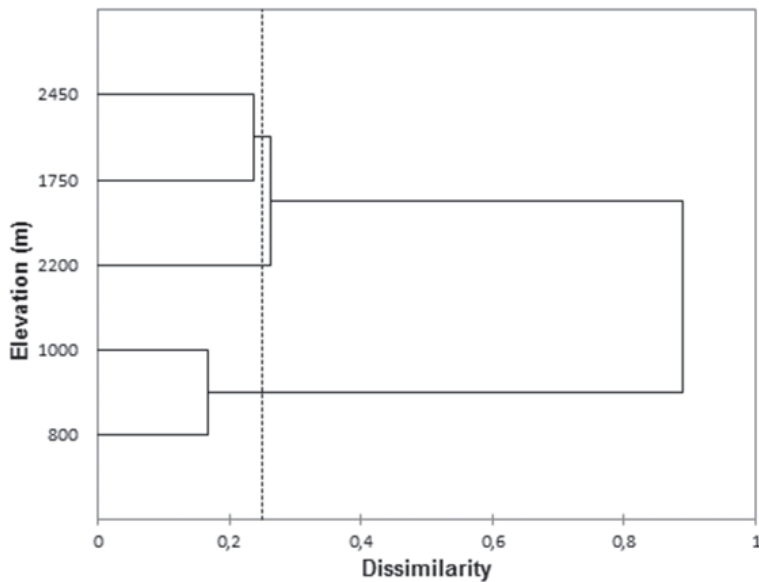
Richness and abundance of Chrysomelidae were different among the five elevations (Table 2). Although 1750 m showed the highest species richness, the greatest abun-

Table 1. Abundance, relative abundance, species richness and relative richness of the seven Chrysomelidae subfamilies.

Subfamilies	Abundance	Relative abundance (%)	Richness	Relative richness (%)
Bruchinae	10	0.4	2	2.2
Cassidinae	21	0.9	9	9.9
Chrysomelinae	8	0.4	6	6.6
Criocerinae	36	1.6	9	9.9
Cryptocephalinae	6	0.3	4	4.4
Eumolpinae	114	4.9	8	8.8
Galerucinae	2123	91.6	53	58.2
TOTAL	2318	100	91	100

Table 2. Richness, abundance and diversity of Chrysomelidae sampled with sweep nets in five elevation sites of Itatiaia National Park.

Elevation	800 m	1000 m	1750 m	2200 m	2450 m
Richness	35	28	43	29	35
Abundance	128	78	384	1246	482
Diversity	2.9	3.0	2.6	2.1	2.5

**Figure 2.** Cluster analysis grouping different elevational sites in Itatiaia National Park, calculated with Bray-Curtis dissimilarity index. The closer to zero, the more similar is the species composition between altitudes.

dance was recorded at 2200 m. The highest site, at 2450 m, was the second in both richness and abundance. Diversity was highest at 1000 m, where the number of species and abundance were the lowest, and lowest at 2200 m, where the number of species was the second lowest and abundance was the highest. Similarity analysis grouped sites at 800 m and 1000 m as the most similar ones. The sites at 1750 m and 2450 m elevations were also quite similar in species composition and similar to the one at 2200 m. However, these three upper sites presented very distinct species of Chrysomelidae compared to the two lower sites (Fig. 2).

Considering that Galerucinae was the most abundant subfamily and presented the highest species richness, its altitudinal distribution was assessed in more detail. The abundance of Galerucinae reached its peak at 2200 m with 1,152 individuals, declining abruptly to 446 individuals at 2450 m. Even so, the highest site showed a greater abundance than the three lowest ones (Fig. 3). The highest species richness of Galerucinae was observed at 1750 m, followed by the two lowest sites, and at 2200 m

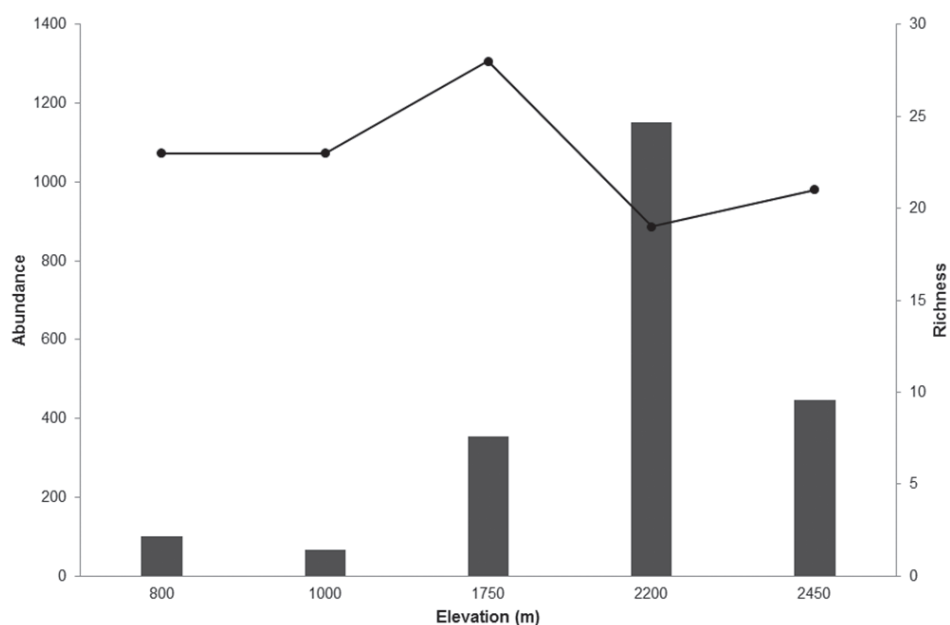


Figure 3. Elevational variation of species richness (line) and abundance (bars) of Galerucinae sampled with sweet nets in Itatiaia National Park.

Table 3. Abundance and species richness of Galerucini and Alticini and the relative abundance and richness of Alticini in each altitudinal site at Itatiaia National Park.

Elevation	Abundance			Richness		
	Galerucini	Alticini	Alticini (%)	Galerucini	Alticini	Alticini (%)
800 m	15	87	85.3	6	17	73.9
1000 m	5	63	92.6	3	20	87.0
1750 m	12	343	96.6	5	23	82.1
2200 m	4	1148	99.7	3	16	84.2
2450 m	3	443	99.3	2	19	90.5
Total	39	2084	98.2	16	37	69.8

the lowest richness was recorded (Fig. 3). The tribe Alticini was more abundant and species-rich than Galerucini and tended to be relatively more abundant and rich with increasing elevation (Table 3). These two groups, although in the same subfamily, seem to show different patterns of abundance distribution across elevational range, with the Alticini being more abundant at the two highest sites and Galerucini at the three lowest ones. Species richness seems also to be different as the mid-elevation site was the one to have more Alticini species but with many species in all elevation sites, and Galerucini decreasing in species richness with increasing elevation (Table 3).

Of the 53 species of Galerucinae only 17 had more than 10 individuals sampled during the whole period. Three out of these 17 species were recorded at only one or

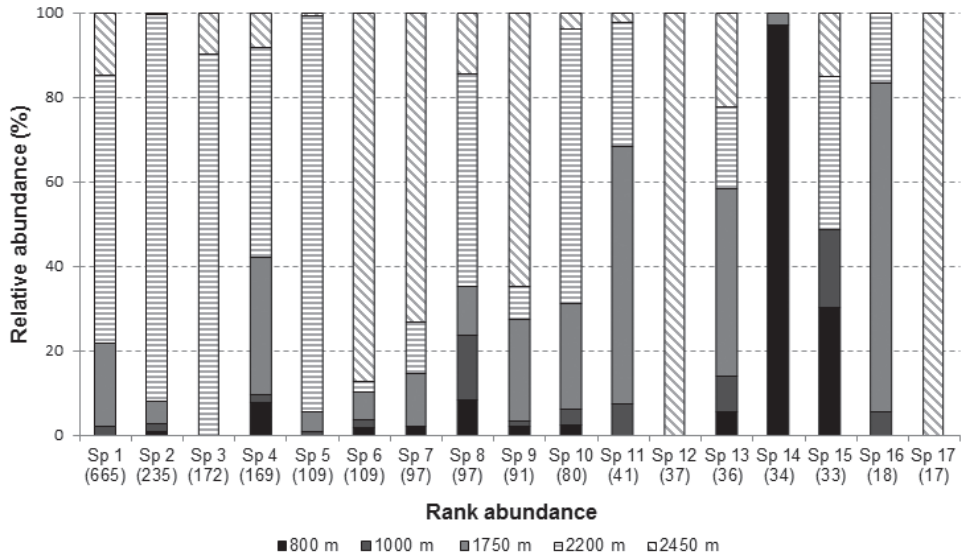


Figure 4. Relative abundance per elevation of the 17 Galerucinae species with more than 10 individuals sampled in the entire study period. Species are arranged from the most (left) to the less (right) abundant one. Number of individuals of each species are within brackets. Texture represents the high fields and color lowest elevations.

two elevations, showing a more restricted altitudinal distribution than the 14 other species, which were collected from three or more elevation sites. This means that there is a significantly greater frequency of species with broad distribution ($\chi^2 = 7.11$; $P < 0.008$). The three species with restricted distribution were precisely those that occurred in *campos de altitude* (2200 and 2450 m) (Fig. 4). Ten out of the remaining 14 species presented a wide distribution, occurring at all elevations, two did not occur only at the lowest site, one did not occur at the lowest and highest sites, and one did not occur at the two highest elevations (Fig. 4).

Temporal distribution

The abundance of individuals and species richness of Chrysomelidae varied widely over time. However, the lowest values were found in the months of the dry season, while the highest were those during the wet season (Table 4). At all elevations a higher average abundance of Chrysomelidae was found in the wet season compared to the dry season, but this difference was only significant at 1000 m and 1750 m (Table 5).

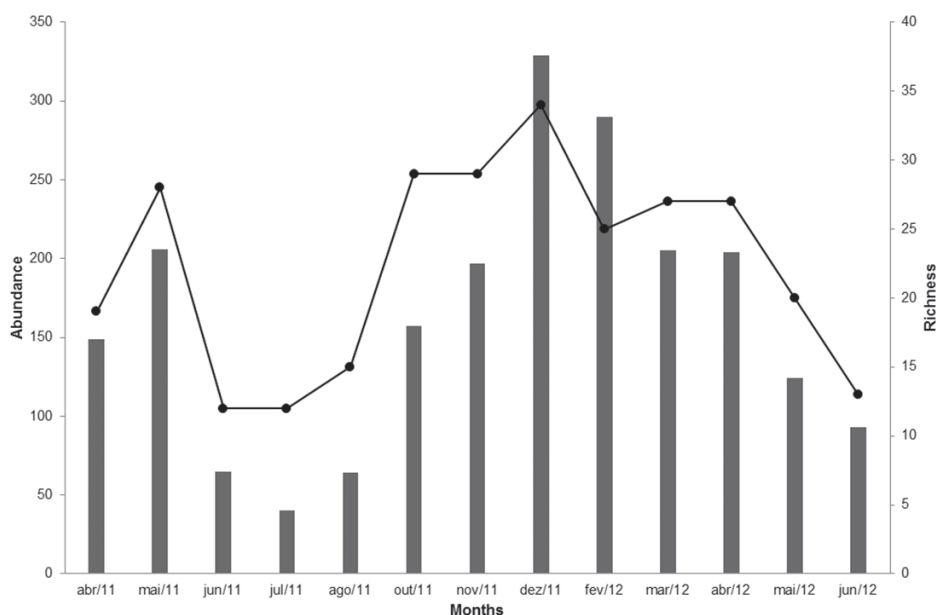
Between the two seasons there is clearly a continuation in the increase or decrease in abundance. The richness and abundance of Galerucinae varied similarly when analyzed throughout the study period (Fig. 5). December 2011 and February 2012, warmer and wetter months, showed the highest abundance, 329 and 290 individuals, and richness,

Table 4. Richness, abundance and Shannon diversity index of Chrysomelidae in Itatiaia National Park from April 2011 to June 2012.

Months	Dry season 2011					Wet season 2011-2012					Dry season 2012		
	A	M	J	J	A	O	N	D	F	M	A	M	J
S	19	28	12	12	15	29	29	34	25	27	27	20	13
N	165	218	67	51	71	178	215	365	303	229	222	131	103
H'	2.1	2.1	2.0	1.9	1.6	2.4	2.6	2.4	2.3	2.5	2.5	2.1	2.0

Table 5. Mean abundance (standard deviation) of Chrysomelidae in the dry (April, May, June, July and August 2011) and wet (October, November and December 2011, and February and March 2012) seasons, compared with Student's t-test. Values followed by * had significant difference ($p < 0.05$).

Elevation	Mean abundance (SD)		t-value	DF	p
	Dry	Wet			
800 m	8.4 (7.0)	11.0 (6.3)	-6.6	8	0.553
1000 m	3.4 (1.5)	6.6 (1.5)	-3.3	8	0.010*
1750 m	13 (17.1)	51 (20.0)	-3.2	8	0.012*
2200 m	63.6 (41.1)	126.2 (68.9)	-1.7	8	0.119
2450 m	24.4 (32.9)	64.2 (22.7)	-2.2	8	0.056

**Figure 5.** Variation of abundance (bars) and richness (line) of Galerucinae sampled with sweep nets during the study period, from April 2011 to June 2012.

34 and 25 species, respectively. The colder and drier months, June, July and August 2011 had the lowest abundance values, 65, 40 and 64 individuals, respectively, and also the lowest richness, ranging from 12 species in June and July to 15 in August (Fig. 5).

Discussion

This study presents the first record of elevation and temporal variation of Chrysomelidae in Itatiaia National Park, Rio de Janeiro State, the oldest national park in Brazil. We collected a total of 2,318 individuals in 91 species over 13 months at five different elevations, with more than 90% of the total sample from the subfamily Galerucinae. Thus, the elevation and temporal patterns of distribution of Chrysomelidae are largely determined by subfamily Galerucinae, especially by the tribe Alticini. The group had the highest richness and abundance at intermediate altitudes and in the rainy season. Most of the more abundant Galerucinae species presented broad elevation ranges but approximately 17% of these species were only collected in the mountaintop sites. The results are discussed in relation to other studies on Chrysomelidae and under a scenario of climate change.

Sanchez-Reyes et al. (2014) studying Chrysomelidae diversity in altitudinal gradient in Mexico using the sweep-net technique also found Galerucinae as the most abundant (82.1%) and species-rich (49%) subfamily. Although the order of importance of the other subfamilies was different from our results in both abundance and species richness, they all had low abundance and richness. Galerucinae has important features that could explain its great abundance in these studies. They are highly specialized insects feeding on a wide range of plant groups, especially the Angiospermae (Konstantinov and Vandenberg 1996) and the tribe Alticini, the far most abundant of the Galerucinae, with 8,000 species (Furth 1988, Konstantinov and Vandenberg 1996), has the ability to jump, which could facilitate their movement through vegetation and consequent collection by traps (Ge et al. 2011).

The most abundant site for Chrysomelidae was at 2200 m and species richness was highest at 1750 m. The highest species richness occurred at an intermediate site as observed in several other studies with insects belonging to different groups (e.g. Janzen 1973, Janzen et al. 1976, McCoy 1990, Fernandez et. al 2010). Furth (2009) in his study with Alticini in Mexico showed that in an altitudinal gradient ranging from 600 to 2400 m, the highest species richness also occurred at the intermediate elevation of 1990 m. However, he only collected at the lowest altitudes during the dry season and mid-rainy season. The fact that lower altitudes are warmer and nearly subtropical in climate shows a possibility that more intense collecting at the lower altitudes would produce higher species richness at lower elevations. Sánchez-Reyes et al. (2014) also found greater species richness of Chrysomelidae at intermediate elevations.

According to Janzen et al. (1976), species richness peaks at middle elevations, rather than at low elevations. Photosynthetic rates and respiratory rates of plants are assumed to be high at low elevations and low at high elevations; as a result, the net accumulation of photosynthate is highest at mid-elevations. An increase in energy available to the intermediate elevation herbivorous community should result in more insect species rather than a mere increase in biomass, because of the subsequent ecological processes (Janzen 1973, Janzen et al. 1976). Also, upper limits of distributions are set mostly by climatic severity and resource restriction, and lower limits mostly by climatic severity and predation (Gagne 1979, Randall 1982a, 1982b, Young 1982, Smiley and

Rank 1986). Therefore, the middle of the mountain would be more favorable to the existence of more species.

Chrysomelidae and Galerucinae abundance increased up to 2200 m and abruptly decreased at 2450 m, which was the second most abundant site, suggesting that this group lives better in higher elevation areas, though peaking at intermediate elevations. Flowers and Hanson (2003) also observed higher values of abundance at intermediate elevations, but the relative importance of Alticini increased with elevation also suggesting that this group is more successful than the others at higher altitudes. This suggests that Alticini and Galerucini should be studied in more detail regarding their altitudinal distribution patterns in order to understand which factors can be important in determining such a difference. In contrast to the abundance, Chrysomelidae diversity remained high when the abundance was low and low when the abundance was high. This pattern was also recorded by Jones et al. (2012) studying the phytophagous family Apionidae (Coleoptera: Curculionoidea) of three different forests, tropical deciduous forest, cloud forest and oak/pine forest. Higher diversity in tropical vegetation was the result of both greater number of species and more uniform abundance patterns. In the oak/pine forest the uniformity of species abundance as low, reducing diversity measures.

On the other hand, Sánchez-Reyes et al. (2014) observed a decrease in Chrysomelidae abundance and an increase in the diversity with increasing elevation. According to these authors, as the Chrysomelidae are phytophagous, plant composition could be seen as the main factor to influence abundance and species richness. However, other factors must also influence the insects at different levels along an elevation gradient, such as temperature, sunlight, wind, etc. as reviewed by Hodkinson (2005).

Most of the common Galerucinae species were broadly distributed over the mountain; however, almost 20% of the species presented quite narrow elevation ranges, only occurring in the *campos de altitude* on the mountaintops, which is considered to be a habitat with high frequency of endemic species (Martinelli 1996). Studies have predicted that climate change will cause mountain species to shift their distribution upslope (e.g. Parmesan 1996, Parkash et al. 2013, Menéndez et al. 2014). In such a scenario we would expect these species which only occur on the mountaintops to be ones most prone to extinction, as the microclimates at the top of the mountain are those most likely to disappear. Moreover, there are other threats that make this habitat especially vulnerable, such as fire and burning, extraction of attractive species of the flora, hunting, and invasive species. It is really urgent to study species biology and their elevation ranges, so that we can predict how organisms alter their distribution and adapt to environmental changes (Maveety et al. 2011) and plan conservation strategies to protect this unique biota, as suggested by Macedo et al. (in press).

The Chrysomelidae presented greater abundance in wetter and warmer months, a pattern already observed in other studies on the group (e.g. Linzmeier and Ribeiro-Costa 2008, 2013, Sanchez-Reyes et al. 2014). The large number of individuals at this time of year seems to be highly related to the environmental requirements of the main group collected in the study, Galerucinae. Most of the species in this subfamily have root-feeding larvae and the adults feed on the leaves. Thus, food availability as well as

abiotic factors at this time of the year favors the development of Galerucinae. Although the Galerucinae species seem to be widely polyphagous (Pokon et al. 2005), which could make it easier for them to survive and reproduce throughout the year, the relatively seasonal climate observed at higher altitudes (e.g. Flinte et al. 2009) may represent a constraint to their occurrence throughout the year. Studies on Chrysomelidae phenologies in mountainous areas at similar latitudes have been showing that these species tend to be more similar to subtropical and temperate species than to those on tropical areas at sea level (e.g. Nogueira-de-Sá et al. 2004, Flinte et al. 2015). Even though, the difference in abundance was only significant at 1000 m and 1750 m, the relative difference between the means of the dry and the wet seasons was lowest at the lowest site. We suggest that our results also point in this direction, but more detailed studies on a finer scale across elevation gradients is necessary to confirm this pattern.

The temporal variation in species richness and diversity followed the same pattern of variation in abundance confirming the importance of seasonality to the diversity of Chrysomelidae.

The results of this study highlight the importance of studying and conserving mountainous areas in Brazil as these are hotspots of biodiversity and endemism (Körner 2002, Martinelli 2007), and also subject to intense threats (listed in Martinelli 2007, Tomzhinski 2012).

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Biology and phenology of three leaf beetle species (Chrysomelidae) in a montane forest in southeast Brazil*

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Abstract

The population phenology of the cassidines, *Coptocycla arcuata* and *Omaspides trichroa*, and the chrysomeline, *Platyphora axillaris*, was studied at Serra dos Órgãos National Park, State of Rio de Janeiro, southeast Brazil. Monthly surveys of larvae and adults were conducted between 2008 and 2011 at approximately 1000 m altitude on their respective host plants, *Cordia polycephala* (Boraginaceae), *Ipomoea philomega* (Convolvulaceae) and *Solanum scuticum* (Solanaceae). This is the first observation of larviparity and host record for *P. axillaris*. Although having different life history traits, all species showed similar phenologies. They were abundant from October to March, months of high temperatures and intense rainfall, with two distinct reproductive peaks in the same season. Abundance dropped abruptly during the coldest and driest months, from May to August. Frequently none of these species were recorded during June and July. This phenological pattern is similar to other Chrysomelidae living in subtropical areas of Brazil. Temperature and rainfall appear to be the major factors influencing the fluctuation of these three species.

Keywords

Population fluctuation, viviparity, host plant, altitude, climate

* Extended version of a presentation to the 2nd European Symposium on the Chrysomelidae, York (England), August 4, 2014

Introduction

Phenology can be considered a temporal dimension of natural history, and because both include timing of growth, reproduction and senescence, they are sometimes used as synonyms (Forrest and Miller-Rushing 2010). However, phenology does not include non-temporal aspects of life history, which in turn can affect phenology. The same authors point out that the proximate causes of phenological events are a combination of an organism's genes and several external environmental factors, such as temperature, precipitation and photoperiod.

The role of abiotic variables in species phenology increases concern in how climatic change will affect species' temporal and spatial distributions. Efforts are being made to predict biotic responses in relation to abiotic changes (see references in Forrest and Miller-Rushing 2010, Cleland et al. 2012). Several studies were recently started on mountains, since differing altitudes can simulate a gradient of environmental conditions similar to increasing latitude but within a small geographical range (Hodkinson 2005), thereby facilitating ecological research. Distribution and population fluctuations of phytophagous insects on mountains depend on a sum of factors such as thermal requirements for growth, temperature tolerance, dispersal ability, host plant quality and distribution, phenological synchrony with host plants, and interactions with competitors, parasites and predators (Alonso 1999, Obermaier and Zwolfer 1999, Lazzari and Lazzarotto 2005, references in Hodkinson 2005, Merrill et al. 2008).

Interestingly, previous studies on Chrysomelidae in Brazil (e.g. Nogueira-de-Sá et al. 2004, Flinte et al. 2009, 2010, 2011) showed that tropical species on mountains exhibit population fluctuations similar to species in subtropical areas, i.e. these beetles did not occur throughout the year as their tropical lowland neighbors, but rather had a restricted occurrence and disappeared during a period of the year. Below we describe aspects of the life history and phenology of three leaf beetle species in a tropical montane forest.

Methods

Surveys were undertaken along the main road of the Serra dos Órgãos National Park (22°26'56"S and 42°59'5"W) in the county of Teresópolis, at approximately 1000 m altitude, characterized by montane rain forest. The Park lies in a mountainous area of the State of Rio de Janeiro, southeast Brazil, with elevations extending from 80 to 2263 m a.s.l. The climate in the region is tropical mesothermic (Köppen 1936), with a short dry season, mild summers and lower temperature due to the altitude. During the study, June to August were the coldest (mean temperature of 15.2 °C) and driest (mean of 81.1 mm monthly rainfall) months, while December to February were the warmest (mean temperature of 20.9 °C) and wettest (mean of 350.2 mm monthly rainfall) months (data from the National Institute of Meteorology at 980 m altitude, from 2008 to 2011).

Our study focuses on three abundant chrysomelid species previously observed by the author in the area, two cassidines and one chrysomeline. Study periods varied by species, but generally corresponded to the period from November 2008 to June 2011. Host plants were marked and thoroughly inspected for insects in periodic surveys, but it was not uncommon for plants to be accidentally cut down or to disappear during the study, which can explain some differences in host numbers between consecutive surveys. Host plant numbers and survey periods are presented below for each study species.

Coptocycla (Podostraba) arcuata (Swederus, 1787) (Cassidinae: Cassidini) feeds on the small shrub, *Cordia polycephala* (Boraginaceae) (Flinte et al. 2008), and was observed once or twice per month from November 2009 to June 2011. This species also feeds on *C. urticifolia* in the area (Flinte et al. 2008), but in a much lower frequency (Flinte, pers. obs.). Twenty plants of *C. polycephala* were surveyed from November 2009 to July 2010, and 30 plants from August 2010 to June 2011, an overall total of 20 months and 33 surveys.

Omaspides (s. str.) trichroa (Boheman, 1854) (Cassidinae: Stolinae) feeds on the vine *Ipomoea philomega* (Convolvulaceae) (Flinte et al. 2008) and was surveyed one to four times per month from November 2008 to March 2011, a total of 29 months and 69 surveys. Because leaves almost completely disappeared during some months of the year, the number of plants inspected varied between five and 24.

Platyphora axillaris Germar, 1824 (Chrysomelinae) feeds on the shrub *Solanum scuticum* (Solanaceae) and was studied from February 2009 to June 2011 (between one and four surveys per month). A total of 29 months and 78 surveys were conducted for this species. The number of plants surveyed varied from 14 to 46. There are no published accounts of this species.

During inspection, adults and larvae of all species, and eggs of *O. trichroa*, were counted and observations were made regarding life history and behavior traits. Beetles were on occasions brought to the laboratory and reared in plastic containers with host plant leaves to complement field observations and to obtain parasitoids. Parasitized egg masses of *O. trichroa* found in field were brought to the lab to obtain parasitism rates within clutches. The total number of records of adults and larvae on upper and lower sides of the leaves was also registered. Although it is possible that the same individual was recorded more than once, adults and larvae of the studied species are mobile, so their location could vary from one survey to another. Beetle, plant and parasitoid specimens are deposited in the collection of the Laboratório de Ecologia de Insetos, Universidade Federal do Rio de Janeiro, Brazil.

Due to the different numbers of host plants inspected on each survey we calculated the density of insects per plant for each beetle species to describe patterns of phenology. In addition to adults and larvae, densities were also calculated for egg masses and larval aggregations of *O. trichroa*, and for young larvae of *C. arcuata*, as eggs are difficult to find in field. Densities were calculated separately for each survey, multiplied by 100 (to avoid decimals) and finally the mean density was determined for each month. Thus, a monthly mean density of 200, for example, indicates that for that stage, on average, 200 individuals were found per 100 plants on a given month, or two individuals per

plant. Plant phenology was evaluated simply by the presence or absence of new leaf shoots for each individual inspected on each survey. The percentage of host plants with new shoots was calculated for each survey, dividing the number of plants with new shoots by the number of plants inspected and multiplying the result by 100. The mean percentage was then calculated for each month. The monthly mean density of beetles was correlated (Pearson correlation) with plant phenology and climate variables (temperature and rainfall). Lagged correlations of one, two and three months were made as well. The percentage of plants occupied by beetles (adult or larva) was also calculated to evaluate the intensity of attacks on plants and the spatial distribution of beetles on their host plants. Here, for each survey, the number of attacked plants was divided by the number of surveyed plants and multiplied by 100 to be expressed as percentage; then the mean and maximum percentages (considering all surveys) were established.

