

# Leaf-mining chrysomelids

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“There are more things in heaven and earth, Horatio, than are dreamt of in your philosophy.”  
(Act I, Scene 5, Lines 66-167)

“To be or not to be; that is the question” (Act III, Section 1, Line 58)  
both quotes from “The Tragedy of Hamlet, Prince of Denmark”  
by William Shakespeare (1564-1616)

## Abstract

Leaf-mining is the relatively prolonged consumption of foliar material contained within the epidermal layers, without eliciting a major histological response from the plant. This type of herbivory is relatively uncommon in the Chrysomelidae and has been reported in 103 genera, representing 4% of the approximately 2600 described genera and amounting to over 500 reported species, or 1-2% of the 40-50,000 described species. Larvae in the following subfamilies are known leaf-miners, with numbers and percentages of taxa also being included. The subfamily Zeugophorinae consists of one genus with reported leaf-mining species, or 25% of the total genera; there are twelve reported leaf-mining species, about 17-20% of the species described in the subfamily and about 60-70 described species in the Zeugophorinae, all believed to be leaf-miners. The subfamily Criocerinae comprises two genera of reported leaf-miners, representing 10% of the described genera, and two reported leaf-mining species, accounting for less than 1% of the approximately 1450 species described in the Criocerinae. The Galerucinae has two reported leaf-mining genera, representing less than 1% of the approximately 500 genera described. There are approximately 20 reported species of leaf-mining galerucines, accounting for less than 1% of the approximately 7000 species described in the subfamily. The Alticinae has nineteen reported leaf-mining genera, representing about 3% of the approximately 500 genera described. There are 65 reported species of leaf-mining flea-beetles, or about 1-2% of the 4000-8000 species described in the Alticinae. The Hispinae is represented by 78 genera that have been reported as leaf-miners, or 40% of the approximately 200 genera described. There are over 400 reported leaf-mining hispines, accounting for 14% of the over 3000 species described in the subfamily. There is a single reported genus of leaf-mining in the Cassidinae, representing less than 1% of the 159 genera described. Only six species of cassidines have been reported as leaf-miners, accounting less than 1% of the 2760 species in the Cassidinae. The reported geographical distribution and host plants are summarized for most of the over 500 species of suspected or documented leaf-mining chrysomelids (Table 1). Larval chrysomelids can be classified

into two morphological categories: the eruciform, less modified type (Galerucinae and some Alticinae); and the flattened, sometimes onisciform type characteristic of the Zeugophorinae, many Alticinae, the Cassidinae, and the Hispinae. There are no published data on the larval structure of leaf-mining criocerines. Larval leaf-mining chrysomelids are reported to have rather broad host-plant feeding preferences. For adults, the ranges are broader. The Index of Feeding Range (IFR) is introduced herein as a scalar to quantify the feeding range of the larvae (IFR<sub>l</sub>) and adults (IFR<sub>a</sub>). For the Zeugophorinae, IFR<sub>l</sub> is 2.0 and IFR<sub>a</sub> 2.9. The plant families (and genera, parenthesized) most commonly reported serving as host-plants for the Zeugophorinae are the Salicaceae (*Salix* and *Populus*), the Betulaceae (*Betula* and *Corylus*), and the Celastraceae. For adult zeugophorines, 55% of the reported species only feed on one plant genus, and 82% of the reported species feed on one plant family only. For the Galerucinae, IFR<sub>l</sub> is 1.0 and IFR<sub>a</sub> 2.4. The plant families (and genera, parenthesized) most commonly reported serving as host plants for the Galerucinae are the Asteraceae (several genera) and the Chenopodiaceae (*Atriplex*, *Chenopodium*, *Suaeda*, etc.). For adult galerucines, 32% of the reported species only feed on one plant genus, and 60% of the reported species only feed on one plant family. For the Alticinae, IFR<sub>l</sub> is 2.7 and IFR<sub>a</sub> (excluding the data for *Phyllotreta nemorum*) is 3.8. The plant families most commonly reported to be serving as host plants for the Alticinae are Brassicaceae, Lamiaceae, Asteraceae, Plantaginaceae, Scrophulariaceae, Polygonaceae, and Poaceae, but many more families and numerous genera are reported as host plants. For adult alticines, 47% of the reported species only feed on one plant genus, and 71% of the reported species only feed on one plant family. For the Cryptostomes (Hispinae + Cassidinae), IFR<sub>l</sub> 1.6 and IFR<sub>a</sub> is 3.02. The plant families (and genera, parenthesized) most commonly reported as host plants for the Hispinae in the Old World are Arecaceae (*Cocos*, *Metroxylon*, and numerous other palm genera), Pandanaceae (*Pandanus* and *Freycinettia*), and Zingiberaceae. Numerous Leguminosae, Asteraceae, Poaceae, and Verbenaceae have been reported as host plants for the Hispinae in the New World. For larval Cryptostomes, 77% of the reported species feed on one plant species. In adult Cryptostomes, 51% of the reported species

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only feed on one plant species. Leaf-mining chrysomelids are uni- or bivoltine, particularly in temperate zones, but they can be trivoltine or multivoltine in the tropics. Natural biological enemies of the immature stages of leaf-mining chrysomelids are abundant but, in most cases, these organisms seem to be unable to control outbreaks of leaf-mining chrysomelids. Leaf-mining appears to have arisen independently multiple times in the Chrysomelidae, typically from most recent common ancestors which were exophytic. Leaf-mining mostly occurs in the Hispinae, and it may have evolved from ancestors living between closely appressed leaves of monocotyledons. Several leaf-mining chrysomelids, especially hispines, are economically important as pests of major crops; others are used as biological control agents of weeds.

## An introduction to leaf-mining insects

### *What is leaf-mining?*

Leaf-mining is the consumption of foliar material contained within the epidermal layers, without eliciting a major histological response from the plant. The study of leaf-mines is termed ‘minology’ (Hering, 1951). Mines may have a thin rim of callus tissue (Hering, 1951). Leaf-miners consume developmentally differentiated tissue and their tunneling activities do not elicit a major proliferation of undifferentiated tissue (Connor & Taverner, 1997). Superficially similar-looking structures on leaves, known as pseudomines, are caused by a variety of microorganisms, including fungi and viruses; feeding activities of non-leaf-mining insects; or as a reaction of plants to margin-feeding (Hering, 1951).

Mining leaves is one of several modes that invertebrates have of feeding and living inside plants (endophyty). Other endophytic ways of living may elicit a response from the plant in the form of exudate production (Langenheim, 2003; Santiago-Blay *et al.*, 2002) and/or gall formation. Numerous insects bore or otherwise penetrate the shoot (trunk, branches, stems, buds, flowers, fruits, or seeds) or the roots, causing significant economic damage (Metcalf & Metcalf, 1993).

Other insects and mites dwell inside leaves, eliciting a major histological response, forming enlargements of anomalous tissue, known as galls or cecidia (singular, cecidium < Greek, *kekis* (κεκίς), or gall; Ananthakrishnan, 1984; Byers, 2002; Csóka *et al.*, 1998; Darlington, 1968; Felt 1940; Labandeira & Phillips, 1996a, 2002; Lindquist *et al.*, 1996; Meyer, 1987; Shorthouse & Rohfritsch, 1992). Apparently there is a report of mites as leaf-miners of forest canopies in Queensland (Australia) but this find has not been followed-up with additional published reports. Mani (1964) indicates that “some species of ... Chrysomelidae... have been reported to give rise to galls”, although no further details are given. The only known chrysomelid gall-makers are the Sagrinae and *Ortholema samalkotensis* (Criocerinae) (Heinze 1943). Jolivet has seen many sagrine galls in Upper Volta in Africa; in Vietnam, he frequently saw adults simultaneously hatching at the start of the rainy season.

Sagrinae larvae are borers into semi-rigid stems and, when the larva pupates, it makes a cocoon within the stem gall. Currently, only sagrine larvae of the Old World genus *Sagra* and the New World genus *Atalasis* are known to make galls. However, except for anecdotal observations, nothing is known about the larvae of *Megamerus* and other Gondwanian sagrines. Most of them are probably gallicolous, but there are likely to be exceptions in Australia. *Megamerus*, for instance, is said to be gallicolous in Madagascar (Jolivet to Santiago-Blay, personal communication, July 2003).

A leaf-mining organism is one in which, minimally, one of its life stages actively tunnels or mines the usually flattened expansions of shoots, the leaves. Leaves of vascular plants have three parts: base, petiole, and blade (or lamina). The largest and most often flattened portions of leaves are usually known as the blades, although graminologists (students of grasses, Poaceae) also refer to entire leaves as ‘blades’. Leaf-miners overwhelmingly consume the relatively softer tissue, or parenchyma, contained between the epidermal layers, although some leaf-miners tend to consume vascular tissues (Hering, 1951).

Leaf-mining is largely restricted to the larvae of about a dozen families of the four major holometabolous insect orders: Coleoptera (Buprestidae and Chrysomelidae), Lepidoptera (Nepticulidae, Gracillariidae (*sensu lato*), Incurvariidae, Tischeriidae, Coleophoridae, Eriocraniidae, and Opostegidae), Diptera (Agromyzidae, Anthomyiidae, and Tephritidae), and Hymenoptera (Tenthredinidae). In numerous species of insects, including leaf-mining chrysomelids, the pupa and to a lesser extent the adult, also dwell within the mine. The larvae of leaf-miners produce a relatively long-lived behavioral record of their recent, as well as ancient herbivory, hence providing a unique window into the nature of ancient insect-host-plant associations and possible coevolution (*Fossil evidence of leaf-mining insects*, below).

There are other chrysomelids with tunneling tendencies (albeit, not in leaves). In Central America, Vencl *et al.* (2004) discovered that larvae of *Neolema approximata* Jacoby eat ovules and flower parts, and that larvae of *Neolema sallaei* Jacoby bore into the scandent stems of two species of Commelinaceae. Also, one species of criocerine feeds on seeds of Commelinaceae, and some species of *Crioceris* feed in fruits of *Asparagus* (Asparagaceae). Jolivet once found a galerucine, *Agetocera filiformis* Laboissière, feeding on the fruits of the vine *Cayratia japonica* (Thunberg) Gagnepain (Vitidaceae) in Thailand. Other ecologically unusual feeding tendencies of normally leaf-feeding chrysomelids have been observed, such as members of the Lamprosomatinae feeding on rodent excreta in the Florida Keys or galerucines feeding on snake wounds in Indonesia (Jolivet to Santiago-Blay, personal communication, June 2003). Hering (1951) reported cases of stem-mining insects.

In summary, “there are more things in heaven and earth, Horatio, than are dreamt of in your philosophy....” according to Hamlet.

“*To be or not to be*”... a leaf-mining chrysomelid  
Occasionally, it is difficult to precisely define what a leaf-mining insect is. For instance, in the eumolpine tribe Spilopyrini (e.g., *Stenomela*, *Hornius*, *Bohumiljanina*, and probably *Spilopyra*), the first instar larvae are diggers, eating their way into leaf buds to feed and emerging from buds frequently (Jolivet to Santiago-Blay, personal communication, June 2003). As the larvae grow larger (approximately from the second instar onward), they feed on the leaf surface (Jolivet to Santiago-Blay, personal communications, April, June 2003). I have excluded spilopyrines from Table 1, a compendium of the reported leaf-mining chrysomelids of the world.

One of the most dramatic examples of behavioral variability in leaf-mining is *Clitea picta* Baly (Alticinae) larvae, which may bore into leaves from the midrib, young shoots, spines and axils of branches, and occasionally developing fruits (Zaka-ur-Rab, 1991). Cases of organoxeny, or feeding in an unusual plant organ, are rare in leaf-mining Chrysomelidae. Some species of *Longitarsus* (Alticinae) have larvae that “are root feeders, but sometimes [they have been] reported to be leaf-miners” (Jolivet & Hawkeswood, 1995).

As a general rule, species in the hispine tribes Botryonopini, Anisoderini, Aporidini, Callispini, Leptispini, and Eurispini of the Old World Hispinae and in the Oediopalpini, Cephaloleiini, Hybosispini, Arescini, and Alurnini of the New World Hispinae, are not leaf-miners. They have been omitted from Table 1. Even so, some exophytic taxa that typically are ‘strip miners’, have been reported (probably erroneously) to be leaf-miners. For instance, Hering (1957) reports that “various species of the genera *Arescus* and *Chelobasis* were frequently found in communal mines on *Heliconia*, a genus of Heliconiaceae. Maulik presumes that this communal living in a single mine must frequently give rise to hybridization. This seems all the more plausible since leaf-mining Hispinae normally pupate within the mine and the emerging imagines, which in Coleoptera always remain for some time in the mine to tan and harden their exoskeleton necessary for chewing their way out, might thus easily find a suitable mate. If the emergence of different species took place in a single mine simultaneously, it is very reasonable to assume that in all probability hybridization will ensue” (emphases added by JASB). However, Strong (1983), who has studied *Chelobasis bicolor* (Pic), makes no mention of leaf-mining on these hispines. Neither *Arescus* nor *Chelobasis* are ‘leaf-miners’, instead, they are ‘strip feeders’, eating on the surface and not between the upper and lower epidermis of the leaves (Strong to Santiago-Blay, personal communication, June 2003).

Some members of the Old World hispine tribe Cryptonychini have also been omitted from Table

1, as their larvae feed temporarily on leaf buds and the larger larval instars live on stems (e.g., Kalshoven, 1981; Maulik, 1938; Spaeth, 1933, 1936; Uhmman 1942, 1952, 1963). Mariau (2001) indicates that both the larval and adult stages of Cryptonychini live between the leaflets of unopened buds forming the spear of the leaf frond. Others species of the Cryptonychini, such as species of *Plesispa*, seem to eat the adaxial and abaxial surfaces of the leaves, but mining often seems to be the case (Maulik, 1919; Jolivet to Santiago-Blay, personal communication, June 2003). I have included all species of *Plesispa* for which I could find host-plant records in Table 1. In contrast, species in the genus *Callistola* are browsers, but there is one record (Cox, 1996; Cox to Santiago-Blay, personal communications, May 2003) where a ‘*Callistola* sp.’ is recorded as a leaf-miner. This record is in error (Cox to Santiago-Blay, personal communications, June 2003) and I have excluded all species of *Callistola* from Table 1.

In the hispine tribe Gonophorini, “larvae are, according to the species, either leaf-miners or free-living larvae between the leaves” (Jolivet & Hawkeswood, 1995). I have included as many gonophorines for which I could find some documentation on their host-plant associations in Table 1.

The conceptual difficulties in defining leaf-miners are also present in some other groups of insects (Hering, 1951). For example, in the cecidomyiids (Diptera), blister galls described by cecidologists may merge imperceptibly with leaf mines (Gagné, 1994). The difference evidently hinges on the degree of production of cecidogenic nutritive callus or other anomalous tissues before the structure can be termed a ‘gall’. Similarly, the “distinction between browsing and mining at times could be subtle” (Jolivet to Santiago-Blay, personal communication, May 2003). “[Leaf-scratching] larvae among Hispinae could be also occasionally miners” (Jolivet to Santiago-Blay, personal communication, June 2003).

#### *Leaf-mining insects are only found in the four major holometabolous orders*

Within the Hexapoda, leaf-mining is apparently restricted to the four major holometabolous insect orders: Coleoptera, Diptera, Lepidoptera, and Hymenoptera. It is estimated that 10 000 species of insects are leaf-miners (Connor & Taverner, 1997). All feed on vascular plants, including ferns, or pteridophytes (ferns and their allies), gymnosperms (conifers, gnetaleans, ephedraceans, and *Ginkgo*), as well as extinct seed-fern clades such as corytosperms (Rozefelds, 1988), and flowering plants (Labandeira, 2002a). Species of leaf-miners are particularly abundant in numerous families of relatively basal Lepidoptera (Askew, 1980; Auerbach & Simberloff, 1984; Connor & Taverner, 1997; Kristensen, 1999; Labandeira *et al.*, 1994; Opler, 1973; Powell, 1980), where they also have left fossil evidence (Labandeira, 2002a,b). The thirteen lepidopteran superfamilies

(and the 34 families parenthesized) reported to have leaf-mining species are, as follows: Heterobathmioidea (Heterobathmiidae), Eriocranioidea (Eriocraniidae and Acanthopteroctetidae), Nepticuloidea (Nepticulidae and Opostegidae), Tischerioidea (Tischeriidae), Palaephatoidea (Palaephatidae), Incurvarioidea (Incurvariidae, Prodoxiidae, Adelidae, and Heliozelidae), Tineoidea (Gracillariidae, Bucculatricidae, Douglasiidae, and Roeslerstammidae), Gelechioidea (Oecophoridae, Elachistidae, Coleophoridae, Momphidae, Cosmopterygidae, Scythrididae, and Gelechiidae), Copromorphoidea (Carposinidae and Epermeniidae), Yponomeustoidea (Glyphipterigidae, Acrolepiidae, Argyrestitidae, Yponomeutidae, Heliodinidae, Ochsenheimeriidae, and Lyonetiidae, the latter often included with the Tineoidea), Tortricoidea (Tortricidae), Pyraloidea (Pyalidae), and Pterophoroidea (Pterophoridae) (Connor & Tavener, 1997; Heppner, 1998; Kristensen, 1999). Powell (1980) suggests that feeding preferences among ‘microlepidopterans’ have evolved following “specialized larval feeding niches or horizons within communities... rather than along botanical evolutionary lines”.

In Diptera, twelve higher taxa (and seventeen families, parenthesized) that have leaf-mining species include the nematoceran Tipulomorpha (Tipulidae), Culicomorpha (Ceratopogonidae and Chironomidae), and Bibionomorpha (Cecidomyiidae and Sciaridae); the brachyceran Empidoidea (Dolichopodidae), and the cyclorrhaphan Aschiza (Phoridae and Syrphidae), Calyptratae (Anthomyiidae and Scathophagidae), Acalyptratae Diopsoidea (Psilidae), Tephritoidea (Tephritidae), Luaxanioidea (Luaxaniidae), Opomyzoidea (Agromyzidae, notorious for having numerous pestiferous species), Carnoidea (Chloropidae), as well as Ephydroidea (Drosophilidae and Ephydriidae) (Colless *et al.*, 1991; Connor & Tavener, 1997; Disney, 1994; Evenhuis, 1994; Labandeira, 2003; Needham *et al.*, 1928). These families are quite unrelated phylogenetically. Labandeira (2003) estimates that there are at least 25 independent originations of leaf-mining in the Diptera, when these cases are evaluated at the subfamilial/familial level or higher. Their mining is concentrated in herbaceous plants, instead of woody plants as leaf-mining insects in the Coleoptera, Hymenoptera, and Lepidoptera (Labandeira, 2003). Among aquatic nematocerans, most host plants include the Poaceae and the Cyperaceae, and less commonly herbaceous dicotyledoneous plants (Hering, 1951; Labandeira, 2003).

Leaf-mining is not as common in the other two holometabolous insect orders, namely the Hymenoptera and the Coleoptera. In the Hymenoptera, leaf-mining has been reported in about 100 species of symphytans, including the families Argidae, Pergidae, and Tenthredinidae (Connor & Tavener, 1997; Naumann *et al.*, 1991; Smith, 1995). Most symphytan larvae are phytophagous and the Selandriinae (Tenthredinidae) are almost exclusively on ferns. The Blasticotomidae (Hymenoptera) are petiole miners of ferns (Needham *et al.*, 1928).

In the Coleoptera, leaf-mining has been described in at least five superfamilies, placed in nine families (parenthesized): Buprestoidea (Buprestidae, Trachydinae); Bostrichoidea (Anobiidae); Cucujoidea (Nitidulidae, species of *Xenostrogylus* and of *Anister*); Tenebrionoidea (Mordellidae, Ptininae, *Ptinus antillanus* Bellés); and the Chrysomeloidea [Chrysomelidae (details in this chapter), Platypodidae (*Phylloplatypus pandini* Kato), and Curculionidae *sensu lato*, species of *Orchestes*, *Prionomerus*, *Rhamphus*, *Ciopus*, and others; Belidae; and Attelabidae] (Connor & Tavener, 1997; Crowson, 1981; Hespeneheide, 1991; Hespeneheide & Kim, 1992; Kato, 1998; Lawrence, 1991; Lawrence & Britton, 1991; Lawson, 1991; Needham *et al.*, 1928; Paulian, 1988; Philips *et al.*, 1998; Wilcox, 1979). In the chrysomelids, or leaf beetles, leaf-mining has been reported for the subfamilies Zeugophorinae, Criocerinae, Alticinae-Galerucinae (Trichostomes *sensu* Jacoby 1908, or Galerucinae, *sensu lato*), and Hispinae-Cassidinae (Cryptostomes *sensu* Chapuis 1874-1875, or Cassidinae, *sensu lato* Staines (2002a,b)) have leaf-mining representatives.

The Coleoptera have more phytophagous species than any other order of insects, yet a smaller proportion of beetle groups have this *modus vivendi* than do the Lepidoptera. Within the Chrysomelidae, only the hispine chrysomelids are relatively well known. This is partly attributable to the fact that some are prominent agricultural pests. Why are there so few leaf-mining Coleoptera? Connor & Tavener (1997) suggest that lack of speciosity in leaf-mining insects suggests the lack of adaptive radiation, implying that the evolutionary benefits of being a leaf-mining coleopteran have been outweighed by the drawbacks, such as an elevated incidence of parasitoidism. Nevertheless, there are numerous known leaf-mining beetles that still need to be described (Hespeneheide, 1991). In fact, there are many more non-chrysomelid beetle leaf-mining taxa than hispines, at least in Central America. The perception that there is a depauperate nonhispine leaf-miner fauna is an artifact of the taxonomy of those other groups. For instance, the current number of buprestids for the La Selva Biological Station (Costa Rica) is 167 leaf-mining species out of 218 total for the family (72%), more than twice as many species as there are leaf-mining hispines. There are three major groups (Rhynchitidae, Prionomerinae, Tachygoninae) and one minor (Camarotinae) group of weevil leaf-miners at La Selva. At the moment, Hespeneheide has separated 55 species of weevils. In the Tachygoninae, 21 of 26 species are undescribed; there are twelve leaf-mining species of rhynchitids. The issue is that hispines are larger in size and relatively well-known taxonomically. The buprestids and weevils frequently are small (often <3 mm) and very poorly known taxonomically. For example, 113 of La Selva’s 167 buprestid leaf-mining species are undescribed, and virtually all the weevils are undescribed as well. There are several very large genera of leaf-mining buprestids

in the Old World, and they are relatively poorly known. The question posed above cannot be answered at this moment due to the lack of sufficient data (Hespenheide to Santiago-Blay, personal communication, July 2003).

Why are there no non-holometabolous leaf-mining insects? Perhaps a combination of reasons may help to explain this. Firstly, numerous hemipteroid insects (heteropterous and homopterous Hemiptera and their allies), many of which are phytophagous, have piercing-sucking mouthparts, and produce relatively small holes to feed on cells' protoplasts. Undoubtedly, hemipteroid insects have mechanical difficulties creating holes large enough to maneuver through the inside of the leaf blade. Interestingly, just as many hispines, a number of species from several hemipteroid lineages live between appressed leaves, including taxa, such as the Termitaphididae and Thaumastocoridae, both in the order Heteroptera (Schuh & Slater, 1995), as well as numerous Coccoidea (Carver *et al.*, 1991). And yet, they have not occupied the leaf-mine adaptive zone. Secondly, many nonholometabolous (paleopteroid and orthopteroid) insects tend to have large appendiculate immature stages that lack a vermiform facies, rendering leaf-mining physically difficult. Thirdly, it appears that the leaves or leaf-like structures of aquatic plants, where many paleopteroid, orthopteroid, and hemipteroid insects live, are too thin for a typical immature insect to inhabit. However, while size could be a factor for the later instars, the earlier instars can be minute. Although hemimetabolous groups evolved prior to the diversification of angiosperms (Kukalová-Peck, 1991; Labandeira, 2002a; Labandeira & Sepkoski, 1993) and most likely were fixed on using food materials that were always available, such as dead leaves of nonangiosperms, algae, or other animals, the targeted plant tissues by insects that feed using the piercing-and-sucking method are the same in gymnosperms or angiosperms (Labandeira & Phillips, 1996b). Hence, the lack of leaf-mining hemipteroid insects is probably unrelated to gymno- or angiospermy (Labandeira to Santiago-Blay, personal communication, July 2003). In addition, other major insect orders containing leaf-mining insects also originated prior to the diversification of angiosperms (Kukalová-Peck, 1991; Labandeira 1997, 1998, 1999, 2002a; Labandeira & Sepkoski, 1993) and their leaf-mines are often excellently preserved in the Mesozoic fossil record (Anderson & Anderson, 1989; Rozenfelds, 1988; Zherikhin, 2002).

#### *Fossil evidence of leaf-mining insects*

Despite the numerous biases of preservation (Crampton *et al.*, 2003; Labandeira, 2002a), highly characteristic mines preserved in fossil plants have been reported for several orders of insects, including several families of Lepidoptera, Diptera, and for a number of unidentified insects as early as the Cretaceous, some 100 millions of years ago (Ma) (Labandeira,

2002a,b; Labandeira *et al.*, 1994; Lang, 1996; Stevenson, 1992; Wilf *et al.*, 2001) and extending to the late Jurassic/Early Cretaceous boundary ( $\approx 142$  Ma) (Rozenfelds, 1988), and the early Triassic to late Middle Triassic (230-225 Ma) of Kazakhstan, Australia, and South Africa (Anderson & Anderson, 1989; Labandeira, 2003, personal observations; Rozenfelds & Sobbe, 1987; Zherikhin, 2002). Additional examination of older fossils may reveal evidence for an older origin for this *modus vivendi*. There is no evidence in the fossil record of leaf-mining mites (Labandeira to Santiago-Blay, personal communication, July 2003), although there are numerous documented fossil mites (Labandeira, *et al.*, 1997; Petrunkevitch, 1955).

There seems to be no reported evidence of leaf-mining chrysomelid larvae in the fossil record (Santiago-Blay, 1994), but it is probable that mines with patterns characteristic or suggestive of chrysomelids may have been overlooked or remain to be discovered. Until recently, many paleobiologists would often disregard rocks containing fossil plants with evidence of damage in favor of material exhibiting paleobotanically diagnosable and complete leaves (Allmon to Santiago-Blay, pers. comm., July 2003; Labandeira to Santiago-Blay, personal communication, July 2003). Recently, Wilf *et al.* (2000) (summarized by Pennisi, 2000) described feeding marks probably caused by rolled-leaf hispines (Cephaloleiini or Arescini). These Cretaceous feeding marks, which were produced by strip feeders on monocotyledoneous plants, not by leaf-miners, are the oldest known external feeding damage by chrysomelids and they are represented by damage types from multiple life stages. There is material in the Dakota Formation (100 Ma) of Nebraska and Kansas which has feeding marks that suspiciously resembles chrysomelid damage (Labandeira to Santiago-Blay, personal communication, July 2003). Also, there are a number of described *Sceleonopla* and other fossil hispines in tribes known to have leaf-mining genera (Santiago-Blay, 1994; Santiago-Blay *et al.*, 1996; Staines & Sanderson, 2000). The presence of leaves with characteristic feeding marks, particularly in the company of a leaf-mining chrysomelid body-fossils, would be strongly suggestive evidence for the existence of this behavior during the Cretaceous and perhaps the Jurassic periods.

Changes in the frequency of leaf-mining and other more host-specific types of damage have also been considered as evidence for major and sudden changes in the patterns of insect herbivory at the Cretaceous-Tertiary extinction event (Labandeira *et al.*, 2002a,b). Interestingly, Wilf *et al.* (2001) suggest that a prolonged increase in leaf-mining from the relatively humid and warm-temperate late Paleocene ( $\approx 56$  Ma) to the more subtropical early Eocene ( $\approx 53$  Ma) to the relatively drier and subtropical middle Eocene ( $\approx 43$  Ma) may have been related to global paleoclimatic changes and concomitant vegetation shifts from what we now know as the central Rocky Mountain region of the USA.

## Introduction to leaf-mining chrysomelids

### *Taxonomic distribution of leaf-mining chrysomelids*

In this paper, I use the classification of Seeno & Wilcox (1982). Some of the drawbacks of Seeno & Wilcox (1982) are caused by the difficulties in some groups, particularly the natural delimitations, if any, between the Galerucinae + Alticinae (Trichostomes) and the Hispinae + Cassidinae (Cryptostomes), in addition to the position of numerous other taxa, as well as recent advances from more detailed studies at all levels of biological resolution, from the molecules to the ecosystem. Nevertheless, Seeno & Wilcox (1982) have served students of the Chrysomelidae well, and have presented the best comprehensive system. Until the higher classification of the Chrysomelidae becomes more stable and generally accepted as a practical tool of communication that reflects some presumed past events, I find it useful to follow Seeno & Wilcox's (1982) 'catalogue classification' (as it is sometimes referred to) with the appropriate and occasional caveats.

Leaf-mining is relatively uncommon in the Chrysomelidae and is found in 103 reported genera, representing 4% of the approximately 2600 genera described and amounting to over 500 reported species, or 1-2% out of the 40-50,000 species described (Lopatin, 1984; Jolivet to Santiago-Blay, personal communication, March 2003). Larvae in the following subfamilies are known leaf-miners, with numbers and percentages of taxa included, as well. The subfamily Zeugophorinae consists of one genus with reported leaf-mining species, or 25% of the total genera; there are twelve reported leaf-mining species, about 17-20% of the species described in the subfamily and about 60-70 species described in the Zeugophorinae, all believed to be leaf-miners (Jolivet to Santiago-Blay, Schmitt to Santiago-Blay, and Verma to Santiago-Blay independent personal communications, May through July 2003). The subfamily Criocerinae comprises two genera, representing 10% of the described genera, and two reported leaf-mining species accounting for less than 1% of the approximately 1450 species described in the Criocerinae (Jolivet to Santiago-Blay, Schmitt to Santiago-Blay, and Vencl to Santiago-Blay, independent personal communications, May 2003). The Galerucinae has two reported leaf-mining genera, representing less than 1% of the approximately 500 genera described. There are approximately 20 reported species of leaf-mining galerucines, accounting for less than 1% of the approximately 7000 species described in the subfamily (Jolivet to Santiago-Blay, personal communication, July 2003). The Alticinae has nineteen reported leaf-mining genera, representing about 3% of the approximately 500 general described. There are 65 reported species of leaf-mining flea-beetles, or about 1-2% of the 4000-8000 species described in the Alticinae (Schmitt to Santiago-Blay, personal communication, May 2003). The Hispinae is repre-

sented by 78 genera which have been reported as leaf-miners, or 40% of the approximately 200 genera described. There are over 400 reported leaf-mining hispines, accounting for 14% of the over 3000 species described in the subfamily (Mariau, 2001). There is a single reported genus of leaf-mining in the Cassidinae, representing less than 1% of the 159 genera described. Only six species of cassidines have been reported as leaf-miners, accounting less than 1% of the 2760 species names in the Cassidinae (Borowiec, 1999).

In the Zeugophorinae, a subfamily with only a handful of described genera, all studied species of *Zeugophora* have leaf-mining species. However, as in most leaf-mining chrysomelids, "at present all that can be said is that the larvae of the Indian species of Zeugophorinae are presumably leaf-miners and their host-plants have not been recorded." (Verma to Santiago-Blay, personal communication, July 2003). A total of twelve species are reported to be leaf-mining zeugophorines (Table 1).

With regard to leaf-mining, the Criocerinae represents a mysterious and fascinating group. With only two species being reported as leaf-mining criocerines (Table 1), many more are expected to be documented, particularly among minute forms that inhabit the tropics (see Vencl *et al.*, 2004, for examples of tropical endophytic criocerines).