Results

Biological and behavioral traits

Coptocycla arcuata deposits single, flattened, membranous eggs, and *O. trichroa* deposits a mass of hard elliptical eggs which are guarded by the mother; both species lay eggs on the underside of leaves ($n = 6$ for *C. arcuata* and $n = 167$ records for *O. trichroa*). The solitary larvae of *C. arcuata* carry an exuvio-fecal shield, resembling an elliptical blob of wet feces (Fig. 1A). The larvae of *O. trichroa* occur in large (59.6 ± 16.1 ($n = 113$)) maternally-guarded aggregations. Individual larvae bear a reduced shield composed more of exuvia than feces (Fig. 1B). Larvae of both species exhibited repeated and rapid flexing movements of shields when disturbed. Adults of *C. arcuata* tended to fly when approached. *Platyphora axillaris* is larviparous and its greenish larvae are deposited singularly and remain solitary throughout their development, later becoming brownish in colour (Fig. 1C). No maternal care was observed for this species. When manipulated, larvae regurgitate, as do adults, which additionally feign death as a defense. Larvae of all three species and adults of *O. trichroa* were mainly found on the underside of leaves, while adults of *C. arcuata* and *P. axillaris* preferred the upper side (Table 1). Field observations showed that *C. arcuata* pupates on the underside of leaves ($n = 22$ records) and *O. trichroa* on stems ($n = 17$ records of aggregations). Pupae of *P. axillaris* were only observed in the lab, buried in the soil placed at the bottom of the rearing container.

The phoretic wasp *Emersonella pubipennis* Hansson, 2002 (Hymenoptera: Eulophidae) (Fig. 1B) oviposited on freshly laid eggs of *O. trichroa*. Egg parasitism within clutches was 97.9% (ranging from 95 to 100%; $n = 8$ egg masses), but the percentage of parasitized clutches in the population is unknown. Even when parasitized, *O. trichroa* mothers continued to care for their eggs. For this species we also obtained *Brachymeria* sp. (Hymenoptera: Chalcididae) parasitoids from pupae, and a tachinid fly species from prepupa. On one occasion, a Vespidae wasp was observed attacking a group of larvae

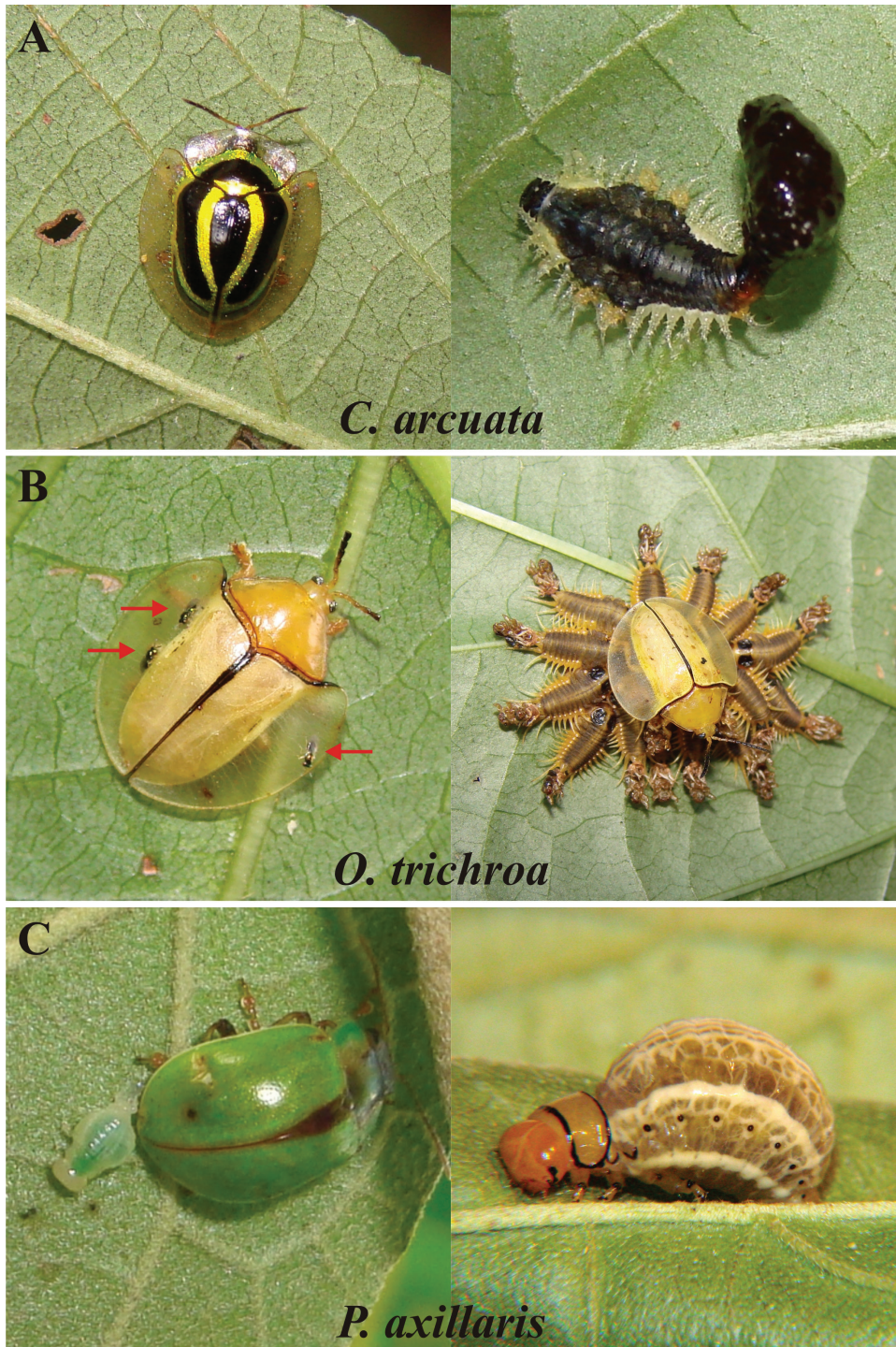


Figure 1. Adults and larvae of the study species: *Coptocycla arcuata* (A), *Omaspides trichroa* (B) and *Platyphora axillaris* (C), in a montane rain forest in southeast Brazil. Arrows in B show phoretic wasps.

Table 1. Percentage and total number of records of adults and larvae (larval aggregations for *O. trichroa*) on the upper and lower side of host plant leaves.

Species	Stage	Upper side (%)	Lower side (%)	N
<i>Coptocycla arcuata</i>	Adults	61.5	38.5	422
	Larvae	1.5	98.5	67
<i>Omaspides trichroa</i>	Adults	2.9	97.1	888
	Larval aggregations	0.0	100.0	190
<i>Platyphora axillaris</i>	Adults	76.2	23.8	632
	Larvae	8.3	91.7	223

without a caring mother (Khattar, pers. comm.). It approached the group, grasped a larva, turning it over, and flew away, returning soon after to grasp another one. When the same wasp moved towards a nearby group of larvae with attending mother, the mother made rapid movements in its direction, driving the wasp away. An unidentified species of tachinid fly emerged from a *P. axillaris* larva brought from the field.

Population fluctuations

Densities of the three chrysomelid species varied similarly throughout the year, with higher numbers from October to March (spring and summer), and lower numbers or even absence of beetles from June to August (Fig. 2). The period of absence varied between species, being shorter in *P. axillaris* (one or two months) and larger in *O. trichroa* (five months). Fluctuations in densities (per 100 plants) of different stages also followed similar trajectories for the three species, as follows.

Omaspides trichroa was studied during two whole reproductive seasons, 2009/2010 and 2010/2011. Adults and egg masses started to be found in September 2009 in the first season and in October 2010 in the second season, and larvae always appeared one month later. Densities of egg masses and larvae peaked right away, then decreased abruptly in November (eggs) and December 2009 (larvae), increasing again and peaking once more in January (eggs) and February 2010 (larvae). Exactly the same pattern was observed in the following season, with exception that densities of eggs and larvae decreased together in December 2010. Density of adults also showed this bimodal pattern of occurrence in two consecutive seasons. Densities of all stages then decreased rapidly and disappeared completely from May until the following season. Studies on *C. arcuata* started in the beginning of the reproductive season 2009/2010 and extended until the end of the season 2010/2011. Adults were first found in September, and larvae one month later. Density of young larvae (as an approximation of the egg stage) and total larval density varied similarly, peaking in the first season in January 2010 and in the second season in December 2010, decreasing and reaching another peak in March 2010 and February 2011. Adults of this species also showed two peaks of occurrence. *Platyphora axillaris* was studied also during seasons 2009/2010 and 2010/2011. Densities of adults peaked at least twice in

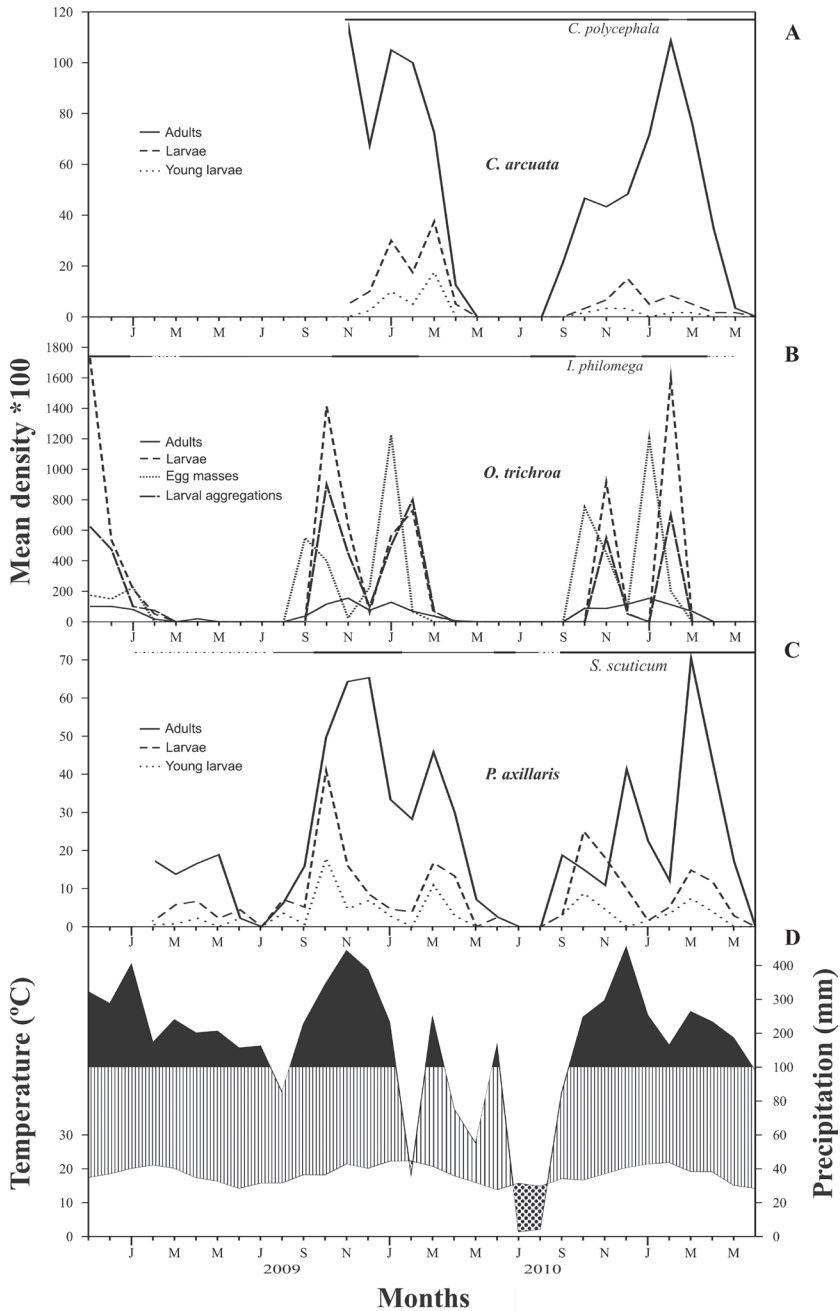


Figure 2. Population phenology of *C. arcuata* (A), *O. trichroa* (B) and *P. axillaris* (C) in a montane forest at 1000 m altitude between November 2008 and June 2011. A climatic diagram (data obtained from a meteorological station in the same site) is given for the same period as surveys (D). Dotted area = dry period; striped area = humid period; black area = super-humid period. The line above species fluctuations represents the percentage of host plant with new leaf shoots, the dotted line being < 25% of plants in this phase; fine line between 25% and 75%; thick line > 75%.

each reproductive season, once or twice in the end of the year and then again in March, and their larvae earlier in October and a second time in March, during two consecutive seasons. Overall, densities of all stages showed two peaks in each reproductive season for the three species, suggesting the existence of two generations per year, i.e. bivoltine reproduction. Numbers of all species decreased in April and some completely disappeared in subsequent months, increasing again in September (Fig. 2).

The seasonal fluctuation of beetle densities correlated with variations of temperature and rainfall throughout the year, with high numbers coinciding with super-humid periods (precipitation above 100 mm per month) and warmer months in the study area (Fig. 2). Significant correlations were obtained in most cases between beetle densities, both adult and larval, and temperature and precipitation values (Table 2). On the other hand, plant phenology, more specifically the presence of new leaf shoots, was only positively related to density of *O. trichroa* adults, but not for larval aggregations. The majority of host plants of the two other species seem to be adding new leaves throughout the year (Fig. 2), although neither the intensity of this production per plant nor the nutritional quality of leaves were measured. Lagged correlations of one, two and three months did not show more significant results.

Although fluctuation patterns were similar among species, their numbers could differ by an order of magnitude, especially for *O. trichroa*, in which larval density reached 17 times that of the adults (for larval aggregations the number was six times higher than adults). For the other two species, adults were generally more abundant than larvae (Fig. 2). Maximum density was 2.7 adults per plant for *O. trichroa*, 1.8 for *C. arcuata* and 0.9 for *P. axillaris*. Larval maximum density was 37.0 individuals per plant for *O. trichroa*, but considering larval aggregations, maximum density dropped to 0.7 per plant, similar to 0.6 found for the larvae of the other two species. The mean percentage of plants occupied by any beetle, adult or larva, was 31% for *O. trichroa*, 30.9% for *C. arcuata* and 16.1% for *P. axillaris*, varying from a minimum of zero for all three species to a maximum of 70%, 80% and 38.9%, respectively, of attacked plants per survey.

Table 2. Correlations (Pearson) between monthly mean density of adults and larvae of *C. arcuata*, *O. trichroa* and *P. axillaris* and monthly mean temperature, total precipitation per month and monthly mean percentage of plants with new shoots. For *O. trichroa* densities of larval aggregations are given. Number of months used are given by n.

Species	Stage	Temperature (°C)	Precipitation (mm)	Plants with new shoots
<i>Coptocycla arcuata</i>	adults	r = 0.922*** (n=20)	r = 0.493* (n=20)	r = -0.191 (n=20)
	larvae	r = 0.655** (n=20)	r = 0.267 (n=20)	r = 0.014 (n=20)
<i>Omaspides trichroa</i>	adults	r = 0.665*** (n=29)	r = 0.702*** (n=29)	r = 0.410* (n=29)
	aggregations	r = 0.422* (n=29)	r = 0.260 (n=29)	r = 0.280 (n=29)
<i>Platyphora axillaris</i>	adults	r = 0.608*** (n=29)	r = 0.728*** (n=29)	r = 0.319 (n=18)
	larvae	r = 0.218 (n=29)	r = 0.558** (n=29)	r = 0.336 (n=18)

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Discussion

This study describes aspects of the natural history and phenology for three Chrysomelidae species occurring at 1000 m altitude in SE Brazil. Our results document that, despite differences in life history traits occurring among these three taxonomically distinct species, all present a similar two-peak pattern of reproduction during the warmest and wettest months of the year. Below our findings are discussed in the context of previous reports on Neotropical Chrysomelidae.

Earlier studies documented that *O. trichroa* feeds on only a single plant species at the study area, whereas *C. arcuata* feeds on two related plants (Flinte et al. 2008), which was confirmed in this work. Field observations also confirmed the findings of these authors that *C. arcuata* and *O. trichroa* are oviparous and construct an exuvio-fecal shield as larvae (Fig. 1A, B). However, the observations that *P. axillaris* is larviparous (Fig. 1C) and feeds on *S. scuticum*, are unique and reported here for the first time. *Platyphora* is a neotropical genus (Daccordi 1996), containing species closely associated with Solanaceae host plants (Jolivet and Hawkeswood 1995), with viviparous habits (Vasconcellos-Neto and Jolivet 1994, Bernardi and Scivittaro 1991, Schroder et al. 1994, Olckers 2000, Windsor et al. 2013) and some species showing maternal care (Windsor et al. 2013). Together with egg covering, female site selection and maternal care, viviparity is likely a mean of defending the vulnerable egg stage (Hilker 1994).

The preferences of adults of *C. arcuata* and *P. axillaris* for the upper side of leaves (Table 1) can be related to possible defenses of aposematic and cryptic coloration, respectively, but experiments are necessary to test this hypothesis. Additionally, many species of *Platyphora* are known to have chemical defenses, secreting secondary plant metabolites through elytral and pronotal exocrine glands (Pasteels et al. 2001). On the other hand, adults of *O. trichroa*, mainly represented by mothers, were found more often on the underside of leaves, where they can protect their young inconspicuously. Larvae of all species were recorded frequently on the underside of leaves, where it is harder for flying visual predators to detect them. Nogueira-de-Sá and Vasconcellos-Neto (2003) obtained similar results for young larvae of three other Cassidinae species and suggest that their position is explained by female site selection, in an effort to protect immature stages from visually oriented natural enemies and unfavorable abiotic conditions. Indeed, it has recently been shown that maternal oviposition choices (site/leaf) significantly impact the effectiveness of larval tortoise beetle defenses and survival (Vencl et al. 2013). The fleshy larvae of *P. axillaris* seem especially vulnerable compared to those of Cassidinae, which have a dorsal shield (a common defense in the subfamily – Olmstead 1996) and/or maternal care (a defense limited to Chrysomelinae and Cassidinae – Windsor and Choe 1994). However, they do regurgitate when disturbed, a potentially defensive behavior amongst many chrysomelids (Pasteels et al. 1988). Nonetheless parasitoids were capable of circumventing these defenses as were found attacking *O. trichroa* and *P. axillaris*. Cassidinae and Chrysomelinae are frequently parasitized by Hymenoptera and Tachinidae (Diptera) (Cox 1994, 1996). According to Caignet et al. (2008), more than half of the tortoise beetle species of Panama have egg parasitoids

of the Eulophidae family, mostly *Emersonella* spp., while larvae and pupae parasitoids are mainly of *Brachymeria* and *Conura* (Chalcidae) species. Interestingly, an egg parasitoid, *E. pubipennis*, was foretic on female *O. trichroa* adults, and a *Brachymeria* species attacked pupae, similar to the pattern found in Panama (Cuignet et al. 2008). Besides these parasitoids, a vespid wasp was observed predating larvae of *O. trichroa* in a group without attending mother. Although most accounts of predation on cassidines are by piercing/sucking insects, mandibulate predators have been found attacking cassidines that lack or have reduced shields (Cox, 1996), as is the case of *O. trichroa*.

Clearly, the three Chrysomelidae species have very different life histories and a distinct array of defenses. *Platyphora axillaris* is larviparous with no maternal care, while *O. trichroa* is oviparous, with females caring for their young and larvae carrying an exuvio-fecal shield on their dorsum; both species are monophagous at the study area. *Coptocyclus arcuata*, on the other hand, is oligophagous, feeding on two plant species, but oviparous without maternal care and with larvae also carrying a shield. Despite these significant differences between the three species, they showed very similar population phenologies (Fig. 2), which may suggest that external factors are mostly influencing their fluctuations. Adult densities for all species were significantly related to temperature and precipitation, and in the case of *O. trichroa* also to leaf flushing, while larval densities varied: in *C. arcuata* and *O. trichroa* they were related to temperature, and in *P. axillaris* to precipitation. Thus, climate seems to affect the species fluctuations directly and, at least for *O. trichroa*, also indirectly via host plant. Indeed, climate and/or resources are frequently used to explain insect population fluctuations (e.g. Wolda 1978, Demster and Pollard 1981, Medeiros and Vasconcellos-Neto 1994, Monteiro and Macedo 2000, Nogueira-de-Sá and Vasconcellos-Neto 2003, Nogueira-de-Sá et al. 2004).

Our findings corroborate other studies on Chrysomelidae in the same area (Flinte et al. 2009, 2010, 2011), where species reproduce during the hot rainy months and practically disappear when temperatures and rainfall drop, probably undergoing diapause as adults. Although taking place in a tropical latitude, the study was conducted at ca. 1000 m altitude, which approximates subtropical conditions. In their review on population phenologies of tortoise beetles in Brazil, Nogueira-de-Sá et al. (2004) discuss that climate tends to be more important for cassidines in subtropical areas, where species usually have a well defined reproductive season and overwinter in diapause. This is clearly supported by Medeiros and Vasconcellos-Neto (1994) studying five chrysomeline species on Solanaceae in South Brazil. One of these species, *Platyphora anastomozans*, showed two peaks in its reproductive season, in December and in March, exactly like the *Platyphora* species in this study. The existence of two well defined abundance peaks in the same reproductive season observed in our study indicates two generations per year occurring in the favorable season (spring and summer), explained as follows. After overwintering, adults immediately start laying eggs (in the case of *C. arcuata* and *O. trichroa*) or larvae (for *P. axillaris*), generating the first peak in abundance. The emerging adults lead to the second peak of abundance, and they reproduce in the same season, resulting in a second generation of immatures.

By the end of the reproductive season, adults overwinter during the driest and coldest months (Fig. 2). The importance of climate in species phenology is proven by the strong correlations found between the different stages and variables of temperature and precipitation (Table 2). It is interesting to notice that there are also two distinct peaks of precipitation in each of the seasons 2009/2010 and 2010/2011, in November and March, and in December and March, respectively.

Variation in the order of magnitude of species numbers, especially the much larger density of *O. trichroa* larvae, can possibly be explained by the behavior of maternal care, which increases immature survivorship (Windsor and Choe 1994, Chaboo et al. 2014). Thus, maximum density of *O. trichroa* larvae per plant was much higher than for the other species. However, considering *O. trichroa* larval aggregations, their maximum density on plants was similar to larvae of the other species, ca. 0.6 per plant. Adult maximum density ranged from 0.9 individuals per plant in *P. axillaris* to 2.7 in *O. trichroa*, i.e. more or less 1 individual per plant on periods of high abundance. Considering that, on average, no more than 31% of each plant species was occupied by any specimen of the studied species, these densities on plants indicate that beetles are not evenly distributed on their host plants. Nevertheless, attack on plants varied greatly along the year and were more intense on the months of higher densities, reaching 80% of plants attacked by *O. trichroa* in one of the surveys.

Despite considerable differences in life history traits and systematic position among the three chrysomelid species, our data suggest that they are bivoltine, disappearing during the unfavorable period of lower temperatures, a pattern similar to species in subtropical regions and other species already studied in the same area. The climatic variables of temperature and precipitation seem to be important drivers for species phenologies. In light of the undergoing climatic changes, studies on insects and their host plants on mountains can provide an important tool for studying the responses of species to changing environmental conditions, predicting possible future scenarios and collaborating with species conservation efforts.

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Leaf beetles are ant-nest beetles: the curious life of the juvenile stages of case-bearers (Coleoptera, Chrysomelidae, Cryptocephalinae)

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Abstract

Although some species of Cryptocephalinae (Coleoptera: Chrysomelidae) have been documented with ants (Hymenoptera: Formicidae) for almost 200 years, information on this association is fragmentary. This contribution synthesizes extant literature and analyzes the data for biological patterns. Myrmecophily is more common in the tribe Clytrini than in Cryptocephalini, but not documented for Fulcidacini or the closely-related Lamprosomatinae. Myrmecophilous cryptocephalines (34 species in 14 genera) primarily live among formicine and myrmecines ants as hosts. These two ant lineages are putative sister-groups, with their root-node dated to between 77–90 mya. In the New World tropics, the relatively recent radiation of ants from moist forests to more xeric ecosystems might have propelled the association of cryptocephalines and ant nests. Literature records suggest that the defensive behavioral profile or chemical profile (or both) of these ants has been exploited by cryptocephalines. Another pattern appears to be that specialized natural enemies, especially parasitoid Hymenoptera, exploit cryptocephaline beetles inside the ant nests. With the extant data at hand, based on the minimum age of a fossil larva dated to 45 mya, we can infer that the

origin of cryptocephaline myrmecophily could have arisen within the Upper Cretaceous or later. It remains unknown how many times myrmecophily has appeared, or how old is the behavior. This uncertainty is compounded by incongruent hypotheses about the origins of Chrysomelidae and angiosperm-associated lineages of cryptocephalines. Living with ants offers multiple advantages that might have aided the colonization of xeric environments by some cryptocephaline species.

Keywords

Myrmecophily, Camptosomata, Larvae, Biology, Clytrini, Cryptocephalini

Introduction

With approximately 40,000 species documented, the Chrysomelidae, commonly called leaf beetles, are one of the most diverse insect groups on Earth. They are well known as phytophages, specializing on all parts of plants, from roots to fruits and flowers. Within this broad lineage, whose origin has been dated from the Middle Jurassic (Wang et al. 2014), numerous instances of plant host-switching have been recorded with clades specialized on certain plant families. In some immature stages, we also find remarkable diet switching to detritivory and myrmecophily (“ant loving”). Such habitat and diet shifts involve behavioral, morphological and chemical changes, yet these are unevenly or poorly studied across Chrysomelidae.

This study focuses on the monophyletic Camptosomata branch of leaf beetles (Gómez-Zurita et al. 2008, and references therein), comprised of two subfamilies: Cryptocephalinae Gyllenhal (127 genera; *ca.* 5300 species) and Lamprosomatinae Lacordaire (13 genera; *ca.* 250 species) (Chamorro 2014a, b). Cryptocephalinae is currently classified into 3 subtribes: Fulcidacini, Clytrini, and Cryptocephalini. Camptosomata has been poorly studied despite its large diversity within Chrysomelidae and several remarkable features in their life cycle, behavior and morphology.

Camptosomates are commonly referred to as “case-bearers” because of the unusual larval behavior of retaining a maternal covering of feces around each egg, carrying and reconstructing it as a protective structure, and ultimately modifying it as a pupation chamber. Schaller (1783) is the first illustrated description of a leaf beetle larvae carrying a case. Since then, Erber’s (1988) synthesis of camptosomate case-bearing behavior has helped us recognize this behavior as a synapomorphy of Cryptocephalinae + Lamprosomatinae. The case functions as a domicile and protective covering from environmental conditions (e.g. desiccation) and/or from predators and parasitoids (e.g., camouflage). The Greek name “camptosomata”, literally “curved body”, was established by Chapuis (1874) (Camptosomes), presumably describing the characteristic J-shape of the soft larva in both Cryptocephalinae and Lamprosomatinae. This curvature results in the anus being located near the legs, so fecal pellets are more easily manipulated in case construction (Erber 1988). Brown and Funk (2005) studied the morphological variation across life stages, construction

behavior, and investigated some functions in one species. Two recent treatments on Camptosomata, Chamorro (2014a, b) for adults and a catalog by Chaboo et al. (in press) for juveniles, can now stimulate recognition of new ecological and evolutionary patterns in Camptosomata and aid future research on this major branch of leaf beetles. Chaboo et al. (in press) searched literature records for 354 species (6.7%) of the 5300 recognized camptosomate species, and documented multiple instances of host ant associations (in contrast to the commonly known host plant use of both adult and larvae).

Although myrmecophilous associations can be found in at least 35 beetle families, including varied behavioral and morphological characteristics (Mynhardt 2013), it is not widely known among entomologists, even among ant and leaf beetle biologists, that some Camptosomata appear to seek food and shelter in ant nests. This paper builds on Chamorro (2014a, b) and Chaboo et al. (in press) to further synthesize the literature record, bring focus to the association of some Cryptocephalinae species with ants, and evaluate what pattern, if any, exists.

Chevrolat (1835) was the first to mention case-bearing leaf beetles inside ant nests. Although myrmecophily in leaf beetles has been known for almost 200 years, it remains poorly studied. Within the Chrysomelidae, myrmecophily has evolved in two subfamilies, Eumolpinae, and Cryptocephalinae (Jolivet and Petitpierre 1981, and references therein). Of the 354 species for which some data on juvenile stages exist, only Clytrini and some Cryptocephalini exhibit myrmecophily (Jolivet 1988, Fig. 1 A–D). To date, no case of myrmecophily has been documented for Fulcidacini (the third tribe of Cryptocephalinae) and Lamprosomatinae.

Jolivet (1952) published on myrmecophily for *Lachnaia* Chevrolat and *Tituboea* Lacordaire. Brothers et al. (2000) reported that approximately 20 species of Clytrini are commensals in the nests of more than 30 ant species; yet, a small number of these associations are formally documented. Schöller and Witte (2007) hypothesized myrmecophily as a synapomorphy at least for the subtribe Clytrina, however, a phylogeny of this subtribe and the Camptosomata clade and more detailed observations and broader taxon sampling are needed to understand the full picture of these leaf beetle association with ants.

Ants are not the only hosts of some Camptosomata. *Griburius montezuma* (Cryptocephalini) has been reported as living in nests of bird (Beamer 1926) and of packrats *Neotoma* Say & Ord, 1825 (Mammalia: Rodentia; Riley et al. 2001, Riley et al. 2002). *Oomorphus* Curtis (Lamprosomatinae) larvae were also found in packrat nests (Flowers et al. 1994, Riley et al. 2002, Jolivet and Verma 2002). Nothing is known about these peculiar associations; it might be that these larvae were accidentally introduced in these nests (i.e. incorporated through plant materials). However, we cannot ignore that in nature there are several examples of commensals, saprophages, hibernators, occupying these kind of habitats, thus their presence in these nests might indicate a remarkable new association that requires further study. We will not discuss this association further in this paper.

Challenges of myrmecophily

Ant nests are considered to be well-protected environments, with storage of food items and stable microclimatic conditions. Wilson (1971) and Hölldobler (1972) argued that the insect colony and its immediate environment can be compared to an ecological island, partitioned into many micro-habitats that symbiotic organisms are continuously attempting to colonize. Several myrmecophilous organisms are known to profit from these assets by inhabiting them (Geiselhardt et al. 2007, and references therein). In fact, more than 10,000 social parasite species have been reported in ant nests (Thomas et al. 2005). Coleopterans are common commensals in ant nests (Hölldobler and Wilson 1990). For cryptocephalines, this relationship is based only on the documented presence of the beetle in the ant nest. The degree and quality of the relationship has not been investigated except for a few species for which life histories are known.

The exploitation of ant nests presents some formidable challenges. Wilson (1971) remains the classic overview to non-ants living with ants. Finding the host ants, especially the nest, is the first challenge, but entering the fortress of these aggressive and hostile animals requires behavioral, morphological, and chemical changes to fool the host. A myrmecophile can live outside the nest, being associated with ant trails and even migrating with the ants as they move; they could follow trails or hitchhike on the ants. The host ant can be tricked into carrying invaders inside the nest, and even into feeding them. For example, adult clavigerine staphylinid beetles have glands with oily secretions and associated trichomes that wick the chemicals and fool their host ants into carrying them into the nest and feeding them (Kistner 1982). There may also be great morphological changes to mimic ants, as seen in other beetle groups (e.g. *Myrmex* Sturm (Curculionidae: Otidoccephalini). Once accepted inside the ant nest, the ‘uninvited guest’ insect has some trophic options as predators (of ants or other arthropod inhabitants), scavengers (nest refuse, dead bodies), fungivores, herbivores (eating stored grain and leaves), parasitoids, and thieves (e.g. regurgitated food). An invading insect can also choose from a variety of places or niches to live, such as refuse piles, storage chambers, and brood chambers. Research is more advanced on other insect myrmecophiles (e.g. Carabidae: Paussinae; Staphylinidae) and may provide useful models to guide research on the cryptocephaline myrmecophiles.

Materials and methods

Existing literature on ant-camptosoma associations was synthesized (Table 1). Beetle names were validated in Chaboo et al. (in press), with family- and genus-group names and authors following Bouchard et al. (2011), Löbl and Smetana (2010), and Seeno and Wilcox (1982). Ant names were validated using AntWeb (<http://www.antweb.org>). In order to trace the evolution of cryptocephaline myrmecophiles and their hosts, existing information on the phylogenetic patterns among Formicidae was extracted from Moreau and Bell (2013), Brady et al. (2006), Rabelling et al. (2008), and Schultz

and Brady (2008). Author's names for all genera and species of ants and beetles cited in the text are given in Table 1.

Terminology: we use the terms 'myrmecophily' and 'myrmecophilous' in a broad sense, meaning casual or intimate association of the beetle with ants. Such interactions could involve different forms, from mutualism (benefits for both associates), parasitism (host resources necessarily drained for parasite's own reproduction), commensalism (with no direct effect on the host), predation (direct feeding/damage to the host), or inquilinism (the 'guest' obtains shelter and other resources from the host without damaging host). For extended definitions and discussion of the latter terms see Parmentier and Michel (2013 and references therein). Myrmecophiles are often differentiated as 'protective' or 'symphiles' according to their strategies (Geiselhard et al. 2007 and references therein). We also follow Mynhardt (2013 and references therein), as a glossary and modern critique of the terms historically used in the study of myrmecophily.

Figure 1 photographs were taken by Matthias Schöller with a Nikon D5100 mounted on a stereo microscope, and the photos stacked with CombineZP software (<http://www.hadleyweb.pwp.blueyonder.co.uk>).

Results

Our synthesis of the literature reveals that 34 species of Cryptocephalinae have been associated with ants. The following ant groups host cryptocephalines: Dolichoderinae (1 species), Dorylinae (1 species) Formicinae (13 species), Myrmicinae (16 species); 11 species were reported on an undetermined host ant. Of the latter, 4 cryptocephaline genera are included in this category for which there is no other ant record. These associations represent approximately 0.6% of current species diversity of Cryptocephalinae. In summary, 14% of the 127 Cryptocephalinae genera are associated with ants at some level, as truly myrmecophilous. We found several previously unnoticed patterns in the ant associations of camptosomate genera and species. Regarding the extent of myrmecophily within Camptosomata, we found that ant associations are documented only in two tribes, Clytrini and Cryptocephalini (Fig. 1). Both tribes show distinct patterns of ant association — clytrines appear to be able to exploit several subfamilies of ants, including Formicinae, Myrmicinae, Dolichoderinae, and Dorylinae, while cryptocephalines appear to be restricted to the Formicinae and Myrmicinae.

Data extracted from literature and synthesized here suggest that myrmecophily in Cryptocephalinae is rare or simply unknown, being more frequent in Clytrini (Fig. 2 A–F). Cryptocephalini is currently composed of 54 genera (Chamorro 2014b). Out of these, six genera of Cryptocephalini (11%), have records of association with ants, while Clytrini has 62 genera (Chamorro 2014b), with 12 genera (19%) associated with ants (Table 2). Within the Clytrini, almost all documented cases of myrmecophily are in the subtribe Clytrina, except for two genera in the subtribe Megalostomina (i.e. *Coscinoptera*, and *Megalostomis*) and two genera in Babiina (*Helioscopa*, *Saxinis*).

Table 1. Known ant host of Cryptocephalinae. CL=Clytrini, CR=Cryptocephalini.

Taxon	Beetle species	Tribe	Source
Dolichoderinae ants			
<i>Tapinoma erraticum</i> Latreille	<i>Labidostomis taxicornis</i> (Fabricius)	CL	Barbier 1976, Erber 1988
Dorylinae ants			
<i>Dorylus</i> sp.	Clytrinae larvae follow the migrations of their hosts outside the nest during day or night	CL	Jolivet 1952
Formicinae ants			
<i>Camponotus</i> sp.	<i>Clytra</i> (<i>Clytra</i>) <i>laeviuscula</i> Ratzeburg	CL	Paulian and Villiers 1939
<i>Camponotus ligniperdus</i> Latreille	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Wasmann 1894a, Skwarra 1927, Jolivet 1952, Medvedev 1962
<i>Camponotus</i> (Latreille)	<i>Clytra</i> sp.	CL	Medvedev 1962, Lee and Morimoto 1991, Jolivet and Hawkeswood 1995
<i>Camponotus melleus</i> Say	<i>Coscinoptera dominicana dominicana</i> (Fabricius)	CL	Wasmann 1894a, Cockerell (1891)
<i>Camponotus</i> (<i>Myrmosericus</i>) <i>rufoglaucus</i> Jerdon	<i>Hockingia curiosa</i> Selman	CL	Selman 1962
<i>Camponotus</i> sp.	<i>Clytrasoma maschwitzi</i> Schöller	CL	Schöller and Witte 2007
<i>Camponotus</i> sp.	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)		
<i>Camponotus</i>	Clytrine	CL	Jolivet 1978
<i>Cataglyphis cursor</i> Fonscolombe	<i>Clytra</i> (<i>Clytraria</i>) <i>atraxaphidis</i> (Pallas)	CL	Xamheu 1899, Jolivet 1952
<i>Cataglyphis bicolor</i> (Fabricius)	<i>Clytra</i> (<i>Clytraria</i>) <i>atraxaphidis</i> (Pallas)	CL	Medvedev 1962
<i>Cataglyphis cursor</i> Fonscolombe	<i>Clytra</i> (<i>Clytraria</i>) <i>atraxaphidis</i> (Pallas)	CL	Jolivet (1952)
<i>Cataglyphis bicolor</i> Fabricius	<i>Clytra</i> (<i>Clytraria</i>) <i>atraxaphidis</i> (Pallas)	CL	Xamheu (1899), Medvedev (1962)
<i>Cataglyphis</i> Förster	<i>Clytra</i> sp.	CL	Medvedev 1962, Lee and Morimoto 1991, Jolivet and Hawkeswood 1995
<i>Cataglyphis cursor</i> Fonscolombe	<i>Lachnaia</i> (<i>Lachmaia</i>) <i>tristigma</i> (Lacordaire)	CL	Medvedev 1962
<i>Cataglyphis cursor</i> Fonscolombe	<i>Lachnaia</i> (<i>Lachmaia</i>) <i>tristigma</i> (Lacordaire)	CL	Xamheu 1899
<i>Cataglyphis</i> Förster	<i>Lachnaia</i> Chevrolat in Dejean	CL	Jolivet and Hawkeswood 1995
<i>Formica pallidefulva</i> Latreille	<i>Anomoea flavokansiensis</i> Moldenke	CL	Stiefel et al. 1995, LeSage and Stiefel 1996, Stiefel and Margolies 1998
<i>Formica sanguinea</i> Latreille	<i>Clytra</i> (<i>Clytra</i>) <i>laeviuscula</i> Ratzeburg	CL	Wasmann 1894a, Donisthorpe 1927, Jolivet 1952, Lapeva-Gjonova 2013
<i>Formica pratensis</i> DeGeer	<i>Clytra</i> (<i>Clytra</i>) <i>laeviuscula</i> Ratzeburg	CL	Wasmann 1894a, Skwarra 1927, Jolivet 1952
<i>Formica fusca</i> L.	<i>Clytra</i> (<i>Clytra</i>) <i>laeviuscula</i> Ratzeburg	CL	Reineck 1928, Erber 1988

Table 1. Continued.

Taxon	Beetle species	Tribe	Source
<i>Formica rufa</i> L.	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Chevrolat 1835, Märkel 1841, Rosenhauer 1842, Brauns 1864, Collet 1883, Fowler 1890, Wasmann 1894a, Donisthorpe 1908, Donisthorpe 1927, Skwarra 1927, Jolivet 1952, Medvedev 1962, Lapeva-Gjonova 2013
<i>Formica rotundata</i> Klug	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Medvedev 1962, Erber 1988
<i>Formica exsecta</i> Nylander	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Brauns 1864, Wasmann 1894b, Skwarra 1927, Jolivet 1952, Medvedev 1962
Possibly <i>Formica congerens</i> Nylander	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Hislop 1872
<i>Formica sanguinea</i> Latreille	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Wasmann 1894a, Skwarra 1927, Jolivet 1952, Medvedev 1962, Medvedev 1962
<i>Formica pratensis</i> DeGeer	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Skwarra 1927, Jolivet 1952, Wasmann 1894a, Erber 1988
<i>Formica rufo-pratensis</i> Forel	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Skwarra 1927, Erber 1988
<i>Formica pressilabris</i> Nylander	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Skwarra 1927, Erber 1988
<i>Formica gagates</i> Nylander	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Wasmann 1894a, Skwarra 1927, Jolivet 1952, Medvedev 1962
<i>Formica uralensis</i> Ruzsky	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Skwarra 1927, Medvedev 1962
<i>Formica</i> sp.	<i>Clytra</i> (<i>Clytra</i>) <i>quadripunctata</i> (L.)	CL	Priefert 1926, Selman 1988
<i>Formica rufa</i> L.	<i>Clytra</i> sp.	CL	Chevrolat 1835
<i>Formica</i> L.	<i>Clytra</i> sp.	CL	Medvedev 1962, Lee and Morimoto 1991a
<i>Formica fusca</i> L.	<i>Clytra</i> sp.	CL	Medvedev 1962
<i>Formica fusca</i> L.	<i>Clytra</i> sp.	CL	Samsšínák 1956, Medvedev 1962
<i>Formica</i> sp.	<i>Coscinoptera dominicana dominicana</i> (Fabricius)	CL	Riley 1874b
<i>Formica obscuripes</i> Forel	<i>Coscinoptera dominicana dominicana</i> (Fabricius)	CL	Riley 1874b
<i>Formica selysii</i> Bondroit	<i>Pachybrachis anoguttatus</i> Suffrian (found inside the ant nest)	CR	Schöller 1995
<i>Formica fusca subaenescens</i> Emerton	<i>Coscinoptera dominicana dominicana</i> (Fabricius)	CL	Jolivet 1952, Wasmann 1894a
<i>Formica obscuripes</i> Forel	<i>Coscinoptera dominicana dominicana</i> (Fabricius)	CL	Cockerell 1891, Jolivet 1952, Riley 1874
<i>Formica neoclara</i> Emery	<i>Coscinoptera dominicana franciscana</i> (LeConte)	CL	Slosser 2003

Table 1.Continued.

Taxon	Beetle species	Tribe	Source
<i>Formica fusca subaenescens</i> Emerton	<i>Coscinoptera vittigera</i> (LeConte)	CL	Wasmann 1894a, Jolivet 1952
<i>Formica fusca</i> L.	<i>Coscinoptera vittigera</i> Probably <i>C. dominicana</i> (Fabricius)	CL	Cockerell 1891, Wasmann 1894a, Jolivet 1952
<i>Formica</i>	Clytrine	CL	Jolivet 1978
<i>Lasius niger</i> L.	<i>Cryptocephalus (Burlinius) ocellatus ocellatus</i> Drapiez	CR	Schöller 1995
<i>Lasius niger</i> L.	<i>Clytra (Clytra) laeviuscula</i> Ratzeburg	CL	Fiori 1948, Wasmann 1894a, Erber 1988
<i>Lasius alienonigra</i> Forst.	<i>Clytra (Clytra) laeviuscula</i> Ratzeburg	CL	Skwarra 1927, Erber 1988
<i>Lasius alienus</i> Forst.	<i>Clytra (Clytra) laeviuscula</i> Ratzeburg	CL	Skwarra 1927, Fiori 1948, Erber 1988
<i>Lasius neglectus</i> Van Loon, Boomsma & András-Falvy	<i>Clytra (Clytra) laeviuscula</i> Ratzeburg	CL	Selman 1988, Espadaler and Bernal 2009
<i>Lasius niger</i> L.	<i>Clytra (Clytra) laeviuscula</i> Ratzeburg	CL	Donisthorpe 1927
<i>Lasius niger</i> L.	<i>Clytra (Clytra) laeviuscula</i> Ratzeburg	CL	Donisthorpe 1927
<i>Lasius flavus</i> (DeGeer)	<i>Clytra (Clytra) quadripunctata</i> (L.)	CL	Wasmann 1894a, Skwarra 1927, Jolivet 1952, Medvedev 1962
<i>Lasius</i> Latreille	<i>Clytra</i> sp.	CL	Medvedev 1962, Lee and Morimoto 1991, Jolivet and Hawkeswood 1995
<i>Lasius neglectus</i> Van Loon, Boomsma & András-Falvy	Clytrinae larvae	CL	Nagy et al. 2009
<i>Lasius fuliginosus</i> Latreille	<i>Cryptocephalus (Burlinius) fulvus fulvus</i> (Goeze)	CR	Donisthorpe 1927
<i>Plagiolepis</i> sp.	<i>Tituboea macropus</i> (Illiger)	CL	Medvedev 1962, Erber 1988
Myrmicinae ants			
<i>Aphaenogaster subterranea</i> Latreille	<i>Clytra (Clytra) laeviuscula</i> Ratzeburg	CL	Fiori 1948, Erber 1988
<i>Aphaenogaster (Myrmica) testaceopilosa</i> Lucas	<i>Tituboea octosignata</i> (Fabricius)	CL	Lucas 1850
<i>Aphaenogaster testaceopilosa</i> Lucas	Cryptocephaline	Undetermined	Wasmann 1894a, Xambeu 1899, Medvedev 1962, Jolivet 1952
<i>Atta mexicana</i> (F. Smith) (Larvae saprophagous)	<i>Megalostomis dimidiata</i> Lacordaire	CL	Rojas 1989, Navarrete-Heredia (2001) (as accidental)
<i>Atta</i> Fabricius	<i>Megalostomis dimidiata</i> Lacordaire	CL	Moldenke 1970
<i>Atta</i> nest (digging on)	<i>Megalostomis dimidiata</i> Lacordaire	CL	Agrain 2010
<i>Atta texana</i> (Buckley)	<i>Megalostomis dimidiata</i> Lacordaire (as <i>M. major</i> Crotch). 2.5m depth.	CL	Waller and Moser 1990, Della Lucia 1993, Navarrete-Heredia 2001 (as accidental)
<i>Atta</i>	Clytrine	CL	Jolivet 1978
<i>Atta mexicana</i> (F. Smith)	<i>Pachybrachis</i> sp. On external ant debris	CR	Márquez-Luna and Navarrete-Heredia 1994, Navarrete-Heredia 2001 (as accidental)

Table 1. Continued.

Taxon	Beetle species	Tribe	Source
<i>Atta mexicana</i> (F. Smith)	<i>Griburius</i> sp. (misspelled as <i>Griburium</i>). On external ant debris,	CR	Márquez-Luna and Navarrete-Heredia 1994, Navarrete-Heredia 2001 (as accidental).
<i>Crematogaster lineolata</i> (Say)	<i>Anomoea</i>	CL	Stiefel and Margolies 1998
<i>Crematogaster lineolata</i> Say (the ants carries the eggs to their nest)	<i>Anomoea flavokansiensis</i> Moldenke	CL	Stiefel and Margolies (1998)
<i>Crematogaster mimosa</i> Santschi	<i>Hockingia curiosa</i> Selman	CL	Selman 1988, Erber 1988, Jolivet 1991
<i>Crematogaster sjostedti</i> Mayr	<i>Hockingia</i> Selman	CL	Selman 1962
<i>Crematogaster</i> (<i>Crematogaster</i>) <i>nigriceps</i> Emery	<i>Isnus petasus</i> Selman	CR	Selman 1962, 1988; Hocking 1970, Jolivet 1986
Nest of <i>Crematogaster peringueyi</i> Emery	Clytrine cases	CL	Péringuey (1898)
<i>Crematogaster</i> sp.	<i>Coenobius macarangae</i> Gressitt (living on myrmecophyte)	CR	Jolivet 1991
<i>Crematogaster</i> sp.	<i>Cadmus macarangae</i> Gressitt (living on myrmecophyte)	CR	Jolivet 1991
<i>Messor clivorum sevani</i> Kar.	<i>Clytra</i> (<i>Clytraria</i>) <i>valeriana valeriana</i> Ménétriés	CL	Medvedev 1962
<i>Messor</i> Forel	<i>Clytra</i> sp.	CL	Jolivet and Hawkeswood 1995
<i>Messor barbarus</i> L.	<i>Lachnaia vicina</i> Lacordaire.	CL	Barbier 1976, Erber 1988
<i>Messor barbarus capitatus</i> Latreille	<i>Tituboea biguttata</i> (Olivier)	CL	Fiori 1957
<i>Messor</i> spp.	<i>Tituboea biguttata</i> (Olivier)	CL	Erber 1988
<i>Messor barbarus</i> L.	<i>Tituboea biguttata</i> (Olivier)	CL	Medvedev 1962, Jolivet 1952
<i>Messor barbarus capitatus</i> Latreille	<i>Tituboea biguttata</i> (Olivier)	CL	Medvedev 1962
<i>Messor barbara</i> (L.)	<i>Tituboea</i> Lacordaire	CL	Barbier 1976
<i>Messor barbara</i> L.	Clytrine	CL	Barbier 1976
<i>Mymica rugulosa</i> Nylander, queen using larval case for colony founding	<i>Cryptocephalus morarei</i> (L.)	CR	Schöller 1999
<i>Pheidole</i> sp. Queen with eggs and workers on larval case	<i>Cryptocephalus anceps</i> Suffrian	CR	Schöller 1999
<i>Tetramorium caespitum</i> L.	<i>Clytra</i> sp.	CL	Girard 1873
<i>Tetramorium caespitum</i> L.	<i>Clytra</i> sp.	CL	Escherich and Emery 1897, Jolivet 1952, Medvedev 1962
<i>Tetramorium caespitum</i> L.	<i>Smaragdina concolor</i> (Fabricius)	CL	Xambeu 1899, Medvedev 1962, Erber 1988
<i>Tetramorium vespitum</i> L.	<i>Smaragdina concolor</i> (Fabricius)	CL	Jolivet 1952
Leaf cutting ant nest	<i>Megalostomis dimidiata</i> Lacordaire	CL	Agrain 2010
Undetermined ants			

Table 1.Continued.

Taxon	Beetle species	Tribe	Source
Eat detritus and Humus, associated with ants	<i>Anomoea</i>	CL	Moldenke 1970, Jolivet and Hawkeswood 1995
Myrmecophile	<i>Clytra</i> sp.	CL	Escherich 1899, Erber 1988
Ant eggs	Clytrine	CL	McAtee 1932
As myrmecophiles	Clytrine	CL	Jolivet 1952
As myrmecophiles	Clytrine	CL	Doguet 1992
Dead leaves in ant nests	Clytrine	CL	Johnson and Triplehorn 2004
In ant nests	Clytrine	CL	Jolivet 1991
Larvae that overwinter as antinquilines	Clytrine	CL	Erber 1988, Steifel et al. 1995, Jolivet 1996
Ant host	<i>Coscinoptera dominicana dominicana</i> (Fabricius)	CL	Riley 1882, Wasmann 1894a, Van Dyke 1925, Wickham 1896
Ants on <i>Acacia</i> tolerate ants	Cryptocephaline	CR	Jolivet 1996
Ant nests	<i>Cryptocephalus</i> Geoffroy	CR	Donisthorpe 1927, Kasap and Crowson 1976
Ant host	<i>Helioscopa</i> Gistel	CL	Jolivet and Hawkeswood 1995
Associated with ants, myrmecophiles, or submyrmecophiles	<i>Labidostomis</i> Chevrolat in Dejean	CL	Jolivet 1952, 1978; Selman 1988, Erber 1988
As obligate or facultative antinquilines	<i>Lachnaia</i> Chevrolat in Dejean	CL	Erber 1988
Myrmecophilous larvae	<i>Lachnaia italica italica</i> Weise	CL	Regalin et al. 2006
Found in the vicinity of ant nest)	<i>Macrolenes dentipes</i> Olivier	CL	Schöller 1998
As myrmecophiles	<i>Megalostomis</i> Chevrolat	CL	Jolivet and Hawkeswood 1995
Found in the vicinity of ant nest)	<i>Pachybrachis anoguttatus</i> Suffrian	CR	Schöller 1998
In ant nests	<i>Saxinis (Boreosaxinis) saucia</i> LeConte	CL	Van Dyke 1925, Hatch 1971

Discussion

Since most records found in the extant literature are the product of a chance finding of the beetles in association with the ant nests, and not of a directed search, it is not clear how widespread ant associations really are. Below we discuss some patterns of ant associations we recognized in our synthesis. The study of myrmecophilous beetles has revealed an extraordinary amount of adaptations (Mynhardt 2013), therefore, further research on other beetle lineages may provide useful touchstones to guide theoretical or empirical research on cryptocephaline myrmecophily.

Quality of available data. Records of myrmecophilous species summarized in Table 1 have accumulated over the last 180 years since Chevrolat (1835) first reported a crypto-

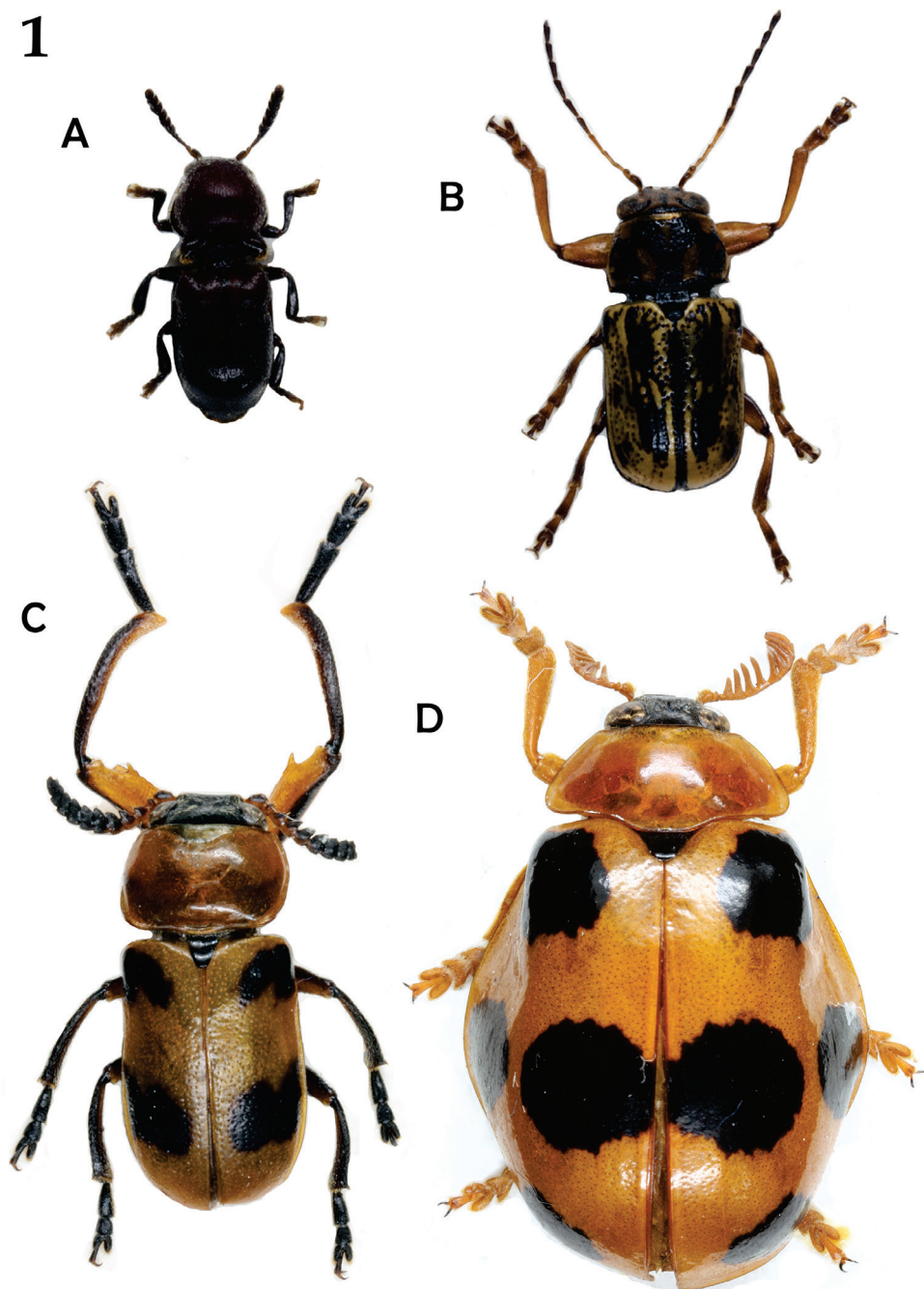


Figure 1. Some Cryptocephalinae associated with ants; **A** *Hockingia curiosa* Selman **B** *Pachybrachis pallidulus* Suffrian **C** *Macrolenes dentipes* (Olivier) **D** *Clytrasoma balyi* Monrós (not to scale). Photos: Matthias Schöller.