Within the Trichostomes *sensu* Jacoby, or Galerucinae + Alticinae, the Galerucinae has two genera that are known to have leaf-mining species: one species of *Galerucella* and all the known species of the genus *Monoxia*. Blake (1939) and other researchers noted the need to understand the difficult galerucine genus *Monoxia*, where most of the species studied by me are leaf-miners. A total of 20 species are reported as leaf-miners (Table 1). In contrast, in the Alticinae there are 19 leaf-mining genera (*Aphthona*, *Apteropeda*, *Argopistes*, *Argopus*, *Chaetocnema*, *Clitea*, *Dibolia*, *Epitrix*, *Februa*, *Hippuriphila*, *Longitarsus*, *Mantura*, *Mniophila*, *Ochrosis*, *Phyllotreta*, *Psylliodes*, *Schenklingia*, *Sphaeroderma*, and *Throscoryssa*) that are known to have some or all of their species as leaf-miners. A total of 65 species are reported to be leaf-mining alticines (Table 1). These genera belong in several seemingly unrelated groups of the Alticinae (Seeno & Wilcox, 1982).

Within the Cryptostomes *sensu* Chapuis, the Hispinae have 78 known or suspected leaf-mining genera (*Acanthodes*, *Acentroptera*, *Achymenus*, *Agonita*, *Anisostena*, *Asamangulia*, *Aspidispa*, *Baliosus*, *Balyana*, *Brachycoryna*, *Carinispa*, *Cassidispa*, *Chaleridiona*, *Chalepus*, *Charistena*, *Chrysispa*, *Clino-carispa*, *Cnestispa*, *Coelaenomenodera*, *Corynispa*, *Crapedonispa*, *Cyperhispa*, *Dactylispa*, *Di cladispa*, *Dorcat hispa*, *Downesia*, *Enischnispa*, *Euprionota*, *Freycinetispa*, *Gestronella*, *Glyphuroplata*, *Gonophora*, *Heptispa*, *Heterispa*, *Hispa*, *Hispellinus*, *Hispoleptis*, *Isopedhispa*, *Javeta*, *Klitispa*, *Metaxypera*,

*Micrispa*, *Microrhopala*, *Nonispa*, *Ocnosispa*, *Octhispa*, *Octotoma*, *Octouropata*, *Odontota*, *Oncocephala*, *Oxychalepus*, *Oxyroplata*, *Pentispa*, *Pharangispa*, *Phidodonta*, *Physocoryna*, *Pistosia*, *Platochispa*, *Platypria*, *Plesispa* (but see remarks in “*To be or not to be ... a leaf-mining chrysomelid*” above), *Polyconia*, *Prionispa*, *Probaenia*, *Promecotheca*, *Prosopodonta*, *Rhabdotohispa*, *Rhadinosa*, *Sceleonopla*, *Spilispa*, *Stenopodius*, *Stenostena*, *Stehispa*, *Sumitrosis*, *Temnochalepus*, *Trichispa*, *Uroplata*, *Xenochalepus*, and *Wallacispa*). A total of 410 species are reported to be leaf-miners (Table 1).

In contrast, the Cassidinae has only one leaf-mining genus, *Notosacantha*, which also has been placed in the Hispinae (Borowiec, 1995; Medvedev & Eroshkina, 1988). A total of six species are reported to be leaf-mining cassidines (Table 1).

Considerably more leaf-mining chrysomelids will be revealed. For example, Frost (1931) and Hespeneide (1991) reported rearing many species of leaf-mining hispines from plants at Barro Colorado Island (Panama) and La Selva (Costa Rica), as well as hispines from several species of *Cecropia* (Cecropiaceae) in central Panama. As researchers conduct careful field and laboratory observations and the life histories of other chrysomelids are studied, particularly those in taxa previously documented as leaf-miners (e.g. the hispine *Octotoma*, c.f. Staines, 1989), more chrysomelid leaf-mining taxa will be documented, particularly within the hispines. I have not located reports of leaf-mining for the other subfamilies of the Chrysomelidae, although this life habit is suspected for the Orsodacninae and the Aulacoscelinae (Jolivet to Santiago-Blay, personal communications, 2003).

#### *How many species of leaf-mining chrysomelids are/were there?*

I estimate that there are approximately 2500 species of leaf mining chrysomelids, principally located in the hispines. However, in addition to the intrinsic difficulties in estimating “how many species?” (May 1990), it is also difficult to know how many leaf-mining species there are among the Chrysomelidae because the larval stages, larval-adult associations (e.g., Lee & Furth, 2000), and basic biological research on most species, particularly those with root-feeding larvae, still remains to be done for over an estimated 95% of the species. In other cases, the literature is not clear as to whether a species is a leaf-miner and, if so, what the host-plants of the larvae and of the adults are. The works of Buhr (1955,1956), Ford & Cavey (1985), Frost (1924), Jolivet (1989a), Jolivet & Hawkeswood (1995), Maulik (1931,1932,1933a,b), Needham *et al.* (1928), Hering (1951,1957), Staines (2002b), Staines & Staines (1989,1992), and Wade (1935), among numerous others, contain discussions, lists, and/or bibliographies of leaf-mining insects from different regions of the world. Their data, as well as those

from many other papers (see *References* below), and unpublished data, have been used in Table 1.

### **Life history of leaf-mining chrysomelids**

The biology of several leaf-mining chrysomelids has been reported in detail. While there is considerable variability in life history, some typical patterns and variations are described below, elaborated in Figures 1-5, and summarized in Figure 7.

#### *Egg*

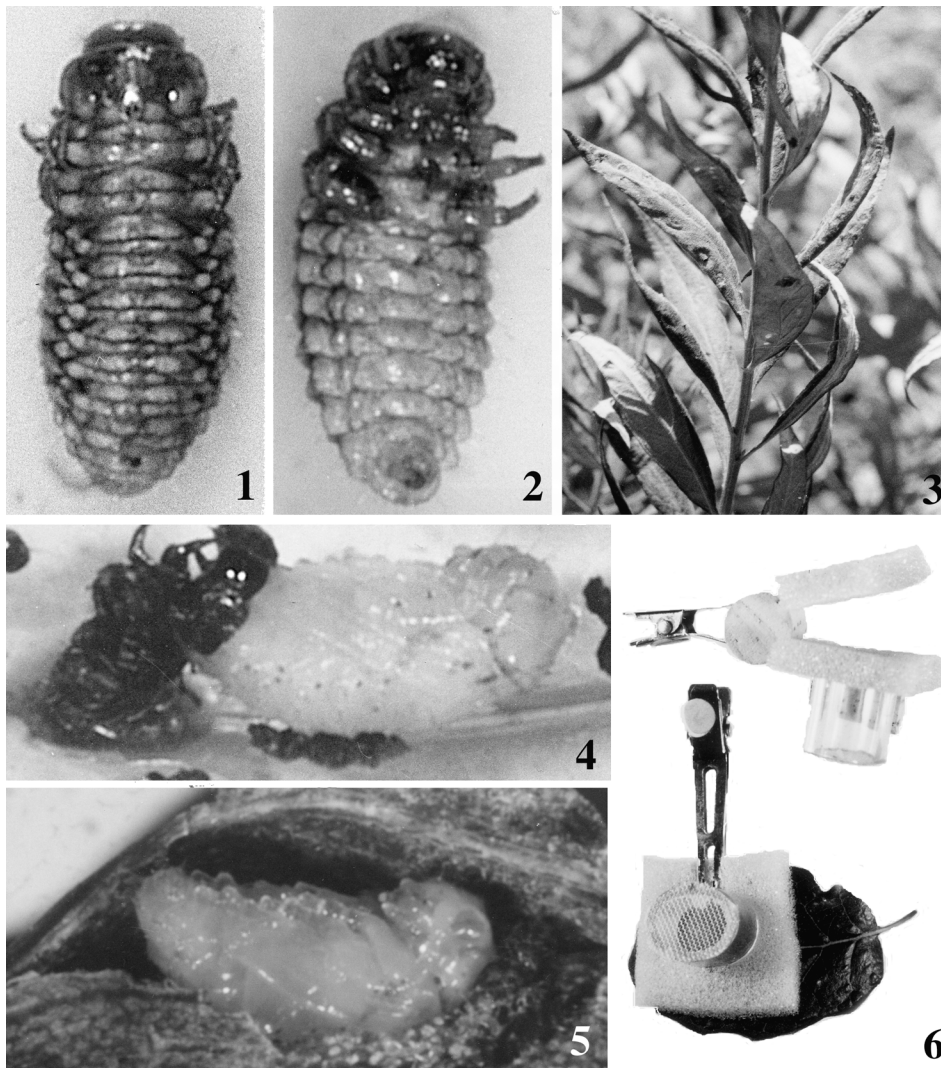
The fine ultrastructure of leaf-mining chrysomelid eggs appears to have been all but overlooked. Memmott *et al.* (1993) reported that egg structure is useful in distinguishing three sympatric, congeneric species of *Chalepus* (Hispinae) that share three species of Central American *Lasiacis* bamboos (Poaceae) as host-plants. For a comprehensive discussion of insect eggs, see Hinton (1981).

#### *Timing and location of oviposition*

Like typical insects, after emerging from diapause (if present), leaf-mining chrysomelid beetles feed and mate. Shortly after copulation, depending on the species, eggs are laid on different locations of the leaf, either abaxially, or adaxially, or in a cavity made by the female on the blade (Chittenden, 1902; Monrós & Viana, 1947; Sen & Chakravorty, 1970). The act of oviposition by several leaf-mining chrysomelids has been observed, and it is relatively simple. Leaf-mining chrysomelids tend to lay relatively few eggs per oviposition bout on or in host-plant leaves (Chittenden, 1902; Ford & Cavey, 1985). For the hispine *Dicladispa armigera* (Olivier), oviposition follows shortly (less than three to four days) after copulation and most eggs are deposited during the first week of adult life (Sen & Chakravorty, 1970).

Several hispines, including *Baliosus nervosus* (Panzer), *Dicladispa armigera* (Olivier), *Promecotheca couruleipennis* Blanchard, and *P. cumingi* Baly lay eggs singly, in a space excavated by the female on the upper portion of leaves or leaflets (Teixeira *et al.*, 1999; West & Lothian, 1948). The hispines *Microrhopala vittata* (Fabricius), *M. xerene* (Newman), and *Odontota dorsalis* oviposit abaxially in small masses consisting of three to five eggs per cluster or for each of several rows (Clark, 1983; Needham *et al.*, 1928). In some species, such as *Heterispa costipennis* Boheman, females may lay as little as one egg per leaf or several eggs, dispersed or clustered, per leaf (Monrós & Viana, 1947). Some species of *Sceloenopla* (Hispinae) lay eggs, eight per oviposition bout, inside an ootheca deposited on the mesophyll of the abaxial surface of young *Cecropia* spp. leaves (Andrade, 1984; Jolivet, 1989b). Females may cover the excavations with an exudate made out of chewed leaflet bits and feces (Boldt & Staines, 1993; Dharmadhikari *et al.*, 1977; Zaka-





Figs. 1 and 2. Eruciform larva of *Monoxia* spp. 1. Dorsal. 2. Ventral.

Fig. 3. Sacculate or blotch mines caused by *Monoxia guttulata* (LeConte) on *Artemisia douglasiana* Besser (Asteraceae).

Figs. 4 and 5. Different stages of pupation in *Monoxia* spp. in larval mine in a *G. humilis*. In Figure 5, note the presence of larval exuvium (to the left) still partially attached to pupae.

Fig. 6. Side and top views of clip cages used by the author in host-plant feeding preference experiments by *Monoxia* beetles.

ur-Rab, 1991; Fig. 7). In contrast, the hispine *Odontota dorsalis* (Thunberg) lays its eggs in small groups on the lower surface of the leaves, although it also covers them with a “sticky substance partially covered with an excrementitious secretion” (Chittenden, 1902). According to Chittenden (1902), the secretion “appears to possess some caustic properties, for the place of an egg mass can always be seen on the upper side of the leaf as a small brown spot. It [the secretion] hardens very rapidly, and becomes so tough and firmly adherent to the eggs that these cannot be taken out from a mass without destroying them.”

Fecal matter is used by numerous chrysomelids to cover their eggs (Müller & Hilker, 2004). For instance, Clark (1983) suggests that *Microrhopala* (Hispinae) anal secretions, likely feces, which soon darken and harden, cover and probably protect the eggs (Cappuccino, 1991b; Damman & Cappuccino, 1991; Hodson, 1942). Field experiments have dem-

onstrated that this material reduces egg mortality from predators and parasitoids significantly, particularly that of eggs located at upper tiers in *M. vittata* egg clusters (Damman & Cappuccino, 1991). In the case of the hispine *Odontota dorsalis*, it is believed that the feces, with which eggs are covered, make eggs more cryptic (Wheeler, 1987). This material also glues eggs to the leaf (Taylor, 1937). Nevertheless, natural enemies of eggs from non-leaf-mining chrysomelids may also be attracted by chemicals released by the eggs (Müller & Hilker, 2004). However, the dark material with which female hispines *Octotoma scabripennis* Guérin-Méneville and *Uroplata girardi* Pic cover their eggs is liquid from the colleterial glands, not feces (Harley, 1969; Cilliers, 1987a).

#### *Total fecundity and some correlates of oviposition*

The hispine *Trichispa sericea* Guérin-Méneville can lay up to 747 eggs in a season (Ravelojaona, 1970).



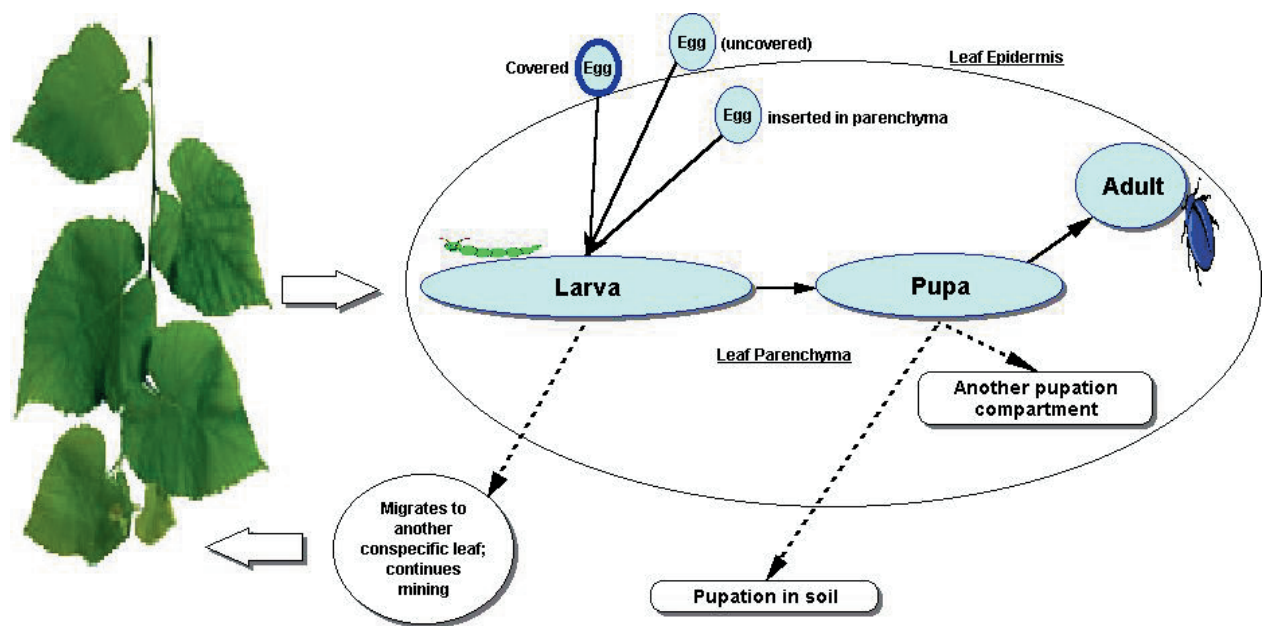


Fig. 7. Typical life history of leaf-mining chrysomelids, with some variations (usually represented by dashed line).

The total number of eggs a female can oviposit during her life can reach 100 or more for a *D. armigera* female, although most larvae die during hatching (Sen & Chakravorty, 1970). The hispine, *Promecotheca reichei* Baly lays 16 to 25 eggs during her life (Hinton, 1981). These numbers fall well within the range for the Chrysomelidae, 10 to 2800 oviposited eggs during the life of a single female (Hinton, 1981).

In some species, the eggs are partially forced into the leaves' tissues, through the tissue that has already been partially eaten by the adult female (Hodson, 1942). The hispine, *Asanmagulia cuspidata* Maulik, oviposits just under the leaf-blade epidermis of sugar cane, *Saccharum officinale* Linné (Zaka-ur-Rab, 1991). The hispine *Platypria coronata* Guérin-Méneville can lay one to three eggs, all located just under the lower epidermis.

The number of eggs laid by *Platypria coronata* (Guérin-Méneville) apparently varies, depending on whether it has fed recently on the leaf that is used as the site of oviposition on its host-plant, the legume *Pueraria phaseoloides* (Roxburgh) Benth (Bernon & Graves, 1979). West & Lothian (1948) suggest that there must be intraspecific food competition in *Baliosus nervosus* hispines feeding on *Tilia americana* leaves. The hispine *Pentispa suturalis* (Baly) lays one to six eggs, most of them apically and adaxially on *Baccharis bigelovii* leaves. Small *B. bigelovii* leaves tend to receive only one *P. suturalis* egg, perhaps a mechanism that reduces competition for food (Boldt & Staines, 1993; Hespenheide, 1991; Teixeira *et al.*, 1999). The chemical determinants of oviposition in leaf-mining chrysomelids appear to be unknown.

#### Larva

Using head capsule measurements from preserved samples, Boldt & Staines (1993) found that *Pentispa suturalis* has three larval instars. Other species, such as *Di cladispa armigera* (Hispinae), have four instars (Sen & Chakravorty, 1970). Samples from exuviae can be difficult to measure since the head capsules tend to separate along their epicranial sutures. However, field observations are often carried out *in situ* by placing the mined larvae against a light source.

#### Hatching and penetrating the leaf

Larvae are the pre-eminently active mining stage of leaf-mining insects. Newly emerged larvae may begin mining a leaf on the upper (adaxial) or on the lower (abaxial) epidermis, depending on the location of the egg from which the larvae eclose. Newly hatched *Dibolia borealis* Chevrolat (Alticinae) larvae enter leaves by making a slit on the epidermis and chewing their way in to inner tissues (Needham *et al.*, 1928). *Throscoryssa citri* Maulik (Alticinae) larvae mine leaves, entering through the lower surface of the blade and exit leaves through an exit hole on the upper surface at night (Zaka-ur-Rab, 1991). Both *Octotoma scabripennis* and *Uroplata girardi* (Hispinae) penetrate the leaf promptly after hatching (Cilliers, 1987a). However, when larvae of the hispines *Promecotheca caeruleipennis* and species of the hispine genus *Microrhopala* hatch, they penetrate first through the maternally-laid exudate layer that surrounds the egg and is glued to the leaf, and then enter the leaf. In leaf-mining chrysomelids, such as the hispine *Baliosus nervosus*, whose eggs have been deposited in an excavation made by the mother, the larvae invade the mesophyll-rich parenchyma upon hatching. Newly hatched *B. nervosus* larvae that were experimentally placed on an unchewed surface of

*Tilia americana* Linné host leaves were unable to penetrate the epidermis (West & Lothian, 1948). In all cases, penetration of the epidermis opens a direct avenue for the start of the leaf-mining habit. In contrast to some lepidopteran leaf-miners, all known leaf-mining chrysomelid larvae are devoid of a case (Hering, 1951).

#### Leaf occupancy

The number of mines in a leaf vary with the size and the temporal availability of the leaf (Williams, 1989b). *Microrhopala xerene* (Newman) has many more mines per leaf on the earlier germinating and larger leaved *Aster puniceus* Linné (Asteraceae) than on the sympatric, later germinating and smaller leaved *A. simplex* (Willdenow).

The number of individuals per mine, and the functional significance of the mines, vary per species. In some cases, such as that of *Microrhopala xerene*, the mines are large enough to contain up to four immature members of the species (McCauley, 1938), while in some other species, mines may contain up to two or three conspecifics (Harley, 1969; Lee, 1990; Wheeler, 1980). In *Odontota scabripennis* and *Uroplata girardi*, the number of individuals in a mine is inversely proportional to the size of the larval tenants (Harley, 1969).

The larvae of some species of leaf-mining chrysomelids stay in the same leaf during their entire life (Williams, 1989a); the larvae of other species change leaves, sometimes up to three times (Hering, 1951; Wheeler, 1987), generating a new mine for each switch. For instance, several larvae of *Zeugophora scutellaris* Suffrian (Zeugophorinae) may find themselves living in a single chamber when several independent mines become confluent. Yet, when mining is completed only one living larva is found. Needham *et al.* (1928) do not explain whether this is caused by cannibalism, lack of sufficient food, or other reasons. Upon hatching, larvae of *Odontota dorsalis* penetrate one leaflet of *Robinia pseudo-acacia* (Leguminosae). The first hatched larvae or “leader” and the other larvae from the same clutch, or ‘followers’, occupy the same mine, and they burrow communally during their first instar (Chittenden, 1902). Several days later, the larvae exit the leaves and disperse, each larva mining a different leaflet. Interestingly, on occasion, two more mature *Odontota horni* Smith larvae have been found in the same mine (Buntin & Pedigo, 1982). The solitary larvae of *Pentispa suturalis* (Hispiniae) usually mine two or three *Baccharis bigelovii* leaves during their life (Boldt & Staines, 1993). *Platypria andrewesi* Weise (Hispiniae) larvae consume foliar tissue briefly out of several small pocket-like mines (Zaka-ur-Rab, 1991). In some leaf-mining insects, larvae may change host-plant species during development (Hering, 1951).

Intraleaf feeding preferences have been documented in some species of leaf-mining chrysomelids. Among a substantial number of differences (Inoue, 1996), larvae of *Argopistes coccinelliformis* Csiki

and *A. biplagiatus* Motschulsky occupy different niches of their oleacean host-plants. These species start mining on different surfaces of their host-plant leaves: on the upper surface for *A. coccinelliformis* and on the lower surface for *A. biplagiatus*. Occasionally, more frequently for *A. coccinelliformis* than for *A. biplagiatus*, larvae change mines, perhaps as a result of fecal accumulation. Later, older larvae of *Argopistes coccinelliformis* may re-enter the host leaves from the lower surface and *Argopistes biplagiatus* from the upper surface (Inoue, 1990b, 1996). Similar pattern preferences have been noted for *Octotoma scabripennis* Guérin-Méneville and *Uroplata girardi* Pic (Harley, 1969). The anatomical and chemical determinants of this larval feeding behavior are apparently unknown, although it is generally believed that larvae of leaf-mining insects tend to avoid the leaf veins (Hering, 1951).

#### Morphological modifications

In the context of evolutionary biology, adaptations are traits that are presumed to have been brought forth by the action of natural selection (Rose & Lauder, 1996). Although anecdotal natural history cases certainly can be compelling and often form the basis for more detailed analyses, evidence for adaptation is best attained by experimental and comparative biomechanical studies coupled with a sound phylogenetic analysis (Orzack & Sober, 2001; Ross & Lauder, 1996). In this strict sense, there are no traits among the leaf-mining chrysomelids that have been experimentally shown to be specifically adaptive or linked with an adaptive radiation event. However, many traits are compelling candidates, including a flattened body and spines on some adults as adaptations for leaf-mining (Hering, 1951).

Leaf-mining chrysomelid larvae have a broad spectrum of larval types from fully-legged eruciform to very flat, disc-shaped, or onisciform shapes. In some genera, such as *Chalepus* (Hispiniae) and *Phyllotreta* (Alticinae), the legs are well developed; in the hispine *Baliosus* they are minute, whereas in the zeugophorine *Zeugophora* and the hispine *Octotoma*, larvae are apodous. Nevertheless, leaf-mining chrysomelid larvae seem to be placed in two gross morphological categories: first, the less modified or eruciform type found in the Galerucinae and some Alticinae; second, the flattened type occurring among Zeugophorinae, many Alticinae, Cassidinae, and the Hispiniae. Morphological data for leaf-mining larval criocerines are not yet available.

The first type, the slightly or unmodified eruciform larvae, is represented by galerucines such as species of *Galerucella* spp. and *Monoxia* spp. and by some alticines, including *Aphthona* and *Phyllotreta* (Böving, 1927, 1929; Grandi, 1959; Lawson, 1991). Both galerucine and alticine larvae, which appear only minimally modified for mining leaves (Needham *et al.*, 1928; Lawson, 1991) tend to be orthosomatic, have nine to ten abdominal segments in galerucines and ten in alticines, bear legs, display four to five

palmate teeth on mandibles, and posses small, one to two segmented antennae. Some hispine larvae, such as species of *Microrhopala*, have subcylindrical bodies that taper posteriorly, an occiput with two posteriorly projecting lobes, a fused clypeus and frons, a mandible projecting slightly over the labrum, absent labial palpi, postgenae that are lateral to the gula, antennae displaced anterodorsally, some mouthparts that are adnate and hyperhirsute, and an expanded maxillolabial complex and ligula; labial palps that are involuted, a thorax that is only lightly sclerotized, a constricted mesothoracic segment, the presence of legs, and ambulacral projections occurring on the abdomen (McCauley, 1938).

In addition to the overall body shape, there are many other modifications that leaf-mining chrysomelid larvae may have. When present, such modifications tend to be concentrated on the head. This is exemplified by the second type of overall body shape in larvae of leaf-mining chrysomelids, the flattened, or depressed, type (Grandi, 1959), which has two variants.

This is the first variant of the second type of leaf-mining chrysomelid larvae and is represented by *Dibolia femoralis* Redtenbacher and *Sphaeroderma rubidum* Gruells (Alticinae), as well as by some hispine leaf-miners, such as *Sceloenopla* near *bidens* (Fabricius) which have conspicuously depressed bodies (Costa *et al.*, 1988). In addition, these larval types have reduced body setation, legs, vestigial ambulatory lobes, a head capsule with prognathous or slightly declined mouthparts, an occipital area with posteriorly expanded projections, involuted labial palps, and antennae that are displaced anterodorsally. *Phyllotreta nemorum* Linné and *Psylliodes chrysocephala* Linné (Alticinae), which also belong in this type, have a sclerotized plate on the last visible abdominal tergite (Grison *et al.*, 1963). The hispine *Odontota dorsalis* also is slightly modified but only minimally depressed dorsoventrally (Needham *et al.*, 1928).

The second variant of the flattened larval type is represented by species of the zeugophorine, *Zeugophora*. These larvae are apodous and have: a body that is obviously flattened and enlarged anteriorly; a flattened head capsule with a prognathous or slightly declivous head that is somewhat retracted in the prothorax; two thorax-penetrating posterodorsolateral projections; three-segmented antennae; labrum with long, spatulated bristles; long, depressed mandibles; three-segmented maxillae having large, sclerotized stipites and cardines located beyond the labium; involuted labium with large, spatulated bristles and contiguous, reduced, or vestigial labial palpi; no coronal suture; frontal sutures in direct contact with occipital foramen; thorax with two large apodemata; thoracic and abdominal ambulatory lobes, and a nine-segmented abdomen (Lawson, 1991; Lee, 1990; Needham *et al.*, 1928). The long thoracic setae in *Zeugophora abnormis* LeConte larvae may assist larvae moving inside the mines (Frost, 1924; Monró

& Viana, 1947). A flattened body may constitute an advantage in gas exchange.

Hispine larvae tend to be flattened as well, albeit, as a group they show the greatest range of body variation within leaf-mining chrysomelids. Hispine larvae lack the forked projection in the eighth abdominal segment present in cassidines. However, because of its peculiar combination of traits – mining larvae that lack posterior abdominal projections and overall tortoise-shape body-like cassidines – *Notosacantha* has been variously placed in the Hispineae or in the Cassidinae (Borowiec, 1995; Medvedev & Eroshkina, 1988; Rane *et al.*, 2000; Staines, 2002b). Hispine larvae are approximately 5–10 mm long, pale-colored, except for the dark eighth abdominal segment, which tends to be darker; orthosomatic; have four or six stemmata; and all eighth abdominal segments frequently bear lateral projections (Lawson, 1991; Jolivet, 1989a).

As body forms become increasingly flattened, particularly for the hispines, lateral processes become broader and interlacing, making the larvae onisciform. This condition gives them appearance of water pennies (Coleoptera: Psephenidae) (Anderson *et al.*, 2002; Maulik, 1932; Jolivet, 1989a). However, extreme body flattening, is not exclusive to hispines that mine leaves. Larvae of the leaf-browsing *Platyauchenia latreille* Castelnau, as well as species of *Arescus* and *Chelobasis*, are extremely flattened, approximating 1 mm in thickness (Maulik, 1931, 1933a). Presumably this is a restriction on the range of allowable body forms imposed on organisms living amid the crevices between appressed leaves over evolutionary time (Maulik, 1931).

The heads of hispine larvae have a full spectrum of variation, ranging from subglobular (as in species of *Prosopodonta*) to progressively flattened heads that have large posterior elongations on the epicranium. As flattening progresses, so does the prognathation and reduction of mouthparts and antennae (Maulik, 1931). Larvae of *P. latreillei* exhibit a great reduction in mouthparts (Maulik, 1933a). The prothorax enlarges correspondingly and tends to be more extensively connected to the head, at times by heavily sclerotized tergites. Also, there is a reduction in the meso- and metathorax, as well as greater differentiation between the thoracic segments, which tend to be larger, legged, and devoid of spiracles, except for a pair between the pro- and mesothorax. The abdominal segments are generally smaller, apodous, and bear spiracles. In general, leaf-mining hispine larvae have reduced, fleshy legs, such as *S. maculata* Andrade or are apodous in the case of species of *Octotoma* (Crowson, 1955; Steinhausen, 1966; Peterson, 1979).

The fused, or connate, sclerotized eighth and ninth abdominal segments are common in many genera of hispine larvae, such as species of *Prosopodonta* spp., as are the projections on the last visible body segment (Maulik, 1933b). Maulik (1931) believed that the hardened eighth/ninth abdominal segment

may serve to further enlarge mines, since these larvae are large, in order to allow for the accumulation of detrimental feces and other frass. "By moving [this segment] the insect is able to make a clearing, or it [the frass] may thrust it outside if need be" (Maulik, 1931). Several hispine larvae, such as species of *Dactylispa*, have the terminal spiracles located on the abdomen, which are protected by the distal projections, or papillae, inside the spiracular opening, or the opening positioned at a very oblique angle to the longitudinal axis of the spiracular trunk (Maulik, 1932, 1933b).

#### *Patterns of mines in leaf-mining chrysomelids*

The dwellings made by leaf-mining larvae inside leaves are known as mines. Mines have several basic morphologies and biological functions, such as waste disposal and development, and those functions are often compartmentalized (e.g., the alticine *Dibolia*). Extensive discussion of these subjects for leaf-mining insects can be found in Hering (1951).

*Types of mines.* There are many types of feeding damage done to plants, including leaf-mines (Hargrove, 1986; Hering, 1951; Labandeira, 2002a; Wilf *et al.*, 2001). There is often a wealth of gross morphological patterns in the mines of leaf-mining insects, and chrysomelids are no exception. A useful pictorial depiction of common, extant leaf-mine damage with examples from each of the four orders of leaf-mining insects is available online (<http://www.leafmines.co.uk/index.htm>). As a group, the mines produced by leaf-mining chrysomelids vary in shape and dimensions, although most are of the blotch type, also known as blister type (see illustration in Wheeler, 1987).

Mines of many chrysomelids are elongated and serpentine, such as those of *Phyllotreta nemorum* (Alticinae) and of many hispines, including *Octotoma plicatula* (Fabricius) (Needham *et al.*, 1928). In other cases, such as the galerucine *Monoxia guttulata* (LeConte) (Fig. 3) and species of *Microrhopala* (Hispinae), their mines are more sacculate or blotchy (Needham *et al.*, 1928). In *Octotoma scabripennis* and *Uroplata girardi*, mines are broader and compartmentalized, contain several separated feeding galleries.

*Patterns of mines in leaf-mining chrysomelids: sources of intraspecific variation.* The shape of the mines varies with developmental stage and age of the larvae. In *Zeugophora annulata* and in species of the fern-feeding alticine *Schenklingia*, mines of early larvae are broadly linear; those of late larvae are wider (Lee, 1990; Kato, 1991). Kogan & Kogan (1979) depict a wide range of variation in mine size, as well as leaf area covered, on the hispine *Odontota horni*. In *O. horni*, some of the mines can be circular. The size of the mine is monotonally proportional to the size of the larvae. In hispines, for instance, mines produced in palm leaves can reach 20 cm long

and 2 cm wide (Mariau, 1988). Gressitt (1957) reports that mines of several species of *Promecotheca* exceed 30 cm in length, and that a compound mine of *P. violaceae* Uhmann produced by two or more larvae was 60 cm long.