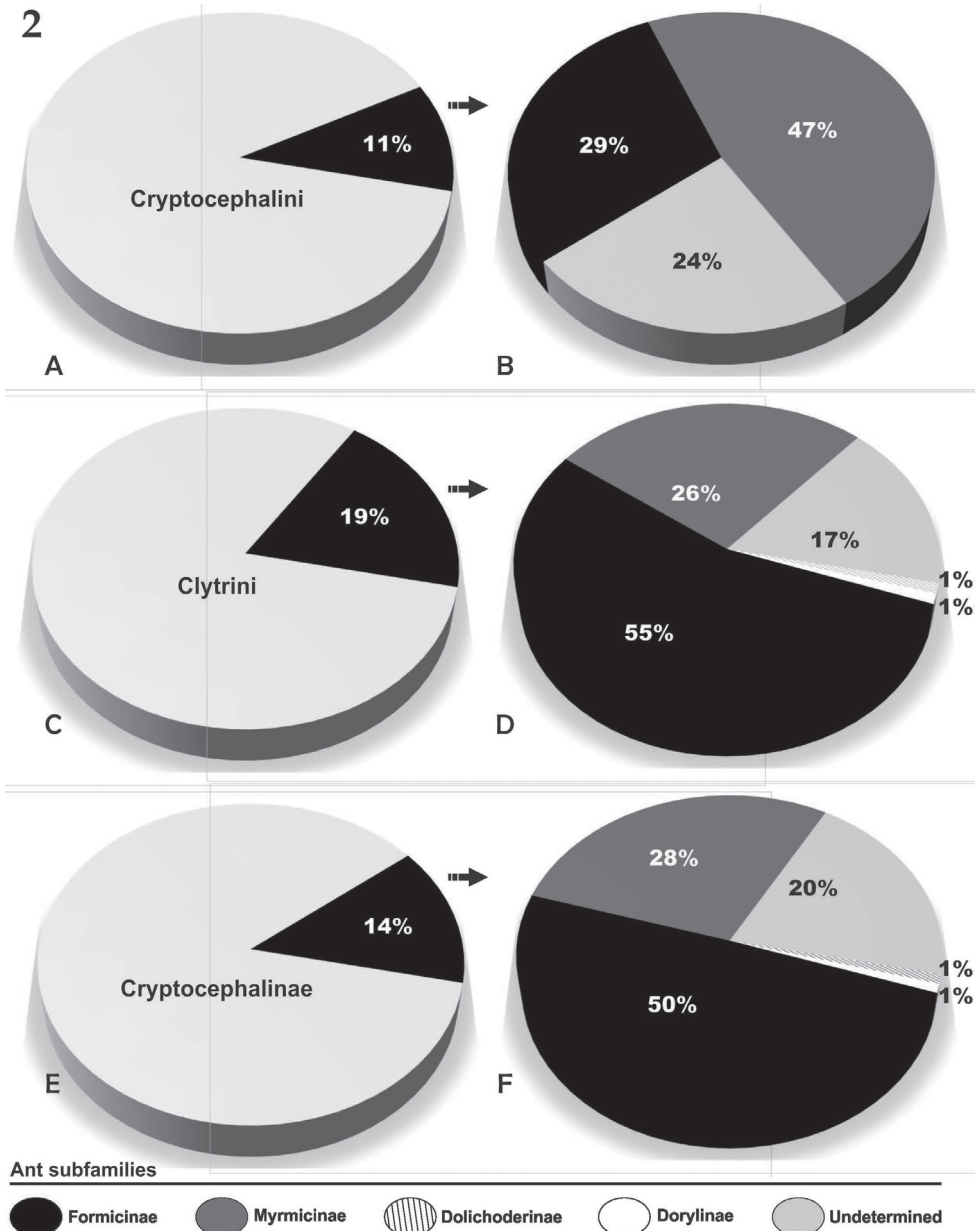


Figure 2. Ant association records. Each pie chart indicates ant association records expressed as percentages, different color tones refer to each ant subfamilies as indicated in the color reference below: **A–B** records within the tribe Cryptocephalini **C–D** records within the tribe Clytrini **E–F** records within the whole subfamily.

cephaline-ant association. We believe a collection bias exists in these data. For instance, some ant nests are the focus of a great deal of study and subsequent excavation (e.g. *Atta* nests); these species would, as a result, have more records of myrmecophilous species

Table 2. The number of Cryptocephalinae genera associated with ant hosts.

Tribe / Genus	Myrmecophilous species number	Number of ant genera recorded as host
Clytrini		
<i>Anomoea</i> Agassiz	1 + undet.	2 + undet.
<i>Clytra</i> Laicharting	4 + undet.	7 + undet.
<i>Clytrasoma</i> Jacoby	1	1
<i>Coscinoptera</i> Lacordaire	2	2 + undet.
<i>Helioscopa</i> Gistel	undet.	undet.
<i>Hockingia</i> Selman	1 + undet.	2
<i>Labidostomis</i> Germar	1 + undet.	1 + undet.
<i>Lachnaia</i> Chevrolat	1 + undet.	2 + undet.
<i>Macrolenes</i> Chevrolat	1	undet.
<i>Megalostomis</i> Chevrolat	2 + undet.	2 + undet.
<i>Saxinis</i> Lacordaire	1	undet.
<i>Smaragdina</i> Chevrolat	1	1
<i>Tituboea</i> Lacordaire	3 + undet.	3
Undetermined	11	5 + 6 undet.
Cryptocephalini		
<i>Cryptocephalus</i> Geoffroy	1 + undet.	1 + undet.
<i>Cadmus</i> Erichson	1	1
<i>Coenobius</i> Suffrian	1	1
<i>Griburius</i> Haldeman	1 undet.	1
<i>Isnus</i> Weise	1	1
<i>Pachybrachis</i> Chevrolat	1 + 2 undet.	2 + undet.
Undetermined	2	1 + undet.

inhabiting them than other ant nests that are more difficult to study (e.g. *Dorylus*) or simply understudied. Verifying the accuracy of host records presented here has not been our primary goal, so some records presented here may not hold up to future scrutiny and/or data (through additional fieldwork and/or examination of museum vouchers). Finally, some species of cryptocephalines have received more study than others, and hence, their host patterns are not in common with other species. For instance, the Palearctic *Clytra* (*Clytra quadripunctata*) is one of the most studied cryptocephaline species, and has consequently been recorded from ant nests of 12 species within 3 genera in 2 different subfamilies. If more fieldwork were conducted on all myrmecophilous cryptocephaline species, the pattern of host use might be very different.

Taxonomic patterns of host use. All records examined here indicate that myrmecophilous cryptocephalines are specialists on the formicoid ants, a branch of Formicidae, which include the most common ant species as well as the major invasive species (Brady et al. 2006). The sister-group to the formicoids, the poneroid clade, does not appear to be exploited by cryptocephalines. This formicoid clade has been estimated to range between 105–120 mya (Brady et al. 2006) and 107–119 (Moreau and Bell 2013), but the subfamilies and genera of interest to this study are much younger, and will be covered below.

The most striking pattern that emerges from the assembled data relates to *Clytra*. Members of this genus have the broadest host range, with records from some of the more core formicines such as the carpenter ants (*Camponotus*) and *Formica* ants, but also from the myrmicines *Aphaenogaster*, *Messor*, and *Tetramorium*. While many species of *Camponotus* and *Formica* can be found commonly in forested environments (and often, in fact, co-occur), species of *Messor* are found in more xeric environments, and are herbivorous, seed-harvesting ants (the former are generalist predators). However, Brady et al. (2006) estimated the root-nodes of formicines and myrmicines to be roughly 77–82 mya, and concluded these two subfamilies are sister-groups of each other. Moreau and Bell (2013) recovered the root node of formicines at between 74.9 and 90.3 mya, and myrmecines between 79.3 and 89.8 mya; this study did not recover the two subfamilies as sister-groups, but instead found ectatommines and heteroponerines nested between the two families (but lacking branch support). Today cryptocephalines are associated with both the formicines and myrmecines. Within *Clytra*, we see some degree of host specificity, exemplified by *Clytra* (*Clytra*) *laeviuscula* having an affinity for species of *Lasius*, *Clytra* (*Clytra*) *quadripunctata* being associated with species of *Formica*, and *Clytra* (*Clytraria*) *atraxidis* being recovered only from species of *Cataglyphis* (Table 1). This last observation suggests that something of the ant's defensive behavioral profile or chemical profile (or both) have been exploited by these beetles, and through this exploitation, a certain degree of evolutionary canalization has taken place. Otherwise, we would likely see a plethora of generalist beetles exploiting all manners of ant subfamilies; the data herein reported do not support that hypothesis.

Below we summarize some of the broad challenges of myrmecophily mentioned above (see (Hölldobler and Wilson 1990). Myrmecophilous cryptocephalines appear to use different strategies to live near, enter, or inhabit ant nests. The following discussion analyzes the quality of data available for each challenge posed by the ants' well-defended fortress.

1) *Finding the host ant*. In some Clytrini, the female oviposits on a leaf and drops the egg, after being intricately covered by feces, to the ground. Ants then carry the eggs, or the first instar larvae within its fecal case, inside the nest (Jolivet 1991, Schöller 2011). Some egg cases are attached to the substrate by a peduncle; Jolivet and Petitpierre (1981) mentioned that ants cut the peduncle in those cases. They also remark that 'naked' eggs, i.e. lacking a case, are eaten by the ants.

2) *Living outside the nest*. Some species have been found on external ant debris and are known to feed on it. The biologic meaning of this have not yet been studied, it might be that debris is a rich food source, or possibly, it provides the beetle or larvae with some sort of camouflage.

3) *Trail following*. Jolivet (1952) mentioned that Clytrini larvae follow the migrations of the nomadic *Dorylus* ants (army ants, Formicidae: Dorylinae) during day or night, and that the clytrine adults interact with ants near or inside the nest. This sug-

gests that in some cases, all life stages of camptosomates are capable of interacting with ants. In the case here, the presence in the adults of deep grooves for the reception of appendages (such as antennae and legs) and the cryptic nature of the presence of their head within the prothorax, suggests this to be true.

4) *Entering the ant nest.* All myrmecophiles must enter and remain in the ant nests without being expelled or killed (Hölldobler and Wilson 1990, Lenoir et al. 2001). The inquiline must be adopted, or at least tolerated inside the nest, and this is usually accomplished by chemical mimicry [e.g. *Trichopsenius* Horn (Coleoptera: Staphylinidae) inside *Reticulitermes* Holmgren nests (Isoptera: Rhinotermitidae) (Lenoir et al. 2001, and references therein)]. Erber (1988) indicates that *Hockingia curiosa* might live obligatorily in ants nest, the genus mimics the body form of *Crematogaster* ants in Tanzania. The adults exhibit interesting myrmecophilous organs, which consist of two setae bearing tubercles on the pronotum (Fig. 1A), possibly with a secretory function. *Isnus petasus* also bears long setae on the lateral pronotal margins (Selman 1962). Secretory hairs or bristles and special glands (e.g. adoption glands *sensu* Hölldobler 1970 or defense glands) are not uncommon in myrmecophilous insects (Hölldobler and Wilson 1990) and they may discharge mimicking, appeasing, tranquilizing, repellent or deadly chemicals. Detailed anatomical and scanning electron microscopy might reveal such organs in Cryptocephalinae and chemical analysis will reveal the nature of the exudates. Cryptocephaline adults studied thus far bear a paired basolateral seta on the pronotum.

5) *Evolution towards living and surviving in ant nests.* Once inside an ant nest, whether temporarily or long-term, every myrmecophile is faced with new challenges, from avoiding being detected as an enemy, to finding a safe micro-habitat within the ant complex, to finding food, and carrying on its life cycle.

5a) *Avoiding being eaten by ants.* Cryptocephalinae adults exhibit some typical chrysomelid defenses – chemical sequestration and secretion of toxic compounds (e.g. reflex bleeding) (Selman 1988), mimicry (Hespenheide 1999), defensive stridulation (Monrós 1953, Schmitt 1994), thanatosis (Monrós 1953, Selman 1988), aposematic coloration (Selman 1988, and references therein), gregarious behavior (Monrós 1953); and, as mentioned above, at least some species are thought to have complex myrmecophilous organs (Selman 1988). Egg, larval and pupal cases provide physical protection against predators (Wallace 1970, Root and Messina 1983, Schöller 2014). Furthermore, they are also cryptic and work as a barrier against desiccation, this last function being important as it has been observed that camptosomates are relatively more sensitive to desiccation than other chrysomelids (Root and Messina 1983). The larval cases are sometimes armored with plant trichomes (Chaboo et al. 2008). Camptosomata that develop within the ant nest have to leave it as adults, and are consequently faced with attacks by ants. Species that develop in the vicinity of the nest may be attacked as well. *Clytra* (*Clytra*) *laeviuscula* responds with thanatosis when attacked by ants and

when the ants lose interest in the beetle, it walks away or flies off quickly. The adults of *Labidostomis taxicornis* and *Lachnaea pubescens* do not exhibit thanatosis; instead, they move quickly to avoid being attacked, and typically do not survive the ant attacks if caught (Schöller pers. obs.). Nevertheless, defense or antipredator devices of the larvae against ant attacks largely remain unknown.

5b) *Avoiding other dangerous organisms in the ant nest.* In reports of associations with ants, hymenopterans are the most frequent parasitoids of eggs and larvae of the Camptosomata (Erber 1988). Bethyridae wasps are known specialized parasitoids of coleopteran larvae (Evans 1964); many bethylid females are wingless, and their small size and flat body allow them to locate prey in hard-to-access places, such as ant nests. Nagy (1969) found the bethylid *Mesitius horvathi* Kieffer attacking a clytrine. Mutillids (velvet ants; Mutillidae) were also found to attack the enclosed larvae or pupae of species of Coleoptera, including some cryptocephalines (Lawrence and Britton 1991) that live in the ant nests (Brothers et al. 2000). Brothers (1975) could not trace a parallel between the evolution of the mutillids and that of their hosts, so colonization of new hosts is likely a common pattern. Mutillids are thought to have evolved from parasitoids of ground-nesting Hymenoptera, however, host fidelity is not high and host-shifts to distantly related hosts (even in different orders) have apparently occurred. Brothers et al. (2000) indicate that more host records of mutillids parasitizing Clytrini are expected to be found, while the occurrence of Cryptocephalini species as hosts of mutillids in association with ants need to be confirmed. The larvae of mutillid wasps may be parasitoids of host stages which are enclosed in some sort of “hard” package and which are not actively feeding (Brothers 1972, 1989). In ant associations, the well-known occurrences of mutillids always involve parasitism of chrysomelid beetles living in the ant nests and having hard cases. It is unknown whether other mutillid species attack ants directly.

Within the proctotrupomorph Hymenoptera (most of the formerly recognized superfamilies of Parasitica; Sharkey et al. 2007) are a number of ant-specialist lineages. The Universal Chalcidoidea Database (Noyes 2015) cites just under 700 parasitic chalcidoid species that have been recorded from Chrysomelidae; among these species, five have been recorded from *Cryptocephalus*, and none from the other myrmecophilous genera covered herein. Within Ichneumonidea, 77 genera and over 200 species are known parasitoids of chrysomelids, with 7 species of *Cryptocephalus* recorded as hosts (Yu et al. 2012), including *Gelis acarorum* (L.) and *Dimophora evanialis* Gravenhorst (Schöller 1999). Together with members of the aculeate Bethyridae and Mutillidae, the parasitoid pressure on cryptocephalines to escape parasitism is rather high, and utilizing a refugia such as an ant nest would release the parasitoid pressure significantly on these beetles.

5c) *Microhabitat specialization within the nest and diet:* An ant nest presents multiple places to live, including open chambers, refuse heaps (“kitchen midden”), brood chambers or nurseries (heavily defended but high-quality food), and fungus gardens

for those ants that cultivate fungi. Presently it is unknown where cryptocephaline myrmecophiles live within the ant nest. Some of these sites can offer different degrees of protection and different resources to exploit, yet nothing is known about the selection mechanism employed by myrmecophilous cryptocephalines among the different nest chambers. The only insight may be provided by the relation between the food inside the ant nest and the diet of the beetle larvae. Leaf beetles show a general pattern of adults and larvae living on the same host plants. However, some cryptocephalines show a further distinction where the larval and adult stages can have different habitats and diet; this is particularly true for Clytrini and Cryptocephalini. Some species have zoosaprophagous and phytosaprophagous larvae (Schöller 1998). The myrmecophilous larvae appear to feed on ant droppings and pellets (Erber 1988; Lapeva-Gjonova 2013); others feed on detritus (LeSage 1985, 1986; Erber 1988, Stiefel 1993), leaf litter or dead insects collected by the ants (Schöller 1998); or, on ants or ant bodies (Riley 1882). Schöller (1995) posits that zoosaprophagy may be an important aid for the development of larvae inhabiting arid and semi-arid regions, when plant foliage is scarce. Even if some interactions between ants and their associates are known (i.e. social parasitism), the precise behavioral characters and payoffs are not so clear. It is believed that most of the nest associates take advantage of the nest micro-habitat, living as commensals on dead ants and assorted detritus from the ant fungus garden (Waller and Moser 1990).

Fungi inside an ant nest can provide food or can pose a threat to cryptocephalines. Ants such as the Attini (the leafcutter ants) cultivate fungi and these fungus gardens may provide both a micro-habitat to live in and a larder of food. Fungi are commonly known to negatively affect immature stages of cryptocephalines. Yet, there is only one formal citation by Jolivet and Theodorides (1952) of the fungus *Sporotrichum* sp. affecting the larvae and pupae of *Clytra* (*Clytra quadripunctata*; currently it is impossible to know the specificity of this relationship. Fungal mycelia appear to be part of the case construction (Chaboo et al. 2008).

6.) *Benefits for the host?* Although no chemical recompense is known to be offered by myrmecophilous cryptocephalines, Schöller (1999) found empty larval cases of *Cryptocephalus* species being used as microchorions by certain Formicidae and Araneae. Yet more remarkable, Schöller (1999) also found queens of *Myrmica* and *Pheidole* using cases as a place for colony founding, which indicates that these myrmecophilous systems are rather complex and may be synergistic. However, it should be noted that most strategies of cryptocephalines to enter, reside and leave the ant nests remain largely undocumented.

Strength of host association. The strength of myrmecophilic relationships can vary, as some larvae can survive without actually entering an ants' nest (Erber 1988, and references therein). Within clytrines, adults of *Hockingia* exhibit an extraordinary morphology indicative of a strong integration with ants; yet, when considering the larvae or pupae, they seem to exploit a protective strategy, solely relying on the protection

offered by their cases and a plug-like head. Important evidence to solve this problem might come from the study of known or new myrmecophilous organs, present in camptosomate beetles that would provide appropriate compensation for the ants. Nevertheless, according to present evidence, it is possible to find a plethora of relationships, from mutualism to parasitism. Below we introduce some interesting aspects of the evolutionary challenge faced by cryptocephalines living with ants.

The reports to date suggest some degree of specialization in non-*Clytra* species. *Megalostomis dimidiata* is an *Atta* specialist; *Anomoa*, *Clytrasoma* (Fig. 1D), *Hockingia* (Fig. 1A), and *Isnus petasus* are all *Crematogaster* specialists; *Tituboea biguttata* are harvester ant (*Messor*) specialists; and *Smaragdina concolor* (Fabricius) are known from the pavement ant *Tetramorium*. With respect to these ant species, some aspects of their biology may help explain this degree of specificity. Both *Atta* and *Messor* have long-lived nests, in that they typically remain in one location for several years (Hölldobler and Wilson 1990), and this is largely afforded by having a nearly constant source of food (fungus in the case of *Atta*; seed caches in the case of *Messor*). This sort of stable environment could allow for long-term myrmecophilous relationships to evolve, and in fact, *Atta* species typically harbor a large number of commensal species living among their nests (Waller and Moser 1990). It is also quite intriguing considering that the root node of *Atta* has been estimated to be some 8 my old, more or less a newcomer in evolutionary time, which means its inquiline (*Megalostomis dimidiata*) is likely to be even younger than that.

Regarding the strength of currently known Cryptocephalines/ants associations, Selman (1988) sorted the life histories of the following assemblages: *Clytral/Formica*, and *Hockingia*, *Isnus/Crematogaster* as cases of commensalism, or perhaps parasitism. The author also remarked the importance of the stable temperature within the ant nests as a clear advantage for cryptocephalines. Hitherto, even if these are the most studied cases, we do not know much about the organisms.

Another unusual pattern to emerge from our synthesis is the case of *Dorylus*, a genus that includes army ants, which do not construct a typical ground nest like many other formicids, but instead, a bivouac as needed, and remain constantly in search of prey items (Hölldobler and Wilson 1990, and references therein). Jolivet (1952) offers a very intriguing observation of an unidentified Clytrini whose larvae migrates with a *Dorylus* species; how a relationship such as this can evolve is quite fascinating, but certainly requires further verification beyond this single reference. *Labidostomis taxicornis* is the only known cryptocephaline to be associated with a Dolichoderinae (*Tapinoma erraticum*). Dolichoderines are some of the most notoriously invasive species of ants (entering non-native habitats/regions), with species such as *T. sessile* and *T. melanocephalum* essentially found worldwide. Considering the commonality of *Tapinoma* species, it is reasonable to expect that we would have recorded more cryptocephalines from this group of ants by now if the species actually existed. This dearth of cryptocephaline species associated with such a common, widespread group suggests the relationship between *Labidostomis taxicornis* and *Tapinoma erraticum* is something unique. This may also apply to *Smaragdina concolor*, which has been associated with

the highly invasive pavement ant (*Tetramorium caespitum*). In this case, it would be fascinating to conduct additional fieldwork to determine if the beetle has been able to track its host ant into novel geographic regions, or if it is restrained to the aboriginal home of the ant.

Summarizing, existing evidence indicates multiple routes to myrmecophily in cryptocephalines, even if adults are above-ground herbivores and occasionally interact with ants; their immature stages (eggs, pupae and larvae) are the most exposed stages in terms of ant interaction. Myrmecophilous cryptocephalines can be found in subterranean (e.g. *Megalostomis* larvae found at 2.5m inside *Atta* nest), arboreal (e.g. *Isnus* in *Acacia* ant nests), and terrestrial (e.g. *Pachybrachis* on external debris of *Atta* nests) habitats.

Geography of ant association (Table 3). While the origin of myrmecophily is thought to be monophyletic among Old World genera of Clytrina (Schöller and Witte 2007), it is currently unknown if myrmecophily was inherited or newly acquired by New World cryptocephalines. To date, only two genera of Cryptocephalini have been cited as myrmecophilous in the New World. So far, no records of beetle/ant association have been found for Australian, Madagascan, Oceanian, Oriental, Papua-Melanesian, and Sino-Japanese regions (*sensu* Holt et al. 2013) (Fig. 3). The most remarkable specialized ant interactions known today (i.e. involving complex myrmecophilous organs and myrmecomorphy) are known for the Afrotropical region: Clytrini (*Hockingia*) and Cryptocephalini (*Isnus*), both genera related to *Crematogaster* ants. It is interesting to remark that *Crematogaster* is almost globally distributed today, and have apparently achieved this large distribution range by successive dispersion events since their origin in the mid-Eocene (Blaimer 2012). Actually, in most cases, the ants that have been

Table 3. Genera of Cryptocephalinae by region and ant subfamily. Note all genera belong to the tribe Clytrini except for those marked with (*), which belongs to the Cryptocephalini.

Region	Formicinae	Myrmicinae	Dolichoderinae	Dorylinae	Undet.
Afrotropical	<i>Hockingia</i>	<i>Hockingia</i> , <i>Isnus</i> *, + undet.	-	Undet.	-
Nearctic	<i>Anomoea</i> , <i>Coscinoptera</i>	<i>Anomoea</i> , <i>Megalostomis</i>	-	-	<i>Anomoea</i> , <i>Coscinoptera</i> , <i>Lachnaia</i> , <i>Megalostomis</i> , <i>Saxinis</i>
Neotropical	<i>Megalostomis</i> , <i>Pachybrachis</i> *	<i>Megalostomis</i> , <i>Griburinus</i> **	-	-	<i>Helioscopa</i>
Oriental	<i>Clytrasoma</i>				
Palaearctic	<i>Clytra</i> , <i>Cryptocephalus</i> *, <i>Lachnaia</i> , <i>Pachybrachis</i> *, <i>Tituboea</i> , + undet.	<i>Clytra</i> , <i>Smaragdina</i> , <i>Tituboea</i>	-	-	<i>Clytra</i> , <i>Macrolenes</i> <i>Cryptocephalus</i> *, <i>Lachnaia</i> <i>Pachybrachis</i> *
Saharo-Arabian	<i>Clytra</i>	<i>Lachnaia</i> , <i>Tituboea</i>	<i>Labidostomis</i>	-	-

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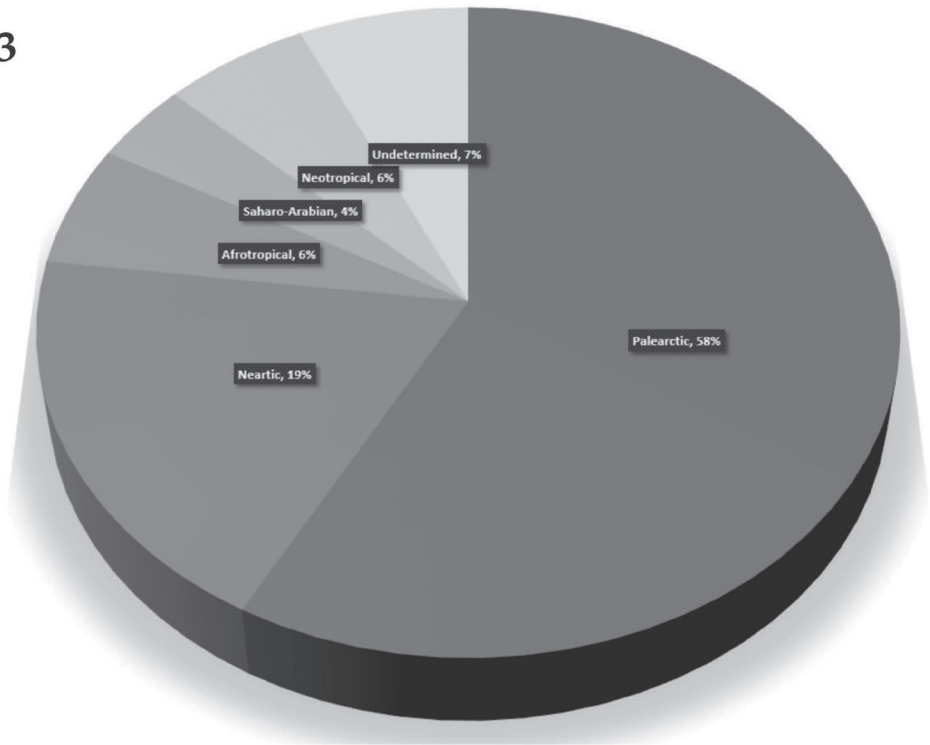


Figure 3. Ant association records by region. The percentage values indicates the fraction of ant association records known for each zoogeographic region.

associated with cryptocephalines are widely distributed, which suggests further records of myrmecophily are to be found for the also widely distributed cryptocephalines. The latter being especially true for the Neotropical region, which is mostly unexplored for myrmecophilous cryptocephalines, despite of its richness in endemic species and genera of ants (Holdobler and Wilson 1990), particularly in the tribe Attini. Finally, some other interesting patterns have been revealed in this study that require further investigation: although there is no myrmecophilous cryptocephaline recorded in Australia, there are three ant genera there that do host cryptocephalines in other parts of the world; even though the species of the dolichoderine *Tapinoma* are cosmopolitan, there is only one extant record for the genus.