If the leaves of the host plant are elongated, mines may also be elongated, constrained by the veins (Hespenheide & Dang, 1999). Several tropical hispines form serpentine mines, which are more characteristic of lepidopteran leaf-miners (Hespenheide & Dang, 1999). Another extreme case is the hispine *Assamangulia cuspidata*, which may produce longitudinal mines of up to 20 cm long (Zaka-ur-Rab, 1991), and mines of the hispine *Promecotheca papuana* Csiki have measured up to 40 cm in length (Howard *et al.*, 2001). *Platypria coronata* larvae mine leaves, starting at the site of eclosion, avoiding large veins, and forming circular mines (Bernon & Graves, 1979). Larvae of *Pentispa suturalis* (Hispinae) mine small leaves and their mines tend to conform to the shape of the leaf (Boldt & Staines, 1993). A few leaf-mining chrysomelids, such as *Dibolia* (Alticinae), make long serpentine mines; *Hippuriphila* and *Phyllotreta* (both Alticinae) make short serpentine mines (Frost 1924).

Some of the most complex leaf-mines of tropical hispines have been called 'blotch lobulate' (Hespenheide & Dang, 1999) and resemble the depiction of digitate, or star mines, or asteronomes, in Hering's (1951) classification. These mines have a central chamber, located under the oviposition place, coated with larval fecal material. Several compartments, or lobes, are produced as the larva feeds at different sites. In some cases, resting and pupation may take place in lobes apparently used only for those activities (Hespenheide & Dang, 1999).

Communally-feeding larvae may change the shape of serpentine mines into those of blotch mines (Fig. 8), as occurs with the genera *Heterispa* and *Oxyroplata* (Hespenheide & Dang, 1999). I am unaware of blotched mines with compartments being transformed into a simpler blotch mine or a blotch mines converted to serpentine or irregular mines. While there can be functional compartmentalization in serpentine and in irregular mines, when there are distinct compartments, they tend to be more frequent in blotch mines.

Despite this variation, the shape of the blotch mines produced by leaf-mining chrysomelids may be characteristic within a taxonomic group (Hodson, 1942). For example, the mines produced by asteracean-feeding larvae of *Monoxia* (Figs. 1 and 2) are consistently simple, often inflated and sacculate, and about 1 cm long at completion (Fig. 3). These kinds of mines have also been reported for the hispine *Pentispa suturalis* (Boldt & Staines, 1993).

*Patterns of mines in leaf-mining chrysomelids: compartmentalization of functions.* Larvae of the hispine *Dicladispa testacea* (Linné) make two mines, one in which they spend the first larval stages, the sec-

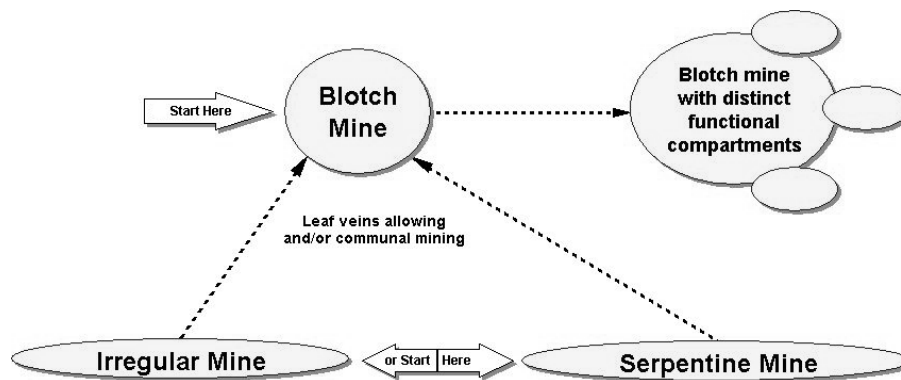


Fig. 8. Developmental transitions between types of leaf-mines; including: irregular, serpentine, blotched, or blotched with functional compartments. I am unaware of blotched mines with compartments being transformed into a simpler blotch mine or a blotch mine turning into serpentine or irregular mines, hence the absence of double arrows connecting those types of mines. While there can be compartmentalization in serpentine and irregular mines, *distinct* compartments tend to be more frequent on mines that resemble blotch mines. This figure is not a phylogenetic hypothesis and the arrows do not imply evolutionary transformations.

ond in which metamorphosis is completed. The disposition of the larval feces varies from species to species and serves as a good example of mine compartmentalization. In *Zeugophora annulata* (Baly), feces are scattered within the mine (Lee, 1990). Larvae of the hispine *Platypria coronata* and of the alticine *Throscoreyssa citri* place their feces towards the center of the mine (Bernon & Graves, 1979; Zaka-ur-Rab, 1991). However, *P. caeruleipennis* and *P. cumingi* larvae defecate on one side of the mine and leave the central space relatively free (Dharmadhikari *et al.*, 1977; Zaka-ur-Rab, 1991). It is unclear whether one side of the mine (right or left) is preferred, or whether such a preference is constant from individual to individual or through time. Larvae of *Dibolia* spp. and of *Baliosus nervosus* defecate in the mine's side branches rather than on the central space of the mine (Hering, 1951; West & Lothian, 1948). Larvae of *Physocoryna expansa* Pic, *Octhispa haematopyga* (Baly), and a species of *Probaenia* lay their feces on special frass-lined resting mines (Hespenheide, 2000; Hespenheide & Dang, 1999). In the latter three species, feeding occurs in tunnels radiating from the resting area (Hespenheide, 2000; Hespenheide & Dang, 1999). Some possible developmental transitions between mines that are serpentine, blotched, or blotched with functional compartments are represented in Figure 8. However, this Figure is not a phylogenetic hypothesis.

### Pupa

Chrysomeloid pupae have been thoroughly studied and diagnosed to the subfamily level (Cox, 1996). Most chrysomelid pupae, including those of leaf-mining species, are exarate, having free appendages. Nevertheless, many leaf-mining hispines have (or almost) obtect pupae, presumably a trait secondarily derived from exophytic ancestors (Cox, 1996). Herein, I uniformly summarize and rearrange Cox's (1996) diagnoses for each of the subfamilies of Chry-

somelidae known to contain leaf-mining taxa. I have included only traits that are relatively easy to observe and are less variable. Readers interested in additional details should consult Cox (1996). Some data for the Galerucinae originate from my studies of *Monoxia* (Figs. 4 and 5).

*Dactylispa javaensis* Maulik pupae have a spiracular presumably protective device on the fifth abdominal segment. Some leaf-mining chrysomelid pupae bear strong, pointy prongs. The impact of pupae on mine enlargement, if any, is probably accidental.

### Abbreviated diagnoses of the pupae of leaf-mining chrysomelids

Pupae of the Zeugophorinae are exarate, whitish, have a setose head, possess four papillae on each antennal segment, lack pronotal anterior tubercles, bear three apical femoral setae, have spiracles on I-VII (VIII), possess relatively unsculptured abdomen, have two bosses, each with four tubercles, and lack urogomphi. Pupae of the Criocerinae are exarate and of variable color, have a glabrous head, possess two to three papillae on each antennal segment, usually bear two pronotal anterior tubercles, lacking apical femoral setae, have spiracles on I-VII (VIII), possess a microspiculed abdomen, lack a boss, and bear paired urogomphi. Pupae of the Galerucinae are exarate, whitish/yellowish, have a setose head, possess two to five papillae on each antennal segment, lack pronotal anterior tubercles, bear one to three apical femoral setae, have spiracles on I-IV (V-VIII), possess a relatively unsculptured abdomen, lack a boss, and lack a urogomphi. Pupae of the Alticinae are exarate, of variable color, have a dorsally setose and ventrally glabrous head (and rest of body), possess two to five papillae on each antennal segment, lack pronotal anterior tubercles, bear one to three apical femoral setae, have spiracles on I-IV (V-VIII), possess a relatively unsculptured abdomen, lack a boss, and bear paired urogomphi or lack it

altogether. Pupae of the Hispinae are (almost) obtect, yellow-brown, have a variably setose head, lack papillae on each antennal segment, lack pronotal anterior tubercles, possess one to five apical femoral setae, bear spiracles on I-IV (V-VIII), have an abdomen that sometimes bears two rows of spinules, lack a boss, and possess a paired urogomphi, or lack it altogether. Pupae of the Cassidinae are (almost) obtect, yellow-brown, have a variably setose head, lack papillae on each antennal segment, lack pronotal anterior tubercles, possess one to five apical femoral setae, bear spiracles on I-IV (V-VIII), have an abdomen that sometimes bears two rows of spinules, lack a boss, and possess paired urogomphi, or lack it altogether. See also Rane *et al.* (2000) for additional details on pupae of leaf-mining Cassidinae.

#### *Biology of the pupae of leaf-mining chrysomelids*

Pupation in leaf-mining chrysomelids takes place in an often specialized leaf-mine, or in cells in the soil which are lined with a smooth inner wall (Cox, 1996). According to Cox (1996), zeugophorines pupate in earthen cells. Among the criocerines, pupae lay inside “whitish cocoons constructed from mouth exudate ... attached to the host-plant or in the soil; or in earthen cells lined with mouth exudate”. *Oulema pumila*, according to Vencel & Aiello (1997), one of only two criocerines known to be leaf-miners, appear to produce a ‘foamy substance’ that coats the pupation chambers in leaves. Additional details of the pupation biology of leaf-mining criocerines are not yet available, although it is known that other criocerines, such as *Liliocercis lilii* Scopoli and *Crioceris asparagi* (Linné) do pupate in the soil. For the galerucine genus *Monoxia* and many hispines, including several North American taxa (Boldt & Staines, 1993; Clark, 1983; Ford & Cavey, 1985; West & Lothian, 1948), as well as Indo-Pacific palmophilous hispines (Mariau, 1988), and the galerucine genus *Monoxia* (Figs. 4 and 5), pupation takes place inside the leaf mine excavated by the larvae. In other leaf-mining chrysomelids, such as species of *Dicladispa*, there is a newer and shorter leaf compartment, known as ‘pupation mine’, in which they pupate (Hering, 1951). Larvae of the cassidine *Notosacantha vicaria* vacate their mined leaves and form a new pupation mine in another leaf (Rane *et al.*, 2000).

Once pupal cells are formed, the leaves of the asteracean that harbor *Microrhopala xerene* hispines inflate slightly and form a hard blister (McCaughey, 1938). Several species of Central American hispines have resting mines in which they pupate (Hespenheide, 2000; Hespenheide & Dang, 1999). Interestingly, the hispine *Dicladispa testacea* (Fabricius) pupates in the “larval mine in leaf midrib” of *Cistus* sp. hosts (Cox, 1996).

On the other hand, in a significant number of leaf-mining chrysomelids, such as *Dibolia borealis*, species of *Argopistes* (both Alticinae), and several other flea beetles, pupation occurs in earthen cells within the soil (Cox, 1996; Frost, 1924; Hering, 1957; Need-

ham *et al.*, 1928). In the hispine *Platypria andrewesi* Weise and in *P. coronata* (Guérin-Méneville), pupation occurs in a special leaf mine excavated before pupation (Bernon & Graves, 1979; Zaka-ur-Rab, 1991). *Platypria coronata* larvae, crawl out of the feeding mine and move to the upper epidermis towards the leaf’s apex following the margin of the leaf. Shortly before reaching the apex, the larvae move mesally, crawl into the leaf, and form pupation mines. During this period (approximately 45 minutes), larvae are susceptible to predation, especially by ants. Chittenden (1902) also reported that the transformation from prepupa to pupa in the hispine *Odontota dorsalis* takes two to three minutes. In the alticine *Clitea picta*, pupation may take place in the mine or in the soil (Zaka-ur-Rab, 1991).

Some hispine pupae, such as those of *Sceloenopla* near *bidens*, are strongly dorsoventrally depressed, allowing for movement within the mines excavated by larvae. Ford & Cavey (1985) reported that prongs on the seventh abdominal sternite of several genera of North American hispines are ambulacral. Some hispine pupae are remarkably fast movers. For instance, in the hispine genus *Anisostena*, pupae have been observed to move at a rate of about 5 cm per second (Ford & Cavey, 1985).

It is not known how leaf-mining larvae arrive at pupation sites located in the soil. Do they crawl down the shoot to reach the soil; do they simply drop; or do they do both? Cox (personal communication to Santiago-Blay, July 2003) suspects that often larval legs, particularly of leaf-mining alticine larvae, are too short to be used in crawling, and it is more likely that they just drop down. Pupation in the soil involves considerable mortality risks, but no one has studied whether such dangers are significantly different from those present when pupating in or on leaves, which are also exposed to parasitoids, predators, and diseases.

#### *Adults*

Once adulthood is reached, some imagoes, such as those of the hispines *Sceloenopla maculata* (Olivier), *Microrhopala*, and *Promecotheca couruleipennis* Blanchard stay inside the larval mine for several days before emerging from the leaf (Andrade, 1984; Clark, 1983; Dharmadhikari *et al.*, 1977). Adults chew a hole in the mined leaf and emerge (Dharmadhikari *et al.*, 1977). Among numerous leaf-miners, emergence holes are species specific features; leaf-mining coleopterans often obliterate these emergence holes as they eat their way out of the mine (Auerbach & Simberloff, 1988). Once beetles emerge, they seek food (see *Host-plant feeding preferences*, below) and mates (see *Reproduction*, below). *Baliosus nervosus* total adult longevity has been estimated as eleven months (West & Lothian, 1948). Adult chrysomelid longevity ranges from a few days to over two years (Hinton, 1981).

## Ecology: the leaf as a habitat for survival and reproduction

Finding a suitable host plant for survival and reproduction has been the subject of considerable research. These areas are important in the context of the greater understanding of insect-hostplant interactions and possible coevolution (Ehrlich & Raven, 1964). In simple terms, the host-seeking process can be divided into: initial (long-distance) orientation; contact (short-range) orientation; and behavior once contact with the host-plant is made (Moldenke, 1971). Very little is known about these phases of herbivory for leaf-mining chrysomelids.

### *Host-plant feeding preferences: the patterns*

When I began compiling these data in 1995, I had only partially realized the immensity of the task. Table 1 is a worldwide list of leaf-mining chrysomelid taxa, including their geographical distribution, host-plants, and their taxonomic authorities, as well as pertinent references. It is not as comprehensive as I would have liked. Nevertheless, I am correcting some deficiencies (listed below) and hope to have additional and detailed quantitative analyses at a later date. Preliminary analyses of the data follow after mention of some associated caveats.

### *Problematic data set*

There are numerous difficulties with the data regarding the feeding behavior of leaf-mining chrysomelids. Firstly, it is often unclear what records are actual feeding events or which are cases of ‘accidental’ sitting, feeding, nibbling, or ovipositing on a plant (Harley 1969; Mullins, 1976; Razzaque & Karin, 1989).

Secondly, there are relatively little experimental and quantitative data on potential host-plant feeding preferences of larvae and adult leaf-mining chrysomelids. However, experimental approaches to leaf-mining are not new. For instance, Buhr (1955) reports an unsuccessful attempt to rear larvae of the Brassicaceae colonizer *Phyllotreta nemorum* (Linné) on a noncruciferous plant, *Allium moly* Linné (Liliaceae). Dominique Mariau has spent a great part of his professional life in the Ivory Coast of Africa opening palm leaves with a knife to insert larvae of several species of Hispinae to test whether they can complete development on artificially-produced mines (Jolivet to Santiago-Blay, personal communication, June 2003). If there are experimental trials, the literature tends to omit whether the used leaves were unexcised and, if excised, how often they were replenished. Experimental studies of feeding behavior by and preferences of leaf-mining chrysomelids are relatively uncommon, unless the species in question is of potential economic importance (see examples in Cilliers, 1987b; Harley, 1969; Hodson, 1942; Kogan & Kogan, 1979; Richerson & Boldt, 1995). Harley (1969) explored the possibility of using

the hispines *Octotoma scabripennis* Guérin-Méneville and *Uroplata girardi* Pic for the biological control of noxious *Lantana* (Verbenaceae) weeds. Beetles as well as larvae were starved – a common part of the protocol in this type of experiments – and caged plants, usually of economic importance, were exposed to the herbivores for a predetermined time, usually 24–48 hours. Subsequently, the evidence of feeding and oviposition were observed on the plants as feeding marks or as deposited eggs, respectively. Cilliers (1987b) used exclusion experiments to demonstrate that the presence of leaf-mining chrysomelids causes significant defoliation, decreased leaf size, flower production, and seed set in *Lantana camara*. Use of leaf-disc tests, standard procedure when the testing potential biological control of weed agents, were used by Vig (1998a, 1998b) to show the feeding preferences of adult *Phyllotreta vitata* (Alticinae) to grasses (Poaceae) and crucifers (Brassicaceae). An important distinction, not always made particularly in the context of applied research, is the ability of adults leaf-mining chrysomelids to oviposit only on a limited suite of plant species although the beetles may have fed on a larger group of plants and occurred on many additional plant species. Observations of species of *Argopistes* have shown that *A. cocconelliformis* oviposits and larvae develop only in new leaves of their oleacean host-plants (Inoue & Shinkaji, 1989). Studies on *Dicladispa armigera*, the rice hispa, have confirmed that sitting, feeding, and ovipositing host-plants need not be on the same plant.

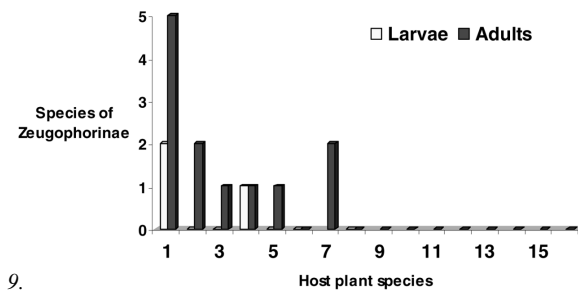
Thirdly, authors frequently do not distinguish between adult and larval feeding. A case in point is that of the *Dicladispa armigera*, the rice hispa, in Bangladesh. Razzaque & Karin (1989) tested the feeding preferences of adult *D. armigera* on several cultivars, including corn, wheat, rice, and several weeds. While numerous plants were heavily used as settling substrates and/or food items by adult *D. armigera*, Razzaque & Karin (1989) reported that only rice (*Oryza sativa* Linné, Poaceae) served as an oviposition site and as the host for larval development. For the purposes of Table 1, when the life-history stage of an insect is not mentioned in a source, I have conservatively assumed that the context refers to adults.

Fourthly, there is rarely published mention of voucher specimens for the insects or plants deposited in a collection, an issue that is especially acute for evidence of leaf-mining. Vouchers would greatly facilitate verification of identifications by subsequent researchers.

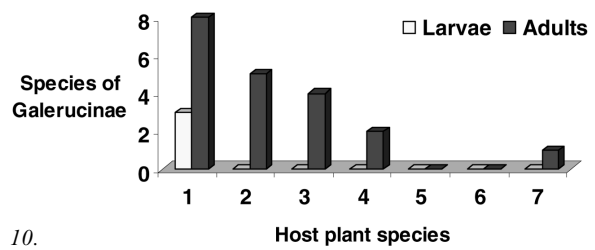
Fifthly, the taxonomic status of numerous leaf-mining chrysomelid genera, as well as of their host plants, varies greatly. In some cases, many species remain to be described, particularly tropical leaf-mining chrysomelids.

Sixthly, in those cases where the genera have been well-studied, I have yet to find a case where there are rigorous phylogenies for both the leaf-mining

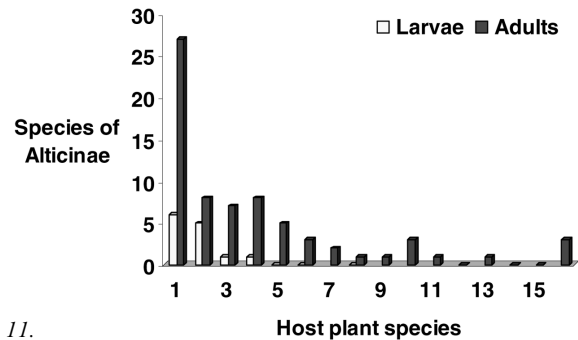




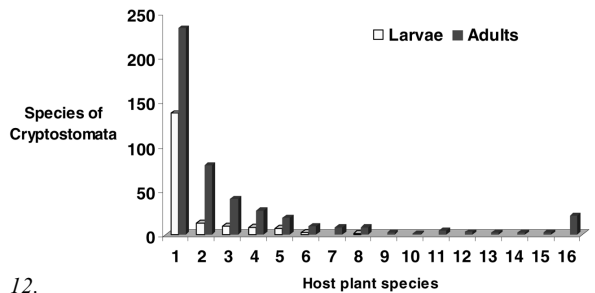
9.



10.



11.



12.

Figs. 9 to 12. Distribution of reported plants serving as hosts for leaf-mining in different subfamilies of the Chrysomelidae. 9. Zeugophorinae. 10. Galerucinae. 11. Alticinae. 12. Cryptostomes (Hispiinae + Cassidinae). While there are less data available for larvae than for adults, simple inspection strongly suggests that the range of plants serving as hosts for leaf-mining chrysomelid larvae is smaller than that of adults. IFR for the comparison of subfamily calculations support this: Zeugophorinae (IFRi = 2.0, IFRA = 2.9), Galerucinae (IFRi = 1.0, IFRA = 2.4), Alticinae (excluding *Phyllotreta nemorum*), IFRi = 2.7, IFRA = 3.8), and Hispiinae (IFRi = 1.6, IFRA = 3.0). For adult zeugophorines, 55% of the reported species only feed on one genus, and 82% of the reported species only feed on one plant family. For adult galerucines, 32% of the reported species only feed on one genus, and 60% of the reported species only feed on one plant family. For adult alticines, 47% of the reported species only feed on one genus, and 71% of the reported species only feed on one plant family. For larval Cryptostomes, 77% of the reported species only feed on one plant species, for adult Cryptostomes, 51% of the reported species only feed on one plant species.

chrysomelid group and its host-plant taxa. This would greatly facilitate tests of coevolutionary hypotheses. Interestingly, Pasteels *et al.* (2003) have found out that the patterns of chemical defenses of chrysomelids are more conserved than insect-hostplant affiliations. Evidently, more species need to be described, alpha taxonomy refined even further, and revisionary works pursued before most of the tests can be implemented.

Seventhly, authors often report the host plant by its common name, only complicating species identification.

Eighthly, the data are scattered over a wealth of languages and countries and are often buried in taxonomic papers, making access difficult.

Ninthly, some of the papers used have summarized information secondarily. Often, in the investigative process, it is difficult to recover the primary data.

#### Data analyses

Clearly, leaf-mining is concentrated into several tribes of what have traditionally been called 'Hispiinae' (Seeno & Wilcox, 1982), now called the 'Cassidinae' (Staines, 2002b, 2004b) or, formerly, the Cryptostomes.

With the exception of four reported fern-feeding species of alticines (two in *Schenklingia* and two in *Febra*) (Kato, 1991, and Samuelson, 1973, respectively) and the *Equisetum* (horsetail) associate (*Hippuriphila moderii* Linné; see Table 1 for references), leaf-mining chrysomelids appear to feed exclusively on angiosperms. No chrysomelids have been reported as gymnosperm miners.

As with leaf-mining insects as a group (Hespenheide, 1991), leaf-mining chrysomelids are believed to be narrow spectrum foliovores or, as Wilcox (1979) says, "They [chrysomelids] usually show some degree of specificity". While leaf-mining chrysomelids certainly have narrower feeding preferences than the Coleoptera as a group (Bernays & Chapman, 1994), numerous leaf-mining chrysomelids have more catholic preferences than usually suspected for leaf-mining organisms, frequently feeding on several congeneric, confamilial, or even rather distantly related plants. Hispiines, which constitute most of the leaf-mining chrysomelids, tend to be more polyphagous as adults than as larvae (Ford & Cavey, 1985) and, as a subfamily, prefer monocotyledonous plants (Borowiec, 1995, 1999; Jolivet, 1989a; Wilf *et al.*, 2000). The same patterns hold true for the remaining subfamilies of leaf-mining chrysomelids.

There are numerous qualitative classifications of the range of host-plant feeding by herbivores (*e.g.*, Hering 1951). In an effort to quantify the degree of polyphagy of a given taxon, I have created an index of feeding range (IFR), which can be calculated as a simple arithmetic average. For a given taxon, the IFR is defined as:

$$\text{IFR} = \frac{\text{total number of entities (e.g. plant species) consumed by organisms in group being compared (e.g. leaf-mining chrysomelids)}}{\text{total number of consumers being compared}}$$

The IFR varies from 1, or strict monophagy, as in many species of leaf-mining hispines, to a very large number, illustrated by the rampant polyphagy of organisms with little discrimination whatsoever, such as the alticine *Phyllotreta nemorum*. The IFR, a scalar quantity (units consumed per organisms doing the consumption, *e.g.*, host-plant species per species of leaf-mining chrysomelid), can be adjusted for the group doing the feeding (*e.g.*, individuals, species, genera, subfamilies, etc.). I have accounted neither for plant phylogeny nor for plant chemical affinity in the IFR calculations presented in this work, although the former can easily be solved by differentially weighing distinct families, orders, or classes of host-plants fed upon by a given organism. The ‘unit’ as well as the ‘entity’ terms can also be adjusted by taxonomic rank (different species, different genera, etc.), or by relative feeding (as in weighed indexes, particularly in the context of experimental trials).

As an example, this is what would have to be done to make a simple quantitative statement about the host-plant species feeding range for the adults of the reported species of leaf-mining Criocerinae (only two species). Firstly, obtain a total number of species that are being consumed by the *Lema quadrivittata* Boheman and by *Oulema pumila* Vencl and Aiello. In this case, a minimum – hence a conservative estimate – of one if Commelinaceae and Piperaceae are counted as one species or one genus. Secondly, calculate the resulting IFR. In this case, the IFR is 1, meaning that the leaf-mining criocerines are monophagous at the level of resolution one is examining, in this case, species. Of course, we could have reached the same conclusion by simple inspection of Table 1.

Highly polyphagous species, such as the alticine *Phyllotreta nemorum* (Linné) have a very high IFR. One should compare similar terms (*e.g.*, subfamilies of leaf-mining chrysomelids, as done below) and be aware of the fact that the results are as good as the data upon which they are based. For example, Vig (1998b) and Vig & Verdyck (2001) have shown how variable feeding preferences can be in several species of *Phyllotreta*. In addition, different activities in the life of an organism may have different sets of ‘host’ ranges. For instance, while staying ‘idle’ may happen almost anywhere, host-plant feed-

ing is more restricted (especially for larvae), and oviposition even more.

The IFR has one major drawback: it does not easily lend itself to account for the chemical affinities of the objects being consumed (*e.g.*, host plants). There are also smaller problems. For instance, what to do when a plant is mentioned only to the level of genus? I counted it, conservatively, as one species, unless there are congeneric host-plants mentioned for the same leaf-mining chrysomelid. In this case, I ignored the *Genus* sp. What follows is a preliminary analysis of the data compiled on host-plant feeding for larvae and for adults (Table 1). More detailed analyses are currently in progress.

It is quantitatively clear that, for each subfamily of leaf-mining chrysomelids, the IFR of larvae is smaller than the IFR of the adults. For the Chrysomelidae, the overall IFR is 1.7 for larvae and 3.1 for adults. Most plants serving as feeding hosts of leaf-mining chrysomelids are from relatively modern lineages (Judd *et al.*, 2002), just as in the Buprestidae (Hespenheide, 1991).

Zeugophorinae: IFRi for larvae (IFRi) is 2.0 and IFR for adults (IFRa) 2.9. The plant families (and genera, parenthesized) most commonly reported serving as host plants for the Zeugophorinae are the Salicaceae (*Salix* and *Populus*), the Betulaceae (*Betula* and *Corylus*), and the Celastraceae. For adult zeugophorines, 55% of the species reported only feed on one plant genus, and 82% of the species reported only feed on one plant family. Figure 9 summarizes the distribution of reported host-plants for larvae and adults in the Zeugophorinae.

Trichostomes. Galerucinae: IFRi is 1.0 and IFRa 2.4. The plant families (and genera, parenthesized) most commonly reported serving as host plants for the Galerucinae are the Asteraceae and the Chenopodiaceae (*Atriplex*, *Chenopodium*, *Suaeda*, etc.). For adult galerucines, 32% of the species reported only feed on one plant genus, and 60% of the species reported only feed on one plant family. Figure 10 summarizes the distribution of reported host plants for larvae and adults in the Galerucinae.

Alticinae: IFRi is 2.7 and IFRa (excluding the data for *Phyllotreta nemorum*) 3.8. The plant families most commonly reported to be serving as host plants for the Alticinae are the Brassicaceae, Lamiaceae, Asteraceae, Plantaginaceae, Schrophulariaceae, Polygonaceae, and Poaceae, but many more families, and numerous genera have been reported as host plants. For adult alticines, 47% of the species reported only feed on one plant genus, and 71% of the species reported only feed on one plant family. Figure 11 summarizes the distribution of reported host plants for larvae and adults in the Alticinae.

Cryptostomes (Hispinae + Cassidinae): IFRi 1.6 and IFRa is 3.02. The plant families (and genera, parenthesized) most commonly reported serving as host plants for the Hispinae are the Arecaceae (*Cocos*, *Metroxylon*, and numerous other palms), Pandanaceae (*Pandanus*, *Freycinettia*), and Zingiberaceae in the Old World. Numerous Leguminosae, Asteraceae,

Poaceae, and Verbenaceae serve as host-plants for hispines in the New World. For larval Cryptostomes, 77% of the species reported feed on one plant species. For adult Cryptostomes, 51% of the species reported only feed on one plant species. Figure 12 summarizes the distribution of reported host plants for larvae and adults in the Cryptostomes.

For central European chrysomelids at least, while the genera tend to be relatively selective in their overall habitat, their feeding preferences are broader (Schöller, 1996). This broad host-plant feeding capability parallels studies in phytophagy on southern California weeds on the Ambrosiinae (Asteraceae) (Goeden & Teerink, 1993): 73% polyphagous and 10.9% endophytic in leaves, although it is somewhat difficult to directly compare these two sets of data.

Many of the host plants listed in Table 1 are common weedy plants. However, as life histories are studied in more detail, additional host plants will be found, and corrections made to previously published reports, particularly if they have emphasized adults instead of larvae (*c.f. Microrhopala*; Clark, 1983).

Some chrysomelids appear to be facultative leaf-miners and they tend to be (potentially or actually) oligo- or polyphagous. Of all leaf-mining chrysomelids listed, the alticine *Phyllotreta nemorum* has the largest number of recorded hosts (134); most host plants are in the Brassicaceae. This species has been recorded on at least 110 crucifers in central Europe and Poland (Lipa *et al.*, 1977), although it does not mine all the species listed. *Phyllotreta vittata* has been associated with 89 host plants from the same region, although it mines only two of them. Interestingly, in his extensive studies of *P. vittata*, Vig (personal communication to Santiago-Blay, April 2003) has never seen this species mining leaves. Similar reports exist for *P. armoraciae* (Vig & Verdyck, 2001). It appears that all these species are facultative leaf-miners as well. If this is correct, the ecological transition from exo- to endophyty may be evolutionarily simple.

#### *Chemical correlates of feeding behavior*

Apparently, there are very few studies on the chemical correlates of feeding behavior in leaf-mining chrysomelids. Some species of *Phyllotreta* are widespread, making one wonder what all the host plants may have in common. In Poland and central Europe alone, over 750 species of insects have been reported for crucifers (Lipa *et al.*, 1977). Nearly all species of *Phyllotreta* (Alticinae) feed on crucifers or on related genera in the Resedaceae and the Cappara-ceae. The only documented exception to this feeding pattern on a species of *Phyllotreta* is *P. vittula* Redtenbacher, which feeds on grasses and cereals, but it is still attracted to crucifers (Kostromitin, 1973; Vig, 1998a,b). Oligophagy is the characteristic feature of species of *Phyllotreta*, but some species are monophagous. The remaining portion of this sec-

tion is restricted to studies on *Phyllotreta armoraciae*. Karoly Vig has generously allowed me to borrow from a recent paper of his (Vig, 1999).