Calibrating the evolutionary history of ants and Camptosomata

Wilson and Hölldobler (2005) pointed out three major events in the evolution of ants: 1) early radiation during mid-Cretaceous aided by complex ground litter (angiosperms assembled); 2) a dominance of ants in the angiosperm-rich tropical forests during the Paleogene; and 3) diet shift events in the dolichoderines, formicines, and certain myr-

micines. These events triggered expansion from tropical forest and general predation, into the canopy and into xeric environments and more specialized feeding behaviors.

According to Brady et al. (2006) myrmecines and formicines are sister-groups, and they split around 75–84 mya (but see Moreau and Bell 2013), and some of them exploit symbiotic relationships. This evolutionary picture favors the scenario for the acquisition of myrmecophily in casebearer species and a date of origin in the upper Cretaceous. The older fossil evidence of cryptocephaline larvae (in their cases) include specimens in Dominican Miocene (20 mya) and Baltic (45 mya) ambers (Grimaldi and Engel 2005, Chaboo et al. 2009, Bukejs and Chamorro 2015), thus the minimum age of case-bearing behavior dates to 45 mya. This data is compatible with Wang et al. (2014), yet it differs from other studies on leaf beetles phylogeny (i.e. Hunt et al. 2007, Gómez-Zurita et al. 2007), which date the origin of Chrysomelidae and Cryptocephalines much later.

Table 2 clearly shows that nearly all of the known records of myrmecophily in the cryptocephalines belongs to the Myrmicinae + Formicinae clade, whose common ancestor date from Mid-Cretaceous, 125–75 mya (Brady et al. 2006, Moreau et al. 2006, Geiselhard et al. 2007). The Dolichoderinae clade has an estimated origin of 65 mya (Ward et al. 2010), and the tribe Tapinomini seems to have originated in the Paleotropics. Ergo, host ants might have been available early during the evolution of Cryptocephalinae, a lineage that began its diversification about 93 mya (Wang et al. 2014).

The evolutionary history of formicoid ants date back to the Upper Cretaceous period (Brady et al. 2006, Moreau and Bell 2013), with genus-level divergences being established later in the Eocene, 50–35 mya; this is also supported by their common presence in amber fossils (Grimaldi and Agosti 2000, Moreau et al. 2006, Dunn et al. 2007, Grimaldi and Engel 2005, LaPolla et al. 2013). Furthermore, the origins of myrmecochory (seed dispersal by ants) were also being established at this same time period (Dunn et al. 2007), which include the associations with Formicinae and Dolichoderinae, and the so called tree-loving ants (*Crematogaster*) which are well known canopy-dwelling herbivores (Rico-Gray and Oliveira 2007). Leaf-cutting Attini are far more recent, about 7–16 mya (Schultz and Brady 2008). Attines are limited to the New World, and most of the 12 genera and 190 species occur in the tropical portions of Mexico, Central and South America (Hölldobler and Wilson 1990). These ants form large, mature colonies with great diversity of myrmecophilous species. Certain leaf-cutting ants, such as species of *Atta*, house a large number of “nest guests”, for which interactions with the host (ants) are poorly understood (Waller and Moser 1990). The sophisticated habit of culturing and eating fungi by these fungus-growing ant species has evolved in other insects groups as Macrotermitine (termites) and certain wood-boring beetles. So far no case of termitophily has been reported for Cryptocephalines; further, termitophily has been regarded as extremely rare and accidental for Chrysomelidae in general (Jolivet and Petitpierre 1981). According to Korb (2008), social evolution was independently acquired by ants and termites lineages, the author remark that one of the major differences is that termites do not depend on food provisioning activities for their hemimetabolous brood; contrariwise ants has become

excellent food providers in order to feed their brood. The latter might be thought as a key innovation in ant evolution, which might have driven the origin of myrmecophily within Cryptocephalines searching for food and shelter in ant nest. In this regard, we hypothesize that the nature of food items available inside the termite nest, as well as the effectiveness of the termite defense mechanisms (Puker et al. 2015, and references therein) might explain the absence of termitophily in Chrysomelidae, a relationship which has in fact been exploited by other lineages of Coleoptera as Elateridae, Passalidae, Melyridae, Scarabaeidae, Tenebrionidae, and Carabidae (Costa and Vanin 2010).

A parallel can be traced between the evolution of ants and cryptocephalines regarding climatic preferences. As mentioned above, the last major evolutionary event in ant evolution, according to Wilson and Hölldobler (2005), was the invasion into the canopy niche, aided by diet shift that allowed certain ant groups to colonizing xeric environments. A similar process can be inferred for the diet shift already discussed above in myrmecophilous casebearers: although extant evidence indicates that these might have occurred simultaneously, the precise interconnection of these processes need to be further analyzed to conclude what sort of evolutionary process predominates in such system. Taking Clytrini as an example, most species are characterized as inhabiting temperate, xeric regions (Lopatin 1999). Furthermore, Agrain and Roig-Juñent (2011), based on new and previous evidence, hypothesized a tropical/subtropical origin for this tribe. According to Cloudsly-Thompson (2001), the Tenebrionidae and, to a lesser extent, the Chrysomelidae, are among the most successful animals of xeric environments, and species of these groups are often the only ones to be seen at-large during the day. Jolivet (2004) analyzed adaptations of Chrysomelidae to xeric regions and he mentioned some potential adaptations of clytrines, such as omnivorous larvae, polyphagous adults, lack of potential competitors (i.e. the author mentions that less than 2% of Chrysomelids live in arid zones), and finally, ant-host protection in subterranean nests (microclimatic, hygienic, and enemy-free space). Schöller (1995) also proposed, as an adaptation to xeric environments, the use of the rectal sclerites as water retention organs. This is a morphological trait exhibited only by the females, and not being shared by males. However, males are short-lived compared to females in many insect species, consequently male longevity may not be adaptive. Moreover, the oviposition process may require a more sophisticated water retention mechanism for the females. We have also observed that most species within the subtribe Megalostomina have thicker elytra (relative to other clytrines in the Neotropical region), such as *Anomoea* or *Lachnaia*; this might help in water retention, in a similar way as the sub-elytral cavity in Tenebrionidae and some other beetles adapted to arid environments (Cloudsly-Thompson 2001 and references therein). Also, Monrós (1953) mentions that adults of *Megalostomis gazella* Lacordaire rest for periods during daytime, and this, together with the subterranean habits of the larvae, might be an adaptive means for living in climatic extremes.

Key evolutionary steps in Camptosomata. Case-bearing and its correlated behavioral and morphological characters are a complex synapomorphy distinguishing the clade Cryptocephalinae + Lamprosomatinae within Chrysomelidae. It is the most obvious

defense mechanism of these immature stages (Poinar 1996) and represents a fundamental evolutionary step within leaf beetles. The habitat shift from living in plants to living inside arboreal or subterranean ant nests is an extraordinarily complex problem. A comprehensive phylogenetic analysis of Camptosomata currently underway by a team of researchers, including a number of authors of this paper, hopes to shed some light on the evolution of the group.

Recently, Parker and Grimaldi (2014) described the earliest known specialized myrmecophile, a rove beetle (Staphylinidae) that dates to the early Eocene (52 mya). This indicates that myrmecophily is an ancient evolutionary phenomenon. The detailed study of fossil larval morphology in Cryptocephalines might also provide evidence of specialized morphology indicative of myrmecophily behavior and it would establish a minimum age for myrmecophily within cryptocephalines. Yet, even though the immature stages of cryptocephalines have been studied (Chamorro 2014b, and references therein) and are well preserved in amber fossils, no data on possible myrmecophily specialized structures or chemical substances are currently known.

Conclusions

Unraveling the evolutionary patterns of the habitat and diets shift in adults and larvae, as well as understanding, the multiple behavioral and morphological adaptations of ant-loving cryptocephalines will require extensive field work and inter-disciplinary approaches. The relationship with ants suggests the acquisition of ethological and morphological characters that are currently poorly studied. Some basic research activities include: field observations; experiments using artificial ant nests; and detailed morphological studies of the adults and immature stages. Also, the study of the degree of the association (facultative vs. obligate), the effects of this association on host plant choice (i.e. tropic selection mediated by ants), and the possibility of linked cladogenesis between ants and cryptocephaline phylogeny and diversification. Cost-benefit analysis will evaluate the role of each member in an association. Description of life cycles, as well as detailed anatomical studies of all stages are necessary, especially the study of myrmecophilous organs and the possible chemical cues involved. The behavioral, morphological, and chemical adaptations of cryptocephaline myrmecophiles are promising areas for further research.

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New contributions to the molecular systematics and the evolution of host-plant associations in the genus *Chrysolina* (Coleoptera, Chrysomelidae, Chrysomelinae)

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Abstract

The taxonomic circumscription of the large and diverse leaf beetle genus *Chrysolina* Motschulsky is not clear, and its discrimination from the closely related genus *Oreina* Chevrolat has classically been controversial. In addition, the subgeneric arrangement of the species is unstable, and proposals segregating *Chrysolina* species into new genera have been recently suggested. In this context, the availability of a phylogenetic framework would provide the basis for a stable taxonomic system, but the existing phylogenies are based on few taxa and have low resolution. In the present study we perform a phylogenetic analysis based on mitochondrial (*cox1* and *rrnL*) and nuclear (H3) DNA sequences from a sample of fifty-two *Chrysolina* species representing almost half of the subgeneric diversity of the group (thirty out of sixty-five subgenera) and most of the morphological, ecological and karyological variation in the genus. In addition, five *Oreina* species from two subgenera have also been analysed. The resulting phylogeny is used to evaluate some of the most relevant taxonomic hypotheses for *Chrysolina*, and also to reconstruct its ancestral host plant associations in a Bayesian framework. Our findings support the paraphyly of *Chrysolina* as currently defined due to the inclusion of *Oreina*, the monophyly of the *Chrysolina* (plus *Oreina*) species including the divergent *Ch. (Polysticta) vigintimaculata* (Clark, 1864), and enable inferences of deep-level evolutionary relationships among the studied subgenera. The plant family Lamiaceae is inferred as the ancestral host of the study group, whose evolution is characterized by continuous host-shifting among pre-existing host plant families. Some *Chrysolina* clades include mixtures of species with different levels of diet breadth, indicating that niche width has varied through time.

Keywords

Coleoptera, Chrysomelidae, *Chrysolina*, *Oreina*, Phylogeny, Insect-plant interaction, *cox1*, *rrnL*, H3

Introduction

The genus *Chrysolina* Motschulsky is a very large and diverse group of leaf-beetles that are mainly distributed in Europe, Asia and Africa (Bieńkowski 2001). Nearly 450 species belonging in 65 subgenera have been recognized (Bieńkowski 2001), and new species are still being described (e.g. Ge et al. 2011, Bourdonné et al. 2013, Lopatin 2011, 2014). However, despite the number of taxonomic studies focused on *Chrysolina* its taxonomy is chronically confused (Kippenberg 2010), and even the circumscription of the genus remains unclear. In fact, the most recent and updated taxonomic review (Bieńkowski 2007) does not contribute a comparative morphological diagnosis to differentiate *Chrysolina* from the closely related genera. In this sense the most controversial case is the one concerning the genera *Chrysolina* and *Oreina* Chevrolat, whose discrimination mainly relies in the ratio between the length of the metasternum and the length of the first abdominal sternite (Weise 1893). It has been suggested that this morphological attribute could be inconsistent (Bieńkowski 2007), thus reinforcing the inclusion of the genus *Oreina* within *Chrysolina* (Chapuis 1874, Bourdonné and Doguet 1991, Daccordi 1994) or conversely the recognition of *Chrysolina* as a subgenus of *Oreina* (Monrós and Bechyné 1956). In addition, taxonomic rearrangements are frequent in *Chrysolina*, including decisions splitting species into new genera (e.g. *Craspeda* Motschulsky [= *Zeugotaenia* Motschulsky]: Bourdonné 2005, *Camerounia* Jolivet: Bieńkowski 2007, *Chalcoidea* Motschulsky: Bourdonné 2012). Likewise, the subgeneric arrangement of the *Chrysolina* species is also unstable (Mikhailov 2000, 2002, Bieńkowski 2001, 2007, Bourdonné 2008, 2012, Kippenberg 2010). This taxonomic instability reflects the lack of a supraspecific systematic for the genus *Chrysolina*, due in part to the absence of a phylogenetic background.

Phylogenetic studies focused on *Chrysolina* are scarce and limited to a reduced number of taxa. Bourdonné and Doguet (1991) proposed the first evolutionary hypothesis for 10 groups of Palaearctic species attending to both their chromosome numbers and host-plant affiliations. From a molecular perspective, Garin et al. (1999) performed a phylogenetic analysis based on mtDNA sequences (*cox1* and *rrnL*) from 30 *Chrysolina* species representing 22 subgenera plus two *Oreina* species. The resulting phylogenetic trees allowed for the identification of monophyletic lineages comprising few species each, but the deep level relationships were poorly resolved. On the other hand, the two *Oreina* species nested within the *Chrysolina* clade, but this relationship was unsupported. Simultaneously, Hsiao and Pasteels (1999) also inferred a molecular phylogeny based on mtDNA markers (12S and *rrnL*) from 16 *Chrysolina* species ascribed to 14 subgenera and 14 *Oreina* species, but the resulting topologies also had low resolution at the basal nodes. *Oreina* species were recovered as a monophyletic lineage that also included *Chrysolina fastuosa* (Scopoli, 1763), and all of them were nested in

the *Chrysolina* clade. Both molecular studies highlighted the reciprocal monophyly of the subgenera *Melasomoptera* Bechyné and *Synerga* Weise, and of *Hypericia* Bedel and *Sphaeromela* Bedel, however discrepancies were observed regarding the systematic position of the subgenera *Colaphodes* Motschulsky and *Taeniochrysea* Bechyné.

Apart from taxonomic purposes, the availability of a phylogenetic hypothesis for the species of *Chrysolina* may allow for the study of evolutionary processes such as their ancestral host plant affiliations. In this regard, this leaf beetle genus constitutes a suitable and interesting study group as most of the species are oligophagous, each of them feeding on a narrow range of closely related plants (Jolivet and Petitpierre 1976, Bourdonné and Doguet 1991). Indeed, the taxonomic conservatism in host plant use found in *Chrysolina* is so high that host use has been frequently coupled with other systematic characters to circumscribe species assemblages (Petitpierre and Segarra 1985, Bourdonné and Doguet 1991, Petitpierre and Mikhailov 2009). The ancestral reconstruction of the trophic affiliations in *Chrysolina* and *Oreina* was addressed in the phylogenetic studies performed by Garin et al. (1999) and by Hsiao and Pasteels (1999), inferring the plant family Lamiaceae as the most likely ancestral host for *Chrysolina* + *Oreina* (Garin et al. 1999) and the Asteraceae for *Oreina* (Hsiao and Pasteels 1999). However, these reconstructions were based on poorly resolved phylogenetic trees from few taxa.

In this work we present the results of a phylogenetic study based on mitochondrial and nuclear DNA sequences from a sample of *Chrysolina* and *Oreina* species, using Bayesian and maximum likelihood (ML) inference approaches. We expand the taxon sampling of previous molecular studies (Garin et al. 1999, Hsiao and Pasteels 1999) through the inclusion of representatives for nearly half of the *Chrysolina* subgenera comprising most of the morphologically defined groups and ecological variation of the genus. In addition, the inferred molecular phylogeny is used to test the validity of a number of taxonomic hypotheses derived from morphological, ecological, chemical and genetic data. Finally, we aim to investigate the evolution of the host plant associations in the genus *Chrysolina*.

Materials and methods

Taxon sampling

We have studied 52 *Chrysolina* species representing 30 out of the ca. 65 subgenera currently recognized for the genus (Bieńkowski 2001, Kippenberg 2010), plus five *Oreina* species from two subgenera. Our sampling includes type species representatives regarding 13 of the studied *Chrysolina* subgenera and one type species for *Oreina*. In addition, several representatives of other genera of the subfamily Chrysomelinae were analysed as outgroups, including a species from the early-divergent genus *Timarcha* Latreille (Gómez-Zurita et al. 2008) (Table 1). Beetles were collected by us in the field or received from colleagues in absolute ethanol and stored in the laboratory at -20 °C

Table 1. Studied taxa, sources, host plants and GenBank accession numbers. Species groups defined by Bourdonné and Doguet (1991) are also indicated. a: Baselga and Novoa (2006), b: Bienkowski 2010, c: Bienkowski 2011, d: Bourdonné 2005, e: Bourdonné and Doguet 1991, f: Cobos 1953, g: Garin et al. 1999, h: Jolivet and Petitpierre 1976, i: Jolivet et al. 1986, j: Koch 1992, k: Lopatin and Mikhailov 2010, l: Mikhailov 2006, m: Petitpierre 1981, n: Rizza and Pecora 1980, o: Vela and Bastazo 1999.

Species	Source	Host(s)	Host(s) references	Bourdonné and Doguet's (1991) group	cox1	rml	H3
<i>Ch. aeruginosa</i> (Faldermann, 1835)	SE Tuva, Siberia, Russia	Asteraceae (<i>Artemisia</i>), Lamiaceae (<i>Thymus</i>)	b		LN833682	LN833808	LN833745
<i>Ch. baetica</i> (Suffrian, 1851)	Murcia, Spain	Lamiaceae (<i>Satureja</i> , <i>Thymus</i>)	i	2	LN833683	LN833809	LN833746
<i>Ch. americana</i> (Linnaeus, 1758)	Almuñecar, Spain	Lamiaceae (<i>Lavandula</i> , <i>Rosmarinus</i>)	b, h	2	LN833684	LN833810	LN833747
<i>Ch. aurichalcea</i> (Gebler in Mannerheim, 1825)	Ticino, Switzerland	Apocynaceae (<i>Vincetoxicum officinale</i>), Asteraceae (<i>Anethum</i> , <i>Artemisia</i> , <i>Aster</i> , <i>Kalimeris</i> , <i>Peasites</i>)	b, j	9	LN833685	LN833811	LN833748
<i>Ch. banksi</i> (Fabricius, 1775)	Balearic Islands, Spain	Lamiaceae, Plantaginaceae	h	2	LN833686	LN833812	LN833749
<i>Ch. bicolor</i> (Fabricius, 1775)	Canary Islands, Spain	Lamiaceae (<i>Sacrocodyx</i> , <i>Salvia</i> , <i>Thymus</i>)	h	2	LN833687	LN833813	LN833750
<i>Ch. carnifex</i> (Fabricius, 1792)	Barcelona, Spain	Asteraceae (<i>Artemisia</i> , <i>Santolina</i>)	b	9	LN833688	LN833814	LN833751
<i>Ch. cerealis gynaenotata</i> (Motschulsky, 1860)	Altai, Siberia, Russia			2	LN833689	LN833815	LN833752
<i>Ch. colasi</i> (Cobos, 1952)	Granada, Spain	Lamiaceae (<i>Sideritis glacialis</i>)	o	1	LN833690	LN833816	LN833753
<i>Ch. convexicollis</i> (Jakobson, 1901)	SE Tuva, Siberia, Russia	Asteraceae (<i>Artemisia</i>)	c		LN833691	LN833817	LN833754
<i>Ch. costalis</i> (Olivier, 1807) (= <i>Ch. obsoleta</i> Brullé, 1838 <i>sensu</i> Bienkowski 2014 unpubl.)	Canary Islands, Spain	Ranunculaceae (<i>Ranunculus</i>)	e	2	LN833714	LN833818	LN833777
<i>Ch. diluta</i> (Germar, 1824)	Granada, Spain	Plantaginaceae (<i>Plantago</i>)	h	3	LN833693	LN833819	LN833756
<i>Ch. eurina</i> (Friedvaldszky, 1883: 17)	Mundybakh, Kemerovskaya oblast', Russia	Asteraceae (<i>Tanacetum vulgare</i>)	b	9	LN833694	LN833820	LN833757
<i>Ch. fastuosa</i> (Scopoli, 1763)	Lleida, Spain	Lamiaceae (<i>Galeopsis</i> , <i>Lamium</i> , <i>Leonorus</i> , <i>Prunella</i>)	h, i	2	LN833695	LN833821	LN833758
<i>Ch. femoralis</i> (Olivier, 1790)	Girona, Spain	Lamiaceae (<i>Satureja</i> , <i>Thymus</i>)	h, i	2	LN833696	LN833822	LN833759
<i>Ch. fuliginosa</i> (Olivier, 1807)	Lleida, Spain	Asteraceae (<i>Centaurea</i>)	h	9	LN833697	LN833823	LN833760
<i>Ch. gemina</i> (Brullé, 1838)	Canary Islands, Spain	Lamiaceae (<i>Lavandula</i>)	h	2	LN833698	LN833824	LN833761
<i>Ch. geminata</i> (Paykull, 1799)	Lleida, Spain	Hypericaceae (<i>Hypericum</i>)	b	10	LN833699	LN833825	LN833762
<i>Ch. huemochloru</i> (Gebler, 1823)	Ust'-Koksa, Altai Republic, Russia	Apiaceae (<i>Aegopodium</i> , <i>Angelica</i> , <i>Conioselinum</i> , <i>Heracleum</i> , <i>Pleurospermum</i>)	c		LN833700	LN833826	LN833763

Species	Source	Host(s)	Host(s) references	Bourdonné and Doguet's (1991) group	cox1	rnl	H3
<i>Ch. haenoperna</i> (Linnaeus, 1758)	La Coruña, Spain	Plantaginaceae (<i>Plantago</i>)	m	7	LN833701	LN833827	LN833764
<i>Ch. helioides</i> (Suffrian, 1851)	Málaga, Spain	Apiaceae (<i>Ferula</i>)	h	4	LN833702	LN833828	LN833765
<i>Ch. herbacea</i> (Dufschmid, 1825)	Teruel, Spain	Lamiaceae (<i>Mentha</i>)	b, h	2	LN833703	LN833829	LN833766
<i>Ch. hyperica</i> (Forster, 1771)	Bragança, Portugal	Hypericaceae (<i>Hypericum</i>)	b	10	LN833704	LN833830	LN833767
<i>Ch. jakobovici</i> (Weise, 1894)	Sayan Mts., Tuva, Russia				LN833705	LN833831	LN833768
<i>Ch. janbechyni</i> Cobos, 1953 [= <i>Ch. curvilinea</i> (Weise, 1884)]	Murcia, Spain	Asteraceae (<i>Artemisia</i>)	f	9	LN833692	LN833832	LN833755
<i>Ch. kocheri</i> (Codina Padilla, 1961)	Smimou, Morocco	Plantaginaceae (<i>Plantago coronopus</i>)	d	3	LN833706	LN833833	LN833769
<i>Ch. kuesteri</i> (Heliessen, 1912)	Tejeda, Granada, Spain	Lamiaceae, Scrophulariaceae (<i>Linaria</i>)	b, e	1	LN833707	LN833834	LN833770
<i>Ch. lepida</i> (Olivier, 1807)	Huésca, Granada, Spain	Asteraceae (<i>Mantischaea salmantica</i>)	e	9	LN833708	LN833835	LN833771
<i>Ch. lucida</i> (Olivier, 1807)	Almería, Spain	Lamiaceae (<i>Mentha</i>)	h	2	LN833709	LN833836	LN833772
<i>Ch. lucidicollis grossepunctata</i> (Lindberg, 1950)	Canary Islands, Spain	Scrophulariaceae (<i>Linaria</i>)	e	1	LN833710	LN833837	LN833773
<i>Ch. marginata</i> (Linnaeus, 1758)	Girona, Spain	Asteraceae (<i>Achillea</i>)	b, e, h	9	LN833711	LN833838	LN833774
<i>Ch. affinis mesatlantica</i> (Kocher, 1958)	Moyen Atlas, Morocco			2	LN833712	LN833839	LN833775
<i>Ch. obscura</i> (Suffrian, 1851)	Var, France	Apiaceae	e	4	LN833713	LN833840	LN833776
<i>Ch. oirota</i> Lopatin, 1990	Ivanovsky massif, Kazakhstan	Asteraceae (<i>Saussurea latifolia</i>), Lamiaceae (<i>Lamium</i>)	k		LN833715	LN833841	LN833778
<i>Ch. pedicris</i> (Gebler, 1823)	Sekisovka, Kazakhstan	Apiaceae (<i>Seseli</i>)	c		LN833716	n.a.	LN833779
<i>Ch. peregrina</i> (Herrich-Schaeffer, 1839)	Balearic Islands, Spain	Apiaceae (<i>Daucus, Phoeniculium</i>)	g, h	8	LN833717	n.a.	LN833780
<i>Ch. perforata</i> (Gebler, 1830)	Erzin, Russia	Asteraceae, Lamiaceae	c		LN833718	LN833842	LN833781
<i>Ch. petipierrei</i> Kippenberg, 2004	Lleida, Spain				LN833719	LN833843	LN833782
<i>Ch. polita</i> (Linnaeus, 1758)	Girona, Spain	Lamiaceae (<i>Lycopus, Mentha, Origanum, Satureja</i>)	b, h, i	2	LN833720	LN833844	LN833783
<i>Ch. quadrigenina</i> (Suffrian, 1851)	Bragança, Portugal	Hypericaceae (<i>Hypericum</i>)	h	10	LN833721	LN833845	LN833784
<i>Ch. reitteri</i> (Weise, 1884)	Susuz, Turkey				LN833722	LN833846	LN833785
<i>Ch. rossia</i> (Illiger, 1802)	Torino, Italy	Lamiaceae (<i>Mentha piperita</i>), Scrophulariaceae (<i>Linaria, Veronica</i>)	b, n	1	LN833723	LN833847	LN833786
<i>Ch. rufouenea</i> (Suffrian, 1851)	Zamora, Spain	Apiaceae (<i>Carum verticillatum</i>)	a, i	8	LN833724	LN833848	LN833787
<i>Ch. soiana</i> (Jakobson, 1924)	Kulumsy range, Olsky pass, Russia				LN833726	LN833849	LN833789

Species	Source	Host(s)	Host(s) references	Bourdonné and Doguet's (1991) group	cox1	rrnL	H3
<i>Ch. sturmi</i> (Westhoff, 1882)	Chelyabinsk, Russia	Asteraceae (<i>Cirsium</i>), Lamiaceae (<i>Glechoma</i>), Scrophulariaceae (<i>Linaria</i>)	b		LN833727	n.a.	LN833790
<i>Ch. sylvatica</i> (Gebler, 1823)	Kulumsy range, Olsky pass, Russia	Ranunculaceae (<i>Aquilegia glandulosa</i>)	l		LN833728	LN833850	LN833791
<i>Ch. timarchoides</i> (Brisout de Barneville, 1882)	Girona, Spain	Apiaceae (<i>Bupleurum</i> , <i>Heracleum</i>)	h	4	LN833729	LN833851	LN833792
<i>Ch. tundralis</i> (Jakobson, 1910)	Serebryansky Mount, Russia	Asteraceae (<i>Arnica</i> , <i>Saussurea</i>), Lamiaceae (<i>Lamium purpureum</i>)	c		LN833730	LN833852	LN833793
<i>Ch. vernalis pyrenaica</i> (Dufour, 1843)	Lleida, Spain	Plantaginaceae (<i>Plantago</i>)	m	7	LN833731	LN833853	LN833794
<i>Ch. viridana</i> (Kuster, 1844)	KwaZulu-Natal, South Africa				LN833732	n.a.	LN833795
<i>Ch. vigintimaculata</i> (Clark, 1864)	Riofrio, Granada, Spain	Lamiaceae (<i>Mentha</i>)	h	2	LN833733	LN833854	LN833796
<i>Ch. wollastoni</i> (Bechyné, 1957) [= <i>Ch. rutilans</i> (Wollaston, 1864)]	Canary Islands, Spain	Lamiaceae (<i>Mentha</i>)	h	2	LN833725	LN833855	LN833788
<i>Oreina cacaliae</i> (Schrank, 1785)	Lleida, Spain	Asteraceae (<i>Adenostyles</i> , <i>Petasites</i>)	i	6	LN833735	LN833857	LN833798
<i>Oreina fairmatiriana</i> (De Gozis, 1882) [= <i>Oreina splendidula</i> (Fairmaire, 1865)]	Lleida, Spain	Apiaceae, Asteraceae (<i>Senecio</i>)	e	6	LN833739	LN833858	LN833802
<i>Oreina ganglbaueri</i> (Jakob, 1953)	Lleida, Spain	Apiaceae (<i>Angelica</i> , <i>Hemideum</i> , <i>Meum</i>)	i	5	LN833736	LN833859	LN833799
<i>Oreina speciosa</i> (Linnaeus, 1767)	Massif des Vosges, Haut-Rhin, France	Apiaceae (<i>Angelica</i> , <i>Heliosiadium</i> , <i>Laerppitium</i> , <i>Peucedanum</i>)	i	5	LN833737	n.a.	LN833800
<i>Oreina speciosissima</i> (Scopoli, 1763)	Lleida, Spain	Asteraceae (<i>Adenostyles</i> , <i>Cirsinus</i> , <i>Petasites</i> , <i>Senecio</i>)	i	6	LN833738	LN833860	LN833801
<i>Lamprolina aeneipennis</i> (Boisduval, 1835)	Mount Keira, NSW, Australia				LN833734	LN833856	LN833797
<i>Paropsis atomaria</i> Olivier, 1807	Molonglo Gorge Nature Reserve, ACT, Australia				LN833740	LN833862	LN833803
<i>Paropsissterna linuata</i> (Marsham, 1808)	Black Mountain, ACT, Australia				LN833741	LN833861	LN833804
<i>Phyllocharis cyanicornis</i> (Fabricius, 1801)	Royal National Park, NSW, Australia				LN833742	LN833863	LN833805
<i>Poropteromela epipleuralis</i> Lea, 1916	Mount Moombil, NSW, Australia				LN833743	LN833864	LN833806
<i>Timarcha sinuatoollis</i> Fairmaire 1861	Lleida, Spain				LN833744	LN833865	LN833807

before processing. Voucher specimens are deposited for long-term storage at the DNA and tissue collection of the Biodiversity, Systematics and Evolution group (Bio6Evo) of the University of the Balearic Islands.