*Phyllotreta armoraciae* feeds on several cruciferous plants to the same extent as it does on horseradish, *Armoracia rusticana* Gaertner, Mey, and Scherbius (Brassicaceae), but it rejects more than half the investigated species (Nielsen *et al.*, 1979a). Both accepted and rejected cruciferous species contain glucosinolates in large quantities. Glucosinolates are known as important feeding stimulants for *P. armoraciae* and for other species of *Phyllotreta* (Hicks, 1974). Horseradish contains mainly allylglucosinolate but 2-butyl- and benzylglucosinolate are detected as well, in traces. In spite of the fact that *Brassica nigra* (Linné) Koch, *Alliaria petiolata* (M.B.) Cavara *et* Grande, *Iberis umbellata* Linné, and *Thlaspi arvense* Linné (all Brassicaceae) have a very similar glucosinolate content as horseradish (Kjaer, 1976), *P. armoraciae* feed only on *B. nigra*. *Nasturtium microphyllum* Bönningh (Tropaeolaceae), *Sinapis alba* Linné, and *Sisymbrium officinale* (Linné) Scopoli do not contain allylglucosinolate but, under laboratory conditions, they were all eaten in appreciable amounts by *P. armoraciae*. Glucosinolate mixtures isolated from *N. microphyllum*, *S. officinale*, *Alyssum saxatile* Linné, and from *Cardamine amara* Linné were more stimulatory than the glucosinolate mixture from horseradish. No correlation was found between plant acceptability and stimulatory activity of glucosinolate mixtures isolated from the aforementioned plants (Nielsen *et al.*, 1979a).

Usually, crucifer-feeding insects can discriminate between different glucosinolate containing plant species. According to Nielsen *et al.* (1979a), the horseradish flea beetle, *Phyllotreta armoraciae* (Koch), cannot recognize horseradish solely by its glucosinolates content or by the hydrolysis products released from glucosinolates. In further experiments, two flavonol-glycosides were isolated from water extracts of horseradish leaves. Larsen *et al.* (1982) identified the flavonol-glycosides as 3-*O*-[2-*O*-( $\beta$ -D-xylopyranosyl)- $\beta$ -D-galactopyranosyl]-kaempferol (compound I) and it was present at high concentration in the leaves throughout the growing season. A second compound, 3-*O*-(2-*O*-( $\beta$ -D-xylopyranosyl)- $\beta$ -D-galactopyranosyl]-quercetin (compound II) is less phagostimulatory to *P. armoraciae* than compound I. Combinations of allylglucosinolate and compound I are more stimulatory than any of the compounds alone (Larsen *et al.*, 1982; Nielsen *et al.*, 1979b).

Flavonol-glycosides with different sugar moieties are widely distributed compounds in crucifers. It seems that *P. armoraciae* is able to distinguish kaempferol-glycosides with different sugar moieties. Simultaneous presence of kaempferol glycoside (compound I) and glucosinolates could be the key stimulus determining the recognition of horseradish by *P. armoraciae* suggesting that other feeding stimulants also contribute to the palatability of different host-plant species to the horseradish flea beetle.

Vig has observed *Phyllotreta armoraciae* feeding on *Capsella bursa-pastoris* (Linné) Medic., *Arabis* sp., and on *Alyssum saxatile* Linné (all Brassicaceae), even under stressful laboratory conditions. *P. armoraciae* also ate small amounts of leaves from *Brassica napus* Linné, *Barbarea vulgaris* R.Br., and *Alliaria petiolata* (Vig & Verdyck, 2001).

#### *Ecological correlates of feeding by leaf-mining chrysomelids*

Numerous abiotic and biotic factors have been associated with the presence (and abundance) or absence of leaf-mining chrysomelids. Over 65 years ago, Maulik (1937) insightfully discussed the importance of both types of factors on hispine-host-plant associations. In cases where the host-plant is present and the phytophagous insect absent, Maulik suggests that “the host plant can throw off its insect enemies under certain conditions”. Conversely, if the phytophagous insect is present and the host-plant is absent, “the former [namely, the insect] must have another host-plant on which it is able to adapt itself”.

#### *Abiotic factors: stress and shade*

An outbreak of the hispine *Odontota dorsalis* in the Appalachian mountains of southwestern Virginia (USA) was tentatively attributed to drought-stress, possibly because of changed physical and chemical conditions. That stress made the host plants more attractive to would-be herbivores. In this case, *O. dorsalis* fed on six sympatric trees belonging to four different vascular plant families: *Acer saccharum* (Aceraceae), *Quercus prinus*, *Q. rubra* (Fagaceae), *Robinia pseudoacacia* (Leguminosae), *Crataegus coccinea*, and *Prunus serotina* (Rosaceae).

Abundant circumstantial evidence scattered throughout the literature suggests that the larvae of some leaf-mining chrysomelids prefer leaves located on relatively shadier portions of plants. For instance, late in the 19th century, Packard (referred by Hodson, 1942,) reported that the foliage of host basswoods (*Tilia americana*, Tiliaceae) is destroyed by the hispine *Baliosus nervosus*, with the exception of the [foliage] of very tall trees. Ford & Cavey (1985) report larvae of the hispine *Anisostena nigrita* (Olivier) mine blades of *Schizachyrium scoparium* (Poaceae) when the leaves were shaded, but not when exposed to direct sunlight (Cappuccino, 1991a,b; Damman & Cappuccino, 1991). They noted that hispine mines tend to occur in shaded or partially shaded leaves. Ford & Cavey (1985) also observed that, when host plants are located in sun-exposed areas, mines, if any, occur in drooping or lower branches which are more likely to contain shaded leaves. These observations suggest a negative relationship between sunlight exposure and presence of hispine mines.

#### *Biotic factors: host-plant and natural enemies*

Obviously, host plant is a major correlate for the presence (and abundance) of leaf-mining chrysomelids (Table 1). Most leaf-mining chrysomelids have a relatively narrow host-plant range. In species of the galerucine genus *Monoxia*, it appears that most species are narrowly oligophagous, at least as adults. Thousands of host-plant preference studies using clip cages (Fig. 6) holding unexcised leaves of potted composites and chenopods (most reported host plants of the genus) clearly point to adult stenophagy to monophagy. Since over 100 plant genera were used in these studies, and they most likely represented a wide spectrum of leaf structures and chemistries, I hypothesize that both chemistry and surface morphology are important determinants of feeding behavior. Perhaps the best demonstration of this feeding eclecticism on leaf-mining chrysomelids is the case of a possible new species, *Monoxia* near *inornata* Blake. Experimental studies show that, as adults, this gum plant (*Grindelia* spp., Asteraceae) associate feeds on every species of *Grindelia* tested, as well as on several other confamilial species in different tribes of asteraceans (Santiago-Blay, 1990). However, in all the cases, the leaves of the plant species fed upon by *Monoxia* near *inornata*, were relatively coriaceous, glaucous, and of moderate thickness, suggesting that, in this case, gross leaf morphology is related to feeding behavior. The preference for certain leaf thickness is so striking that, with some experience, one can learn to accurately guess, within a taxonomic range, which host plants are likely to be eaten by the adults of this species. In connection with the biocontrol of weeds, Harley (1969) reports that starving adults, not larvae, of *Octotoma scabripennis* and *Uroplata girardi* almost choose not to feed on plants other than their hosts.

*Sceloenopla maculata* (Olivier) is freer to feed on *Cecropia lyratiloba* var. *nana* when the *Azteca* ants (Formicidae), which typically inhabit plants of this genus, do not fully utilize the plants (Andrade, 1984). Leaf-mining chrysomelids have such numerous natural enemies that, in some cases have a significant impact on their populations (see *Natural biological enemies and other mortality factors*, below).

#### *How do plants that are attacked by leaf-mining chrysomelids respond to herbivory?*

In some cases, leaf abscission has been reported in conjunction with severe leaf-mining (West & Lothian, 1948; Inoue & Shinkaji, 1989), but it has been argued that this is simply a generalized response to leaf damage, and not a means to regulate populations of leaf-mining herbivores (Hespenheide, 1991). Some plants form a thin callus, or loose aggregate of parenchyma cells, as a reaction to leaf-mining (Hering, 1951). If the herbivorous attack occurs early in the development of the leaf, serious deformation and leaf asymmetry may follow (Hering, 1951). There are some reports of ‘green islands’ caused by

miners' activities in senescing leaves (Connor & Taverner, 1997; Hespenheide, 1991; Hering, 1951). This possible cytokinin-analogue extends cell growth, hence a source of nourishment, after abscission. At times, mining insects attack fallen leaves and this represents an intermediate between leaf-mining and decomposition (Hering, 1951).

#### *Do leaf-mining chrysomelids attack aquatic plants?*

“There are of course very few aquatic insects that are specialists in feeding on individual species of plants (a caddisfly on a red alga, a midge on a blue green alga, maybe some other midges on [species of] *Potamogeton* [pondweeds, Potamogetonaceae])” (Resh to Santiago-Blay, personal communication, July 2003, bracketed words added by Santiago-Blay; see also Hering, 1951). While no definitive aquatic leaf-mining chrysomelids appear to have been confirmed, there are at least two reports of leaf-mining species on aquatic emergent plants. Gressitt (1960) reports that *Cyperispa thoracostachyi* Gressitt pupates, “at extreme base of larval mines at base of long leaves of large sedges [Cyperaceae], often at or below the surface of water in swamps”. Cox (1996) report of a species of crytonychine hispine, *Callistola* sp. as a miner was a *lapsus* (Cox to Santiago-Blay personal communication, July 2003), he meant *C. thoracostachyi*. Collart (1934), reports that the hispine *Diclidispa viridicyeana* (Kraatz) is associated with the large aquatic grasses of the genus *Vossia*, although he does not indicate where they live with respect to the waterline. Undoubtedly, many other species of leaf-mining chrysomelids feed on emergent plants but it remains to be seen how many, if any, are truly living underwater and how they cope with that environment.

#### *Influence of genetics*

Conspecific populations of chrysomelids have been found to differ on their host-plant feeding preference. Vig (1996) suggests that some of the variation in host-plant feeding preference has a genetic basis. Genetically-influenced changes of host-plant feeding preference may be important in determining the evolutionary history of a lineage of phytophagous organisms.

#### *Spatial and temporal distribution*

The use of chrysomelids, including leaf-mining forms, has been suggested for monitoring local species richness in natural areas (Staines & Staines, 1998).

#### *Spatial distribution*

In a long-term study of Panamanian insects, researchers found that leaf-mining chrysomelids are not equally distributed along an intranational transect of Malaise traps. These leaf-miners, which are not

identified in the source, are most abundant at the highest and wettest station, Cerro Campana (<http://www.stri.org/tesp/Intro%20-%20Insects.htm>), matching well with the seasonality of many organisms in that part of the world (Leigh *et al.*, 1996). Frost (1931), who also studied hispines in Panama, observed that the mines of hispines are scattered on host plants, with one or two mines on a plant.

According to Frost (1931), hispine mines are scattered, “with seldom more than one or two [mines each with one individual] on a single plant”, perhaps because of their low fertility rate (Mariau, 1988). Nevertheless, in species of *Monoxia*, there are several mines on a plant, but just one mine per leaf (Fig. 3). When present, the adults are easy to collect as they are frequently found resting on their host food plant.

There appear to be no published studies of the interaction of leaf-mining chrysomelids and endophytic fungi. However, a splendid case of *Promecotheca papuana* Csiki infected by a fungus is illustrated in Howard *et al.* (2001). Faeth & Hammon (1996) suggest a possible relationship between endophytic fungi and *Cameraria* (Lepidoptera: Gracilariidae) leaf-mining larvae by differentially affecting dispersion and colonization in different host-plants. In addition to the host plant, leaf-mining chrysomelid and parasitoid systems, three trophic interactions involving fungi may prove to be biologically interesting and to be of applied importance for some leaf-mining chrysomelid pests. For instance, Kalshoven (1981) reports that the damage caused in coconut palms by the hispine *Promecotheca soror* is increased by the entry of spores of the fungus *Pestalotiopsis* (*Pestalozzia*). Hering (1951) includes a discussion on heterospecific interactions between leaf-mining insects.

#### *Temporal distribution*

Long-term studies of the oil palm leaf-mining hispine *Coelanomenodera elaedis* Maulik in western Africa have shown sudden shifts from mixed instar populations to synchronized populations of one instar during outbreaks (Bernon & Graves, 1979). For several decades, hispine pests of coconut and oil palms have been studied extensively by Mariau, Lecoustre, and their collaborators. They reported cyclical hispine population changes (Mariau & Morin, 1972), which are tracked by some of their parasitoids (Lecoustre & Reffye, 1984). Modeling the population dynamics, including the potential effects of human intervention (*e.g.*, pesticide applications, pruning, etc.) may help predict and reduce great losses to these hispines (Lecoustre & Reffye, 1984). More cyclically extreme and synchronized population dynamics of chrysomelids have been described by Kovalev (2004). Strogatz (2003) wrote a thought-provoking and fascinating book discussing a multiplicity of systems in which synchronization arises from apparent chaos.

Furthermore, populations of *C. lameensis* Berti

and of *C. minuta* Uhmann are greatly affected by air humidity and food supplies (Mariau & Lecoustre, 2000; Lecoustre & Reffye, 1984). In general, hispines appear to be especially sensitive to humidity and temperature in comparison to other chrysomelids.

Leaf-mining chrysomelids are no different from most other insects in their general life history patterns and voltinism. Also, they have considerable variation in the number of generations with the species and latitude. In temperate zones, leaf-mining chrysomelids are usually univoltine (Hering, 1951). Some cases of bivoltine, such as the galerucine *Monoxia* near *inornata* (referred to as possible new species, Santiago-Blay, 1990) occur in regions with a more moderate climate. *Octotoma scabripennis* and *Uroplata girardi* are trivoltine (Harley, 1969; Cilliers, 1987a). Several generations per year are possible for *Promecotheca caeruleipennis* in Sri Lanka (Dharmadhikari *et al.*, 1977) and up to six for the hispine *Dicladispa armigera* (Sen & Chakravorty, 1970). Some sympatric congeneric species, such as *Argopistes coccinelliformis* and *A. biplagiatus*, differ in their voltinism: the former being a facultative univoltine species (although normally univoltine), the latter an obligatory univoltine (Inoue, 1996).

*Biotic effects on temporal distribution of mining insects.* It seems that many leaf-mining chrysomelids in temperate zones, such as *Dibolia borealis*, *Zeugophora scutellaris*, and *Monoxia* near *inornata*, overwinter in the soil as adults (Needham *et al.*, 1928; Santiago-Blay, unpublished data). There, they are exposed to both abiotic and biotic elements, which can be significant mortality factors (see *Natural biological enemies and other mortality factors*, below). West (1985) documented the negative competitive interaction of oak-browsing lepidopterous larvae on leaf-mining lepidopterans attacking oaks. According to West (1985), browsing larvae are more abundant in the spring, when the nutritional quality of the foliage is higher and, later in the season, when the quality of oak leaves has decreased, the leaf-mining guild is more abundant. Similar multitrophic interactions remain to be discovered for leaf-mining chrysomelids.

### Diapause

There is some variation in the resting stages of leaf-mining chrysomelids. *Argopistes coccinelliformis* and *A. biplagiatus* (Inoue, 1990a; Inoue & Shinkaji, 1989) and many other leaf-mining chrysomelids overwinter as adults. In contrast, *Octotoma scabripennis* and *Uroplata girardi* diapause facultatively as adults (Cilliers, 1987a; Harley, 1969). In these cases, the exact factors involved in diapause are not known. Harvey (1969) speculates that decreased autumn temperatures, shorter photoperiod, and reduced growth rate of the host plant possibly trigger diapause.

Many leaf-mining chrysomelids overwinter-dia-

pause as beetles under debris or in the soil. In species of *Microrhopala*, some overwintering sites have been found near roots about 10 cm under the soil surface (Clark, 1983; Ford & Cavey, 1985; Hodson, 1942; West & Lothian, 1948).

### Defensive behavior and mimicry

It seems that some leaf-mining chrysomelids find mines to be a relatively safe retreat from neighboring predators. For example, Andrade (1984) and Jolivet (1989b) report that leaf-mining species of *Sceloenopla* which feed on Brazilian species of *Cecropia* are protected from aggressive *Azteca* ants. Mines provide an environment with proximity to food and a hideout from some larger predators. However, the mine may prove to be a trap, since it may serve as a *cul-de-sac* from enemies small enough to get in the mine or from interactions with potentially negatively interacting organisms, such as fungi (more on three-trophic interactions in *Spatial distribution*, above).

Many leaf-mining chrysomelids form what appears to be a Müllerian mimicry complex with other beetles, particularly with lycids and lampyrids. The mimicry complexes of chrysomelids have been suspected for a long time (Jolivet, 1989a; Maulik, 1919), and they include species that are leaf-miners and beetles in other coleopterous families. The similarities involve the general body form and coloration patterns and/or the presence/absence of spines (Maulik, 1919). Although the nature of those mimicry complexes has not been experimentally tested, they are believed to be Müllerian (Hespenheide, 1991). However, while the anecdotal reports are interesting and compelling, I have been unable to find experimental evidence for these claims. I know of numerous stories of similarly-colored insects allegedly forming mimicry complexes (*e.g.*, the widespread tropical hispine *Chalepus sanguinicollis* (Linné) and another red and black beetle, the lycid *Thonalmus chevrolati* Bourgeois). Experimental evidence is needed to evaluate all those claims.

### Natural biological enemies and other mortality factors

Like many other leaf-miners, leaf-mining chrysomelids are attacked by numerous parasitoids and other biological natural enemies (Connor & Tavener, 1997). Also, just like any organism, they have to cope with numerous abiotic mortality factors.

### Natural biological enemies

Leaf-mining chrysomelids have many natural biological enemies that regulate their populations. A list and/or discussion of chrysomelid parasitoids can be found in Chittenden (1902), Cox (1994), Fulmek (1962), Gallego *et al.* (1983), Gressitt 1959, Mariau (1975, 1988, 2001), Mariau & Morin (1971, 1974), Teixeira *et al.* (1999), and many others. Santiago-

Blay & Fain (1994) discuss the mite associates of chrysomelids.

*Some observations on general principles involved in controlling leaf-mining chrysomelids by natural biological enemies.* More than 40 years ago, Gressitt noticed a well-documented pattern of insect pests. Many of the most pestiferous leaf-mining chrysomelids, such as several species of *Promecotheca*, “are very scarce on their native hosts under natural jungle conditions, but may become abundant under plantation circumstances or in village areas” (Gressitt, 1959). The fact that parasitoids seem to have broad host preferences, and that they seem to be following the host-plants more than their herbivores, is very useful in biological control.

Parasitoids can use alternative insect hosts when populations of economically important leaf-mining chrysomelids, their usual hosts, are low. For this reason, it is essential to provide alternative cover crops for natural enemies as a source of nectar and shelter (Gallego *et al.*, 1983). In cases of leaf-mining chrysomelids that oviposit into the parenchyma (Lecoustre & Reffye, 1984) and those that cover their epidermally-laid eggs with a theca, parasitoids can penetrate the protective layers and oviposit. Parasitoids seem to be effective in keeping leaf-mining populations at low numbers, including those of oil palm leaf-miners. However, they cannot control rapid outbreaks (Cappucino, 1991; Mariau, 1988), in part because parasitoids tend to have a relatively slow development and life history. The importation of numerous parasitoids has been far from successful, since it seems that they cannot adapt well to conditions outside their native range (Mariau, 1988). In one case, the effect of parasitoids and crawling predators has been experimentally shown to be statistically independent of each other (Memmott *et al.*, 1993). There is still a lot to be learned about natural biological enemies of leaf-mining chrysomelids (Hespenheide & Dang, 1999).

Gressitt (1959) suggests numerous measures for the control of *Promecotheca* pests of palm and cacao plantations in the Pacific Rim, including conservation and mass breeding of natural enemies; destruction of heavily infested host-plants (or their parts, unless parasitoids can be reared and the pests excluded); and periodic censuses that aim to detect early stages of infection. Hespenheide mentions that ‘unusual refuges’, which have been observed in several tropical hispines, may reduce their probability of being parasitized (Hespenheide, 1991).

*Some examples of natural biological enemies of leaf-mining chrysomelids.* In *Monoxia guttulata* Blake, an unidentified tachinid as well as an unidentified parasitic nematode have been detected (Santiago-Blay, unpublished data). Together with abiotic factors, these natural enemies probably contribute significantly to the relatively low population numbers of this species.

Eggs of the alticine *Psylliodes chrysocephala* (Linné) suffer bacterioses and are also attacked by cantharid larvae. Their larvae are parasitized by a variety of hymenopterans, while the pre-pupae and pupae are attacked by carabids as well as various species of nematodes. Adult *P. chrysocephala* are host to fungi (Entomophthorales), gregarine protozoans, and braconids (Grison *et al.*, 1963). *Mantura chrysanthemii* Kowartz, *M. pallidicornis* Waltl, *Phyllotreta nemorum* (Linné), *Sphaeroderma rubidium* Graells (all Alticinae) are attacked by a variety of predatory beetles and/or parasitic wasps, including braconids, chalcids, and ichneumonids (Fulmek, 1962; Grison *et al.*, 1963).

Various species of *Promecotheca* leaf-miners have been controlled by a variety of parasitic hymenopterans in the Pacific Basin (Gressitt, 1959; Dharmadhikari *et al.*, 1977; Taylor, 1937). For example, *P. caeruleipennis* Blanchard and *P. papuana* Csiki have been controlled with *Pediobius parvulus* Ferrari (Eulophidae) and *P. cumingi* by *Dimmnockia javanica* Ferrari (Elasmidae) and, perhaps, by *Achrysocharis promecothecae* Ferrari, (Eulophidae) (Dharmadhikari *et al.*, 1977). The hispines *Coelaenomenodera minuta* and *C. lameensis* Berti and Mariau, both palm leaf-miners, are attacked by several oophagous parasitoids, including *Achrysocharis leptocerus* Waterson (Eulophidae) and *Oligosita longiclavata* Viggiani (Trichogrammatidae), as well as by several larval parasitoids, including *Sympiesis (Dimmnockia) aburiana* Waterson (Eulophidae), *Pediobius setigerus* Kerrich (Eulophidae), *Cotterellia podagrica* Waterson (Eulophidae), and *Closterocerus africanus* Waterson (Eulophidae, perhaps also an egg parasitoid) (Berti & Mariau, 1999). Interestingly, the hispines *Platypria coronata* (Guérin-Méneville) and another palm leaf-miner, *Coelaenomenodera perrieri* Fairmaire, are parasitized by a similar parasitoid complex (Mariau, 1988). African *Balyana* hispines also have numerous hymenopteran parasitoids (Berti & De Chenon, 1987). The larval stages of *D. armigera* suffer about 90% mortality (Sen & Chakravorty, 1970). Together with eggs, these two stages appear to be the most vulnerable in leaf-mining chrysomelids.

The parasite complex of the South American leaf-mining *Hispolepsis* spp. is quite different (Mariau, 1988). Thecae of *Sceloenopla maculata* are attacked by chalcid wasps (Andrade, 1984). Wasp emergence holes, possibly from mymmarids or trichogrammatids have been reported for some undetermined tropical Central American hispine eggs. Pteromalids and chalcids (Hymenoptera) and tachinids (Diptera) have been reported for Central American leaf-mining hispines (Hespenheide, 1991). Additional examples of parasites of leaf-mining chrysomelids can be found in Cappucino (1991a,b), McPheron (1985), and Wheeler & Snook (1986).

#### *Other mortality factors*

Cappucino (1991) studied the mortality factors affecting the hispine *Microrhopala vittata* in south-



central New York State. She discovered that early leaf senescence of its host-plants, *Solidago* spp. (Asteraceae), and its effects on larvae, are partially responsible for the relatively low population densities of beetles. Larval parasitoidism by the eulophid *Chrysonotomyia* spp. is another mortality factor. Exclusion experiments have shown that several Central American species of *Chalepus* suffer significant and independent mortality from both crawling predators, possibly ants, and from parasitoids (Memmott *et al.*, 1993). The coconut leaf-miner, *P. cumingi*, has been reported to be significantly controlled by using several formulations of fungal disease (Dharmadhikari *et al.*, 1977). Damman (1994) discovered that *M. vittata* larvae that eclose in large groups have a greater chance of surviving. However, once in a mine, forming part of a large group decreases adult weight. Mine initiation and larval movement to secondary mines are the most vulnerable stages in the life history of *Microrhopala vittata*.

In addition to the mortality that pathogens and parasitoids cause, host plants of leaf-mining chrysomelids respond to the attack with chemical defenses. According to Zaka-ur-Rab (1991), when *Clitea picta* larvae penetrate the epidermis, “the site of infestation swells a little”, and the host plant, *Aegle marmelos* Correa Serra (Rutaceae), produces exudates on the leaf sites chewed upon by larvae. Resin (a complex mixture of organic chemicals, especially terpenes, insoluble in water) production is a constitutive plant defense against herbivores (Becerra, 2003) and pathogens (Langenheim, 2003; Santiago-Blay *et al.*, 2002). There seems to be no quantitative data on the mortality effect of these defenses.

Another interesting development is the use of plant breeding to control populations of leaf-mining chrysomelids (Zheng *et al.*, 2003). For example, larvae of *Coelaenomenodera lameensis* Berti and Mariau have “great difficulty developing on the hybrid derived from the cross between *E[laeis] guineensis* and *E. oleifera*” (Mariau, 2001).

Many papers, and/or references therein, mention or recommend the use of pesticides to control mining chrysomelids in plantations (*e.g.*, De & Konar, 1954; Dharmadhikari *et al.*, 1977; Hodson, 1942; Zabel *et al.*, 1991). However, Kalshoven (1981) warns that, in the hispine *Promecotheca papuana*, the use of insecticides increases pest populations. I suspect the reason for this observation is the interference of the pesticide with the abundant agents of biological control, mostly parasitic Hymenoptera. In addition, unless systemic pesticides are used, the mining stages of chrysomelids are well protected inside the mines.

### Reproduction

Mating behavior seems to be under more stringent control than feeding behavior. Different species of the flea beetle *Argopistes* (Inoue, 1990a) may mate

before and/or after hibernation. Both *O. scabripennis* and *Uroplata girardi* require more specific feeding and oviposition stimulants (or fewer inhibitors). Hence, fewer plant species are acceptable for feeding and suitable for oviposition (Harley, 1969). For palm mining hispines, Mariau (1988) reports a low fertility rate. However, occasional outbreaks of leaf-mining chrysomelids do occur (*C. minuta* in African oil palms (Mariau, 1988)).

In a study of *Di cladispa armigera*, Sen & Chakravorty (1970) found that beetles may mate for as long as two hours, may mate more than once during a single day, and they are polygamous/polygynous. For *Di cladispa armigera*, the sex ratio is approximately 1:1 and the adults may live for up to two and a half months (Sen & Chakravorty, 1970).

Kirkendall (1984) reported long postcopulatory escorts in *Odontota dorsalis*, and he hypothesized that this behavior has evolved in situations where the probability of encounters between the sexes is high and the cost of reproduction to the female is relatively low. Males that escort females are presumed to have a greater probability of fathering the progeny from the sperm they have introduced into the female. (For oviposition, see *Egg in Introduction to leaf-mining chrysomelids*, above.)

### Evolutionary and biogeography trends

Leaf-mining chrysomelids, like any other specialized organism, represent a unique opportunity to explore the major pathways that evolution may have taken in tailoring a successful mode of life and detailed variations. Some leaf-mining chrysomelids are good subjects to study the possible adaptive radiation of herbivores to their host-plants, as in species of *Monoxia* (Galerucinae) (Santiago-Blay & Virkki, 1996). In addition, several species are economically important (Taylor, 1937; Bernon & Graves, 1979; Mariau, 1988; see *Economic importance*, below). The biology of leaf-mining chrysomelids is quite variable, and I provide selected examples to show the wide range of variation present.

I propose a testable hypothesis that leaf mining in most of the Chrysomelidae arose from ancestors whose larvae were exophytic. However, in the Zeugophorinae, leaf-mining appears to be the retained basal endophytic condition. Figure 13 is a character state transition branching diagram mapped on to a recent chrysomelid phylogeny (Duckett *et al.*, 2004). To simplify this hypothesis, the mapped character, feeding mode (leaf-mining, in this case), is being treated as homologous among the lineages and as having two character states, exo- and endophyty. For a discussion on parsimony, see Johnson (1982). Clearly, this needs not to be the case, at the molecular genetics, morphological, or behavioral levels. Homology should be defined by ancestry and diagnosed by criteria not related to ancestry, such as relative

position, development, histology, etc., as Owen and others said (Kaplan, 1987, 2001; Padian to Santiago-Blay, personal communication, July 2003). Numerous pertinent and fascinating discussions on homology at various levels of the biological hierarchy and in different groups of organisms can be found in Bock & Cardew (1999), Hall (1994), and Scotland & Pennington (2000).

Detailed analyses of what is involved in being 'exo'- or 'endophytic' will probably show that there are multiple genetic, physiological, and morphological mechanisms to attain endophyty, hence, considerable convergence should be expected between those lineages. Note the greater relative abundance of alticine leaf-miners in contrast to the smaller relative abundance of leaf-mining galerucines within the Galerucinae in the 'Trichostomes' (Jacoby) clade. In the 'cassidines' (*sensu* Staines, 2002b, 2004b; Hispines and Cassidines, 'Cryptostomes' (Chapuis)) clade, leaf endophyty may have arisen independently in both the Old and New World, from ancestors with larvae living between appressed leaves. In the scenario depicted in Figure 13, all subfamilies, except Hispinae, had most recent common ancestors with exophytic, usually eruciform larvae. In the Hispinae, particularly those from the Old World, the fairly depressed or onisciform larvae tend to live between appressed leaves of monocotyledonous angiosperms. New World larval hispines have a greater variety of body shapes and host-plant feeding preferences.

#### *Origin and evolution of the leaf-mining habit chrysomelids*

Mines are relatively sealed from the outside, serving as a locale for food and as a relatively buffered shelter, including from UV radiation (Connor & Taverner, 1997). However, these *cul-de-sacs* where leaf-miners live limit the amount of food available (Damman, 1994), area for waste disposal, and escape from predators and parasitoids. As a test of the possible adaptive significance of leaf-mining in the Insecta done by Connor & Taverner (1997), the multiple sister-group comparison method was used to assess whether leaf-mining has resulted in a greater diversification of leaf-mining lineages – a presumed surrogate of adaptive radiation. With the exception of the Lepidoptera, where leaf-mining taxa are exceedingly abundant, all other tested cases of sister taxa with one member being a predominant leaf-miner had the leaf-mining taxon show a mediocre to low species richness. For instance, in the 'Cryptostomes', or the clade formed by almost equally speciose Hispinae and Cassidinae, leaf-mining is ubiquitous in the hispines yet almost absent in the cassidines. This suggests that leaf-mining, as well as leaf-galling for which parallel results have been found, is an evolutionary 'dead-end' for most groups of insects (Connor & Taverner, 1997). However, the

question remains: if leaf-mining is an evolutionary 'dead end', why does it keep appearing in such diverse groups? If the question is reworded to address the homologies related to endophyty, maybe we will find a better explanation.