DNA isolation, PCR amplification and sequencing

Total DNA was purified from beetle head and pronotum using the DNeasy Tissue kit (Qiagen, West Sussex, UK) and following the manufacturer's protocol. Elutions were done in 200 μ L volume and one microliter was used in PCR reactions. Three different molecular markers were selected for the study, including a partial sequence of the mitochondrial 16S rDNA (*rrnL*; primers LR-N-13398 and LR-J-12887; Simon et al. 1994), a partial sequence of the mitochondrial cytochrome c oxidase subunit 1 gene (*cox1*; primers C1-J-2183 and TL2-N-3014; Simon et al. 1994), and a fragment from the nuclear histone 3 gene (H3; primers H3aF and H3aR; Colgan et al. 1998). PCR conditions used 0.2 μ M of each primer and 3.5mM MgCl₂ using a standard protocol of 35 cycles with annealing temperature ranging from 50 to 45 °C (60s) depending on the sample, and denaturation (94 °C) and elongation (72 °C) lasted 30 and 60s, respectively. PCR products were visualized by 1% agarose gel electrophoresis and subsequently purified using MSB Spin PCRapace (Invitex, Berlin, Germany). Sanger sequencing was performed with the same primers as above using the BigDye Terminator Cycle Sequencing kit (Applied Biosystems, Foster City, CA, USA). Sequences were edited and contigs were assembled using BIOEDIT v. 7 (Hall 1999), and deposited at GenBank under the accession numbers referred in Table 1.

Phylogenetic analyses

Heterogeneity in base composition across taxa was explored for each codon position of the protein-coding genes and for *rrnL* using the chi-square test for base frequency differences implemented in PAUP*4.0b10 (Swofford 2003). Multiple sequence alignment was performed using MAFFT 7 online version (<http://mafft.cbrc.jp/alignment/server/>, Katoh and Standley 2013) under default parameters. Molecular markers were checked for combinability using the incongruence length difference (ILD) test (Farris et al. 1994) implemented in PAUP* v4.0b10 (Swofford 2002). The test was run using 100 random stepwise additions and 1000 replicates of heuristic search with tree bisection–reconnection (TBR) branch swapping. The optimal partitioning strategy and evolutionary models for the combined sequence matrix were assessed with Partition-Finder (Lanfear et al. 2012) under the Bayesian Information Criterion (BIC) and using the implemented greedy algorithm.

Bayesian phylogenetic inference was conducted using MrBayes 3.2 (Ronquist et al. 2012). Two independent analyses consisting of four chains each were run for $5 \cdot 10^6$ generations specifying a sampling frequency every 100 generations, and setting a burn-

in fraction of 10%. MCMC convergence and the effective sample sizes (ESS) estimates were checked with TRACER v. 1.5 (Rambaut and Drummond 2007). Additionally, a maximum likelihood search was done using GARLI v.2.01 (Zwickl 2006) and performing 100 bootstrap replicates.

Taxonomic hypotheses testing

Specific hypotheses of monophyly were tested using a ML framework and the Approximately Unbiased test (AU test, Shimodaira 2000) as implemented in the CONSEL program (Shimodaira and Hasegawa 2001). We compared our molecular phylogenetic hypothesis with some of the most relevant systematic proposals for the genus *Chrysolina* (see results). Prior to the evaluation of each taxonomic scenario, a ML phylogenetic analysis was performed in GARLI v.2.01 using the same partitioning scheme and models as in the phylogenetic searches described above, but enforcing the monophyly of the taxa of interest. Once the resulting ML trees were obtained, their per site log-likelihoods were calculated using RAxML v8.0.X program (Stamatakis 2014) and used as input data in CONSEL.

Ancestral character reconstruction

Ancestral host plant affiliations were reconstructed using BayesTraits v. 2.0 (Pagel and Meade 2013) selecting the MCMC mode and the “multistate” model of evolution (Pagel et al. 2004). To take into account phylogenetic uncertainty, reconstructions were based on 1000 randomly selected post-burnin Bayesian trees from the phylogenetic analysis in MrBayes 3.2. Following the manual’s recommendations (<http://www.evolution.rdg.ac.uk/BayesTraitsV2.0Files/TraitsV2Manual.pdf>), the reversible-jump (RJ) MCMC with a hyperprior approach was chosen, and the interval of 0–30 for the RJ-hyperprior implementing an exponential distribution was applied. The “addM-RCA” command was used to calculate the posterior distribution of ancestral character states at selected nodes in the Bayesian *Chrysolina* tree. A total of $10 \cdot 10^6$ generations were run, with samples taken every 100 iterations and discarding a burn-in fraction of 10%. Results of the MCMC runs including the ESS values were analysed in TRACER v. 1.5.

We also used BayesTraits to evaluate different ancestral host plant affiliations scenarios at the root of the *Chrysolina* tree. Analyses were conducted by enforcing the ancestral state of the most recent common ancestor (mrca) for the core *Chrysolina* node (excluding the divergent species *Ch. vigintimaculata*) to be one of the eight host plant families recorded for the studied *Chrysolina* species. MCMC was used to explore the samples and the space rate parameter of 1000 post-burnin trees generated in the MrBayes analysis. We performed two independent runs of $10 \cdot 10^6$ generations for each one of the constrained searches, and sampling rate parameters every 100 generations.

The constrained runs were then compared by calculating the Bayes factors between the best and second best models based on the harmonic mean of the likelihood from each analysis as indicated in BayesTraits manual.

Results

Sequence data and phylogenetic analysis

Lengths of the amplified gene fragments ranged from 581 to 794 bp for *cox1*, 278 to 512 bp for *rrnL*, and 294 to 363 for H3. Total length of the concatenated DNA sequence matrix was 1682 bp. In *cox1*, 48.36% of the aligned positions were variable, indicating high divergence level among the studied sequences. Indeed, accumulation of mutations for *cox1* was higher than for the other markers, as shown by the pairwise sequence divergence (*p*-distance), which ranged between 0.0063 and 0.2236 (average: 0.1331 ± 0.0105) for *cox1*, 0.0012 and 0.1723 (average: 0.0924 ± 0.0100) for *rrnL*, and 0.0027 and 0.1077 (average: 0.0641 ± 0.0108) for H3. Also, *cox1* and *rrnL* sequences showed the well-known A+T bias typical of insect mtDNA (69.9% and 76.4%, respectively), whereas base frequency was more balanced in the nuclear H3 marker (54.8%). Chi-squared tests for bias in base composition showed no significant heterogeneity in our datasets ($P > 0.99$). On the other hand, ILD test revealed no evidence of incongruence among molecular markers ($P = 0.24$), and we therefore performed all subsequent phylogenetic analyses following a supermatrix approach.

The best-fit partitioning scheme selected by PartitionFinder under BIC divided the data into seven subsets, each with its own model of molecular evolution (Table 2). The effective sample size value for each parameter sampled from the MCMC analysis was always >200 . Bayesian and ML searches resulted in almost the same topology (Figures 1 and 2), with few discrepancies affecting only unsupported relationships such as the placement of the species *Chrysolina bicolor* (Fabricius, 1775), the position of the subgenus *Sulcicollis* (Fairmaire, 1887), and the internal branching pattern of the three species of the subgenus *Chrysolina s. str.* Motschulsky. Both phylogenetic approaches also yielded similar results in terms of nodal support, differing mainly in the values associated to some of the basal nodes of the core *Chrysolina* clade, which were higher in the Bayesian analysis (e.g. nodes K, D and T). The resulting phylogenetic trees revealed the paraphyly of the genus *Chrysolina* as currently described, due to the inclusion of the *Oreina* representatives within the *Chrysolina* clade (Figures 1 and 2). The genus *Oreina* is also recovered as a paraphyletic clade that includes the species *Chrysolina haemochlora* (Gebler, 1823). The results showed the monophyly of the studied *Chrysolina* (plus *Oreina*) species [clade A, Bayesian posterior probability (*pp*)=1, bootstrap=100] excepting the African taxa *Chrysolina (Polysticta) vigintimaculata*, which showed a higher affinity with outgroup taxa. In addition, the monophyletic status of the subgenera with more than one species sampled in the study was recovered in all cases excepting *Anopachys* Motschulsky, *Chalcoidea*, *Timarchoptera*

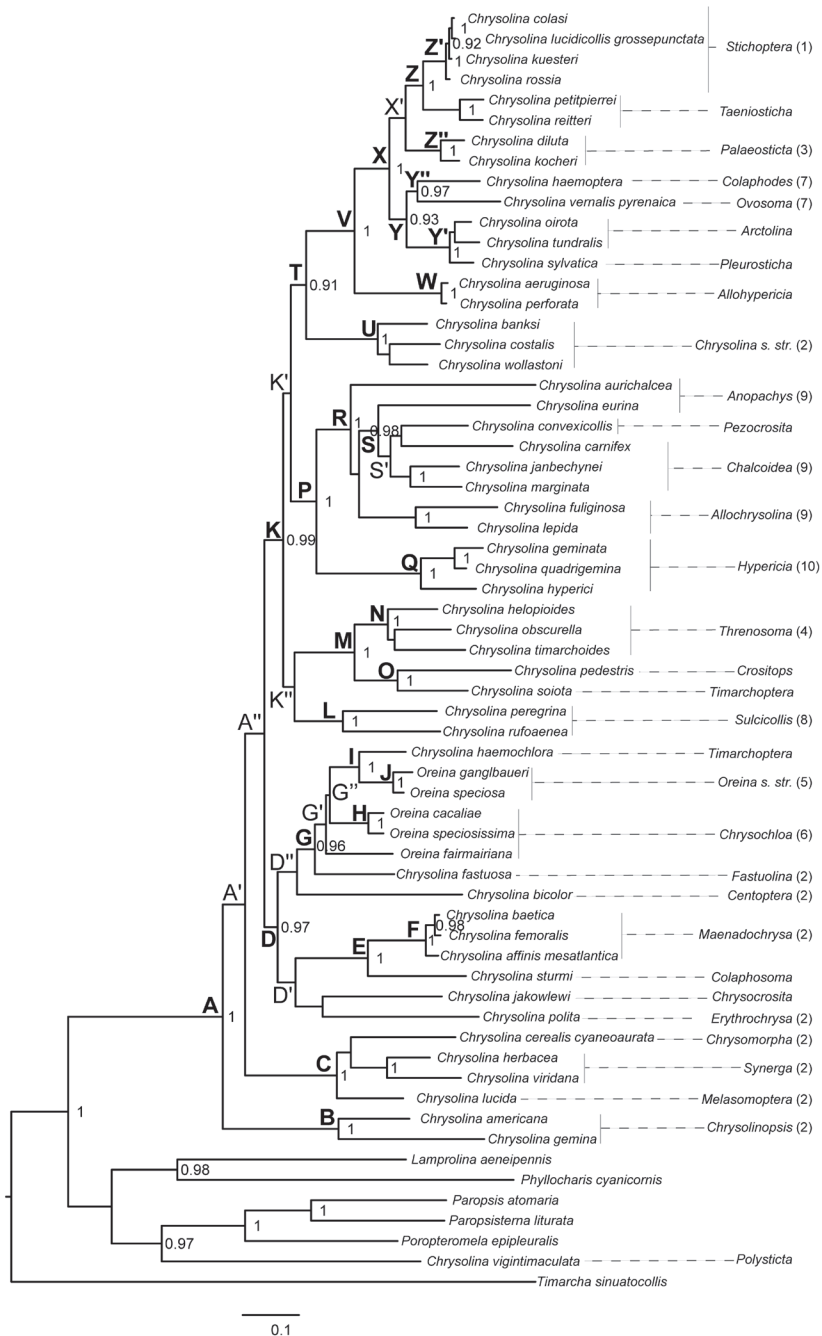


Figure 1. Bayesian phylogenetic tree obtained from the combined analysis of *cox1*, *rrnL* and H3. Node numbers represent Bayesian posterior probability values. Only support values higher than 0.9 are shown. Numbers accompanying the subgeneric classification of the *Chrysolina* species on the right correspond to the systematic groups defined by Bourdonné and Doguet (1991). Clades mentioned in the text are highlighted.

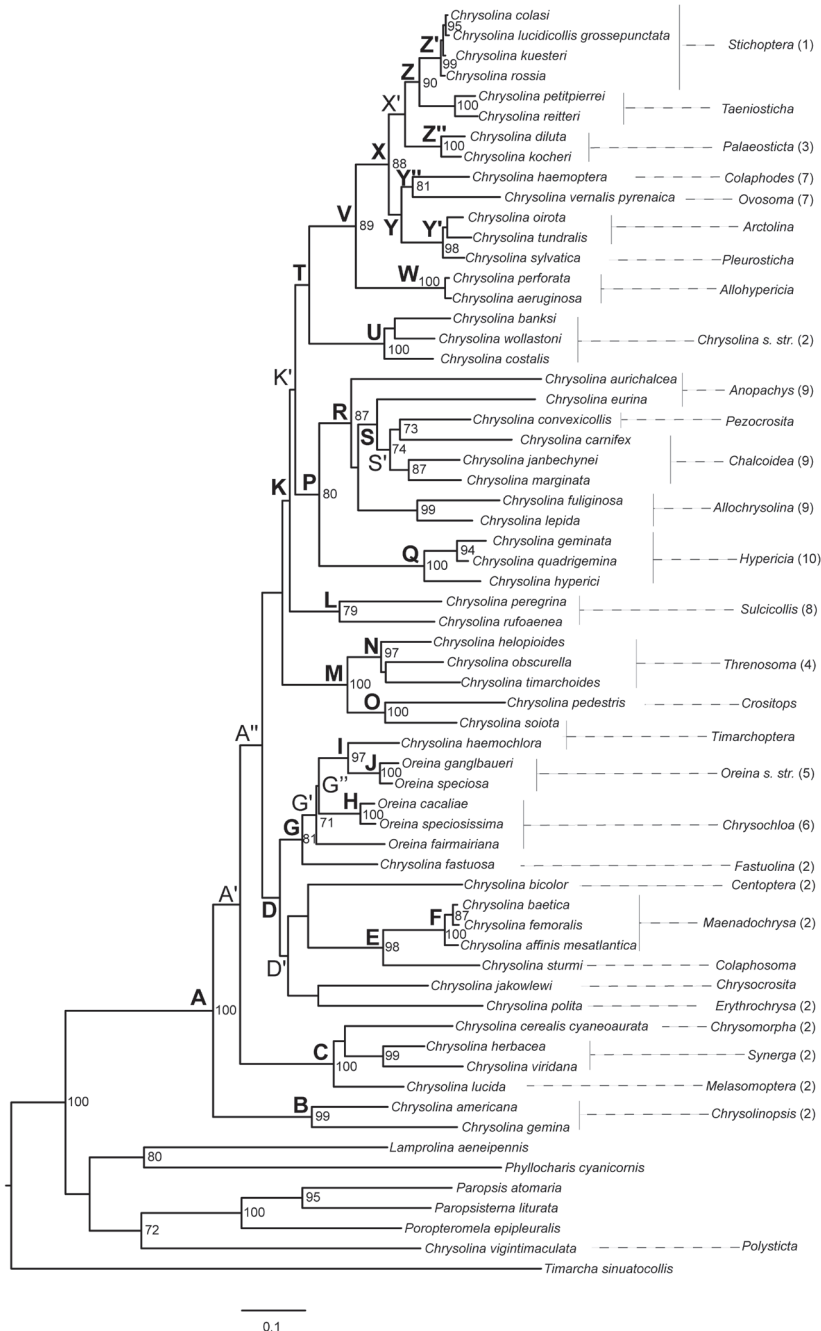


Figure 2. Maximum likelihood phylogenetic tree obtained from the combined analysis of *cox1*, *rrnL* and H3. Node numbers represent bootstrap support values. Only support values higher than 0.7 are shown. Numbers accompanying the subgeneric classification of the *Chrysolina* species on the right correspond to the systematic groups defined by Bourdonné and Doguet (1991). Clades mentioned in the text are highlighted.

Table 2. Optimal partitioning strategy and evolutionary models selected using PartitionFinder under the Bayesian Information Criterion.

Partition	Model
<i>cox1</i> codon pos. 1	GTR+I+G
<i>cox1</i> codon pos. 2	HKY+I+G
<i>cox1</i> codon pos. 3	GTR+G
<i>rrnL</i>	GTR+I+G
H3 codon pos. 1	SYM+G
H3 codon pos. 2	JC
H3 codon pos. 3	HKY+I+G

Table 3. Inferred phylogenetic relationships among *Chrysolina* and *Oreina* subgenera and their statistical supports. Nodes have been coded according to Figures 1 and 2.

Node (Bayesian posterior probability; ML bootstrap)					Subgenera included		
B (1.00; 99)					<i>Chrysolinopsis</i>		
C (1.00; 100)					<i>Chrysomorpha</i>		
					<i>Melasomoptera</i>		
					<i>Synerga</i>		
D (0.97; <70)					<i>Centoptera</i>		
					<i>Chrysocrosita</i>		
					<i>Erythrochrysa</i>		
	E (1.00; 98)				<i>Colaphosoma</i>		
					<i>Maenadochrysa</i>		
	G (0.96; 81)				<i>Fastuolina</i>		
					<i>Oreina</i> subgenus <i>Chrysochloa</i>		
		I (1.00; 97)				<i>Oreina</i> s. str.	
<i>Timarchoptera</i> partim.							
K (0.99; <70)					<i>Sulcicollis</i>		
	M (1.00; 100)				<i>Threnosoma</i>		
		O (1.00; 100)				<i>Crositops</i>	
						<i>Timarchoptera</i> partim.	
	P (1.00; 80)				<i>Hypericia</i>		
		R (1.00; 87)				<i>Anopachys</i>	
						<i>Allochrysolina</i>	
			S' (<0.9; 74)				<i>Chalcoidea</i>
							<i>Pezocrosita</i>
	T (0.91; <70)				<i>Chrysolina</i> s. str.		
		V (1.00; 89)				<i>Allohypericia</i>	
						X (1.00; 88)	
				Y (0.93; <70)	Y' (1.00; 98)		
						<i>Pleurosticha</i>	
				Y'' (0.97; 81)	<i>Colaphodes</i>		
					<i>Ovosoma</i>		
			Z (1.00; 90)				<i>Stichoptera</i>
							<i>Taeniosticha</i>

Motschulsky and *Oreina* subgenus *Chrysochloa* Hope. The inferred topology allowed for the identification of four main monophyletic subgenera assemblages within the core *Chrysolina* clade with high support values in at least one of the resulting trees (clades B, C, D and K). Within these main lineages, it was also possible to identify systematic relationships among subgenera at different phylogenetic levels. The inferred groups of phylogenetically related subgenera and their statistical supports are summarized in Table 3.

Testing for monophyly of key groups

Constrained ML searches were used to evaluate a number of taxonomic hypotheses for *Chrysolina* and *Oreina* using the AU test (Table 4). The phylogenetic scenarios that were rejected in the analyses included the systematic placement of *Oreina* as a different genus from *Chrysolina* ($P=0.016$), the synonymy of subgenera *Paraheliostola* L. N. Medvedev and *Timarchoptera* (Mikhailov 2002, $P=0.001$), the suggestion of a close relationship

Table 4. Results of the Approximately Unbiased test (AU test, Shimodaira 2000). Statistically significant P values are indicated in bold ($P < 0.05$).

Hypothesis of monophyly	Authorship	AU test
<i>Ch. timarchoides</i> + <i>Maenadochrysa</i>	Bienkowski (2001)	0.000
<i>Palaeosticta</i> + <i>Taeniosticha</i>	Bourdonné (2005)	0.198
<i>Craspeda</i> as a different genus from <i>Chrysolina</i>	Bourdonné (2005)	0.007
<i>Allochrysolina</i> + <i>Chalcoidea</i> + <i>Pezocrosita</i>	Bourdonné (2012)	0.205
<i>Allochrysolina</i> + <i>Chalcoidea</i> + <i>Pezocrosita</i> as a different genus from <i>Chrysolina</i>	Bourdonné (2012)	0.003
Species "group 2"	Bourdonné and Doguet (1991)	0.000
Species "group 6"	Bourdonné and Doguet (1991)	0.527
<i>Allochrysolina</i> + <i>Anopachys</i>	Hsiao and Pasteels (1999)	0.215
<i>Colaphodes</i> + <i>Taeniochrysa</i>	Hsiao and Pasteels (1999)	0.000
<i>Paraheliostola</i> + <i>Timarchoptera</i>	Mikhailov (2002)	0.001
<i>Ch. haemochlora</i> + <i>Threnosoma</i>	Mikhailov (2005)	0.000
<i>Chalcoidea</i> + <i>Hypericia</i>	Pasteels et al. (2003)	0.066
<i>Anopachys</i> species		0.212
<i>Chalcoidea</i> species		0.383
<i>Chrysochloa</i> species		0.528
<i>Oreina</i> as a different genus from <i>Chrysolina</i>		0.016
<i>Ch. vigintimaculata</i> + rest of the <i>Chrysolina</i> species + <i>Oreina</i>		0.165
Species feeding on Apiaceae		0.000
Species feeding on Asteraceae		0.000
Species feeding on Lamiaceae		0.000
Species feeding on Plantaginaceae		0.000
Species feeding on Ranunculaceae		0.001
Species feeding on Scrophulariaceae		0.000

between *Threnosoma* Motschulsky and *Ch. (Timarchoptera) haemochlora* (Mikhailov 2005, $P < 0.001$), the reciprocal monophyly of *Colaphodes* and *Taeniochrysa* (Hsiao and Pasteels 1999, $P < 0.001$), the inclusion of *Chrysolina timarchoides* (Brisout, 1882) within the subgenera *Maenadochrysa* Bechyné (Bieńkowski 2001, $P < 0.001$), the recognition of *Craspeda sensu* Bourdonné 2005 as a different genus from *Chrysolina* ($P < 0.01$), the segregation from *Chrysolina* of the subgenera *Allochrysolina* Bechyné, *Chalcoidea* and *Pezocrosita* Jakobson (Bourdonné 2012, $P < 0.01$), the monophyly of the *Chrysolina* species belonging to the “group 2” described by Bourdonné and Doguet (1991) ($P < 0.001$) (Table 1), as well as the monophyly of the *Chrysolina* species feeding on hosts from the same plant family (Apiaceae, Asteraceae, Lamiaceae, Plantaginaceae, Ranunculaceae and Scrophulariaceae; $P \leq 0.001$ in all cases). Conversely, the molecular data could not reject the reciprocal monophyly of several taxa assemblages, such as *Chrysolina vigintimaculata* and the rest of the studied *Chrysolina* species ($P = 0.165$), *Chrysolina* species belonging to the “group 6” described by Bourdonné and Doguet (1991) ($P = 0.527$) (Table 1), subgenera *Allochrysolina* and *Anopachys* (Hsiao and Pasteels 1999, $P = 0.215$), subgenera *Chalcoidea* and *Hypericia* (Pasteels et al. 2003, $P = 0.066$), subgenera *Allochrysolina*, *Chalcoidea* and *Pezocrosita* (Bourdonné 2012, $P = 0.205$), and the subgenera *Palaeosticta* Bechyné and *Taeniossticha* Motschulsky (Bourdonné 2005, $P = 0.198$). Also, the monophyly of the sampled species concerning the subgenera *Anopachys*, *Chalcoidea* and *Oreina* subgenus *Chrysichloa* could not be rejected ($P \geq 0.212$ in all cases).