#### *Distribution of leaf-mining in the Chrysomelidae*

Except for species of *Zeugophora* (Zeugophorinae), where larvae primitively mine leaves and adults feed mostly on members of the Salicaceae (*Populus* spp. and *Salix* spp.), the mining habit seems to have arisen independently several times in the Chrysomelidae, from ancestors feeding externally. Only two species of criocerines have been reported as leaf-miners, hence, proposing generalizations is out of the question. For the criocerines, Vencl & Aiello (1997) hypothesize that endophyty is the basal condition. This is based on the fact that endophyty is present in the hypothesized outgroup of the Chrysomelidae, including the Bruchidae and the Cerambycidae (Crowson, 1981). Endophytous larvae neither produce a larval shield (Vencl to Santiago-Blay, personal communication, May 2003), nor are they covered with a slimy protective mucilage (Crowson, 1981). Larval shields and slimy covers, which are made out of fecal material, are produced only by exophytic larvae. Other presumed defenses of exophytic larvae include living in a hardened case (Clytrinae, Cryptocephalinae, and Chlamisinae), dorsal defensive glands (Chrysomelinae and some Galerucinae), and lateral spines as well as excremental dorsal shields in Cassidinae *sensu antiquo* larvae, among others. By forcing endophytic criocerine larvae that feed on stems to be exophytic, it can be tested whether they can produce a shield. The production of a shield in a normally endophytic larva is considered strong evidence that this endophyty is a recently acquired condition, probably through a reversal from a basal exophytic larva (Fig. 13). Vencl (personal communication to Santiago-Blay, May 2003) has shown that all criocerine stem borers tested produce shields, suggesting that their endophyty is a reversed condition from an exophytic most recent common ancestor. The alternative hypothesis is that the endophytic larvae have retained the basal characteristic and have independently evolved the capacity to produce a larval shield. In criocerines, for example, leaf mining is considered a phylogenetically reversed behavior. Perhaps more species of *Oulema* and of *Lema* are leaf-miners (Jolivet to Santiago-Blay, personal communication, April 2003). Vencl and Aiello, and many others (*e.g.*, Kalshoven, 1957) believe that endophyty, including leaf-mining, is the basal condition for chrysomelids. Schmitt (1988) hypothesized that the mining habit may have been a retained synapomorphy with a distant ancestor in common with the Hispinae but he now considers that view very unlikely (Schmitt to Santiago-Blay, personal communication, April 2003).

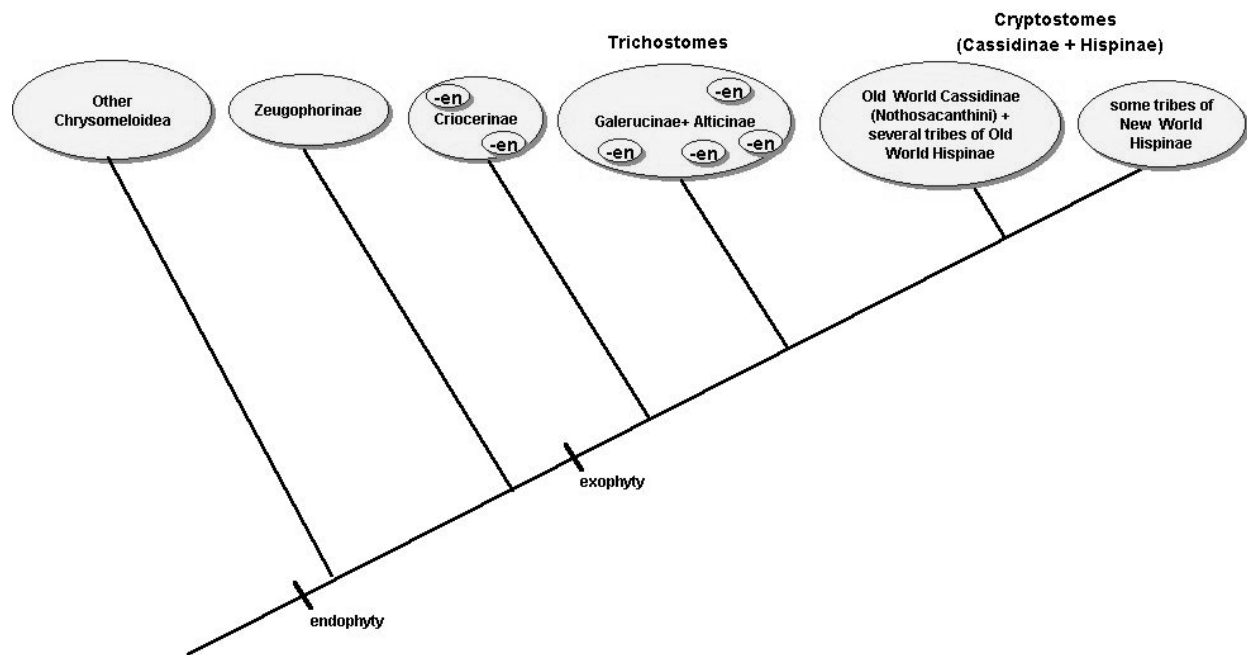


Fig. 13. Character state transitions for subfamilies of the Chrysomelidae containing leaf-mining taxa mapped into a recent phylogeny (data from Duckett *et al.*, 2004). To simplify this hypothesis, the mapped trait, feeding mode, is being treated as a homologous character with two states: exo- and endophyty. The tick mark '—' represents a synapomorphy for the subtended group, in the context of the Chrysomeloidea. A tick mark '—' preceded by '-en', ('en' means endophyty) represents a homoplasy (reversal) for the subtended group, such as tribes in the Cassidinae + Hispinae, etc. The small ovals with an associated '-en' also represent a hypothetical reversal, in this case for a smaller subset, such as a few species in a genus or, less likely, all species in a genus. The number of ovals within the families or group of families is not in exact numerical scale. In the Zeugophorinae, leaf-mining appears to be the retained basal condition. Note the greater relative abundance of alticine leaf-miners, as indicated by the greater number of '-en', in contrast to the smaller relative abundance of leaf-mining galerucines within the Galerucinae + Alticinae clade. In the 'cassidines' (*sensu* Staines 2002b, 2004b, Hispines + Cassidines or Cryptostomes (Chapuis)) clade, leaf endophyty may have arisen independently in both the Old and New World, from ancestors with larvae living between appressed leaves. Tribes of the Cassidinae + Hispinae having leaf-mining genera are parenthesized (and not placed inside small ovals). These include the Callohispidini, Exothispini, Coelaenomenoderini, Promecothecini, Gonophorini, Oncocephalini, Hispini (Old World hispines) and the Prosopodontini, Sceloenoplini, Hispoleptini, Chalepini, Uroplatini (New World hispines). Within the Cassidines, only the Nothosacanthini has leaf mining taxa. The tribes Botryonopini, Anisoderini, Aroidini, Callispini, Leptispini, Eurispini, and Cryptonychini (Old World hispines) and the Cephaloleiini, Hybospini, Arescini, and Alurnini (New World hispines), as well as the remaining tribes of the Cassidines, which are not leaf-miners, are omitted from the figure. While a basal division between Old and New World Cryptostomes has been indicated, this decision simply follows the traditional classification of many authors, including Seeno & Wilcox (1982). I am unaware of a comprehensive phylogeny for the group that would support this or any other global system for the Cryptostomes (Staines to Santiago-Blay, personal communication, June 2003), although there is a classification for part of the group (Borowiec, 1995). The placement of two or more taxa, represented by the smaller ovals, inside one of the larger ovals (more inclusive taxa) does not imply such less inclusive taxa are sister taxa or monophyletic. Details can be found in *Evolutionary and biogeography trends*.

Later in the evolution of Chrysomelidae, leaf-mining appears in one species of *Galerucella* and in many (probably all) species of *Monoxia*, (both genera are placed in the section Schematizites of the Galerucinae; Seeno & Wilcox, 1982). Some of the chenopod-feeding *Monoxia* larvae seem to bore and live in the unopened flower buds or fruits. Several unrelated alticines are leaf-miners and in many of them the congeneric species are not miners. For example, as larvae, most species of *Psylliodes* are root feeders. However, the pestiferous species *P. chrysocephala* feeds on both the petiole and the blade of crucifer leaves and later on the harder parts of the shoots (Grison *et al.*, 1963).

The Hispinae + Cassidinae (or Cassidinae, *sensu lato* of Staines 2002b, 2004b) are divided into four functional feeding groups: free-living leaf feeders,

sheath, appressed, or rolled-leaf feeders, leaf-miners, and stem borers. Frost (1924) suggested that hispine ancestors fed on materials in decay located between the closely appressed leaves. Several species of *Prosopodonta* live between or mine closely appressed leaves (Maulik, 1931.) Likewise, larvae of *Gyllenhaleus* spp., *Cryptonychus* spp., and others, feed on unopened leaf buds of the African and Central American plant genus *Costus* spp. (Costaceae) and on the African plant genus *Amomum* (Zingiberaceae), respectively, penetrating at a later time into the stem (Collart, 1928; Maulik, 1932; Spaeth, 1933; Staines, 2004b). Crowson (1955) believes that two ecological lineages of hispines evolved from ancestors living between closely appressed leaves: one lineage with free living larvae and the other with leaf-miners.

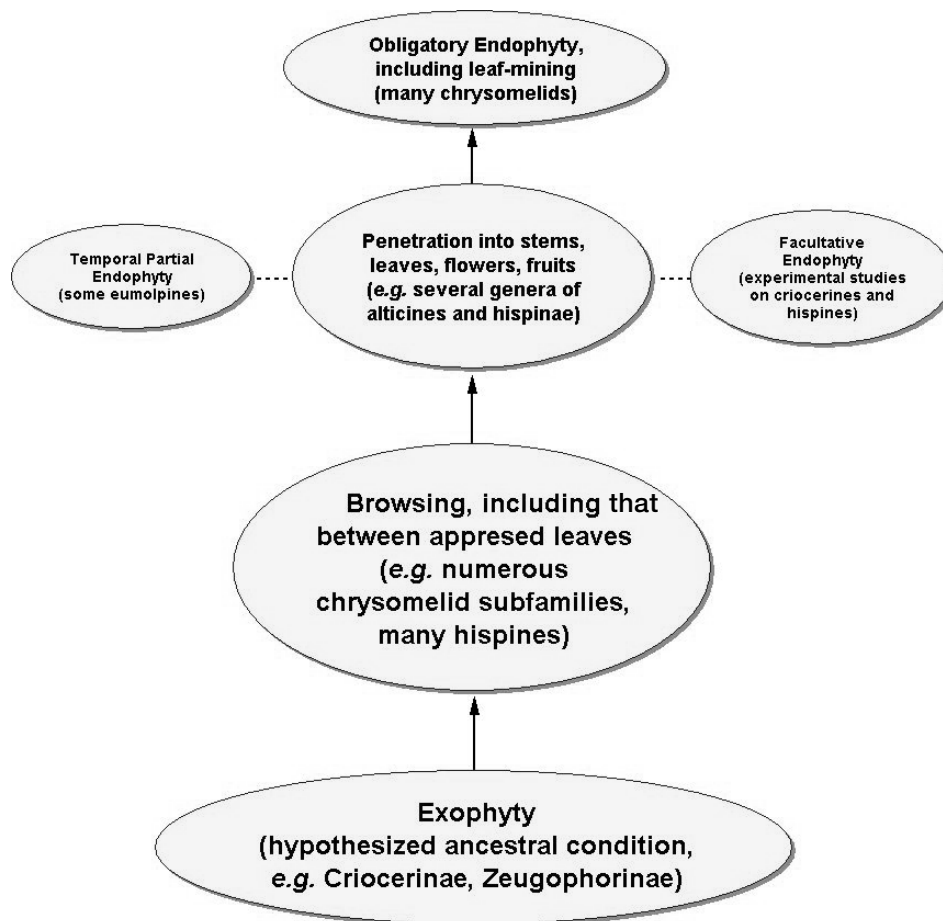


Fig. 14. Hypothetical feeding ecology transitions leading to leaf-mining in the Chrysomelidae, with examples.

*Sceloenopla* *af. bidens* larvae are typically found on shoot-leaf junctions ('axils'), as well as on mining leaves (Costa *et al.*, 1988), suggesting external folioivory as a possible evolutionary pathway to leaf-mining. This is not surprising since Hering (1951) described cases of leaf-mining insects that eat their way through a stem in moving from leaf to leaf. Other insect miners move to non-leafy parts of the shoot. This is because leaves may be too small or atrophied in those plant species for the insects to complete, or even undergo, development (Hering, 1951).

Figure 14 summarizes the hypothetical ecological transitions, from a browsing to an obligatory leaf-mining larva.

#### *Why is leaf-mining absent in most of the Chrysomelidae?*

With exception of hispines, leaf-mining is relatively uncommon in the Chrysomelidae. A rapid perusal of Table 1 shows the tremendous speciosity of leaf-mining hispines in the Indo-Pacific region. These groups need to be studied carefully, including the use of experimental approaches, such as mating experiments which are so commonly done for laboratory-reared *Drosophila* (Diptera), so that their genealogical relatedness, often inferred from diag-

noses based on morphological studies (Rowe, 1988), can be documented. For the time being, I have assumed that the inferences concerning their species status are correct.

Another striking aspect of leaf-mining hispines of the Indo-Pacific region is their speciosity in a few host-plant families (Arecaceae, Pandanaceae, and Zingiberaceae), genera, or species (*c.f.* Table 1). Gressitt (1957, 1963) and Monteith (1970) pointed this out many years ago. Gressitt suggested that speciosity was related to: 1. geographical isolation (allopatric speciation model, Mayr, 1970); 2. low population numbers (low effective population size ( $N_e$ ), random genetic drift, shifting balance and their impact on speciation and evolution, Wright, 1968-1978); 3. changing environment (and possible selection, Darwin, 1859; Fisher, 1999); and 4. ongoing genetic recombination due to rejoining of formerly isolated populations (*e.g.*, New Guinea). Gressitt (1957) noted also that in "many New Guinea insect groups... [there are] one or two widespread forms, with other species differentiated in montane areas".

Hawkeswood & Takizawa (1997) suggest that the colder climate of Australia, not the lack of suitable hosts, is largely responsible for the relative paucity of hispines in Australia compared to neighboring New Guinea. Gressitt (1957) discusses the bioge-

ography of hispines in numerous landmasses of the Pacific Basin. He suggests that because hispines tend toward monophagy and are mediocre flyers, most of their diversity in this region is caused by vicariant instead of dispersal events.

Numerous species of leaf-mining chrysomelids, sometimes congeners, occur sympatrically, even in the same host-plant species (Riley & Enns, 1979). Except for the case of *Odontota mundulus* (Sanderson) and *O. scapularis* (Olivier), there are no observations on how often reproduction isolation is broken down in heterospecifics. In the case of the congeneric species of *Odontota*, Riley & Enns (1979) report mating between *O. mundulus* and *O. scapularis*, but no hybrids that could be recognized externally have been found. The genetic and other biological correlates of these patterns are unknown.

### *Biogeographical patterns*

Leaf-mining chrysomelids are distributed worldwide. At the broadest scale, leaf-mining chrysomelids tend to be more speciose in the tropics, undoubtedly due to the presence of the mostly tropical hispines in those latitudinal ranges, particularly the Oriental biogeographic region (Anand, 1984; Gressitt *et al.*, 1961). This pattern is also followed by leaf-mining Buprestidae (Hespenheide, 1991). Perhaps the only exception to this is the apparent scarcity of leaf-mining forms in australotropical zones, but this may be caused by the lack of extensive surveys of South America and Africa. Evidence that Wilf, Cúneo, and Labandeira are currently garnering suggests that the lineages of Neotropical leaf-miners are ancient, as are the forests upon whose foliage they fed, and that those lineages extend, minimally, to the late Paleocene-Early Eocene (*circa* 55 Ma). In addition, the Neotropical site being explored by them, located in Argentina, is the single deposit with the greatest diversity and number of leaf-mines in the fossil record, with the possible exception of the Dakota Formation (mid Cretaceous,  $\approx$  100 Ma) of Nebraska and Kansas (Labandeira to Santiago-Blay, personal communication, July 2003).

At the scale of the ecosystem, in the discussion of the distribution of leaf-mining buprestids in and Guanacaste (both in Costa Rica, Central America), Hespenheide (1994) suggests that both historic biogeography and recent climatic conditions explain the higher diversity in leaf-miners in the more stable and southern (closer to South America) tropical lowland rainforest, La Selva (Costa Rica), in contrast to the highly seasonal and northern tropical lowland dry forest, Guanacaste, also in Costa Rica.

At the scale of individual plants, Janzen (1968) suggested that host plants are analogous to the real islands of the island biogeography theory. Several studies have discussed biogeographical patterns of mining insects on species of oak (*Quercus*). The species of oak studied were introduced to northern Florida (United States) during the second half of the

19th century. Among the seventeen leaf-mining insect species found, three were beetles, one of which was the hispine, *Baliosus nervosus*. The isolation of small *Quercus* host trees decreased the susceptibility of leaf-mining insects to parasitoidism (Faeth & Simberloff, 1981). However, that decrease was not followed by population increases because on small isolated *Quercus* trees leaf-mining insects are recruited from neighboring host-plants. Although in the studies of Auberbach & Simberloff (1984, 1988) *B. nervosus* was one of the rare taxa, those authors concluded that similar relative diversities of leaf-miners on host plants are partially determined by the presence of taxonomically-related host plants in the neighborhood. Those plants supply both new leaf-mining recruits, as well as natural biological enemies (Faeth & Simberloff, 1981; Faeth *et al.*, 1981). In addition, other factors, such as the biology of the leaf-miner species and abiotic factors, are also important correlates of population abundance and diversity.

After a multi-year study of insects colonizing *Polygonum perfoliatum* Linné, Wheeler & Mengel (1984) concluded that polyphagous insects are the first to colonize a plant that is new to an area. Thereafter, oligophagous insects of taxonomically-related plants colonize the new host-plant. Parasitoids appear to be tracking host plants closer than the insects they parasitize (Auberbach & Simberloff, 1984, 1988; Hespenheide, 1991; *etc.*).

### **Economic importance**

As a group, leaf-mining chrysomelids vary in their economic importance as herbivorous biocontrol agents of weeds or as pests of important crops.

#### *Leaf-mining chrysomelids as agents of weed biocontrol*

The relative success of some chrysomelids in controlling weeds (DeBach & Rosen, 1991; Goeden & Andrés, 1999) has alerted students of this family to the possibility of using host specific leaf-mining chrysomelids to attempt to control some weeds. For example, *Octotoma scabripennis*, *Uroplata girardi*, and a few other hispines have been used successfully for biocontrol of the weed, *Lantana camara* (Verbenaceae) (Cilliers, 1977, 1983, 1987a,b; Harley, 1969; Staines, 1989; Tucker & Singh, 1993; Winder & Harley, 1982; Winder *et al.*, 1984). Although Winder & Harley (1982) gave a relatively low weight to leaf-mining as an attack type on species of *Lantana*, a combination of factors have brought this weed under control in some parts of the world. More recently, Broughton (2000) critically reviewed the literature on the biocontrol of *L. camara* and concluded that the hispine *Uroplata girardi* is the most successful biocontrol agent.

There can be drawbacks to relying on a limited

number of biocontrol agents. In this case, generalist predators, including spiders, predatory heteropterans, neuropteran larvae, and ants attack *U. girardi* and *O. scabripennis* in several parts of the world. Also, low temperatures negatively affect these two biocontrol agents, hence their effectiveness is somewhat reduced because their populations are lowered during the winter. Although a cool-adapted biotype of *U. girardi* has been introduced to Australia, no data appear to be available on their relative establishment success (Broughton, 2000). Consequently, additional efforts have been undertaken to identify multiple host-specific, compatible biocontrol agents of weeds, including herbivores, such as leaf-mining chrysomelids and pathogens (Harley *et al.*, 1995; Gillett *et al.*, 1991; Goeden & Ricker 1974, 1975, 1976a,b,c; Wheeler & Mengel, 1984). Regrettably, the biology of numerous, non-economically important insects remains unknown, even if they are included in studies on their potential economic significance (Goeden & Teerink, 1993).

According to Tucker & Singh (1993), "A number of leaf-mining beetles (Chrysomelidae) have been used successfully in Australia and Hawaii in controlling lantana, *Lantana camara*, and could be introduced into Florida. However, such introductions are frequently delayed or denied by various federal or state committees that must evaluate the risk-benefit picture. There has been some opposition to the introduction of biological control agents due to the fear that the introduced insects or pathogens will attack other plants once their primary food source has been consumed. Also, a weed of economic importance to one may be a desirable plant of value to others. In resolving such conflicts, the economic impact of the weed in croplands must be compared with the negative aspects indicated by those who oppose its control by such introductions."

Many European herbaceous crucifers are attacked by the alticine *Phyllotreta nemorum* Linné in early growth stages. This causes such damage to the plants that they cannot recover at later growth stages (Hering, 1951). However, interest in using *P. nemorum* and other insect herbivores to control cruciferous weeds has continued (Lipa *et al.*, 1977). Sometimes, trees considered 'less desirable', such as *Ostrya virginiana* (Miller) K. Koch., are attacked by *Baliosus nervosus* hispines sparing the more desirable host plant (and ornamental tree) *Tilia americana* of some of its ravages.

In contrast, many leaf-mining chrysomelids have minimal impact on plant populations (Hespenheide, 1991; Hespenheide & Dang, 1999). For example, while at least ten species of *Dibolia* alticines are leaf-miners in Europe, their economic impact seems minimal (Grison *et al.*, 1963). Likewise, a species of *Monoxia*, probably *M. grisea*, was found in densities of up to 100-500 in 3 × 3 × 3-foot plots of *Artemisia tridentata* Nuttall (Asteraceae) plants in 1961 but, "none of the plants that were heavily attacked in 1961 showed adverse effects in 1962". When biological control of weeds is being contemplated,

it is important to consider the effect that biocontrol agents may have on economically-important crops (Hilgendorf & Goeden, 1981).

#### *Leaf-mining chrysomelids as pests*

About a dozen species of leaf-mining chrysomelids, particularly hispines (Anand, 1984; Maulik, 1919), are very important economically. The damage they inflict consists mainly of eating away leaf tissue. In the case of rice, two species of leaf-mining hispines have been implicated in the transmission of a phytopathogenic virus. The cultivars affected and their pestiferous leaf-mining chrysomelids are briefly discussed below.

#### *Palms (Arecaceae)*

In some cases, attack by leaf-miners is devastating to the host-plants, such as oil palms, *Elaeis guineensis*, and coconut palms, *Cocos nucifera* (Bernon & Graves, 1979; Dharmadhikari *et al.*, 1977; Mariau, 1988). For instance, the sometimes cyclical outbreaks of *Coelaenomenodera elaeidis* Maulik and of numerous other palm hispines reduce foliage and oil production of the oil palm, *Elaeis guineensis* (Bernon & Graves, 1979; Lecoustre *et al.*, 1980) and of the coconut palm, *Cocos nucifera* Linné (Howard *et al.*, 2001; Mariau, 2001, 2004). Lepesme (1948) and Howard *et al.* (2001) review insects on palms worldwide.

Foreign exploration-importation efforts have taken place to control pestiferous leaf-mining chrysomelids (Cochereau, 1972). Two relatively successful cases are the control of the coconut leaf-mining hispines, *Promecotheca* spp. and *Brontispa longissima* Gestro. In both these cases, imported eulophids have contributed to the relative success of the foreign importation of natural biological control agents (Cochereau, 1972). Biological control of *Coelaenomenodera elaeidis* was attempted in West Africa by introducing a Malagasy larval parasitoid (*Chrysonotomyia* sp.) of a congeneric hispine. These efforts failed to control hispine populations in the wild since it appears that the parasitoid could not adapt to the fact that *C. elaeidis* larvae die right after being parasitized, reducing the availability as a food source for the internally developing parasitoid larvae (Mariau, 1988). Similar relative failure stories in long term biological control hold true for several species of *Promecotheca* spp. and for *Hispolepsis subfasciata* (Mariau, 1988).

Augmentation of native parasitoids has also been considered to control *C. elaeidis*. It has been noted that *C. elaeidis* and another hispine, *Platypria coronata*, a leaf-miner of a legume cover crop in oil palm plantations, share some parasitoids (Bernon & Graves, 1979). Perhaps one of the best-known cases of biological control is that involving the control of *Promecotheca caerulipennis* by the mite *Pyemotes ventricosus* (Newport) in Fiji (Taylor, 1937). Other cases of mite-chrysomelid associations are summarized in Santiago-Blay & Fain (1994).

*Rice, Oryza sp. (Poaceae)*

*Dicladispa armigera* (Olivier) is a pest of rice (Rawat & Singh, 1980; Razzaque & Kari, 1989; Sen & Chakravorty, 1970) and can cause severe damage to this crop. Several species of hispines, including *Dicladispa* sp., *Trichispa sericea* Guérin-Méneville, and the exophytic galerucine *Sesselia pussila* (Gerstaecker) are vectors of the rice yellow mottle virus (RYMV) in Africa (Banwo *et al.*, 2001a,b). Other chrysomelids reported as vectoring viruses are listed in Crowson (1981).

*Soybean, Glycine max Linné (Leguminosae)*

The leaf-mining hispines, *Odontota horni* and *Baliosus nervosus*, have been suggested as potential pests of soybean, *Glycine max*, particularly if they are present in conjunction with other crop pests (Buntin & Pedigo, 1982; McPherson & Ravlin, 1983; Wheeler & Stimmel, 1983). A multiherbivore attack, including a major pest, such as the leaf-mining dipteran *Liriomyza trifolii* (Burgess), and unnamed chrysomelids, can exacerbate risks of yield reductions (*e.g.*, *Phaseolus vulgaris* Linné in Cuba, Heyer *et al.*, 1989).

*Other cultivars*

Adult alticines, such as *Sphaeroderma rubidum*, have been reported as a pest of artichoke (*Cynara cardunculus* Linné) in the western Mediterranean basin (Grison *et al.*, 1963). *Chaetocnema tibialis* Illiger, a flea beetle, is a pest of sugar beets in some parts of Europe (Zabel *et al.*, 1991). Major infestations of *Citrus* spp. by alticine, *Throscoryssa citri*, larvae may cause severe defoliations (Zaka-ur-Rab, 1991). Several species of *Dactylispa* hispines are considered pestiferous in cichona (probably *Cinchona officinales* Linné, Rubiaceae), kapok (probably *Ceiba* sp., Bombacaceae), coffee (*Coffea arabica*, Rubiaceae), and maize (*Zea mays*, Poaceae) in southeastern Asia and eastern Africa (An *et al.*, 1985; De & Konar, 1954).

*Ornamental trees*

The hispine *Odontota dorsalis* has been reported to be a major pest of *Tilia americana* trees in Washington, DC (Chittenden, 1902). At that time, chemical control measures, some of which would be considered unacceptable by today's standards, were recommended. *Odontota dorsalis* attacks on *Robinia pseudoacacia* are so severe that, "leaves are turned brown as if scorched by fire" (Needham *et al.*, 1928). Numerous hispines attack palms, many of which are becoming widespread because they are used as ornamental trees. Some palms have become invasive (Svenning, 2002) and there is no research yet on how their leaf-mining complex would change as they are introduced into new localities.

**Collecting and rearing leaf-mining chrysomelids**

As long as the host plants are known, the ease of collection and rearing of leaf-mining insects, while in the mines, has been repeatedly noted (*e.g.*, Ford & Cavey, 1985; Hespenheide, 1991; Hering, 1951; Kato, 1991; Lee & Furth, 2000). However, at times, it is difficult to find adults or mines in large numbers. As collecting, rearing, and associating life stages are achieved, future studies on leaf-mining chrysomelids should concentrate on answering some potentially interesting ecological and evolutionary questions.

If there is a lack of environmentally-controlled facilities, plant cuttings can simply be placed in a container (*e.g.*, a plastic bag containing a piece of wet cotton suffices, provided with regular air circulation, or a tightly sealed wire mesh) away from direct sunlight and low temperatures (Gressitt, 1959). Placing cuttings in a container with water or transplanting whole plants, while keeping everything in enclosures, is another easy method to rear leaf-mining insects. Sealed containers (bags, cups) with adequate ventilation not only allow collection of the emerging adults but also of parasitoids. See Ford & Cavey (1985) for additional details.

Mass-rearing of leaf-mining chrysomelids and of their natural enemies has been improved by 'experimental minology', the use of 'artificial mines' (Gallego *et al.*, 1983; Hering, 1951). This technique has been used for at least a century (Hering, 1951) by many, including by Mariau in Africa. Artificial mines are created by inserting a long and thin object, such as a needle or knife, inside a leaf, and forming a cavity that mimics a mine. Some species, such as the hispine *Promecotheca cumingii* seem to accept these human-created dwellings. However, the authors admit that "constant practice is needed to perfect the procedure".

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personal communication, June 2003). However, I have decided to “keep to an imperfect solution” and hope that more additions and corrections can be made to this work by other workers.

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*Table 1.* Taxa, geographical distribution, host plants (arranged alphabetically by family), and selected references of leaf-mining Chrysomelidae of the world. This list is not exhaustive. Host plant data for most chrysomelids, particularly for larvae, are not known.

Scientific names and authors of species are given as completely and updated as I could. In all cases, an effort was made to find the most up-to-date name for each taxon by using revisionary works and catalogues (e.g., Uhmman, 1957, 1958b, 1964). To save space, I have omitted subgeneric and subspecific ranks. Schmitt *et al.* (1998) was used to complete the information for authors of chrysomelid names. Except for hispines, the scientific names of leaf beetles are listed alphabetically, by genus, within subfamily in order to facilitate location for non-specialists. In the Hispinae, genera are listed with tribes, for each the Old and the New World. In numerous cases, data are given only for genera ('Genus' sp.) as I was unable to find more detailed data. Members of the Orsodacninae and the Aulacoscelinae are not included as there are no records of them as leaf miners (Jolivet & Hawkeswood, 1995; Jolivet to Santiago-Blay, personal communications, April 2003). Beetle and plant synonymies have been omitted to save time and space. Blackwelder (1982) and numerous other works were used to update names and geographical distribution. The geographical distribution given is the maximum reported in references found, however, this may vary depending on host plant distribution. As much as possible, I have used the modern names for the geographical regions of the world, particularly for those in the Pacific Region, all extracted from the web. Gressitt *et al.* (1961), as well as the website, <http://www.infoplease.com/countries.html>, proved very useful for that task. Staines (2003b) provides coordinates for some of those islands or archipelagos. Bailey (1976); Brummitt & Powell (1992); Everett (1980); Greuter *et al.* (2000); Germplasm Resources Information Network (GRIN) Taxonomy (Agricultural Research Service, United States Department of Agriculture) <http://www.ars-grin.gov/npgs/tax>; Halladay & Beadle (1983); Harvard University (1968); Heywood *et al.* (1964, 1968, 1972, 1976, 1980); IPNI (International Plant Names Index)<sup>1</sup> <http://www.uk.ipni.org/index.html> or <http://www.us.ipni.org/index.html>; Krüssmann (1984); Mabblerly (1987); Munz & Keck (1973); Quattrocchi (1999); Plant Names (Australian National Botanical Gardens) <http://www.anbg.gov.au/anbg/names.html>; Plants Database (United States Department of Agriculture, Natural Resources Conservation Service) [http://plants.usda.gov/cgi\\_bin/topics.cgi](http://plants.usda.gov/cgi_bin/topics.cgi); The Trustees (1993), and Tropicos (Missouri Botanical Garden, St Louis, MO) <http://mobot.mobot.org/W3T/search/vast.html>; were used to complete or correct nomenclatural (including authorship) information for host plants. However, in several cases, there are different views about the nomenclatural status of insect and/or plant names. I was unable to find the author(s) of thirteen plant scientific names; those names have been noted with the phrase 'unable to find name'. As much as possible, host plants listed are those of the larvae but, when stated by the authors, I have annotated the host-feeding stage association. In those cases, the notation 'larvae' (implying that the adult also feeds on that host plant) or 'adult' has been added next to the host plant, if the source makes such difference. If not stated, I have assumed (and recommend readers to do the same) that host plant records are, as far as known, for adults. In the case of several alticine genera (e.g., *Epitrix*, *Phyllotreta*) and of some hispine genera (e.g., *Plesispa* in the tribe Cryptonychini), it appears that some of the species can, on occasion, be leaf-miners and I have, very reluctantly, included them in Table 1. However, I have not distinguished the host plants where these insects mined from those where larvae are exophytous. Further studies will clarify many of those records. In cases where less species specific statements are made, such as "name of the taxon" are leaf miners', I have entered a taxon as a leaf miner if references on other congeners have pointed out the leaf mining habit, except for the hispines where it appears that it is relatively safe to assume leaf-mining for all genera in the tribes Prosopodontini, Sceloenoplinae, Hispoptini, Chalepini, Uroplatini (New World hispines), as well as Callohispanini, Exothispini, Coelaenomenoderini, Promecothechini, Gonophorini, Oncocephalini, Hispini (Old World hispines) (Seeno & Wilcox, 1982). The Old World hispine tribe Cryptonychini has been omitted as their larvae feed on leaf buds, they are only temporary herbivores on the buds, and the larger larval instars live on stems. Actually, many hispines, such as the species in the tribes Oediopalpini, Cephaloleiini, Hybosispini, Arescini, and Alurnini (of the New World Hispinae) and Botryonopini, Anisoderini, Aroidini, Callispini, Leptispini, and Eurispini (of the Old World Hispinae) are not leaf-miners. Many of those non leaf-mining hispines live between the appressed or in rolled leaves of their host plants (Maulik 1933a, b), thus, they are not included in this table. Other hispines, such as species of *Estigmene* (Maulik, 1932), *Lasiochila* and others, bore the internodes of bamboos (Kalshoven, 1957), and they are not listed. Numerous other suspected leaf-miners have been excluded because I have been unable to find published host plant association data. The suffix '-ceae' is used for plant families, as in Apiaceae (= Umbelliferae), Arecaceae (= Palmae), Asteraceae (= Compositae), Brassicaceae (= Cruciferae), Lamiaceae (= Labiatae), and Poaceae (= Gramineae). I have retained the use of Leguminosae, instead of using the names Caesalpiniaceae, Fabaceae, and Mimosaceae. Some hispine and host plant data are given only to genera. Common names are avoided as much as possible, but, if listed, they appear in quotation marks, and I have given the best approximation of a scientific name possible. It is important to recall that, in general, host plant ranges of adults are broader than those of larvae. Some illustrations (= illustr.) of adults, and/or immature stages, and/or feeding damage are noted. A detailed analysis of the data is in progress.

Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<b>ZEUGOPHORINAE</b>					
<i>Zeugophora abnormis</i> (LeConte)	Canada, United States	<i>Populus alba</i> Linné (Salicaceae)			Frost 1924, Needham <i>et al.</i> 1928
<i>Z. andrewesi</i> Jacoby	India	<i>Santalum album</i> Linné (Santalaceae)			Jolivet 1977, Jolivet to Santiago-Blay (pers. comm., June 2003)
<i>Z. annulata</i> (Baly)	eastern Asia, Japan	<i>Euonymus sieboldiana</i> Blume, <i>Euonymus</i> sp., <i>Tripterygium</i> sp. (Celastraceae)			Jolivet 1977, Lee 1990 (illustr.), Medvedev and Zaitzev 1978 (illustr.), Nakane 1955 (illustr.)
<i>Z. atra</i> Fall	Canada, United States	<i>Populus</i> sp. (Salicaceae)			Balsbaugh and Hays 1972, Wilcox, no date, a (illustr.)
<i>Z. consanguinea</i> Crotch	central to eastern United States	<i>Populus</i> sp. (Salicaceae)			Needham <i>et al.</i> 1928, Wilcox, no date, a (illustr.)
<i>Z. flavicollis</i> (Marsham)	Europe, Great Britain, Asia	<i>Populus alba</i> Linné, <i>P. canadensis</i> Michaux, <i>P. deltoides</i> Marshall (larvae), <i>P. nigra</i> Linné (larvae), <i>P. tremula</i> Linné, <i>P. virginiana</i> Linné (larvae), <i>Populus</i> sp., <i>Salix</i> sp. (several species mentioned by Buhr 1955, 1956, all larvae)			Buhr 1955, 1956; Cox 1996 (illustr.); Hering 1957; Kaszab 1962 (illustr.); Jolivet 1948; Medvedev and Zaitzev 1978; Maček 1986; Pagony 1993 (illustr.); Pál and József 1977; Surányi 1942; Szontagh 1982; Szontagh and Tóth 1977 (illustr.)
<i>Z. puberula</i> Crotch	central to eastern United States	<i>Populus tremuloides</i> Michaux, <i>Populus</i> sp., <i>Salix</i> sp. (Salicaceae)			Clark 2000; Needham <i>et al.</i> 1928; Wilcox, no date, a (illustr.)
<i>Z. scutellaris</i> Suffrian	United States, central Europe, Siberia, Asia	<i>Populus acuminata</i> Rydberg, <i>P. alba</i> Linné, <i>P. deltoides</i> Marshall, <i>P. grandidentata</i> Michaux, <i>P. nigra</i> Linné, <i>Populus</i> sp., <i>Salix</i> sp. (several species mentioned by Buhr 1955, all larvae, Salicaceae)			Böving and Craighead 1931 (illustr.); Buhr 1955; Cavey 1994; Csiki 1900; Erdős 1935; Hering 1957; Jolivet 1948; Kaszab 1962; Koch 1992; Lawson 1991 (illustr.); Lopatin 1984; Medvedev and Zaitzev 1978 (illustr.); Needham <i>et al.</i> 1928 (illustr.); Riley and Enns 1979; Steinhausen 1978 (illustr.); Wilcox, no date, a (illustr.)
<i>Z. subspinoso</i> Fabricius	Canada, United States, Europe, Great Britain, Asia	<i>Corylus avellana</i> Linné, <i>Corylus</i> sp. (Betulaceae), <i>Populus alba</i> Linné, <i>P. nigra</i> Linné, <i>P. tremula</i> Linné, <i>Populus</i> sp., <i>Salix</i> sp. (several species mentioned by Buhr 1955, all larvae) Salicaceae			Buhr 1955, Csiki 1900, Grandi 1959 (illustr.), Hering 1957, Jolivet 1948, Kaszab 1962, Medvedev and Zaitzev 1978, Steinhausen 1966
<i>Z. turneri</i> Power	central Europe, especially in mountains, Great Britain	<i>Betula verrucosa</i> Ehrhart (Betulaceae), <i>Populus tremula</i> Linné, <i>P. nigra</i> Linné, <i>Populus</i> spp. (Salicaceae)			Hering 1957, Jolivet to Santiago-Blay (pers. comm., June 2003)
<i>Z. varians</i> Crotch	United States	<i>Populus</i> sp. (Salicaceae)			Needham <i>et al.</i> 1928
<i>Zeugophora vitinea</i> (Oke)	Australia	'climbing vines', possibly species in the Celastraceae or Sapindaceae			Reid 1989
<i>Zeugophora</i> sp. Both subgenera ( <i>Zeugophora</i> and <i>Pedrillia</i> ) herein included.	Old World (mostly tropics) including east Africa, Madagascar, India, China, and Japan	<i>Betula</i> sp., <i>Corylus</i> sp. (Betulaceae), <i>Euonymus</i> sp., <i>Tripterygium</i> sp. (Celastraceae), <i>Juglans</i> sp. (Juglandaceae), <i>Populus</i> spp., <i>Salix</i> spp. (Salicaceae), <i>Santalum</i> sp. (Santalaceae)			Jolivet 1977, Jolivet and Hawkeswood 1995
<b>CRIOCERINAE</b>					
<i>Lema (Neolema) quadrivittata</i> Boheman	Argentina	Commelinaceae			Monrós '1959' (1960)
<i>Oulema pumila</i> Vencel and Aiello	central Panamá	<i>Peperomia</i> sp. (Piperaceae)			Vencel and Aiello (1997) (illustr.)
<b>GALERUCINAE<sup>2</sup></b>					
<i>Galerucella pusilla</i> (Duftschmidt)	Europe, Great Britain	<i>Lythrum</i> sp. (Lythraceae)			Cox 1996 (illustr.); Hering 1951, 1957 (illustr.)
<i>Monoxia<sup>3</sup> angularis</i> (LeConte)	western North America	<i>Atriplex</i> sp., <i>Beta vulgaris</i> Linné, <i>Chenopodium album</i> Linné, <i>Chenopodium</i> sp. (Chenopodiaceae)			Blake 1939 (illustr.)

<i>M. apicalis</i> Blake	southwestern United States	Chenopodiaceae	Blake 1939 (illustr.), Santiago-Blay and Virkki 1996
<i>M. batisia</i> Blatchley	southeastern United States	<i>Batis maritima</i> Linné (Bataceae)	Blake 1939 (illustr.)
<i>M. beebei</i> Blake	Santa Inez Island, Gulf of California, Mexico	<i>Atriplex barclayana</i> (Bentham) D. Dietrich (Chenopodiaceae) or <i>Amaranthus watsonii</i> Standley (Amaranthaceae)	Blake 1937 (illustr.), 1939 (illustr.)
<i>M. brisleyi</i> Blake	southwestern United States	<i>Atriplex semibaccata</i> R. Brown, <i>Chenopodium album</i> Linné (larvae) Chenopodiaceae, 'a wild desert plant'	Blake 1939 (illustr.)
<i>M. consputa</i> (LeConte)	western United States	<i>Chrysothamnus nauseosus</i> (Pallas ex Pursh) Britton <i>Grindelia</i> sp. (Asteraceae) larvae, <i>Atriplex</i> sp. (Chenopodiaceae) larvae; <i>Quercus</i> sp. (Fagaceae), 'ground cherry', 'ground nut', 'gum', 'Gipsey flower', 'hackberry'	Blake 1939 (illustr.); Böving 1929 (illustr.); Böving and Craighead 1931 (illustr.); Essig 1958; Needham <i>et al.</i> 1928
<i>M. debilis</i> LeConte	southwestern United States	<i>Beta vulgaris</i> Linné, <i>Chenopodium album</i> Linné (Chenopodiaceae), <i>Populus</i> sp. (Salicaceae)	Blake 1939 (illustr.), Cooley 1916
<i>M. elegans</i> Blake	western United States	<i>Atriplex canescens</i> (Pursh) Nutall, <i>Beta vulgaris</i> Linné, <i>Chenopodium</i> sp. (Chenopodiaceae), <i>Sorghum bicolor</i> (Linné) Moench (Poaceae)	Blake 1939 (illustr.)
<i>M. grisea</i> Blake	western Canada and United States	<i>Artemisia tridentata</i> Nuttall, <i>Artemisia</i> sp., <i>Solidago</i> sp. (Asteraceae)	Banham 1962, Blake 1939 (illustr.), Halford <i>et al.</i> 1973
<i>M. guttulata</i> (LeConte)	western United States	<i>Artemisia douglasiana</i> Besser larvae, <i>Artemisia</i> sp. (Asteraceae)	Blake 1939 (illustr.), Santiago-Blay (unpl. data), Santiago-Blay and Virkki 1996
<i>M. inornata</i> Blake	western United States	<i>Grindelia squarrosa</i> (Pursh) Dunal, <i>Grindelia</i> sp., <i>Solidago</i> sp. (Asteraceae)	Blake 1939 (illustr.), Kirk and Balsbaugh 1971
<i>Monoxia</i> sp.(near <i>M. inornata</i> Blake)	United States	<i>Grindelia humilis</i> Hooker and Arnold (Asteraceae)	Blake 1939 (illustr.), Halford <i>et al.</i> 1973, Santiago-Blay 1990, Santiago-Blay (unpl. data)
<i>M. minuta</i> Blake	southwestern United States and northern Mexico	<i>Chrysothamnus</i> sp. (Asteraceae)	Blake 1939 (illustr.)
<i>M. obesula</i> Blake	United States	<i>Atriplex</i> sp. (Chenopodiaceae) larvae, <i>Chenopodium</i> sp.	Blake 1939 (illustr.), Cavey to Santiago-Blay (pers. comm., circa 1990's), Santiago-Blay (unpl. data)
<i>M. obtusa</i> Blake	northern Mexico, Baja California, islands in Gulf of California (Mexico)	<i>Atriplex</i> sp. (Chenopodiaceae)	Blake 1939 (illustr.), Fall 1927
<i>M. pallida</i> Blake	western United States	<i>Beta vulgaris</i> Linné, <i>Chenopodium</i> sp. larvae (Chenopodiaceae), <i>Medicago sativa</i> Linné (Leguminosae)	Blake 1939 (illustr.), Cranshaw <i>et al.</i> 1990, Kondratieff to Santiago-Blay (pers. comm., circa 1990's), Lawson 1991 (illustr.)
<i>M. puberula</i> Blake	western United States	<i>Lepidium alyssoides</i> A. Gray (Brassicaceae), <i>Atriplex confertifolia</i> (Torrey) S. Wats (larvae), <i>Gutierrezia sarothrae</i> (Pursh) Britton and Rusby, <i>Gutierrezia</i> sp. (Chenopodiaceae)	Blake 1939 (illustr.), Hatch 1971, Santiago-Blay (unpl. data), Santiago-Blay and Virkki 1996
<i>M. schizonycha</i> Blake	western United States	<i>Chrysothamnus</i> sp. (Asteraceae), <i>Beta vulgaris</i> Linné (Chenopodiaceae)	Blake 1939 (illustr.)
<i>M. semifasciata</i> Jacoby	Guatemala, Nicaragua	Unknown	Maes 1998
<i>M. sordida</i> (LeConte)	western United States and Baja California (Mexico)	<i>Artemisia</i> sp., <i>Gutierrezia sarothrae</i> (Pursh) Britton and Rusby, <i>Iva axillaris</i> Pursh (Asteraceae),	Blake 1939 (illustr.), Hatch 1971, Smith 1930, Santiago-Blay (unpl. data)



Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<i>Monoxia</i> nr. <i>sordida</i>	southwestern United States	<i>Atriplex confertifolia</i> (Torrey) S. Wats, <i>Beta vulgaris</i> Linné, <i>Chenopodium</i> sp. (Chenopodiaceae), <i>Lycium pallidum</i> Miers (Solanaceae) <i>Prosopis</i> sp. (Leguminosae)			Ward <i>et al.</i> 1977
<b>ALTICINAE<sup>2</sup></b>					
<i>Aphthona cyparissae</i> Koch	Europe	<i>Euphorbia</i> sp. (Euphorbiaceae)			Grandi 1959, Kaszab 1962
<i>A. nigrilabris</i> Duvivier	India, China	<i>Euphorbia hirta</i> Linné, <i>E. hypericifolia</i> Linné (Euphorbiaceae)			Chen 1934, Zaka-ur-Rab 1991
<i>Apteropeda bellidiastrum</i> (Linné)	Europe, Great Britain	Lamiaceae			Hering 1957
<i>A. globosa</i> Illiger	Europe, Great Britain	<i>Ajuga</i> sp., <i>Galeobdolon</i> sp., <i>Lamium</i> sp., <i>Prunella</i> sp., <i>Stachys</i> sp., <i>Teucrium</i> sp. (Lamiaceae), <i>Veronica</i> sp. (Scrophulariaceae)			Hering 1957, Koch 1992
<i>A. nigritarsis</i> Gebler	eastern Europe	<i>Anemone</i> sp. (Ranunculaceae)			Hering 1957
<i>A. orbiculata</i> Marsham	Europe, Great Britain	<i>Aster</i> sp., <i>Bellis perennis</i> Linné, <i>Bellis</i> sp., <i>Centaurea nigra</i> Linné, <i>Cirsium</i> sp. (Asteraceae), <i>Ajuga reptans</i> Linné, <i>Ajuga</i> sp., <i>Galeopsis</i> sp., <i>Lamium</i> sp., <i>Prunella</i> sp., <i>Satureja</i> sp., <i>Stachys</i> sp., <i>Teucrium scorodonia</i> Linné, <i>Teucrium</i> sp. (Lamiaceae), <i>Circaea</i> sp. (Onagraceae), <i>Plantago lanceolata</i> Linné, <i>Plantago</i> sp. (Plantaginaceae), <i>Primula</i> sp. (Primulaceae), <i>Saxifraga granulata</i> Linné (larvae) (Saxifragaceae), <i>Digitalis purpurea</i> Linné, <i>Digitalis</i> sp., <i>Kickxia</i> sp., <i>Linaria</i> sp., <i>Pedicularis</i> sp., <i>Rhinanthus glaber</i> Lamarck (larvae), <i>R. graminis</i> unable to find name, <i>Rhinanthus</i> sp., <i>Scrophularia</i> sp., <i>Sibthorpia</i> sp., <i>Verbascum</i> sp., <i>Veronica</i> sp. (Scrophulariaceae)			Buhr 1955, 1956; Hering 1957; Kaszab 1962 (illustr.); Koch 1992; Surányi 1942; Teixeira <i>et al.</i> 1999
<i>A. splendida</i> Alluaud	Europe, Great Britain	<i>Ajuga chamaepitys</i> (Linné) Schreber, <i>Ajuga</i> sp., <i>Veronica</i> sp. (Lamiaceae), <i>Plantago</i> sp. (Plantaginaceae)			Hering 1957, Koch 1992
<i>Apteropeda</i> sp.	Europe, north Africa	<i>Bellis</i> sp., <i>Solidago</i> sp. (Asteraceae), <i>Ajuga</i> sp., <i>Origanum</i> sp., <i>Prunella</i> sp. (Lamiaceae), <i>Plantago</i> sp. (Plantaginaceae), <i>Primula</i> sp. (Primulaceae), <i>Saxifraga</i> sp. (Saxifragaceae), <i>Digitalis</i> sp., <i>Rhinanthus</i> sp., <i>Veronica</i> sp. (Scrophulariaceae)			Buhr 1956; Hering 1951 (illustr.), 1957; Jolivet and Hawkeswood 1995; Konstantinov and Vandenberg 1996
<i>Argopistes biplagiatus</i> Motschulsky	eastern Siberia, Korea, Japan, China	<i>Fraxinus japonica</i> Blume, <i>F. mandshurica</i> Ruprecht var. <i>japonica</i> Maximowicz, <i>Ligustrum japonicum</i> Thunberg, <i>L. lucidum</i> W. T. Aiton, <i>L. obtusifolium</i> Siebold and Zuccarini, <i>L. ovalifolium</i> Hasskarl, <i>Osmanthus fragans</i> (Thunberg) Loureiro, <i>O. heterophyllus</i> (G. Don) P. S. Green, <i>Osmanthus x fortunei</i> Carr, <i>O. ilicifolius</i> (Hasskarl) Mouille, <i>Syringa reticulata</i> (Blume) H. Hara, <i>S. vulgaris</i> Linné (Oleaceae)			Chen 1934; Gressitt 1963; Inoue 1990a, 1990b, 1996; Lee 1992

<i>A. coccinelliformis</i> Csiki	Korea, Japan, Ryukyu Islands (Japan), Taiwan, southeastern Asia, Micronesia	<i>Ligustrum japonicum</i> Thunberg, <i>Osmanthus heterophyllus</i> (G. Don) P. S. Green, <i>Osmanthus x fortunei</i> Carr (Oleaceae)	Inoue and Shinkaji 1989; Inoue 1990a, 1990b, 1996; Lee 1992; Samuelson 1973
<i>Argopus ahrensi</i> Germar	southern and central Europe	<i>Clematis flammula</i> Linné, <i>C. maritima</i> Linné, <i>C. recta</i> Linné, <i>C. vitalba</i> Linné, <i>Clematis</i> sp. (Ranunculaceae)	Grison <i>et al.</i> 1963, Hering 1957, Kaszab 1962, Koch 1992, Lee and Furth 2000
<i>Argopus</i> sp.	Old World	<i>Cirsium</i> sp., <i>Cynara</i> sp. (Asteraceae), <i>Euphorbia</i> sp. (Euphorbiaceae), <i>Quercus</i> sp. (Fagaceae), <i>Phytolacca</i> sp. (Phytolaccaceae), <i>Clematis</i> sp., <i>Pulsatilla</i> sp., <i>Ranunculus</i> sp., <i>Trollius</i> sp. (Ranunculaceae), <i>Citrus</i> sp. (Rutaceae)	Jolivet and Hawkeswood 1995
<i>Chaetocnema aridula</i> (Gyllenhall)	Europe, Asia	Poaceae	Cox 1996, Kaszab 1962, Koch 1992, Medvedev and Zaitzev 1978
<i>C. basalis</i> Baly	India, Sri Lanka	<i>Brassica campestris</i> Linné (Brassicaceae), <i>Crotolaria juncea</i> Linné (Leguminosae), <i>Oryza sativa</i> Linné, <i>Triticum vulgare</i> Linné (Poaceae), <i>Solanum melongena</i> Linné (Solanaceae)	Zaka-ur-Rab 1991
<i>C. concinna</i> (Marsham)	Europe, Asia, Morocco, and Canada (introduced)	<i>Rumex crispus</i> Linné (Polygonaceae)	Koch 1992, Vig to Santiago-Blay (pers. comm., May 2003)
<i>C. tibialis</i> Illiger	Europe, Asia	<i>Atriplex hastata</i> Linné, <i>Beta</i> sp., <i>Chenopodium album</i> Linné, <i>Salicornia europaea</i> Linné (Chenopodiaceae)	Hering 1957, Kaszab 1962, Medvedev and Zaitzev 1978 (illustr.), Zabel <i>et al.</i> 1991
<i>Clitea picta</i> Baly	India, China	<i>Aegle marmelos</i> (Linné) Correa Serra (Rutaceae)	Cox 1996, Chen 1934, Zaka-ur-Rab 1991
<i>Clitea</i> sp.	southeast Asia	<i>Aegle</i> sp., <i>Citrus</i> sp., <i>Zanthoxylum</i> sp. (Rutaceae)	Jolivet and Hawkeswood 1995
<i>Dibolia borealis</i> Chevrolat	central United States	<i>Plantago lanceolata</i> Linné, <i>P. major</i> Linné, <i>P. rugelii</i> Dcne., <i>Plantago</i> sp. (Plantaginaceae)	Böving and Craighead 1931 (illustr.); Byers 2002; Clark 2000; Lawson 1991 (illustr.); Needham <i>et al.</i> 1928 (illustr.); Riley and Enns 1979; Wilcox 1954
<i>D. cryptocephala</i> Koch	Europe, western part of former Soviet Union	<i>Alisma</i> sp. (Alismataceae), <i>Eryngium campestre</i> Linné, <i>Eryngium</i> sp. (Apiaceae)	Böving and Craighead 1931 (illustr.); Hering 1957; Kaszab 1962; Lopatin 1984
<i>D. cynoglossi</i> (Koch)	Europe, Great Britain	<i>Cynoglossum officinale</i> Linné (Boraginaceae), <i>Marrubium vulgare</i> Linné, <i>Marrubium</i> sp., <i>Tymus</i> sp. (Lamiaceae)	Cox 1996 (illustr.), Hering 1957, Koch 1992
<i>D. depressiuscula</i> Letzner	central and southern Europe	<i>Ballota nigra</i> Linné, <i>Ballota</i> sp., <i>Eresmostachys</i> sp., <i>Galeopsis tetrahit</i> Linné, <i>Lamium purpureum</i> Linné, <i>Marrubium</i> sp., <i>Salvia nemorosa</i> Linné, <i>Stachys</i> sp., <i>Teucrium</i> sp. (Lamiaceae), <i>Veronica pseudochamaedrys</i> Jacquín, <i>Veronica</i> sp. (Schrophulariaceae)	Hering 1951, 1957 (illustr.); Kaszab 1962; Koch 1992; Steinhausen 1966; Surányi 1942
<i>D. femoralis</i> Redtenbacher	central Germany, southern and western Europe	<i>Salvia austriaca</i> Jacquín, <i>S. nemorosa</i> Linné, <i>S. pratensis</i> Linné, <i>S. verticillata</i> Linné, <i>Salvia</i> sp. (Lamiaceae)	Grandi 1959 (illustr.), Hering 1957, Kaszab 1962, Koch 1992
<i>D. foersteri</i> Bach	central and western Europe, especially in mountains	<i>Stachys officinalis</i> (Linné) Trev., <i>Stachys</i> sp. (Lamiaceae)	Hering 1957, Kaszab 1962, Koch 1992
<i>D. heringi</i> Selman	Ethiopia	<i>Leucas martinicensis</i> (Jacquin) R. Brown (Lamiaceae)	Selman 1963 (illustr.)

Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<i>D. occultans</i> Koch	Europe	<i>Brunella</i> sp., <i>Leonorus</i> sp., <i>Mentha aquatica</i> Linné, <i>Mentha</i> sp. (several species mentioned by Buhr 1955, all larvae, Lamiaceae)			Buhr 1955, Hering 1957, Kaszab 1962, Koch 1992
<i>D. rugulosa</i> Redtenbacher <i>D. schillingi</i> (Letzner)	central and southern Europe Europe (except northern Europe), Armenia, Caucasus, Daghestan, Kazakhstan, Turkey	<i>Stachys recta</i> Linné, <i>Stachys</i> sp. (Lamiaceae) <i>Salvia pratensis</i> Linné, <i>S. nemorosa</i> Linné, <i>S. verticillata</i> Linné, <i>Salvia</i> sp. (Lamiaceae)			Buhr 1956, Hering 1957, Kaszab 1962, Koch 1992 Buhr 1956, Hering 1957, Kaszab 1962 (illustr.), Koch 1992, Vig to Santiago-Blay, (pers. comm., May 2003)
<i>D. timida</i> Illiger	central Germany to southern Europe	<i>Eryngium campestre</i> Linné, <i>Eryngium</i> sp. (Apiaceae)			Hering 1957, Kaszab 1962, Koch 1992
<i>Dibolia</i> sp.	Holarctic, Africa, Central America	<i>Galeopsis</i> sp., <i>Lamium</i> sp., <i>Nepeta pannonica</i> Linné, <i>Nepeta</i> sp., <i>Stachys</i> sp. (Lamiaceae)			Frost 1924, Hering 1957, Konstantinov and Vandenberg 1996
<i>Epitrix cucumeris</i> Harold	New World, cosmopolitan?	<i>Lycopersicum esculentum</i> Miller, <i>Physalis</i> sp., <i>Solanum americanum</i> P. Miller, <i>S. carolinense</i> Linné, <i>S. melongena</i> Linné, <i>S. tuberosum</i> Linné, (Solanaceae)			Lawson 1991 (illustr.), Needham <i>et al.</i> 1928, Wilcox 1954
<i>Febra insularis</i> Bryant <i>F. venusta</i> Clark <i>Hippuriphila modeeri</i> Linné	Fiji Fiji northeastern United States, almost all Europe, Turkey, Caucasus, Mongolia, Siberia	<i>Acrostichum aureum</i> Linné (Adantiaceae) <i>Nephrolepis</i> sp. (Davalliaceae) <i>Sabal serrulata</i> Roemer <i>et</i> Schultes (Arecaceae), <i>Rutabaga</i> sp. (Brassicaceae), <i>Equisetum</i> sp. (Equisetaceae), <i>Rumex crispus</i> Linné, <i>R. hymenosepalus</i> Torrey, <i>R. obtusifolius</i> Linné (Polygonaceae), 'rye'			Samuelson 1973 Samuelson 1973 Byers 2002, Cox 1996 (illustr.), Kaszab 1962 (illustr.), Medvedev and Zaitzev 1978 (illustr.), Needham <i>et al.</i> 1928, Vig to Santiago-Blay (pers. comm., May 2003)
<i>Hippuriphila</i> sp.	Palaearctic, North America	<i>Equisetum arvense</i> Linné (Equisetaceae), <i>Rumex</i> sp. (Polygonaceae)			Frost 1924, Jolivet and Hawkeswood 1995, Konstantinov and Vandenberg 1996
<i>Longitarsus luridus</i> Scopoli	Europe, Great Britain, Asia	<i>Pulmonaria</i> sp., <i>Symphytum</i> sp. (Boraginaceae), <i>Succisa</i> sp. (Dipsacaceae), <i>Mentha</i> sp., <i>Satureja</i> sp. (Lamiaceae), <i>Plantago</i> sp. (several species mentioned by Buhr 1955, all larvae Plantaginaceae), <i>Ranunculus</i> sp., <i>Clematis</i> sp. (Ranunculaceae)			Buhr 1955, Hering 1957 (illustr.), Kaszab 1962, Koch 1992, Lopatin 1984, Medvedev and Zaitzev 1978
<i>Longitarsus</i> sp.	worldwide	Numerous genera in the Asteraceae, Boraginaceae, Convolvulaceae, Dipsacaceae, Lamiaceae, Linaceae, Plantaginaceae, Ranunculaceae, Schrophulariaceae, Solanaceae, and Thymelaceae. <i>Prunella vulgaris</i> Linné (Lamiaceae) is a doubtful record.			Buhr 1956, Jolivet and Hawkeswood 1995
<i>Mantura chrysanthemii</i> Kowarz	Europe, Great Britain	<i>Polygonum arvense</i> Roemer <i>et</i> Schultes, <i>Polygonum</i> sp., <i>Rumex acetosella</i> Linné, <i>R. scutatus</i> Linné, <i>Rumex</i> sp. (several other species mentioned by Buhr 1956, all larvae) Polygonaceae			Buhr 1955, 1956; Hering 1957 (illustr.); Kaszab 1962; Koch 1992; Lawson 1991 (illustr.)
<i>M. floridana</i> Crotch	eastern and central United States	<i>Plantago</i> sp. (Plantaginaceae), <i>Rumex acetosella</i> Linné, <i>R. altissimus</i> Wood, <i>R. crispus</i> Linné, <i>R. hymenosepalus</i> Torrey, <i>R. obtusifolius</i> Linné (Polygonaceae)			Cox 1996 (illustr.); Balsbaugh and Hays 1972, Böving and Craighead 1931 (illustr.); Clark 2000; Needham <i>et al.</i> 1928
<i>M. matthewsi</i> Curtis	Europe, Great Britain	<i>Helianthemum</i> sp. (Cistaceae)			Hering 1957, Koch 1992

<i>M. mesasiatica</i> Lopatin	Central Asia	<i>Rumex</i> sp. (Polygonaceae)	Lopatin 1984
<i>M. obtusata</i> (Gyllenhal)	Europe, Great Britain	<i>Rumex acetosa</i> Linné, <i>Rumex</i> sp. (Polygonaceae)	Cox 1996 (illustr.), Kaszab 1962, Koch 1992
<i>M. pallidicornis</i> Waltl	Europe, Great Britain	<i>Rumex</i> sp. (Polygonaceae)	Hering 1957 (illustr.)
<i>M. rustica</i> Linné	Europe, Great Britain, Siberia, China	<i>Polygonum aviculare</i> Linné (larvae), <i>Polygonum</i> sp. (larvae), <i>Rheum</i> sp., <i>Rumex conglomeratus</i> Murray, <i>R. crispus</i> Linné, <i>Rumex</i> sp. (larvae) (Polygonaceae)	Buhr 1955, 1956; Gressitt and Kimoto 1963; Hering 1957 (illustr.); Kaszab 1962 (illustr.); Koch 1992; Lopatin 1984; Surányi 1942
<i>M. subobtusata</i> Jansson	Europe	<i>Rumex</i> spp. (several species mentioned by Buhr 1956, all larvae) Polygonaceae	Buhr 1956; Gruev and Doeberl 1997 consider <i>M. subobtusata</i> a synonym of <i>M. obtusata</i> (Gyllenhal 1813)
<i>Mantura</i> sp.	Palaearctic, a few species in New World, Africa, China, Vietnam	<i>Helianthemum vulgare</i> Gaertner (Cistaceae), <i>Polygonum aviculare</i> Linné, <i>Rheum tanguticum</i> Maximowicz ex Balfour, <i>Rheum</i> spp. (several species mentioned by Buhr 1956, all larvae), <i>Rumex acetosa</i> Linné, <i>R. crispus</i> Linné (Polygonaceae)	Buhr 1956, Konstantinov and Vandenberg 1996, Surányi 1942
<i>Mniophila muscorum</i> Koch	Europe	<i>Teucrium scorodonia</i> Linné, <i>Teucrium</i> sp. (Lamiaceae), <i>Digitalis purpurea</i> Linné, <i>Digitalis</i> sp. (Scrophulariaceae), <i>Plantago lanceolata</i> Linné, <i>P. media</i> Linné, <i>Plantago</i> sp. (Plantaginaceae) <i>Pistacia lentiscus</i> Linné (Anacardiaceae), <i>Hypericum perforatum</i> Linné (Hypericaceae), <i>Anagallis arvensis</i> Linné, <i>Anagallis</i> sp. (Primulaceae), <i>Galium verum</i> Linné (Rubiaceae), <i>Solanum dulcamara</i> Linné (Solanaceae)	Hering 1957, Kaszab 1962 (illustr.), Koch 1992
<i>Ochrosis ventralis</i> Illiger	central and south eastern Europe, Great Britain	<i>Lepidium virginicum</i> Linné (Brassicaceae) <i>Alliaria ta</i> (M. B.) Cavara et Grande, <i>Armoracia lapathifolia</i> Usteri, <i>A rusticana</i> Gaertner, Mey, and Scherbius, <i>Armoracia</i> sp., <i>Barbarea vulgaris</i> R. Brown, <i>Brassica napus</i> Linné, <i>B. nigra</i> (Linné) Koch, <i>Cardamine amara</i> Linné, <i>Sinapis alba</i> Linné, <i>Sisymbrium officinale</i> (Linné) Scopoli (Brassicaceae), <i>Nasturtium microphyllum</i> Bönningh (Tropaeolaceae) <i>Cakile americana</i> Nutall, <i>C. edentula</i> Bigelow Hooker (Brassicaceae)	Hering 1957, Koch 1992
<i>Phyllotreta aenicollis</i> (Crotch)	United States	<i>Aecidium virginicum</i> Linné (Brassicaceae)	Needham <i>et al.</i> 1928
<i>P. armoraciae</i> (Koch)	United States and Canada, Europe, Great Britain to eastern Asia	<i>Aethionema</i> sp., <i>Alliaria</i> sp., <i>Alyssoides arduini</i> Fritsch (larvae), <i>Alyssum</i> sp., <i>Anastatica hierochuntica</i> Linné (larvae), <i>Anchonium elichrysifolium</i> Boissier (larvae), <i>Arabidopsis</i> sp., <i>Arabis alpina</i> Linné (larvae), <i>A. arenosa</i> (Linné) Scopoli (larvae), <i>A. hirsuta</i> (Linné) Scopoli (larvae), <i>Arabis</i> spp. (many species listed in Buhr 1955, all larvae), <i>Armoracia rusticana</i> Gaertner, Meyer, and Scherbius <i>Barbarea stricta</i> Andrzejiov-	Böving and Craighead 1931 (illustr.); Buhr 1955; Grison <i>et al.</i> 1963; Hering 1957; Kaszab 1962 (illustr.); Lopatin 1984; Medvedev and Zaitzev 1978 (illustr.); Wilcox 1954; Vig 1999; Vig and Verdyck 2001
<i>P. chalybeipennis</i> (Crotch)	eastern United States		Needham <i>et al.</i> 1928
<i>P. liebecki</i> Schaeffer	southeastern United States		Needham <i>et al.</i> 1928
<i>P. nemorum</i> (Linné)	Europe, Great Britain, northern Africa, eastern Asia		Buhr 1955, 1956; Cox 1996 (illustr.); Grison <i>et al.</i> 1963 (illustr.); Kaszab 1962 (illustr.); Hering 1957 (illustr.); Lipa <i>et al.</i> 1977; Lopatin 1984; Medvedev and Zaitzev 1978 (illustr.); Surányi 1942; Vig 1989 (illustr.), 2000

Taxon	Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
			ski (larvae), <i>B. verna</i> (Miller) Aschers (larvae), <i>B. vulgaris</i> R. Brown (larvae), <i>Barbarea</i> sp., <i>Berteroa incana</i> (Linné) DeCandolle (larvae), <i>Berteroa</i> sp., <i>Biscutella auriculata</i> Linné (larvae), <i>B. auriculata</i> Linné var. <i>erigerifolia</i> DeCandolle (larvae), <i>B. laevigata</i> Linné (larvae), <i>Biscutella</i> sp., <i>Brassica campestris</i> Linné (larvae), <i>B. chinensis</i> Linné (larvae), <i>B. oleraceae</i> Linné, <i>B. napus</i> Linné (larvae), <i>B. nigra</i> (Linné) Koch (larvae), <i>B. rapa</i> Linné, <i>Brassica</i> sp., <i>Brassicella erucastrum</i> O. E. Schulz (larvae), <i>Braya</i> sp., <i>Bunias</i> sp., <i>Calepina</i> sp., <i>Camelina sativa</i> (Linné) Cr. (larvae), <i>Camelina</i> sp., <i>Capsella</i> spp. (several species listed in Buhr 1955, all larvae), <i>Cardamine amara</i> Linné (larvae), <i>Cardamine</i> sp., <i>Cardaminopsis</i> sp., <i>Cardaria draba</i> (Linné) Desvaux (larvae), <i>Cheiranthus alpinus</i> Linné (larvae), <i>C. kewensis</i> unable to find name (larvae), <i>C. senoneri</i> Heldreich and Sartorelli (larvae), <i>Cheiranthus</i> sp., <i>Cochlearia officinalis</i> Linné (larvae), <i>Cochlearia</i> sp., <i>Conringia</i> sp., <i>Coronopus</i> sp., <i>Crambe</i> sp. (several species listed in Buhr 1955, all larvae), <i>Descurainia sophia</i> (Linné) Webb (larvae), <i>Descurainia</i> sp., <i>Diplotaxis cretacea</i> Linné (larvae), <i>D. muralis</i> (Linné) De Candolle (larvae), <i>D. tenuifolia</i> (Juslen) DeCandolle (larvae), <i>Diplotaxis</i> sp. (several more species listed in Buhr 1955, all larvae), <i>Draba</i> sp. (many species listed in Buhr 1955, all larvae), <i>Erophila</i> sp., <i>Eruca sativa</i> DeCandolle (larvae), <i>Eruca</i> sp. (several species listed in Buhr 1955, all larvae), <i>Erucaria myagroides</i> Halacsy (larvae), <i>Erucastrum gallicum</i> (Willdenow) O. E. Schulz (larvae), <i>Erucastrum</i> sp., <i>Erysimum cheiranthoides</i> Linné (larvae), <i>E. diffusum</i> Ehrhart (larvae), <i>E. helveticum</i> (Jacquin) DeCandolle (larvae), <i>E. hieracifolium</i> Linné (larvae), <i>E. hugaricum</i> Zap. (larvae), <i>E. linifolium</i> Linné (larvae), <i>E. pieninicum</i> (Zap.) Pawlowski (larvae), <i>Erysimum</i> spp. (numerous species listed in Buhr 1955, all larvae), <i>Euclidium syriacum</i> (Linné) R. Brown (larvae), <i>E. tenuissimum</i> B. Fedtschenko (larvae), <i>Euclidium</i> sp., <i>Goldbachia laevigata</i> DeCandolle (larvae), <i>Hesperis</i> sp. (several listed in Buhr 1955, all larvae), <i>Hirschfeldia</i> sp., <i>Hugueninia tanacetifolia</i> Reichenbach (larvae),			

*Hutchinsia alpina* Cosson ex Willkomm and Lange (larvae), *Hutchinsia* sp., *Iberis* sp. (many listed in Buhr 1955, all larvae), *Isatis tinctoria* Linné (larvae), *Isatis* sp., *Kremeriella cordylocarpus* (Cosson and Dur.) Maire (larvae), *Lepidim campestre* (Linné) R. Brown (larvae), *L. densiflorum* Schaefer (larvae), *L. heterophyllum* Bentham (larvae), *L. perfoliatum* Linné (larvae), *L. ruderale* Linné (larvae), *Lepidium* sp., *Lesquerella* spp. (several species listed in Buhr 1955, all larvae), *Lobularia maritima* (Linné) Desvaux (larvae), *Lobularia* sp., *Lunaria* sp., *Malcolmia* spp. (several species mentioned by Buhr 1955, all larvae), *Matthiola annua* Sweet (larvae), *Matthiola* sp., *Myagrum* sp., *Neslia paniculata* (Linné) Desvaux (larvae), *Peltaria* sp., *Petrocallis pyrenaica* R. Brown (larvae), *Raphanus raphanistrum* Linné (larvae), *R. sativus* Linné (larvae), *Raphanus* spp. (several species mentioned by Buhr 1956, all larvae), *Rapistrum rugosum* (Linné) Allard (larvae), *R. sylvestre* unable to find name (larvae), *Ricotia lunaria* DeCandolle (larvae), *Rorippa amphibia* (Linné) Bess. (larvae), *R. palustris* (Leys.) Bess. (larvae), *R. sylvestris* (Linné) Bess. (larvae), *Rorippa* spp. (other species mentioned by Buhr 1956, all larvae), *Sinapis alba* Linné (larvae), *S. arvensis* Linné (larvae), *Sinapis* sp. (more species listed by Buhr 1956), *Sisymbrium altissimum* Linné (larvae), *S. loeselii* Linné (larvae), *S. officinale* (Linné) Scopoli, *S. orientale* Linné (larvae), *S. strictissimum* Linné (larvae), *Sisymbrium* spp. (several species listed by Buhr 1956, all larvae), *Texiera glastifolia* Jaubert and Spach (larvae), *Thlaspi* sp. (numerous species listed by Buhr 1956), *Thysanocarpus curvipes* Hooker (larvae), *Turritis glabra* Linné (larvae), *Turritis glabra* Linné (larvae), *Turritis* sp. (Brassicaceae), *Capparis rupestris* Sibthorp and Smith (larvae), *C. spinosa* Linné, *Cleome* sp. (many species listed by Buhr 1955), *Gynandropsis gynandra* (Linné) Briquet (larvae) Capparaceae, *Limnanthes* spp. (several species listed in Buhr 1955, Limnanthaceae), *Reseda* sp. (several species listed in Buhr 1956, all larvae, Resedaceae), *Tovaria pendula* Ruíz and Pavón (larvae) Touvariaceae,

Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<i>P. undulata</i> Kutschera	United States, Europe, northern Africa, Asia	<i>Tropaeolum aduncum</i> Smith (larvae), <i>T. minus</i> Linné (larvae) <i>Reseda</i> sp. (Resedaceae), <i>Tropaeolum majus</i> Linné (Tropaeolaceae), several other genera of Brassicaceae			Cox 1996 (illustr.), Grison <i>et al.</i> 1963, Lopatin 1984, Medvedev and Zaitzev 1978
<i>P. vittata</i> (Fabricius)	central Europe, central and eastern Asia, North America	<i>Berteroa incana</i> (Linné) DeCandolle, <i>Eruca sativa</i> DeCandolle (Brassicaceae) both larvae			Kaszab 1962 (illustr.), Kalshoven 1981 (illustr.); Lipa <i>et al.</i> 1977 (illustr.)
<i>P. vittula</i> (Redtenbacher)	Europe, Asia	<i>Setaria</i> sp. (Poaceae) and numerous plants, particularly of the Brassicaceae and Poaceae. Vig (1998) reports that larvae are <u>not</u> leaf miners but feed on the surface of <i>Agropyron</i> sp., <i>Hordeum</i> sp., <i>Setaria</i> sp., and <i>Zea</i> sp. (Poaceae) leaves.			Chen 1934; Medvedev and Zaitzev 1978; Vig 1996, 1998
<i>P. zimmermani</i> (Crotch)	central and eastern United States	<i>Lepidium virginicum</i> Linné, <i>Raphanus sativus</i> Linné (Brassicaceae)			Clark 2000, Needham <i>et al.</i> 1928
<i>Psylliodes chrysocephala</i> (Linné)	Europe, Ireland, Great Britain, eastern Asia	<i>Brassica napus</i> Linné, <i>B. oleraceae</i> Linné, <i>B. rapa</i> Linné, <i>Brassica</i> sp., <i>Bunias</i> sp., <i>Capsella bursa-pastoris</i> (Linné) Medikus, <i>Lunaria</i> spp. (several species listed in Buhr 1955, all larvae), <i>Raphanus sativus</i> Linné, <i>Raphanus</i> sp., <i>Rapistrum perenne</i> (Linné) Allard, <i>Sinapis arvensis</i> Linné, <i>Sinapis</i> sp., <i>Thlaspi arvense</i> Linné, <i>Thlaspi</i> sp. (Brassicaceae)			Buhr 1955, 1956; Böving and Craighead 1931 (illustr.); Cox 1996 (illustr.), Grison <i>et al.</i> 1963 (illustr.), Hering 1957, Kaszab 1962, Steinhausen 1978 (illustr.)
<i>P. erythroceros</i> Abeille	north Africa	<i>Centaurea</i> sp. (Asteraceae)			Hering 1957
<i>P. hyoscyami</i> (Linné)	central and southern Europe, Great Britain, north Africa, western Asia	<i>Hyoscyamus niger</i> Linné, <i>Hyoscamus</i> sp. (Solanaceae)			Cox 1996 (illustr.), Grison <i>et al.</i> 1963, Hering 1957, Kaszab 1962
<i>P. marcida</i> (Illiger)	central and southern Europe, Great Britain	<i>Brassica</i> sp., <i>Bunias</i> sp., <i>Cakile</i> sp., <i>Lunaria</i> spp. (several species listed in Buhr 1955, all larvae), <i>Raphanus</i> sp. (several species listed in Buhr 1956, all larvae) Brassicaceae			Buhr 1955, 1956; Cox 1996 (illustr.); Hering 1957
<i>P. napi</i> (Fabricius)	Europe, Great Britain, northern Africa, and southeastern Russia, United States	<i>Alliaria officinalis</i> Andrzejewski <i>ex</i> DeCandolle, <i>Barbarea vulgaris</i> Aiton f., <i>Barbarea</i> sp., <i>Brassica</i> sp., <i>Cardamine amara</i> Linné (larvae), <i>Cardamine</i> sp., <i>Crambe</i> sp., <i>Lunaria</i> spp. (several species listed in Buhr 1955, all larvae), <i>Rorippa</i> spp. (several species mentioned by Buhr 1956, all larvae) Brassicaceae			Buhr 1955, 1956; Clark 2000; Hering 1957; Kaszab 1962
<i>P. toelgi</i> Fabricius	Alps (Europe)	<i>Biscutella laevigata</i> Linné (Brassicaceae)			Hering 1957, Kaszab 1962, Koch 1992
<i>Schenklingia hiranoi</i> Takizawa	Japan	<i>Lemmaphyllum microphyllum</i> Pr., <i>Loxogramma salicifolia</i> Makino (Polypodiaceae)			Kato 1991 (illustr.)
<i>S. sauteri</i> Chen	Japan	<i>Colysis elliptica</i> (Thunberg) Ching, <i>C. prothifolia</i> (Don) Pr. (Polypodiaceae)			Kato 1991 (illustr.)

<i>Sphaeroderma bipunctatum</i> Selman	Ethiopia	<i>Dichrocephala chrysanthemifolia</i> DeCandolle (Asteraceae)	Selman 1963 (illustr.)
<i>S. brevicornis</i> Jacoby	India	<i>Bidens pilosa</i> Linné (Asteraceae)	Zaka-ur-Rab 1991
<i>S. guizotiae</i> Selman	Ethiopia	<i>Guizotia schimperi</i> Sch. Bip. (Asteraceae)	Selman 1963 (illustr.)
<i>S. rubidum</i> Graells	southern Europe up to central Germany, Great Britain, northern Africa	<i>Arctium</i> sp., <i>Carduus pycnocephalus</i> Sprengel, <i>Carduus</i> sp., <i>Carthamus</i> sp., <i>Centaurea angustifolia</i> Miller or Schrank (larvae), <i>C. jacea</i> Linné, <i>C. scabiosa</i> Linné, <i>Centaurea</i> sp., <i>Cirsium</i> sp., <i>Cynara scolymus</i> Linné (larvae), <i>Cynara</i> sp., <i>Onopordum acanthium</i> Linné, <i>Onopordum</i> sp., <i>Serratula</i> sp. (Asteraceae), <i>Scabiosa</i> sp. (Dipsacaceae), <i>Circaea</i> sp. (Onagraceae)	Buhr 1955, 1956; Grandi 1959 (illustr.); Grison <i>et al.</i> 1963 (illustr.); Hering 1957 (illustr.); Kaszab 1962
<i>S. testaceum</i> (Fabricius)	Europe, Great Britain	<i>Arctium minus</i> Bernhardt (larvae), <i>Carduus acanthoides</i> Linné (larvae), <i>C. crispus</i> Hudson (larvae), <i>C. nutans</i> Linné (larvae), <i>C. pycnocephalus</i> Linné (larvae), <i>Carduus</i> sp., <i>Cirsium arvense</i> (Linné) Scopoli, <i>C. lanceolatum</i> (Linné) Scopoli Non Hill, <i>C. oleraceum</i> (Linné) Scopoli, <i>C. palustre</i> (Linné) Scopoli, <i>Cirsium</i> sp. (many more listed in Buhr 1955), <i>Onopordum</i> sp., <i>Serratula</i> sp. (Asteraceae)	Böving and Craighead 1931 (illustr.), Buhr 1955, Grison <i>et al.</i> 1963, Hering 1957, Kaszab 1962
<i>S. wedeliae</i> Gressitt	Micronesia (Central and Eastern Carolines), Solomons Islands	<i>Ponapea</i> sp. (Arecaceae), <i>Wedelia biflora</i> DeCandolle (Asteraceae) larvae, <i>Artocarpus</i> sp. (Moraceae), <i>Freycinetia</i> sp. (Pandanaeae)	Samuelson 1973
<i>Sphaeroderma</i> sp.	Worldwide, absent from South America	<i>Ageratum</i> sp., <i>Arctium</i> sp., <i>Bidens</i> sp., <i>Carduncellus</i> sp., <i>Carduus</i> sp., <i>Carthamus</i> sp., <i>Centaurea</i> sp., <i>Cirsium</i> sp., <i>Cynara</i> sp., <i>Dichrocephala</i> sp., <i>Farfugium</i> sp., <i>Galactites</i> sp., <i>Guizotia</i> sp., <i>Lappa</i> sp., <i>Onopordum</i> sp., <i>Petasites</i> sp., <i>Senecio</i> sp., <i>Serratula</i> sp., <i>Silybum</i> sp., (Asteraceae), <i>Commelina</i> sp. (Commelinaceae), <i>Vigna</i> sp. (Leguminosae), <i>Akebia</i> sp. (Lardizabalaceae), <i>Lilium</i> sp., <i>Scilla</i> sp. (Liliaceae), <i>Andropogon</i> sp., <i>Miscanthus</i> sp., <i>Panicum</i> sp., <i>Sasa</i> sp., <i>Smilax</i> sp. (Poaceae), <i>Artocarpus</i> sp. (Moraceae), <i>Musa</i> sp. (Musaceae), <i>Freycinetia</i> sp. (Pandanaeae), <i>Clematis</i> sp. (Ranunculaceae), <i>Coffea</i> sp., <i>Psychotria</i> sp. (Rubiaceae), <i>Salix</i> sp. (Salicaceae), <i>Smilax</i> sp. (Smilacaceae), various Zingiberaceae	Hering 1957, Jolivet and Hawkeswood, Konstantinov and Vandenberg 1996, Lee and Furth 2000
<i>Throscoryssa citri</i> Maulik	India	<i>Citrus</i> sp. (Rutaceae)	Zaka-ur-Rab 1991
<b>HISPINAE<sup>4</sup></b>			
<i>Acanthodes unca</i> Spaeth	Argentina	<i>Quetzalia uruquensis</i> unable to find name (Celastraceae)	Monrós and Viana 1947 (illustr.)



Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<i>Acentroptera basilica</i> Thompson	French Guyana to Argentina	<i>Ananas macrodentes</i> E. Morren	(Bromeliaceae)		Monrós and Viana 1947 (illustr.)
<i>Achymenus inermis</i> Zoubkoff	central Asia	<i>Phragmites communis</i> Trinius	(Poaceae)		Lopatin 1984
<i>Acmenychus</i> sp.	central Asia	<i>Phragmites</i> sp.	(Poaceae)		Jolivet 1989a
<i>Agonita bicolor</i> (Gestro)	Java	<i>Metroxylon</i> sp.	(Arecaceae) larvae		Kalshoven 1957
<i>A. decorata</i> (Gestro)	Sumatra	<i>Coelogyne</i> sp.	(Orchidiaceae) larvae		Kalshoven 1957
<i>A. fossulata</i> (Guérin-Méneville)	western and southern Africa	‘grasses’			Uhmann 1968
<i>A. fuscipes</i> (Baly)	India	‘screwpine’ (possibly <i>Pandanus</i> sp.)	(Pandanaceae)		Anand 1989
<i>A. pallipes</i> (Spaeth)	Java	bamboo	(Poaceae) larvae		Maulik 1937, Kalshoven 1957
<i>A. spathoglottis</i> Uhmann	Java	<i>Arundinacea</i> sp., <i>Coelogyne</i> sp., <i>Phalaenopsis</i> sp., <i>Spathoglottis</i> sp.	(Orchidiaceae)		Maulik 1937
<i>A. suturella</i> (Baly)	Java	<i>Pandanus</i> sp.	(Pandanaceae) larvae		Kalshoven 1957
<i>A. undata</i> Uhmann	Borneo	? orchid	(Orchidaceae) larvae		Kalshoven 1957
<i>Agonita</i> sp.	Asia, Africa	<i>Metroxylon</i> sp., <i>Phoenix</i> sp.	(Arecaceae), <i>Stereospermum</i> sp. (Bignoniaceae), <i>Combretum</i> sp. (Combretaceae), <i>Isoberlinia</i> sp. (Leguminosae), <i>Lophira</i> sp. (Ochnaceae), <i>Arundina</i> sp., <i>Coelogyne</i> sp., <i>Dendrodium</i> sp., <i>Phalaenopsis</i> sp., <i>Spathoglottis</i> sp. (Orchidiaceae), <i>Pandanus</i> sp. (Pandanaceae), <i>Bambusa</i> sp., <i>Hyparrhenia</i> sp., <i>Loudetia</i> sp., <i>Miscanthus</i> sp., <i>Panicum</i> sp., <i>Rottboelia</i> sp., <i>Sporobolus</i> sp., <i>Sorghum</i> sp. (Poaceae), <i>Cissus</i> sp. (Vitaceae), several genera of Zingiberaceae. Staines (2003b) has been unable to confirm records in the Zingiberaceae.		Jolivet 1989a, Staines 2003b, Uhmann 1953
<i>Anisostena ariadne</i> (Newman)	central and eastern United States	<i>Panicum virgatum</i> Linné	(Poaceae) larvae		Cox 1996 (illustr.), Ford and Cavey 1985 (illustr.), Riley and Enns 1979
<i>A. bicolor</i> (Smith)	central and western United States and Mexico	<i>Tripsacum dactyloides</i> (Linné) Linné	(Poaceae) larvae, ‘probable grass feeder’		Staines 1994a, Thomas and Werner 1981
<i>A. bicoloriceps</i> Pic	Paraguay and Argentina	<i>Paspalum</i> sp., <i>Valota insularis</i> (Linné) Chase	(Poaceae)		Monrós and Viana 1947 (illustr.)
<i>A. bondari</i> (Maulik)	Brazil	<i>Olyra</i> sp., <i>Panicum latifolium</i> Humboldt, Bonpland and Kunth	(Poaceae) both larvae		Maulik 1929 (illustr.), Staines 1993
<i>A. cyanea</i> Staines	southern United States and Mexico	<i>Bothriochloa saccharides</i> (Swartz) Rydberg	(Poaceae)		Staines 1994c
<i>A. gracilis</i> (Horn)	southern United States and Mexico	<i>Panicum maximum</i> Jacquin	(larvae)		Noguera 1988 (illustr.), Staines 1994b
<i>A. kansana</i> Schaeffer	central United States	<i>Tripsacum dactyloides</i> (Linné) Linné	(Poaceae) larvae		Riley and Enns 1982, Staines 1994a
<i>A. missionensis</i> Monrós and Viana	Argentina	Poaceae	(larvae)		Monrós and Viana 1947 (illustr.), Staines 1993
<i>A. nigrita</i> (Olivier)	southern Canada and most of United States	<i>Malvastrum auranticum</i> (Scheele) Walpers (Malvaceae) adults; <i>Andropogon</i> sp., <i>Schizachyrium scoparium</i> (Michaux) Nash	(Poaceae) larvae, ‘sweeping grasses of glade communities’		Ford and Cavey 1985 (illustr.), Riley and Enns 1982, Staines 1994c, Thomas and Werner 1981

<i>A. perspicua</i> (Horn)	southwestern United States, Mexico, El Salvador	<i>Acacia constricta</i> Bentham ex A. Gray (Leguminosae) adults, <i>Bothriocloa</i> sp., <i>Sporobolus</i> sp., <i>Tridens</i> sp. (Poaceae)	Staines 1994c, Thomas and Werner 1981
<i>A. prompta prompta</i> Weise	Brazil, Paraguay, Argentina	<i>Panicum leucophaeum</i> Humboldt, Bonpland and Kunth (Poaceae) larvae	Staines 1994b
<i>Anisostena</i> sp.	Canada to Argentina	<i>Bothriocloa</i> sp., <i>Panicum</i> sp., <i>Paspalum</i> sp., <i>Olyra</i> sp., <i>Tripsacum</i> sp., <i>Schizachrium</i> sp., <i>Valota</i> sp. (Poaceae)	Jolivet 1989a, Staines 2002b
<i>Asamangulia cuspidata</i> Maulik	Afganistan, Thailand, India	<i>Oryza sativa</i> Linné, <i>Saccharum officinarum</i> Linné, <i>Saccharum</i> sp. (Poaceae) larvae	Anand 1989, Kalshoven 1957, Kimoto 1999 (illustr.), Maulik 1937; Zaka-ur-Rab 1991
<i>A. horni</i> Uhmann	Taiwan	<i>Saccharum officinarum</i> Linné (Poaceae)	Gressitt and Kimoto 1963, Kalshoven 1957
<i>A. wakkeri</i> (Zehntner)	Australia, Java	<i>Oryza sativa</i> Linné (larvae), <i>Oryza</i> sp. (larvae), <i>Saccharum officinarum</i> Linné (larvae), <i>S. spontaneum</i> Linné (Poaceae) (larvae), 'also ... on wild species of cane and bamboo', and on 'other grasses' (larvae)	Kalshoven 1957, 1981; Maulik 1919, 1937; Needham <i>et al.</i> 1928
<i>Asamangulia</i> sp.	Asia	<i>Bambusa</i> sp., <i>Miscanthus</i> sp., <i>Oryza</i> sp., and <i>Saccharum</i> sp. (Poaceae)	Abdullah and Qureshi 1969, Jolivet 1989a
<i>Aspidispa albertisi</i> Gestro	New Guinea	<i>Korthalsia</i> (Arecaceae)	Gressitt 1957, 1963
<i>A. bicolor</i> Gressitt	New Guinea	<i>Korthalsia beccarii</i> unable to find name (Arecaceae) larvae	Gressitt 1963 (illustr.)
<i>A. calami</i> Gressitt	New Guinea	<i>Calamus</i> sp. (Arecaceae) larvae	Gressitt 1963 (illustr.)
<i>A. daemonoropa</i> Gressitt	New Guinea	<i>Daemonorops</i> sp. (Arecaceae)	Gressitt 1963 (illustr.)
<i>A. flagellariae</i> Gressitt	New Guinea	<i>Flagellaria</i> sp. (Flagellariaceae)	Gressitt 1963 (illustr.)
<i>A. ifara</i> Gressitt	New Guinea	'slender pinnate palms'	Gressitt 1963 (illustr.)
<i>A. korthalsiae</i> Gressitt	New Guinea	<i>Korthalsia</i> sp. (Arecaceae) larvae	Gressitt 1963 (illustr.)
<i>A. lata</i> Gressitt	New Guinea	'rattan'	Gressitt 1963 (illustr.)
<i>A. maai</i> Gressitt	New Guinea	<i>Pinanga</i> sp. (Arecaceae)	Gressitt 1963 (illustr.)
<i>A. palmella</i> Gressitt	New Guinea	? <i>Dieffenbachia</i> sp. (Araceae), 'small palm with pinnae irregularly arranged' (larvae), 'small palms', 'rattan' (Arecaceae)	Gressitt 1960a (illustr.), 1963 (illustr.)
<i>A. papuana</i> Gressitt	New Guinea	<i>Calamus</i> sp., <i>Daemonorops</i> sp. (Arecaceae)	Gressitt 1963 (illustr.)
<i>A. pinangae</i> Gressitt	New Guinea	<i>Pinanga</i> sp., 'rattan' (Arecaceae)	Gressitt 1963 (illustr.)
<i>A. rattana</i> Gressitt	New Guinea	'rattan' (Arecaceae), <i>Freycinetia</i> sp. (Pandanaeae)	Gressitt 1963 (illustr.)
<i>A. rotanica</i> Gressitt	New Guinea	'rattan'	Gressitt 1963 (illustr.)
<i>A. sedlaceki</i> Gressitt	New Guinea	'rattan' larvae	Gressitt 1963 (illustr.)
<i>A. striata</i> Gressitt	New Guinea	'palms and rattans' (Arecaceae)	Gressitt 1963 (illustr.)
<i>A. subviridipennis</i> Gressitt	New Guinea	<i>Korthalsia</i> sp., 'palm' (Arecaceae)	Gressitt 1963 (illustr.)
<i>A. wilsoni</i> Gressitt	New Guinea, Japen Island (west Papua)	'rattan' (Arecaceae)	Gressitt 1963 (illustr.)
<i>Aspidispa</i> sp.	New Guinea	<i>Dieffenbachia</i> sp. (Araceae), <i>Calamus</i> sp., <i>Daemonorops</i> sp., <i>Korthalsia</i> sp., <i>Pinanga</i> sp. (Arecaceae), <i>Flagellaria</i> sp. (Flagellariaceae), <i>Freycinetia</i> sp. (Pandanaeae)	Jolivet 1989a

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<i>Baliosus californicus</i> (Horn)	southwestern United States and Mexico	<i>Ceanothus fendleri</i> Gray (larvae), <i>C. integerrimus</i> Hooker and Arnold, <i>Ceanothus</i> sp. (Rhamnaceae)			Chittenden 1902, Frost 1924, Jones and Brisely 1925, Maulik 1937, Needham <i>et al.</i> 1928
<i>B. conspersus</i> Weise	Brazil, Paraguay, Argentina	<i>Arrabidaea coleocalyx</i> Bureau and K. Schumann (Bignoniaceae), <i>Hippocratea griesebachii</i> Loes. in Engler and Prantl Celastraceae)			Monrós and Viana 1947(illustr.)
<i>B. duodecima</i> (Baly)	Brazil	Bignoniaceae			Maulik 1937
<i>B. nervosus</i> (Panzer)	southeastern Canada and United States	<i>Acer negundo</i> Linné, <i>A. nigrum</i> Michaux, <i>A. rubrum</i> Linné (adults), <i>Acer</i> sp. (adults) (Aceraceae), <i>Eupatorium agerateroides</i> Linné (Asteraceae), <i>Alnus incana</i> (Linné) Moench, <i>A. serrulata</i> (Aiton) Willdenow, <i>Betula alba</i> Linné, <i>Betula</i> sp. (adults), <i>Carpinus caroliniana</i> Walter (adults), <i>Carpinus</i> sp., <i>Corylus americana</i> Walter, <i>Corylus</i> sp. (adults), <i>Ostrya virginiana</i> (Miller) K. Koch (Betulaceae), probably <i>Castanea crenata</i> Siebold and Zuccarini, <i>Quercus agrifolia</i> Nee (larvae), <i>Q. nigra</i> Linné, probably <i>Q. acutissima</i> Carruth., <i>Quercus</i> sp. 'white oaks' adults (Fagaceae), <i>Cassia nictatans</i> Linné, <i>Glycine max</i> (Linné) Merrill, <i>Phaseolus lunatus</i> Linné (adults), <i>P. vulgaris</i> Linné (adults), <i>Robinia pseudoacacia</i> Linné, <i>Robinia</i> sp. (adults) (Leguminosae), <i>Aronia arbutifolia</i> (Linné) Persoon, <i>Amelanchier canadensis</i> (Linné) Med. (adults), <i>Malus malus</i> Linné, <i>M. sylvestris</i> Miller, <i>Prunus americana</i> Marshall, <i>P. virginiana</i> Linné (adults), <i>Prunus</i> sp. (adults), <i>Pyrus arbutifolia</i> (Linné) Linné f. (adults), <i>P. malus</i> Linné (Rosaceae), <i>Citrus aurantium</i> Linné, <i>C. sinensis</i> (Linné) Osbeck (adults) (Rutaceae), <i>Salix</i> sp. adults (Salicaceae), <i>Tilia americana</i> Linné, <i>Tilia</i> spp. (Tiliaceae), <i>Ulmus</i> sp. (adults) (Ulmaceae)			Auerbach and Simberloff 1988, Balsbaugh and Hays 1972, Chittenden 1902, Faeth and Simberloff (1981), Faeth <i>et al.</i> 1981, Ford and Cavey 1985 (illustr.), Frost 1924, Hargrove 1986, Hodson 1942, Kogan and Kogan 1979, Needham <i>et al.</i> 1928 (illustr.), Nicolay and Weiss 1918 (illustr.), Riley and Enns 1979, Robert 1947 (illustr.), West and Lothian 1948, Wilcox 1954
<i>B. parvulus</i> (Chapuis)	Caribbean? (unlikely), Brazil, Paraguay, Argentina	<i>Vernonia sororia</i> DeCandolle (Asteraceae), <i>Dioclea divaricata</i> unable to find name, <i>Meibomia axillaris</i> (Swartz) Kuntze (Leguminosae), <i>Olyra</i> sp. (Poaceae), <i>Urtica</i> sp., (Urticaceae), <i>Cordia salicifolia</i> Cham., <i>C. polystachya</i> Kunth (Boraginaceae), <i>Platymenia foliosa</i> unable to find name			Monrós and Viana 1947(illustr.)
<i>B. productus</i> (Baly)	Costa Rica, Guatemala	unidentified Bignoniaceae (larvae)			Hespenheide and Dang 1999
<i>B. schmidti</i> Uhmman	Bolivia	<i>Banisteria argentea</i> Sprengel (Malpighiaceae) larvae, <i>Guazuma ulmifolia</i> Lamarck (Sterculiaceae) larvae, <i>Guaiacum</i> sp. (Zygophyllaceae)			Maulik 1937; Uhmman 1934 (illustr.), 1937