Ancestral character reconstruction

The Bayesian reconstruction of ancestral host plant associations showed an ancient affiliation with Lamiaceae at the root of the core *Chrysolina* clade (Figure 3, node A, $P = 0.98$; Table 5). This plant family was also recovered as the most likely ancestral host for three of the main clades in our molecular phylogeny (nodes B, C and D; $P = 0.94$, 0.99 and 0.95 , respectively). Within clade D, a host shift from Lamiaceae towards Asteraceae ($P = 0.54$) and/or Apiaceae ($P = 0.37$) was detected for the mrca of *Oreina* and *Chrysolina (Timarchoptera) haemochlora* (clade G'). On the other hand, ancestral host plant reconstruction for node K was ambiguous, recovering associations with multiple families. However, it was possible to identify the occurrence of several host shifts for its derived lineages towards a new trophic association with (i) Apiaceae (node K', $P = 0.62$), (ii) Hypericaceae (nodes P and Q, $P = 0.51$ and 0.97 , respectively), (iii) Asteraceae (node R, $P = 0.94$), (iv) Plantaginaceae (node X, $P = 0.91$), and (v) Scrophulariaceae (node Z', $PP = 0.66$). Nodes W and Y' respectively showed a reversal shift from an ancestral Plantaginaceae host to the original Lamiaceae host family ($P = 0.5$) as well as a new trophic link with Asteraceae ($P = 0.5$).

Results from Bayes factor comparisons of the constraint hypotheses for the ancestral plant family at the root of the core *Chrysolina* clade (node A) corroborated MCMC ancestral state reconstruction, offering positive to very strong statistical support for an ancestral trophic association with Lamiaceae (Table 6).

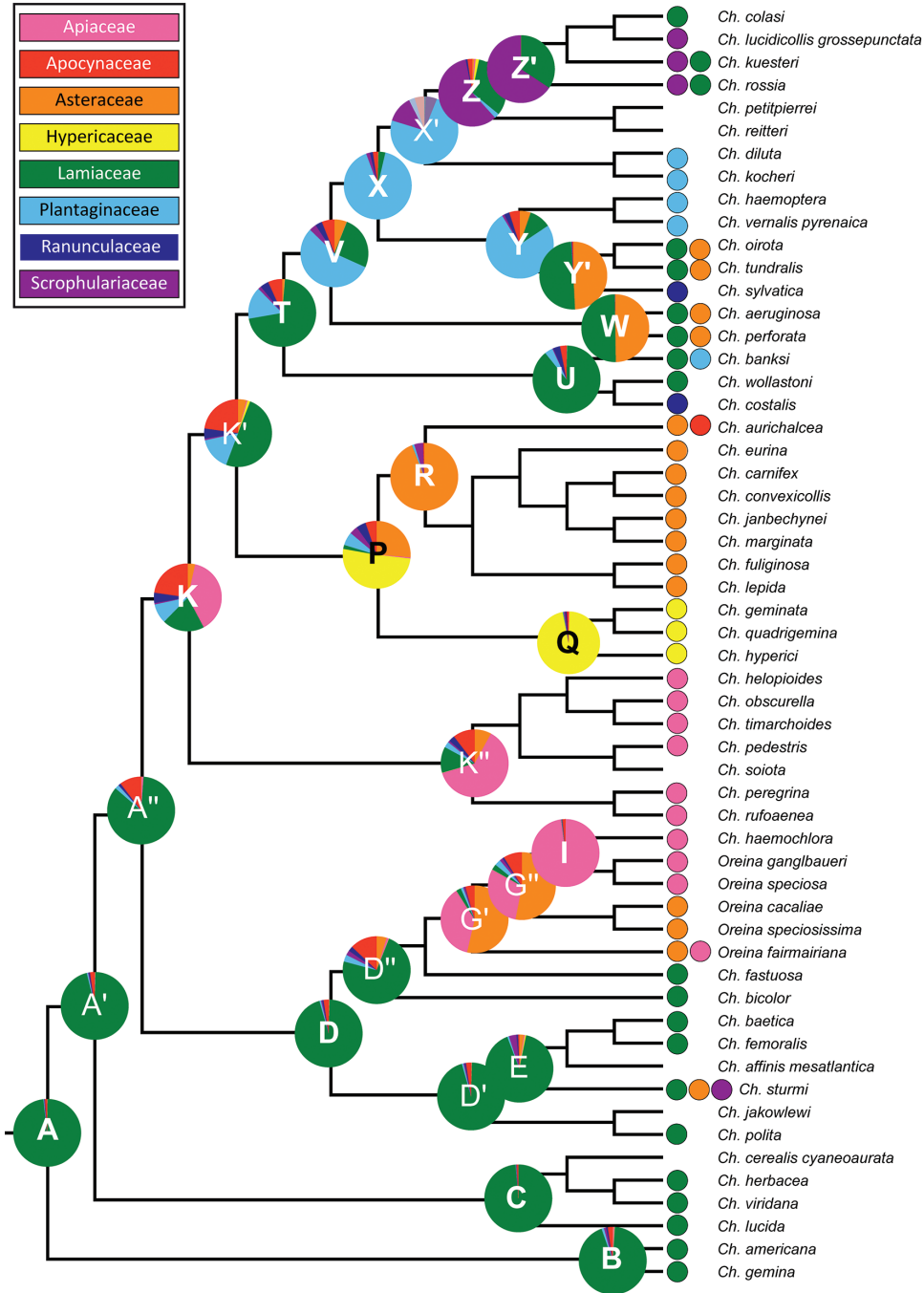


Figure 3. Ancestral reconstruction of host plant affiliations in the studied species of *Chrysolina* and *Oreina*. Terminal taxa are coded according to the available host plants records from the literature (Table 1). Pie charts at selected nodes show probabilities of each state from the Bayesian analysis in BayesTraits. Clades mentioned in the text are highlighted.

Table 5. Posterior probability values of ancestral host-plant affiliations calculated in BayesTraits for the selected nodes in the *Chrysolina-Oreina* phylogeny. The highest probability value(s) for each node are highlighted in bold. Ast.=Asteraceae, Api.=Apiaceae, Hyp.=Hypericaceae, Lam.=Lamiaceae, Plant.=Plantaginaceae, Scro.=Scrophulariaceae, Ran.=Ranunculaceae, Apo.=Apocynaceae.

Node	Host-plant family							
	Ast.	Api.	Hyp.	Lam.	Plant.	Scro.	Ran.	Apo.
A	0.000	0.001	0.000	0.980	0.003	0.002	0.002	0.010
A'	0.001	0.002	0.001	0.959	0.006	0.003	0.006	0.022
A''	0.002	0.010	0.000	0.852	0.020	0.001	0.011	0.104
B	0.002	0.006	0.002	0.937	0.011	0.010	0.008	0.024
C	0.000	0.000	0.000	0.987	0.002	0.002	0.001	0.007
D	0.002	0.001	0.000	0.952	0.008	0.006	0.006	0.024
D'	0.002	0.001	0.000	0.952	0.008	0.006	0.006	0.024
D''	0.048	0.010	0.001	0.732	0.033	0.023	0.024	0.129
E	0.022	0.005	0.006	0.910	0.008	0.036	0.008	0.006
G'	0.536	0.374	0.001	0.023	0.012	0.008	0.002	0.044
G''	0.531	0.300	0.001	0.027	0.029	0.015	0.009	0.089
I	0.001	0.979	0.000	0.001	0.001	0.000	0.002	0.015
K	0.036	0.387	0.000	0.200	0.093	0.007	0.049	0.227
K'	0.040	0.005	0.013	0.499	0.158	0.007	0.049	0.227
K''	0.080	0.624	0.001	0.124	0.028	0.009	0.029	0.104
P	0.262	0.005	0.511	0.019	0.064	0.039	0.047	0.053
Q	0.001	0.002	0.967	0.001	0.003	0.008	0.008	0.010
R	0.941	0.000	0.000	0.000	0.010	0.042	0.001	0.006
T	0.011	0.001	0.001	0.709	0.153	0.015	0.041	0.068
U	0.001	0.001	0.001	0.890	0.039	0.004	0.034	0.031
V	0.059	0.001	0.001	0.257	0.555	0.034	0.033	0.060
W	0.498	0.000	0.000	0.501	0.000	0.001	0.000	0.001
X	0.003	0.000	0.000	0.033	0.908	0.018	0.014	0.023
X'	0.005	0.000	0.001	0.055	0.736	0.128	0.028	0.047
Y	0.052	0.000	0.000	0.103	0.757	0.011	0.026	0.050
Y'	0.492	0.000	0.000	0.498	0.001	0.001	0.002	0.006
Z	0.009	0.008	0.016	0.327	0.023	0.586	0.009	0.023
Z'	0.000	0.000	0.000	0.344	0.000	0.656	0.000	0.000

Discussion

Molecular systematics of *Chrysolina*

The mitochondrial and nuclear genes used here provided an expanded and better-resolved tree topology for the genus *Chrysolina*, significantly improving previous phylogenetic hypotheses. Our results support the reciprocal monophyly of the studied species of *Chrysolina* (plus *Oreina*) including the divergent *Ch. (Polysticta) vigintimaculata*, whose relationship with the core *Chrysolina-Oreina* clade could not be rejected by the AU test. The inferred tree topologies recovered *Ch. vigintimaculata* as a well-

Table 6. Comparing model support with the Bayes factor. Bayes factors were calculated as described in the BayesTraits manual: $BF=2(\ln LhA-\ln LhB)$, where $\ln Lhx$ is the marginal likelihood from the harmonic mean of the post-convergence. The plant family Lamiaceae is the most likely ancestral host at the root of the core *Chrysolina* clade with the highest harmonic mean. The right column indicates the Bayes factor compared against Lamiaceae as the favoured ancestral host. * Indicates positive evidence, ** indicates strong evidence, and *** indicates very strong evidence for the favoured hypothesis.

Host plant family	ln Lh	Bayes Factor
Apiaceae	-62.77	5.27**
Apocynaceae	-63.78	7.30**
Asteraceae	-65.71	11.16***
Hypericaceae	-65.59	10.92***
Lamiaceae	-60.13	-
Plantaginaceae	-62.44	4.61*
Ranunculaceae	-62.57	4.86*
Scrophulariaceae	-63.24	6.20**

differentiated lineage sister to the rest of the ingroup taxa. This species has been traditionally assigned to the subgenus *Atechna* Chevrolat (Bieńkowski 2001), a species of which was included in the phylogenetic analysis of Gómez-Zurita et al. (2008) based on three ribosomal genes and showing a clear divergence from the *Chrysolina-Oreina* clade. In addition, the same pattern was observed in a different phylogenetic study based on five molecular markers (Jurado-Rivera et al. in prep.) that included the species *Ch. (Atechna) striata* (Degeer, 1778). Although more data are needed, the available information indicates that these taxa may represent a lineage of early divergence within *Chrysolina* whose taxonomic status should be further investigated.

The inferred topology also supported most of the current subgeneric taxonomy of *Chrysolina* (Bieńkowski 2001, Kippenberg 2010), since the monophyly of the subgenera screened for more than one species could be demonstrated or alternatively could not be rejected by the AU test. The exceptions in this regard are the synonymy of the subgenus *Paraheliostola* with the subgenus *Timarchoptera* by Mikhailov (2002) and the combination of the species *Ch. (Threnosoma) timarchoides* with the subgenus *Maenadochrysa* by Bieńkowski (2001). In both cases the taxa in question were recovered with support as well-differentiated lineages, thus indicating that such taxonomic decisions could be wrong. Therefore, the subgenus *Paraheliostola* (type species *Ch. soiota* Jacobson, 1924) should be restored according to the present molecular phylogeny. Moreover, the available karyological evidence also conflicts with Bieńkowski's (2001) proposal (Petitpierre 1975, 1981), and we thus agree with Daccordi and Ruffo (2005) and with Kippenberg (2010) in that *Ch. timarchoides* belongs in the subgenus *Threnosoma*.

The new molecular phylogeny also sheds light on the contentious issue of the taxonomic status of *Oreina*. Our analyses supported the inclusion of the studied *Oreina* species within the core *Chrysolina* clade, which was also backed up statistically in the AU test constraining these genera to be reciprocally monophyletic (Table 4). The sam-

ple included the type species of the genus, *O. speciosa* (Linnaeus, 1758), which further strengthens our findings and corroborates previous hypotheses that consider *Oreina* as part of the *Chrysolina* lineage (Chapuis 1874, Bourdonné and Doguet 1991, Daccordi 1994). Moreover, the species feeding on Apiaceae hosts, *O. ganglbaueri* (Jakob, 1953) and *O. speciosa*, were recovered as more closely related to the also Apiaceae feeding *Ch. haemochlora* than to the remainder of the *Oreina* species analysed here, reinforcing our conclusions and highlighting the need for a taxonomic revision for the group. On the other hand, the proposal of considering the genera *Craspeda* and *Chalcoidea* (*sensu* Bourdonné 2005 and 2012, respectively) as separate lineages from the remainder of the *Chrysolina* species is not supported in our phylogenetic framework, although the monophyly of the taxa included in each of them could not be statistically rejected (Table 4). Thus, the recognition of *Craspeda* and/or *Chalcoidea* as valid genera would render *Chrysolina* paraphyletic.

Excluding the divergent species *Ch. vigintimaculata*, *Chrysolina* could be subdivided into four major clades (Figures 1 and 2, clades B, C, D and K). The clades B and C comprised species from the “group 2” defined by Bourdonné and Doguet (1991), all of them feeding on host plants belonging to the family Lamiaceae and with a diploid chromosome number of $2n=24$ (Petitpierre 1975, 1981, 1983). The hypothetical monophyly of the aforementioned “group 2” was statistically rejected by the AU test, thus reinforcing our finding that such an assemblage of species does not constitute a natural group. The clade B included two monotypic subgenera (*Chrysolinopsis* Bechyně and *Taeniochrysea*, *sensu* Bieńkowski 2001) that have been recently regarded as synonyms by Kippengberg (2010), a taxonomic decision that is strongly supported in our phylogenetic analyses. The monophyly of the species nested in clade C were also noted in the phylogenetic study of Garin et al. (1999), excepting the species *Ch. cerealis* (Linnaeus, 1767) that they recovered in a divergent clade as sister to *Ch. fastuosa* with maximum bootstrap support. Here we have analysed the subspecies *Ch. cerealis cyaneoaurata* (Motschulsky, 1860) inferring a clear relationship with the remainder of the members in clade C that is supported with maximum posterior probability and bootstrap values. Genetic distances (*p*-distance) between the sequences deposited in GenBank by Garin et al. (1999) regarding *C. cerealis* and our data for *C. cerealis cyaneoaurata* were unusually high for an intraspecific comparison (*cox1*: 0.14; *rrnL*: 0.08), thus suggesting that the taxa in question do not belong to the same species. It remains to be investigated whether their divergence is due to specimen misidentification or whether *C. cerealis s. str.* and *C. cerealis cyaneoaurata* really are different species. Meanwhile, the results about the systematic position of *Ch. cerealis* should be interpreted with caution.

Clade D defined the monophyletic origin of seven *Chrysolina* subgenera traditionally associated with the “group 2” proposed by Bourdonné and Doguet (1991) plus two *Oreina* subgenera included in “groups 5 and 6”, all of them with a karyotype $2n = 24$ (Petitpierre 1975, 1981, 1983) excepting *Ch. haemochlora* ($2n=27$, Petitpierre and Mikhailov 2009). The affinity between the subgenera *Colaphosoma* Motschulsky and *Maenadochrysa* could be established with confidence agreeing with their shared feeding habits on Lamiaceae species of the tribe Mentheae (Jolivet and Petitpierre 1976, Jolivet

et al. 1986, Bieńkowski 2010). On the other hand, the close relationship recovered in the present work among *Ch. fastuosa* and the studied *Oreina* species is consistent with the findings of Hsiao and Pasteels (1991) based on a different set of molecular markers. The authors concluded that such association was contradicted by strong morphological evidence, highlighting the need of further research on this issue. Our molecular phylogeny not only confirmed the monophyly of these taxa, but also revealed the inclusion of an additional *Chrysolina* species in this clade, *Ch. haemochlora*.

Interestingly, our results regarding the clade K were fully consistent with most species groupings established by Bourdonné and Doguet (1991) based on morphology, karyology and biology of the species ("groups 1, 3, 4, 7, 8, 9, 10 and 2 partim."). Available molecular phylogenies of *Chrysolina* (Garin et al. 1999, Hsiao and Pasteels 1999) failed at recovering supported relationships among these groups, excepting the monophyletic origin of the species belonging in the "groups 1, 3 and 7" inferred by Garin et al. (1999). In contrast, our analyses allowed for the identification of their phylogenetic relationships at deep taxonomic level, and also extended the results to seven *Chrysolina* subgenera not studied by Bourdonné and Doguet (1991). The latter was the case of clade M, where the subgenera *Crositops* Marseul and *Timarchoptera* (more likely *Paraheliostola*, see above) were recovered as the sister lineage of the *Threnosoma* species regarded as "group 4". Indeed, the subgenera *Crositops* and *Threnosoma* are known to share morphological attributes (Mikhailov 2005). Although no information is available for the species *Ch. soiota*, the remainder of the species in clade M feed on Apiaceae and also share a male karyotype $2n=47$ (Petitpierre 1981, 1999, Petitpierre et al. 2004, Petitpierre and Mikhailov 2009), which is highly consistent with their close association recovered here. On the other hand, the existence of a relationship between the Mediterranean subgenus *Threnosoma* and the Siberian subgenus *Timarchoptera* proposed by Mikhailov (2005) was rejected by the AU test. Another subgenus that was not analysed by Bourdonné and Doguet (1991) is represented in our sampling by the species *Ch. (Pezocrosita) convexicollis* (Jakobson, 1901), which appeared in the trees clearly nested within the species "group 9" (clade R) sharing with them a trophic link with Asteraceae. Our phylogenetic hypotheses also allowed for the identification of two main evolutionary lineages within "group 9", on one hand the species belonging in the subgenera *Anopachys* [excluding *Ch. aurichalcea* (Gebler, 1825)], *Chalcoidea* and *Pezocrosita*, all of them feeding on closely related plant species in the family Asteraceae in the tribe *Anthemideae* (*Achillea*, *Artemisia*, *Santolina*, *Tanacetum*; Cobos 1953, Jolivet and Petitpierre 1976, Bieńkowski 2010, 2011, clade S) and sharing a karyotype of $2n=40$ [cytogenetic data for *Ch. eurina* (Frivaldszky, 1883) and *Ch. convexicollis* are not available], and on the other hand the species in the subgenera *Allochrysolina* with a male karyotype $2n=42$ (Petitpierre 1999) and feeding on closely related Asteraceae host plants in the subtribe *Centaureinae* (*Centaurea*, *Mantisalca*, Jolivet and Petitpierre 1976, Bourdonné and Doguet 1991). In turn, the species in "group 9" were recovered as the sister lineage of the species classified in the "group 10" (subgenus *Hypericia*; clade Q), thus contradicting Bourdonné and Doguet's (1991) view that the subgenus *Hypericia* is so differentiated from the remainder of the *Chrysolina* subgenera that it deserves a generic status. Recognition of the genus *Hypericia* would render *Chrysolina* paraphyletic. Also re-

garding this lineage, Pasteels et al. (2003) found that the subgenera *Hypericia*, *Chalcoidea* and *Sphaeromela* are the only Chrysomelinae leaf beetles producing polyoxygenated steroids as defensive toxins, and suggested that they could be raised to a distinct genus. However, our inferred topologies were not compatible with this hypothesis, although the AU test could not reject the constrained monophyly of *Chalcoidea* and *Hypericia*. On the other hand, the well-supported and resolved clade T allowed for the identification of the phylogenetic relationships among four of the systematics groups defined by Bourdonné and Doguet (1991), and also expanded our knowledge regarding the systematic position of four subgenera not included before in any phylogenetic analysis. The species in the subgenera *Chrysolina s. str.* were placed in the “group 2” based on their trophic link with the plant family Lamiaceae but our results clearly contradict this association (clade U), agreeing with their unique male karyotype ($2n=23$; Petitpierre 1975, 1981, 1983). The common ancestry of *Colaphodes*, *Ovosoma* Motschulsky, *Palaeosticta* and *Stichoptera* Motschulsky demonstrated by Garin et al. (1999) was confirmed here, and in addition we show that the subgenera *Allohypericia* Bechyné, *Arctolina* Kontkanen, *Pleurosticha* Motschulsky and *Taeniosticha* also belong in this monophyletic lineage. The close relationship between the subgenera *Arctolina* and *Pleurosticha* has been previously proposed according to their morphology (Bieńkowski 2004) and their karyological resemblances [$2n=26$ (Xy_p), Petitpierre and Mikhailov 2009]. In this regard, our study contributes additional evidence confirming their phylogenetic relatedness (clade Y’). The monophyly of the species adapted to the plant family Plantaginaceae (subgenera *Palaeosticta*, *Colaphodes* and *Ovosoma*) could not be rejected, indicating that they could conform to a natural group, thus expanding Bourdonné and Doguet’s (1991) “group 7”. On the other hand, the *Stichoptera* species of the “group 1” *sensu* Bourdonné and Doguet (1991) were demonstrated to be sister to the morphologically well-defined subgenus *Taeniosticha* (Bourdonné et al. 2013). *Stichoptera* species are characterized by their marked asymmetrical karyotypes (Petitpierre 1999) and their affiliation with Lamiaceae and Scrophulariaceae host plants, but unfortunately no data are available regarding the biology and the cytogenetics of the subgenus *Taeniosticha* to contrast with our molecular results.

Evolution of the host plant associations in *Chrysolina*

The initial stages of the evolutionary history of the genus *Chrysolina* were closely related to the plant family Lamiaceae (Figure 3, node A), which is in line with the pioneering studies based on the karyology and the ecology of the species (Petitpierre and Segarra 1985, Bourdonné and Doguet 1991) and also on mtDNA sequences (Garin et al. 1999). The inferred ancestral association with Lamiaceae was highly favoured in our analyses compared to the alternative hypotheses, including an original affiliation with the family Asteraceae suggested by Crowson (1981).

The most basal clades in our *Chrysolina* phylogeny are those living on Lamiaceae. However, the phylogenetic uncertainty affecting this region of the tree prevents us for drawing firm conclusions about the number of lineages that have adapted to this plant

family at the early stages of the evolution of the genus. In contrast, our phylogenetic analyses allowed for the identification of a minimum of eight host plant family shifts in the *Chrysolina* tree, thus indicating that the feeding spectrum of the extant *Chrysolina* species is the result of frequent and abrupt host shifts in their evolutionary history. While some of these shifts are between plant families belonging to the same order (Lamiaceae, Plantaginaceae, Scrophulariaceae; order Lamiales; APG 2009), others are between distant plant families from different subclasses [shift from families in the subclass Asterids to Hypericaceae (subclass Rosids); APG 2009] or even from more divergent lineages [shifts from Asterids to Ranunculaceae (basal Eudicot); APG 2009]. Three main hypotheses have been proposed concerning the macroevolution of insect–plant associations (Nyman 2010): (i) the ‘cospeciation’ or ‘parallel cladogenesis’ model (Fahrenholz 1913): matching of speciation events between insects and their host plants; (ii) the ‘escape and radiate’ model (Ehrlich and Raven 1964): plants ‘escape’ from herbivory due to novel defences and radiate, followed by colonization of new insect taxa that then radiate on them; and (iii) the ‘sequential evolution’ model (Jermy 1984): insects have little effect on the speciation of their hosts, whereas the diversification of hosts increases possibilities of ecological speciation in insects. The hypothesis of ‘parallel cladogenesis’ between *Chrysolina* lineages and their host plant families can be discarded as the temporal origin of the more closely related host plant families recorded for *Chrysolina* (Lamiaceae and Scrophulariaceae: mrca >65Ma, Bremer et al. 2004) clearly pre-dates the diversification of the *Chrysolina* lineage itself [mrca ca. 40Ma, (ca. 20Ma excluding the divergent subgenera *Atechna*), Gómez-Zurita et al. 2007]. Consistently, this pattern of asynchronous diversification has been found among other phytophagous insect groups and their host plants (Lopez-Vaamonde et al. 2006, McKenna et al. 2009). Regarding the ‘escape and radiate’ model, the existence of coincident radiations at a large scale among host families and the *Chrysolina* lineages is also not possible due to this time lag in their respective origins. Conversely, the ancestral host plant family affiliations inferred for *Chrysolina* seem to fit better the ‘sequential evolution’ model, as deduced from the continuous host-shifting among pre-existing host families that characterizes the evolution of the genus (Nyman 2010). Indeed, some *Chrysolina* clades have experienced multiple host shifts from the ancestral affiliation with Lamiaceae. As an example we could cite the case of the preference for Lamiaceae observed in the derived lineages *Allohypericia* (clade W), *Stichoptera* (clade Z’), *Arctolina* and *Pleurosticha* (clade Y’), which seems to be a back-colonization of this family from ancestors previously adapted to Plantaginaceae. Another case of multiple shifts is illustrated by the transition from Lamiaceae to Asteraceae and then to Apiaceae inferred for the *Oreina* clade, which is highly consistent with previous results based on allozyme data (Dobler et al. 1996) and mtDNA sequences (Hsiao and Pasteels 1999). In addition, convergent shifts to the same host plant family in different *Chrysolina* lineages have also occurred (Apiaceae: clades G’ and K’; Asteraceae: clades G’, R, W’ and Y’, *Ch. sturmi* (Westhoff, 1882) and *Ch. cerealis cyaneoaurata*; Ranunculaceae: *Ch. costalis* (Olivier, 1807) and *Ch. silvatica* (Gebler, 1823); Scrophulariaceae: clade Z’ and *Ch. sturmi*), thus suggesting the existence of evolutionary constraints in host shifts as it has been described in other

phytophagous insects including Chrysomelidae (Futuyma et al. 1993, Futuyma and Mitter 1996, Janz et al. 2001, Nosil 2002). A possible explanation for the continuous and convergent shifts among restricted sets of plant taxa is the phytochemical similarity among the alternative hosts (Feeny 1992), and indeed this seems to be the underlying mechanism in other herbivorous beetle groups (Becerra 1997, Kergoat et al. 2005). It also has been suggested that convergent shifts may not be independent, in the sense that an ancestral trait allowing the colonisation of a given plant group might have been already present in the insect lineages (Janz and Nylin 2008).

Chrysolina leaf beetles are highly specialized herbivores feeding on a narrow range of host plants (Jolivet and Petitpierre 1976, Bourdonné and Doguet 1991). However, despite the high level of specialization, their diet breadth ranges from species feeding on few plant species from the same genus or family (*i.e.*, monophagous or oligophagous, respectively) to more generalist species exploiting few species but from different plant families (*i.e.*, polyphagous). In this regard, Garin et al. (1999) reported the subgenus *Chrysolina s. str.* as the only lineage within the genus experiencing a shift to a generalist feeding habit at the plant family level. Now, our expanded taxon sampling coupled with the availability of a more complete host plant record shows that polyphagy is distributed across the *Chrysolina* tree, although it occurs at a lower frequency than mono- and oligophagy. Moreover, our results suggest that niche widths have varied through time, since some *Chrysolina* clades include mixtures of species with different levels of diet breadth (clades E, G', R, U, Y' and Z'). Oscillations in host range over evolutionary time are thought to play an important role in the diversification of the phytophagous insects (oscillation hypothesis, Janz et al. 2006, Janz and Nylin 2008). Under this model, speciation is driven by successive cycles of expansion of the host-plant range and generation of new species through specialization on different hosts. The oscillations are maintained through the ability to retain essential parts of the genetic “machinery” to utilize ancestral hosts, and therefore the probability of a major host shift seems to be positively influenced by polyphagy (Janz 2011). Our results on *Chrysolina* are still too preliminary to offer any scenario for the evaluation of this hypothesis. However, as it has been shown here, the evolutionary history of the genus is deeply associated with the occurrence of frequent and abrupt host shifts giving rise to the specialization on a restricted set of divergent host plant taxa, which is consistent with the model predictions. Optimizing niche width on the *Chrysolina* phylogeny would help in elucidating whether the diet breadth of the extant polyphagous species indeed represent an event of host range expansion from specialized ancestors, and whether polyphagy has been a transitional stage during host shifts. However, ancestral host range reconstruction will require very detailed information on host plant records and a well-resolved phylogeny for all *Chrysolina* species (Janz and Nylin 2008). In this respect, future research will be directed towards the expansion of the taxonomic sampling and the exploration of additional molecular markers in order to improve phylogenetic resolution. The implementation of DNA-based techniques for the taxonomic identification of the host plants (Jurado-Rivera et al. 2009) would also contribute to our understanding on the evolution of the ecological associations in this large and highly diversified leaf-beetle genus.

Conclusions

The combined phylogenetic analysis of mitochondrial (*cox1* and *rrnL*) and nuclear (H3) DNA sequences allows for the identification of the main evolutionary lineages in a sample of *Chrysolina* species representing almost half of the subgeneric diversity and most of the morphological and ecological variation in the genus. Our results reveal the paraphyly of the genus *Chrysolina* as currently described, due to the inclusion of the *Oreina* representatives within the *Chrysolina* clade. In this regard, the recognition of the genera *Craspeda* and *Chalcoidea* (*sensu* Bourdonné 2005 and 2012, respectively) would also render *Chrysolina* paraphyletic. The molecular phylogeny support for the reciprocal monophyly of the studied species of *Chrysolina* (plus *Oreina*) including the divergent *Ch. (Polysticta) vigintimaculata*, whose relationship with the core *Chrysolina* clade cannot be statistically rejected. The molecular data are consistent with the current subgeneric arrangement of the species, excepting the synonymy of the subgenus *Paraheliostola* with the subgenus *Timarchoptera* by Mikhailov (2002) and the combination of the species *Ch. (Threnosoma) timarchoides* with the subgenus *Maenadochrysa* by Bieńkowski (2001). In addition, our hypothesized molecular phylogeny allows for the identification of deep-level evolutionary relationships among the studied *Chrysolina* subgenera. The Bayesian reconstruction of the host plant associations in the *Chrysolina* phylogeny points to the family Lamiaceae as the ancestral host of the genus, in agreement with previous studies. The feeding spectrum of the extant *Chrysolina* species has been shaped by continuous host-shifting among pre-existing host plant families throughout the evolution of the genus. Many clades include mixtures of species with different levels of diet breadth, indicating that niche width has varied through time.

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Functional morphology of the copulatory organs of a reed beetle and a shining leaf beetle (Coleoptera: Chrysomelidae: Donaciinae, Criocerinae) using X-ray micro-computed tomography*

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Abstract

For more than 100 years it has been known that the sclerotised median lobe of beetles harbours a membranous structure (the "internal sac" or "endophallus") which is everted during copula inside the female genital tract. In order to explore the functional role of this structure and those associated with it, we cryofixed copulating pairs of *Donacia semicuprea* and *Lilioceria lilii* and studied the relative position of the elements of the copulatory apparatus of males and females by micro-computer-tomography.

We found that the everted endophallus fills the lumen of the bursa copulatrix completely. Our data suggest that in *L. lilii* the tip of the sclerotised distal part of the ejaculatory duct, the flagellum, is positioned exactly over the opening of the spermathecal duct inside the bursa copulatrix. The mouth of the bursa copulatrix in *D. semicuprea* is armed with a strong muscle ring, and the whole wall of the bursa is covered externally with a layer of muscle fibres. These morphological differences correspond with differences in mating behaviour: In reed beetles (Donaciinae), females seemingly can control mating to a higher degree than in lily beetles (*Lilioceria* spp.).

Keywords

Aedeagus, endophallus, flagellum, bursa copulatrix, spermatheca, sperm transfer

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Introduction

As the primary role of copulatory organs is to secure transfer of sperm from males to females, they could, in principal, be shaped very simply. A tube, rigid or elastic, and a corresponding basket would do. The fact that copulatory organs are often complex and species-specific has traditionally been explained as a lock-and-key device that guarantees the preservation of the species and prevents waste of time, energy, and sperm by copulations between allospecific partners (Shapiro and Porter 1989). Only since Eberhard's seminal book on "Sexual Selection and Animal Genitalia" (1985) zoologists have learned to interpret the morphology of genitalia in terms of individual fitness maximisation. This paradigm explains why shape and function of male and female copulatory organs are normally species-specific, and it provides a framework for understanding the functional role of peculiar structural elements of the copulatory apparatus.

In beetles, the form of the male copulatory apparatus (aedeagus), especially its median lobe, has found the lively interest of taxonomists (e.g., Kraatz 1881; Weise 1889a and b; Sharp and Muir 1912). Crowson (1955: 114) introduced the basic terminology and a hypothesis on the evolutionary transformation of what he called the "complete cucujoid" aedeagus. According to Crowson, this organ consists of a median lobe – functionally a sclerotised tube, mostly bent, often termed "penis" – and attached elements (see Fig. 1). These latter elements are basically a sclerotised ring around the median lobe from which proximal apodemes and distal parameres arise. We prefer "median lobe" because "penis" is, in our opinion, not a morphological but a functional term. It meant originally "the intromittant organ" (Tuxen 1970: 305). In many Cerambycidae the median lobe hardly, and if, then extremely briefly, enters the female body. On the other hand in, e.g., the sagrine *Mecynodera coxalgica* also the paramere is intromitted. Therefore, the term "penis" seems not just adequate throughout. In addition, we want to avoid any idea of homology of the median lobe and penes in other taxa. Consequently, we use the terminology of Kingsolver (1970) and Clark (1977), with the modification that we use "endophallus" for "internal sac" (following Burke 1959). Among Chrysomelidae, two types of aedeagi are present, those with parameres and those without. The morphology of the female copulatory organs has been largely neglected by taxonomists (an exception is, e.g., Döberl 1986).

However, only few investigators have studied the functional roles of the different elements of the male copulatory apparatus (e.g. Heberdey 1931, Cerezke 1964, LeCato and Pienkowski 1973, Rodriguez et al. 2004) and their interaction with the female copulatory organs during mating. Blunck (1912) studied the reproduction of *Dytiscus marginalis*, including detailed description of the relative position of the copulatory organs during mating and the formation of the spermatophore. Another meticulous investigation was done by Krautwig (1930), on the weevil *Sitophilus granarius*. Goldson and Emberson (1981) reported on the copulation of another weevil, *Hyperodes bonariensis*, and also described the relative position of male and female organs during sperm transfer. Flowers and Eberhard (2006) dissected mated pairs of 12 Neotropical leaf beetle species and described the coupling devices. For the present study, the most

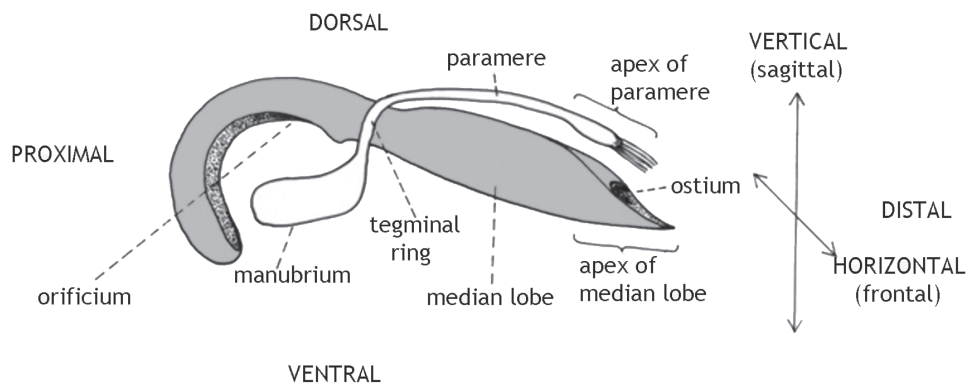


Figure 1. Schematic drawing of the sclerotised part of a Donaciinae aedeagus. The given terms of orientation do not refer to the position within the male abdomen nor within the female during copulation since these structures are rotated during mating. The median lobe is shaded grey. Paramere, tegminal ring and manubrium compose the tegmen.

relevant publication is that by Harnisch (1915) who observed and dissected copulating pairs of several leaf beetle species and depicted the elements of the male and the female copulatory apparatus, isolated and in copula. He speculated that median lobe and the fused parameres act as a clasper organ during copulation in reed beetles (Chrysomelidae: Donaciinae). Döngelhoef and Schmitt (2006) showed that this idea is not congruent with observation of life beetles. The apex of the fused parameres hardly ever gets into physical contact with the female abdomen. Their tip is covered with mechanoreceptors and other sensilla, so that the functional role of the parameres is rather that of "genital feelers" (Döngelhoef and Schmitt 2010) than that of a coupling device.

During copulation, a membranous sac, the endophallus, is everted through the ostium of the median lobe (fig. 1) inside the female bursa copulatrix. The ejaculatory duct transverses the endophallus, ending in a sclerotized tube, the flagellum. In addition, the wall of the endophallus bears sclerites in several beetle species studied so far (Berti and Rapilly 1976, Askevold 1991, Hayashi 2005, Flowers and Eberhard 2006, Döngelhoef and Schmitt 2006).

In earlier papers, Döngelhoef and Schmitt (2006, 2010) argued that the mechanical footing between the mating partners during copulation is achieved by the male's endophallus inflated inside the female's bursa copulatrix. Shape and surface morphology of the external face of endophallus and bursa correspond, so that hemolymph pressure inside the endophallus and high friction between the two surfaces warrant a strong coupling. Exorbitant armour of the endophallus obviously serves additional roles, e.g. it imposes indirect costs to subsequent copulations of the female by injuring the bursa wall (see Crudgington and Siva-Jothy 2000 and the nearly 400 papers citing this publication, according to Google Scholar, last time checked September 10, 2015).

The mating behaviour of leaf beetles in general was described by Jolivet (1999), Bilenkowski (1999) investigated on it in 14 palaearctic species of reed beetles. Konstanti-

nov (2004) studied courtship, copulation and intrasexual competition of *Donacia crasipes* Fabricius, 1775. Here, males perform complex courtship behaviour and females can prevent or/and terminate copulation by kicking with their hind legs. In contrast, lily beetles do not show courtship behaviour. Males simply follow a female, mount when they reach her, and copulate. Females never show special defence behaviour, they either allow the male to mount or they escape. In some cases, females tried to get rid of a mounted male by kicking with their hind legs (Düngelhoef and Schmitt 2006).

We investigated cryofixed pairs of copulating leaf beetles. Male shining leaf beetles (Criocerinae) lack parameres while reed beetles (Donaciinae) possess a so-called complete cucujoid aedeagus. We focused especially on the relative position of male and female genitalia during copulation. We had observed earlier that copulating pairs of reed beetles quickly separate when disturbed, while copulating lily beetles (*Lilioceris lili*) can only be separated by applying considerable force (Düngelhoef and Schmitt 2010). Thus, we expected to find morphological correlates of this behavioural difference.

Material and methods

We collected numerous individuals of *Donacia semicuprea* Panzer, 1796 and *Lilioceris lili* (Scopoli, 1763) in the area of Greifswald (northeast Germany). Copulating pairs were fixed using 70% ethanol at -12 °C (*D.semicuprea*) or liquid nitrogen (*L.lili*). The fixed pairs were stored in 80% ethanol at -40 °C for at least ten days. We prepared them for X-ray micro-computed tomography (micro-CT) analysis by critical point drying (BAL-TEC CPD 030), glued them head downwards on the tip of a little plastic rod of 2 mm in diameter, with the tip of the female abdomen as close to the rotation axis as possible. Three pairs of *D.semicuprea* and two pairs of *L.lili* were scanned under an Xradia Micro XCT-200 (Carl Zeiss X-ray Microscopy Inc.), using the 4× or 10× object lens units, at 30kV and 4W, with a pixel size of 5.36 µm or 2.34 µm. Tomography projections were reconstructed using the reconstruction software provided by XRadia. Volume rendering of image stacks was performed by using Amira 5.4.5 and Amira 5.6.0 (FEI Visualization Science Group, Burlington, USA) using the "Volren" or "Voltex" function.

We use the morphological terms as given in Fig. 1. Thus, "dorsal" does not refer to the back of a beetle but indicates the face of the aedeagus opposite the tegminal manubrium, while "distal" means the end of the median lobe bearing the ostium, i.e. the opening through which the endophallus is everted during copula and the sperm is finally leaving the male body. We use "aedeagus" addressing the complete male copulatory organ, i.e. the median lobe (= penis) plus the tegmen. The tegmen is either – in Criocerinae – v-shaped and attached to the ventral face of the median lobe, or – in Donaciinae – ring-shaped and surrounding the median lobe. Its basal part is formed as a vertical plate, the manubrium. In Donaciinae, the tegminal ring bears dorsally an unpaired projection pointing distad, the paramere.

Results

Liliocerus lili: The median lobe of the aedeagus is inserted in the female abdomen, the endophallus is everted and inflated. We did not make an attempt to trace the ejaculatory duct because we focused on the relative position of male and female copulatory organs. Of the ejaculatory duct only the sclerotised distal part, the flagellum, gets into contact with the female body. The bursa copulatrix is nearly globular (length/height: 1.25/1), its opening is situated at half the length of the last sternite (Figs. 2a, 4).

The tip of the small flagellum is positioned exactly opposite the opening of the spermathecal duct, see Fig. 2b. The spermathecal duct enters the bursa copulatrix through a sclerite that is embedded in the bursa wall. The gap between flagellum tip and duct opening in Figs. 2a and 2b is most probably an artefact caused by shrinking of the tissue during fixation. The space between the wall of the inflated endophallus and the wall of the bursa copulatrix is probably also an artefact.

Fig. 3 shows the massive muscle under the orificium that makes the inflation of the endophallus when it contracts. On the ventral side of the median lobe we see the retractor tendon or muscle of the endophallus stretched through the whole length of the tube from the orificium to the ostium. The endophallus is fully everted through the ostium and fills the bursa copulatrix nearly completely. The opening of the bursa is membranous and is strengthened only by few and delicate muscle fibres (Fig. 4, circle).

Donacia semicuprea: The median lobe is inserted into the female body while the paramere remains outside (Fig. 5). The paramere is slender, its tip is bent towards the

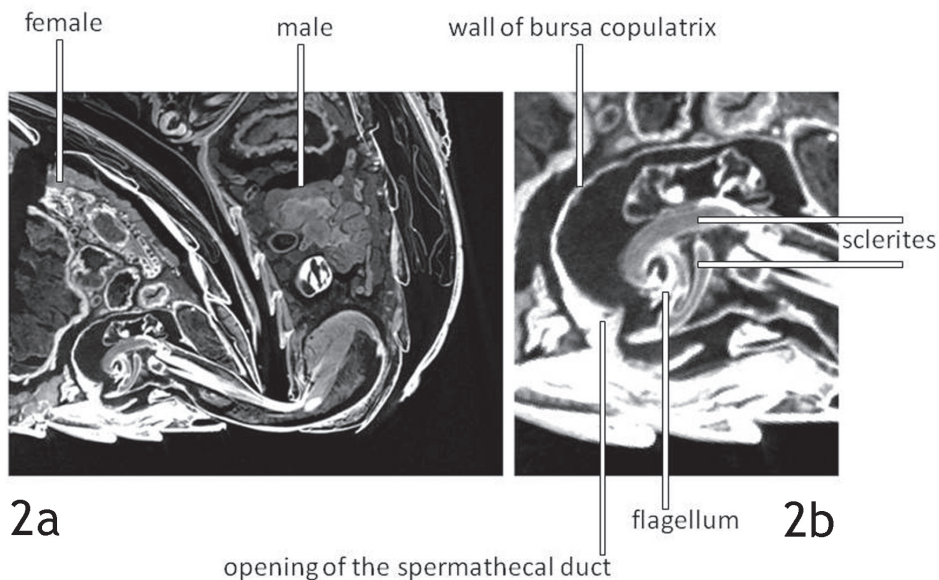


Figure 2. *Liliocerus lili*. Virtual section – sagittal, median – through the abdomina of a mating pair. The endophallus is fully inflated (2a), the flagellum is positioned over the opening of the spermathecal duct (2b).

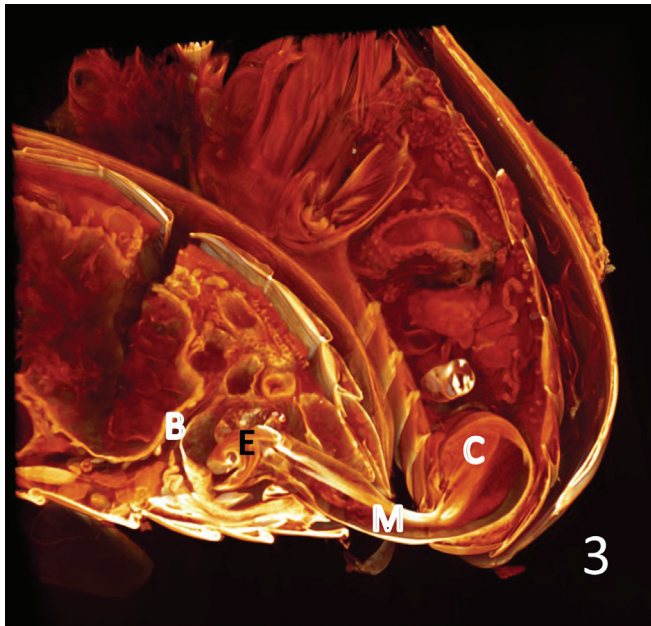


Figure 3. *Lilioceris lili*, copulating pair. Volume rendering of the virtual sections right to the median, digitally stained. The terminal part of the spermathecal duct can be seen immediately left to the bursa wall. The shape of the bursa is nearly globular. B: bursa copulatrix; C: the compound muscle inserting at the manubrium and extending to the lateral rims of the basal orifice of the median lobe; E: endophallus; M: median lobe.

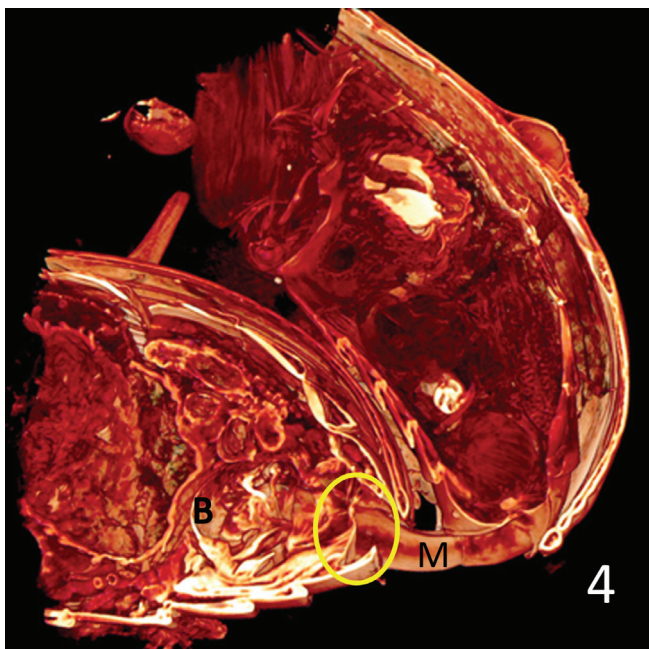


Figure 4. *Lilioceris lili*, as Fig. 3, the opening of the bursa copulatrix and the adjacent part of the bursa wall (circle) do not show significant muscle layers but are mere membranes. B: bursa copulatrix; M: median lobe.

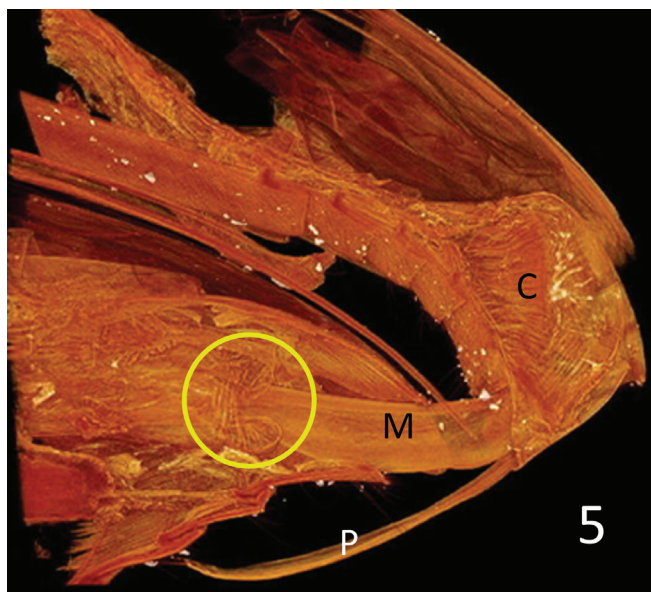


Figure 5. *Donacia semicuprea*. Volume rendering of the virtual sections – sagittal, right to the median – through the abdomina of a mating pair. The opening of the bursa copulatrix (circle) is armed with a conspicuous ring muscle. C: the compound muscle inserting at the manubrium and extending to the lateral rims of the basal orifice of the median lobe; M: median lobe; P: paramere.

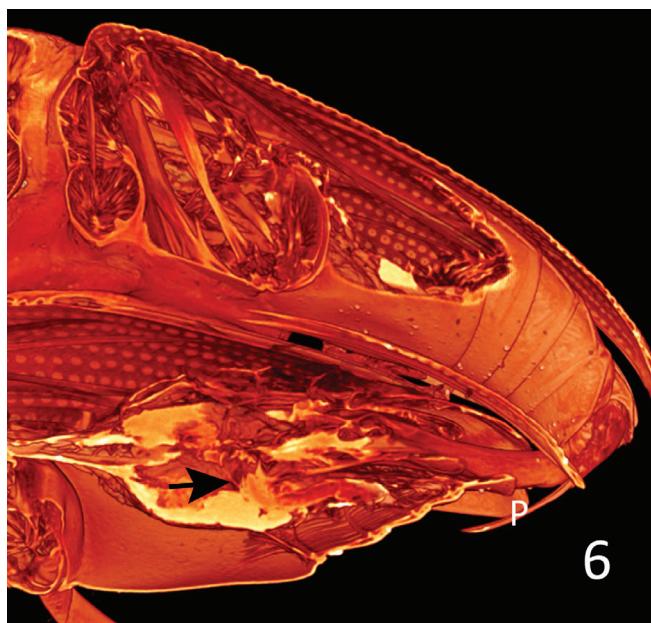


Figure 6. *Donacia semicuprea*, Volume rendering of ca. 390 virtual sections – sagittal, paramedian, tilted to the right – through the abdomina of a mating pair. The bursa is elongate, as seen from the proximal wall (arrow). The yellow shining areas inside the female abdomen are parts of the left ovary. P: paramere.

female abdomen. The paramere is in contact with the female abdomen only through its distal setae. We could not trace the shape and the measurements of the bursa copulatrix because in one pair the endophallus was not yet everted, and in the other two pairs the ovaries were so plump and massive that we could not discriminate the lining of the bursa and the tissue of the ovaries in the proximal part of the bursa. However, we could recognise that the bursa is considerably longer than in *L. lili*.

The tip of the median lobe is inserted into the bursa copulatrix. There is a strong muscular ring around the mouth of the bursa (Fig. 5, circle). Also, the outer surface of the wall of the bursa is covered with a layer of muscular fibres. The inflated endophallus seems to be longish, as is the bursa (Fig. 6). For the same reason as for the bursa we could not reconstruct the distal part of the endophallus.

Discussion

When interpreting the morphological data, we have to take into account that the copulating partners may be fixed in different stages of, e.g. the intromission of the median lobe or endophallus inflation. Moreover, we cannot be certain that the interacting male and female copulatory organs remained exactly as they were in the millisecond when the beetles were cryofixed.

Already Krautwig (1930) found in paraffin sections of copulating pairs of *Sitophilus granarius* that the distal orifice of the ejaculatory duct was placed directly opposite the opening of the spermathecal duct inside the bursa copulatrix. Also Burke (1959) presumes that certain "sclerotized structures serve to effect a close connection between the gonopore of the male and the opening of the spermathecal duct of the female" in weevils. Consequently, we can only speculate that the spout-like opening of the flagellum (see fig. 12 in Düngelhoef and Schmitt 2006) is indeed put over the mouth of the spermathecal duct inside the bursa in *L. lili*. The spermathecal duct opens into the bursa copulatrix through a sclerotised and thickened segment of the bursa wall (see fig. 49 in Berti and Rapilly 1976). We do not know whether or not the endophallus is constantly inflated inside the bursa during copulation. It might well be that the male everts and retracts the endophallus several times after intromission of the median lobe until the mating partners separate.

Our observation that the paramere of *D. semicuprea* remains outside the female body is in concordance with the earlier report of Düngelhoef and Schmitt (2010) and confirms the idea that it functions as a sense organ. Although there are species in which the males insert the parameres in the female body, e.g. the sagrine *Mecynodera coxalgica* (Düngelhoef and Schmitt 2010), it is highly unlikely that the males obtain mechanical footing that way. In nearly all species of Phytophaga studied to date, the parameres – if present at all – remain outside the female abdomen or remain inside the male body and are not even visible during copulation, as, e.g., in weevils and in longicorn beetles (Hubweber and Schmitt 2006, 2010, Düngelhoef and Schmitt 2006, 2010). Our observation that the inflated endophallus in *L. lili* has the same shape as the inner space of the bursa, and that its surface bears denticles and spines (Düngelhoef and Schmitt 2006), together with

the finding that the opening of the bursa and its walls do only bear few and delicate muscle fibres, correspond with an earlier observation (Düngelhoef and Schmitt 2010) that the copulating partners can be separated only by applying considerable force. Similar observations have been reported by Krautwig (1930) for *Sitophilus granarius*. In contrast, the fact that in *D. semicuprea* the inflated endophallus is longish and that the bursa bears a strong muscular ring around its opening and a marked layer of muscle fibres on its outer surface suggests that the female could be able to actively expel the male intromitting organ. This could explain the observation that it is difficult to cryofix copulating pairs in Donaciinae. Furthermore, Bienkowski (1999) and Jolivet (1999) report that females in Donaciinae play a pronouncedly active part in admitting males for mating as well as in terminating the copulation. It may well be that female donaciines can not only press out the male organ from the bursa but also prevent the male from intromitting his median lobe into the bursa by contraction of the sphincter muscle.

In species with a "complete cucujoid aedeagus", the compound muscle (Fig. 3: C, Fig. 5: C) that inserts at the manubrium and extends to the lateral rims of the basal orifice of the median lobe (the so-called ring-muscle, see Harnisch 1915), serves – at least – two different functions. One is to move the paramere, another is to extrude the endophallus during copulation by hemolymph pressure inside the "non-eversible part" of the endophallus (Kumar and Verma 1980). Thus, producing the necessary hemolymph pressure for the inflation of the endophallus has to be coordinated and possibly compromised with the independent movability of the parameres. Consequently, decoupling of these two functions requires differentiation of the "ring" muscle complex and independent neuronal control. Therefore, we speculate that the selective advantage of the loss of parameres in certain lineages of phytophagan evolution (Düngelhoef and Schmitt 2010) was that the massive "ring" muscle could be used exclusively to produce a high hemolymph pressure for the inflation of the endophallus. This compound muscle corresponds to the muscle labelled "RSP1 ... (retractor of the ... tegminal apodeme)" by Kumar and Verma (1908). Kingsolver (1970) described the respective muscle in seed beetles (Chrysomelidae: Bruchinae) as "ventral muscle of the median lobe". In our opinion, it acts rather as an adductor than as a retractor.

The morphological difference between the two species corresponds with differences in mating behaviour. It suggests that in *D. semicuprea* – and probably in all donaciine species – females control admittance of males for mating and the duration of the copulation to a higher degree than in *L. lilii* (and probably in all Criocerinae).

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