<i>B. viridanus</i> (Baly)	Costa Rica, Panama, Brazil, Paraguay, Bolivia, Argentina	<i>Basanacantha spinosa</i> K. Schumann (Rubiaceae), 'Guayabo silvestre'	Monrós and Viana 1947(illustr.)
' <i>Baliosus</i> sp. 1'	Costa Rica	<i>Urera bogitaense</i> unable to find name (Urticaceae) larvae	Hespenheide and Dang 1999
' <i>Baliosus</i> sp. 3'	Costa Rica	<i>Odontonema tubaeforme</i> (Bertoloni) Kuntze (Acanthaceae) larvae	Hespenheide and Dang 1999
<i>Baliosus</i> sp.	New World	<i>Odontonema</i> sp. (Acanthaceae), <i>Acer</i> sp. (Aceraceae), <i>Vernonia</i> sp. (Asteraceae), <i>Alnus</i> sp., <i>Betula</i> sp., <i>Carpinus</i> sp., <i>Corylus</i> sp. (Betulaceae), <i>Arrabidaea</i> sp. and other bignoniaceans, <i>Cordia</i> sp. (Boraginaceae), <i>Cordia</i> sp. (Ehretiaceae), <i>Hippocratea</i> sp. (Celastraceae), <i>Jatropha</i> sp. (Euphorbiaceae), <i>Castanea</i> sp., <i>Quercus</i> sp. (Fagaceae), <i>Bauhinia</i> sp., <i>Desmodium</i> sp., <i>Dioclea</i> sp., <i>Meibomia</i> sp., <i>Robinia</i> sp. (Leguminosae), <i>Banisteria</i> sp. (Malpighiaceae), <i>Sida acuta</i> N. L. Burman (Malvaceae) adults, <i>Olyra</i> sp. (Poaceae), <i>Ceanothus</i> sp. (Rhamnaceae), <i>Amelanchier</i> sp., <i>Malus</i> sp., <i>Prunus</i> sp., <i>Pyrus</i> sp., <i>Rubus</i> sp. (Rosaceae), <i>Basanacantha</i> sp. (Rubiaceae), <i>Citrus</i> sp. (Rutaceae), <i>Salix</i> sp. (Salicaceae), <i>Guacoma</i> sp. (Sterculiaceae), <i>Tilia</i> sp. (Tiliaceae), <i>Ulmus</i> sp. (Ulmaceae), <i>Urera</i> sp., <i>Urtica</i> sp. (Urticaceae), <i>Lippia</i> sp. (Verbenaceae), <i>Guaiacum</i> sp. (Zygophyllaceae)	Gillett <i>et al.</i> 1991, Jolivet 1989a, Staines 2002b
<i>Balyana mariaui</i> Berti and Desmier de Chenon	Madagascar	<i>Cocos</i> sp. (Arecaceae)	Mariau 2001
<i>Balyana</i> sp.	west Africa, Madagascar	<i>Cocos nucifera</i> Linné, <i>Medemia</i> sp., <i>Raphia</i> sp. (Arecaceae)	Jolivet 1989a; Jolivet and Hawkeswood 1995; Mariau 1975 (illustr.), 1988
<i>Brachycoryna dolorosa</i> Van Dyke	western United States	<i>Hemizonia</i> sp., <i>Holocarpa heermannii</i> (Greene), <i>Media elegans</i> D. Don, <i>M. sativa</i> Molina (Asteraceae), <i>Ceanothus cuneatus</i> (Hooker) Rhamnaceae (all adults)	Staines 1986a Staines 1986a
<i>B. hardyi</i> (Crotch)	southwestern Canada and western United States	<i>Ceanothus lucodermis</i> Greene, <i>C. sanguineus</i> Pursh, <i>C. velutisinus</i> Douglas (Rhamnaceae) (all adults)	Staines 1986a Staines 1986a
<i>B. longula</i> Weise	western United States and Mexico	<i>Franseria dumosa</i> A. Gray, <i>Hymenoclea</i> <i>monogyra</i> Torrey and Gray (Asteraceae) (both adults)	Staines 1986a, Noguera 1988
<i>B. melsheimeri</i> (Crotch)	eastern and central United States	<i>Erigeron</i> sp. (Asteraceae) (adults)	Riley and Enns 1979, Staines 1986a
<i>B. montana</i> (Horn)	Canadian and United States Rocky Mountains	<i>Artemisia tridentata</i> Nuttall, <i>Artemisia</i> sp. (Asteraceae) (both adults)	Staines 1986a
<i>B. notaticeps</i> Pic	Bolivia, Paraguay, Argentina	<i>Sphaeralcea</i> sp. (Malvaceae)	Monrós and Viana 1947

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<i>B. pumila</i> Guérin-Ménéville	southern United States to Colombia, also in Jamaica	<i>Baccharis thesioides</i> Humboldt, <i>Baccharis</i> sp. (Asteraceae), <i>Monarda citridora</i> Cervantes, <i>Monarda</i> sp. (Lamiaceae), <i>Phaseolus vulgaris</i> Linné, <i>Phaseolus</i> sp. (Leguminosae), <i>Abelmoschus esculentus</i> (Linné) Moench, <i>Abutilon lignosum</i> (Cavanilles) G. Don, <i>A. americanum</i> (Linné) Sweet (adults), <i>A. peduncularae</i> Humboldt, Bonpland and Kunth, <i>Abutilon</i> sp., <i>Alcea rosea</i> Linné, <i>Alcea</i> sp., <i>Gossypium hirsutum</i> Linné (all adults), <i>Gossypium</i> sp., <i>Malvastrum coromandelinus</i> (Linné) Garcke, <i>M. americanum</i> (Linné), <i>Malvastrum</i> sp., <i>Sida acuta</i> N. L. Burman (larvae), <i>S. cordifolia</i> Linné (adults), <i>S. rhombifolia</i> Linné (adults and larvae), <i>S. spinosa</i> Linné, <i>Sida</i> sp. (Malvaceae) previous five host plants of larvae, <i>Zea</i> sp. (Poaceae) adults, <i>Waltheria americana</i> Linné (Sterculiaceae) adults			Gillett <i>et al.</i> 1991; Maes 1998; Moldenke 1971; Noguera 1988 (illustr.); Staines 1986a, 1991, 1996 (illustr.)
<i>Brachycoryna</i> sp.	southern United States to Argentina	<i>Artemisia</i> sp. (Asteraceae), <i>Abutilon americanum</i> (Linné) Sweet (adults), <i>Abutilon</i> sp., <i>Sida</i> sp., <i>Sphaeralcea</i> sp. (Malvaceae), <i>Waltheria</i> sp. (Sterculiaceae)			Moldenke 1971, Staines 2002b
<i>Carinispa</i> sp. [monotypic genus, <i>C. nevermanni</i> Uhmans]	Central America	<i>Bunchosia costaricensis</i> Rose (larvae), <i>Bunchosia</i> sp., <i>Malpighia glabra</i> Linné (larvae), <i>Malpighia</i> sp. (Malpighiaceae) larvae			Hespenheide and Dang 1999, Jolivet 1989a, Maulik 1937, Staines 2002b (illustr.), Uhmans 1934 (illustr.), 1937 (larvae)
<i>Cassidispa</i> sp. <i>Chaeridiona metallica</i> Baly <i>Chaeridiona</i> sp. <i>Chalepus acuticornis</i> Chapuis	Congo, China, Vietnam tropical Africa, Asia, Australia Asia Mexico, Belize, Guatemala, Nicaragua	<i>Dunbaria</i> sp., <i>Galactia</i> sp. (Leguminosae) <i>Curcuma</i> sp. (Zingiberaceae) larvae <i>Curcuma</i> sp. (Zingiberaceae) <i>Buhinia unguolata</i> Linné (larvae), <i>Bauhinia</i> sp. (Leguminosae) adults, <i>Aloysia gratissima</i> (Gill. and Hooker) Troncoso (Verbenaceae) adults			Jolivet 1989a Maulik 1937, Kalshoven 1957, Stanes 2003b Jolivet 1989a Maes 1998, Maes and Staines 1991, Moldenke 1971, Noguera 1988
<i>C. amabilis</i> Baly	Mexico to Colombia	<i>Chusquea</i> sp. (larvae), <i>Lasiacis nigra</i> Davidse, <i>L. procerrima</i> Hackel, <i>L. ruscifolia</i> (Kunth) Hitchcock (larvae mine <i>Lasiacis</i> sp.), <i>Panicum</i> sp. (Poaceae)			Memmott <i>et al.</i> 1993, Staines 1996, Uhmans 1934 (illustr.)
<i>C. amicus</i> Jacoby <i>C. bacchus</i> (Newman) <i>C. bellulus</i> (Chapuis) (data from several subspecies included) <i>C. bicolor</i> (Olivier)	Mexico southeastern United States Mexico, Guatemala, Nicaragua  eastern half of the United States	<i>Philodendron anisostomum</i> Schott (Araceae) adults 'everglades grasses' <i>Phaseolus</i> sp. (Leguminosae), <i>Oryza</i> sp. (Poaceae) both adults  <i>Panicum clandestinum</i> Linné, <i>P. microcarpum</i> Muhlenberg, <i>P. nitidum</i> Lamarck, <i>P. oligosanthos</i> Schultes (adults), <i>Panicum (Dicanthelium)</i> sp. (Poaceae)			Moldenke 1971 Butte 1968b Butte 1968b (illustr.), Maes 1998, Maes and Staines 1991, Noguera 1988 (illustr.)  Butte 1968b (illustr.), Chittenden 1902, Ford and Cavey 1985 (illustr.), Needham <i>et al.</i> 1928, Riley and Enns 1979

<i>C. cordiger</i> (Chapuis)	Brazil, Paraguay, Argentina	<i>Cordia salicifolia</i> Cham. (Boraginaceae), <i>Olyra</i> sp., <i>Valota insularis</i> (Linné), unidentified Poaceae (Poaceae)	Monrós and Viana 1947 (illustr.)
<i>C. consanguineus</i> Baly	Mexico	<i>Verbesina greenmani</i> Urban (Asteraceae) adults, <i>Benthamantha mollis</i> (Humboldt, Bonpland, and Kunth) Alefeld (Leguminosae) adults, unidentified Poaceae (larvae)	Hespenheide and Dang 1999, Moldenke 1971
<i>C. digressus</i> Baly	Mexico, Costa Rica	<i>Lasiacis nigra</i> Davidse, <i>L. procerrima</i> Hackel, <i>L. ruscifolia</i> (Kunth) Hitchcock (Poaceae), unidentified Tiliaceae (larvae)	Hespenheide and Dang 1999, Memmott <i>et al.</i> 1993
<i>C. hepburni</i> Baly	Mexico	an unidentified species of Leguminosae (adult)	Noguera 1988
<i>C. horni</i> Baly	Costa Rica	<i>Lasiacis nigra</i> Davidse, <i>L. procerrima</i> Hackel, <i>L. ruscifolia</i> (Kunth) Hitchcock (Poaceae)	Memmott <i>et al.</i> 1993
<i>C. parananus</i> Pic	Bolivia, Paraguay, Argentina	<i>Olyra</i> sp., <i>Panicum molle</i> Swartz (Poaceae) all adults	Monrós and Viana 1947 (illustr.)
<i>C. placidus</i> Baly	Mexico, Guatemala	<i>Heliocarpus pallidus</i> Rose (Tiliaceae)	Noguera 1988
<i>C. putzeysi</i> (Chapuis)	Brazil and Paraguay	<i>Paspalum quadrifarium</i> Lamarck (Poaceae) adults	Monrós and Viana 1947 (illustr.)
<i>C. sanguinicollis</i> (Linné)	Florida (United States), West Indies, South America	<i>Panicum leucophaeum</i> Kunth, <i>Paspalum densum</i> Poiret, <i>Sorghastrum setosum</i> Hitchcock, <i>Trichachne insularis</i> (Linné) Nees. (Poaceae) adults	Maulik 1937, Sanderson 1967, Virkki and Santiago-Blay 1998, Wilcox 1975
<i>C. sanguinicollis australis</i> Uhmman	southern Brazil, Bolivia, Paraguay, Argentina	<i>Bromelia caragua</i> unable to find name (Bromeliaceae), <i>Valota insularis</i> (Linné) Chase (Poaceae), <i>Vitex cymosa</i> Bert. (Verbenaceae) all adults	Monrós and Viana 1947 (illustr.)
<i>C. schmidti</i> Uhmman	Nicaragua and Costa Rica	<i>Guazuma</i> sp. (Sterculiaceae), <i>Chusquea</i> sp. (larvae), <i>Lasiacis</i> sp. (larvae), <i>Panicum</i> sp. (Poaceae)	Meas 1998; Maes and Staines 1991; Uhmman 1934 (illustr.), 1937
<i>C. subcordiger</i> Uhmman	Paraguay and Argentina	<i>Aristolochia elegans</i> M.T. Masters. (Aristolochiaceae), <i>Arrabidaea coleocalyx</i> Bureau and K. Schumann (Bignoniaceae), <i>Actinostemon</i> sp. (Euphorbiaceae) all adults	Monrós and Viana 1947 (illustr.)
<i>C. verticalis</i> (Chapuis)	Mexico, Guatemala, Nicaragua	<i>Phaseolus</i> sp. (Leguminosae) adults, flowers of <i>Zea</i> sp. (Poaceae)	Maes 1998, Maes and Staines 1991, Passoa 1983
<i>C. walshii</i> (Crotch)	United States	<i>Bromus</i> sp., <i>Elymus villosus</i> Muehenberg, <i>Hystrix patula</i> Moench (Poaceae)	Ford and Cavey 1985 (illustr.), Thomas and Werner 1981
<i>Chalepus</i> sp.	Canada to Argentina	<i>Acer</i> sp. (Aceraceae), <i>Philodendron</i> sp. (Araceae), <i>Aristolochia</i> sp. (Aristolochiaceae), <i>Centaurea</i> sp., <i>Cyanus</i> sp., <i>Eupatorium</i> sp., <i>Verbesina</i> sp., <i>Vernonia</i> sp., <i>Wedelia</i> sp. (Asteraceae), <i>Betula</i> sp. (Betulaceae), <i>Arrabidaea</i> sp. (Bignoniaceae), <i>Brassica</i> sp. (Brassicaceae), <i>Bromelia</i> sp. (Bromeliaceae), <i>Celastrus</i> sp. (Celastraceae), <i>Terminalia</i> sp. (Combretaceae), <i>Commelina</i> sp. (Commelinaceae), <i>Ipomoea</i> sp. (Convolvulaceae),	Jolivet 1989a, Maes 1998, Maes and Staines 1991, Passoa 1983, Staines 2002b, Ward <i>et al.</i> 1977

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		<i>Cordia</i> sp. (Ehretiaceae), <i>Actinostomon</i> sp. (Euphorbiaceae), <i>Quercus</i> sp. (Fagaceae), <i>Apios</i> sp., <i>Bauhinia</i> sp., <i>Benthamantha</i> sp., <i>Calopogonium</i> sp., <i>Canavalia</i> sp., <i>Cassia</i> sp., <i>Crotalaria</i> sp., <i>Cymbosema</i> sp., <i>Desmodium</i> sp., <i>Dioclea</i> sp., <i>Dolichos</i> sp., <i>Falcata</i> sp., <i>Glycine</i> sp., <i>Lathyrus</i> sp., <i>Meibomia</i> sp., <i>Mucuna</i> sp., <i>Pithecelobium</i> sp. (adults), <i>Prosopis</i> sp., <i>Pueraria</i> sp., <i>Robinia</i> sp., <i>Vicia</i> sp. (Leguminosae), <i>Bambusa</i> sp., <i>Brachiaria</i> sp., <i>Chusquea</i> sp., <i>Elymus</i> sp., <i>Hystrix</i> sp., <i>Lasiacis</i> sp., <i>Olyra</i> sp., <i>Panicum</i> sp., <i>Paspalum</i> sp., <i>Valota</i> sp., <i>Zea</i> sp. (Poaceae), <i>Cerasus</i> sp., <i>Crataegus</i> sp., <i>Malus</i> sp., <i>Pyrus</i> sp. (Rosaceae), <i>Coffea</i> sp. (Rubiaceae) adults, <i>Paullinia</i> sp. (Sapindaceae), <i>Theobroma</i> sp. (Sterculiaceae), Tiliaceae, <i>Aloysia</i> sp., <i>Vitex</i> sp. (Verbenaceae)			
<i>Charistena ruficollis</i> (Fabricius)	Costa Rica to Argentina	<i>Paspalum conjugatum</i> Berg. (Poaceae), <i>Coffea</i> sp. (Rubiaceae) adults			Maes 1998, Maes and Staines 1991, Staines 2002b (illustr.)
<i>Charistena</i> sp.	Colombia to Argentina	<i>Panicum</i> sp., <i>Paspalum</i> sp., <i>Zea</i> sp. (Poaceae)			Staines 2002b
<i>Chrysispa</i> sp.	Sierra Leone (Africa)	<i>Oryza</i> sp. (Poaceae)			Jolivet 1989a
<i>Clinocarispa humeralis</i> (Fabricius)	Trinidad, Tobago, Colombia, Guyana, Suriname, French Guyana, Brazil, Peru	<i>Bambusa vulgaris</i> Schrader ex. Wendland (Poaceae)			Ramos 1996 (illustr.)
<i>Cnestispa acuminata</i> Maulik	Brazil	Leguminosae			Maulik 1937
<i>Cnestispa darwini</i> Maulik	Argentina	<i>Centrosema pubescens</i> Benth., <i>Cymbosema</i> sp., <i>Desmodium discolor</i> Vogel (Leguminosae)			Monrós and Viana 1947
<i>Cnetispa</i> sp.	Colombia to Peru	<i>Centrosema</i> sp., <i>Cymbosema</i> sp., <i>Desmodium</i> sp. (Leguminosae), <i>Bambusa</i> sp., <i>Olyra</i> sp. (Poaceae)			Jolivet and Hawkeswood 1995, Staines 2002b
<i>Coelaenomenodera elaiedis</i> Maulik	west and central Africa	<i>Borassus</i> sp., <i>Cocos</i> sp., <i>Elaeis guineensis</i> Jacquin, <i>Elaeis</i> sp., other palms (Arecaceae)			Bernon and Graves 1979; Berti and Mariau 1999; Chen <i>et al.</i> 1986 (illustr.); Cox 1996 (illustr.); Lepesme 1947 (illustr.); Mariau 1988 (illustr.), 2001; Mariau and Morin 1971, 1974; Morin and Mariau 1971 (illustr.); Maulik 1931 (illustr.); Morin and Mariau 1971; Uhmman 1968
<i>C. lameensis</i> Berti and Mariau	Ivory Coast	<i>Elaeis guineensis</i> Jacquin (Arecaceae)			Berti and Mariau 1999 (illustr.), Mariau 2001
<i>C. minuta</i> Uhmman	west Africa (from Cameroon to Ghana)	<i>Elaeis guineensis</i> Jacquin (Arecaceae)			Mariau 1988, 2001
<i>C. perrieri</i> Fairmaire	Madagascar	<i>Cocos</i> sp. (Arecaceae)			Mariau 1988, 2001
<i>C. speciosa</i> Gestro	Zaire	<i>Elaeis guineensis</i> Jacquin (Arecaceae)			Collart 1934, Lepesme 1947, Mariau 2001, Uhmman 1931
<i>Coelaenomenodera</i> sp. <sup>5-6</sup>	Africa, Madagascar	<i>Borassus</i> sp., <i>Cocos</i> sp., <i>Elaeis</i> sp., <i>Roystonea</i> sp. (Arecaceae), <i>Amonum</i> sp. (Zingiberaceae) (Staines 2003b has been unable to confirm record of <i>Amonum</i> sp.)			Berti and Mariau 1999, Collart 1934, Jolivet 1989a, Mariau 1988

<i>Corynisa</i> sp.	Brazil	<i>Stigmaphyllon</i> sp. (Malpighiaceae)	Staines 2002b
<i>Craspedonisa saccharina</i> Maulik	Trinidad	<i>Saccharum</i> sp. (Poaceae)	Cox 1996 (illustr.), Maulik 1932 (illustr.)
<i>Craspedonisa</i> sp.	Trinidad to Brazil	<i>Saccharum</i> sp. (Poaceae)	Staines 2002b
<i>Cyperispa hypolytri</i> Gressitt	Solomons Islands (Guadalcanal)	<i>Hypolytrum</i> sp. (Cyperaceae)	Cox 1996 (illustr.); Gressitt 1957 (illustr.), 1960a
<i>C. palmarum</i> Gressitt	Solomon Islands (Santa Isabel Island)	'palms', <i>Metroxylon</i> sp. (Arecaceae)	Gressitt and Samuelson 1988 (illustr.)
<i>C. scleriae</i> Gressitt (includes two subspecies listed in Gressitt 1960a)	Solomon Islands (Guadalcanal)	<i>Scleria</i> sp., 'sedge' (Cyperaceae)	Gressitt 1957 (illustr.), 1960a (illustr.)
<i>C. thoracostachyi</i> Gressitt (including two subspecies listed in Gressitt and Samuelson 1988)	Malaita (Solomons Islands)	'palm' (Arecaceae), <i>Thoracastachyum</i> sp. (Cyperaceae) larvae, <i>Pandanus</i> sp. (Pandanaeae)	Gressitt 1960a (illustr.), Gressitt and Samuelson 1988 (illustr.)
<i>Cyperispa</i> sp.	Solomon Islands	<i>Hypolytrum</i> sp., <i>Scleria</i> sp., <i>Thoracastachyum</i> sp. (Cyperaceae)	Jolivet 1989a
<i>Dactylispa aculeata</i> (Klug)	Zaire	'sur cacaoyer'	Uhmann 1968
<i>D. albopilosa</i> (Gestro)	India, Burma (or Myanmar), Thailand, Laos, Vietnam	<i>Andropogon sorghum</i> (Linné) Brotero, <i>Sorghum vulgare</i> Persoon (Poaceae)	De and Konar 1954, Kimoto 1999 (illustr.), Zaka-ur-Rab 1991
<i>D. angulosa</i> (Solsky)	Korea, Japan, China, Siberia	<i>Quercus acutissima</i> Carr, <i>Q. myrsinaefolia</i> Blume., <i>Quercus</i> sp. 'le genus', (Fagaceae), <i>Isodon inflexus</i> (Thunberg) Kudo, <i>Prunella vulgaris</i> Linné var. <i>lilacina</i> Nakai, (Lamiaceae), 'bamboo' (Poaceae), <i>Filipendula multijuga</i> Maximowicz, <i>F. palmata</i> (Pallas) (adults), <i>Filipendula</i> sp. ('he-ye-zi genus'), <i>Malus pumila</i> Miller, <i>Prunus</i> sp., <i>Rosa</i> sp. (Rosaceae)	An <i>et al.</i> 1985, Kalshoven 1957, Nakane 1955 (illustr.), Tan 1993 (illustr.)
<i>D. aspera</i> (Gestro)	Java	<i>Gardenia augusta</i> Merrill (Rubiaceae) adults	Gressitt 1957, Kalshoven 1957
<i>D. bakeri</i> (Gestro)	Java	<i>Saccharum spontaneum</i> Linné (Poaceae) larvae	Kalshoven 1957
<i>D. balyi</i> Gestro	Java	<i>Zea</i> sp. (seedlings) larvae, 'glagah', 'lalang' adults (Poaceae)	Kalshoven 1981
<i>D. bipartita</i> Guérin-Méneville	Philippine Islands, Java	<i>Bambusa blumeana</i> Schultes (larvae), <i>Saccharum spontaneum</i> Linné (adults) (Poaceae), <i>Sterculia</i> sp. (Sterculiaceae) adults	Kalshoven 1957
<i>D. brachycera</i> (Gestro)	India	'grasses' (Poaceae), <i>Lantana camara</i> Linné (Verbenaceae)	Maulik 1937
<i>D. chapuisi</i> (Gestro)	Ethiopia, Uganda, west Africa	<i>Melinis minutiflora</i> Beauvois (Poaceae)	Collart 1934; Maulik 1932 (illustr.), 1937
<i>D. cladophora</i> (Guérin-Méneville)	Philippine Islands	<i>Bambusa blumeana</i> Schultes, <i>Hymenache</i> sp. (Poaceae) both larvae	Kalshoven 1957
<i>D. debilis</i> (Gestro)	Java	<i>Nertera depressa</i> Banks and Soland. <i>ex</i> Gaertner, <i>Plectronia horrida</i> (Blume) Bentham and Hooker f. <i>ex</i> Kurz (Rubiaceae) both larvae	Kalshoven 1957
<i>D. dilaticornia</i> (Duvivier)	'United Provinces', India	<i>Oryza sativa</i> Linné, <i>Panicum</i> sp. (Poaceae)	Maulik 1937
<i>D. discalis</i> Gressitt	New Guinea	'large-leaved shrub'	Gressitt 1963 (illustr.)
<i>D. infuscata</i> (Chapuis)	Philippine Islands	<i>Bambusa blumeana</i> Schultes (Poaceae) larvae	Kalshoven 1957
<i>D. issikii</i> Chûjô	Japan, China	<i>Arundinaria pygmaea</i> Mitter var. <i>glabre</i> Ohwi, <i>A. simonii</i> Rivinus, <i>Phyllostachys bambusoides</i> Siebold and Zuccarini, <i>Oryza sativa</i> Linné (Poaceae)	Chen <i>et al.</i> 1986 (illustr.), Gressitt and Kimoto 1963



Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<i>D. javaensis</i> Maulik	Java	<i>Gardenia</i> sp. (Rubiaceae), 'salam utan', 'kerema' (Myrtaceae?) all larvae			Cox 1996 (illustr.), Kalshoven 1957, Maulik 1931 (illustr.)
<i>D. kamarupa</i> Maulik	India	'plum' (Rosaceae), <i>Guaiacum</i> sp. (Zygophyllaceae)			Maulik 1937
<i>D. kaulina</i> Gestro	China	'bamboo' (Poaceae) larvae			Kalshoven 1957
<i>D. lenta</i> Weise	Tanzania	<i>Oryza sativa</i> Linné (Poaceae)			Banwo <i>et al.</i> 2001a
<i>D. leonardi</i> (Ritsema)	Thailand, Cambodia, Laos, Vietnam, China, Sumatra	<i>Ceiba pentandra</i> (Linné) Gaertner (Bombacaceae) adults, <i>Helicteres</i> sp. (Sterculiaceae) larvae			Kalshoven 1957, 1981 (illustr.); Kimoto 1999 (illustr.)
<i>D. luhi</i> Uhmman	China	<i>Anthraxon hispidus</i> (Thunberg) Makino (Poaceae) larvae			Gressitt and Kimoto 1963, Kalshoven 1957
<i>D. manterii</i> (Gestro)	Malacca (Malaysia), Sumatra, Java	<i>Lagerstroemia</i> sp. (Lytraceae) adults, <i>Cinchona ledgeriana</i> Moens <i>ex. Trimen</i> , <i>Cinchona</i> sp. seedlings (Rubiaceae) larvae, <i>Curcuma</i> sp. (Zingiberaceae) adults			Kalshoven 1957, 1981 (illustr.); Maulik 1937; Staines 2003b
<i>D. masoni</i> Gestro	Korea, Japan, China, Siberia	<i>Petasites japonicus</i> (F.Schmidt) and other Asteraceae			An <i>et al.</i> 1985, Gressitt and Kimoto 1963
<i>D. melanaria</i> (Motschulsky)	Guinea, Gabon, west Africa, Nigeria, Uganda,	<i>Panicum</i> sp. (Poaceae)			Cox 1996 (illustr.), Maulik 1932 (illustr.), Uhmman 1968
<i>D. nemoralis</i> (Gestro)	Java	<i>Rubus moluccanus</i> Linné (larvae) (Rosaceae)			Kalshoven 1957
<i>D. pallipes</i> (Kraatz)	Tropical Africa	<i>Setaria chevalieri</i> Stapf (Poaceae) larvae			Uhmman 1968
<i>D. parbatya</i> Maulik	eastern Himalayas, northern India, southern China	<i>Rubus</i> sp. (Rosaceae)			Gressitt and Kimoto 1963, Maulik 1937
<i>D. pubicollis</i> (Chapuis)	tropical Africa	Commelinaceae			Uhmman 1931, 1968
<i>D. puncticollis</i> Gestro	Democratic Republic of Congo, Congo, Fernando Poo, Spanish Guinea, Nigeria, Natal (South Africa)	<i>Theobroma cacao</i> Linné (Sterculiaceae) larvae			Uhmman 1931, 1968
<i>D. semecarpus</i> Gressitt	New Guinea	? <i>Semecarpus</i> sp. (Anacardiaceae)			Gressitt 1963 (illustr.)
<i>D. sjoestedti</i> Uhmman	China	<i>Bambusa multiplex</i> (Loureiro) Raeuschel, <i>B. tuldoidea</i> Munro, <i>B. subspinosa</i> McClure, <i>Bambusa</i> spp. (larvae), <i>Lingmania cerocissima</i> McClure, <i>L. chungii</i> McClure, <i>Lingmania</i> sp. (larvae), <i>Sinobambusa tootsik</i> (Makino), ? <i>Sinobambusa</i> sp. (larvae) Poaceae			Cox 1996 (illustr.), Gressitt and Kimoto 1963, Kalshoven 1957 (illustr.)
<i>D. spinigera</i> (Gyllenhal)	tropical Africa	Poaceae			Uhmman 1968
<i>D. spinosa</i> (Weber)	India, Burma (or Myanmar), Thailand, Laos, Vietnam, China, Sumatra, Java, Borneo, Sulawesi (= Celebes Island)	<i>Imperata cylindrica</i> (Linné) Beauvois (adults), <i>Panicum palmifolium</i> J. König (larvae), <i>Rottboellia exaltata</i> Linné f. (larvae), <i>Saccharum officinarum</i> Linné (larvae), <i>S. spontaneum</i> Linné (adults), <i>Zea mays</i> Linné (larvae) (Poaceae)			Chen <i>et al.</i> 1986 (illustr.), Gressitt 1957, Kalshoven 1957, Kimoto 1999 (illustr.)
<i>D. spinulosa</i> (Gyllenhal)	tropical Africa	Cyperaceae, <i>Anropogon</i> sp. (Poaceae)			Uhmman 1968
<i>D. subquadrata</i> (Baly)	Korea, Japan, China	<i>Castanea crenata</i> Siebold and Zuccarini, <i>Castanopsis cuspidata</i> (Thunberg) Schottky, <i>Quercus acutissima</i> Carr, <i>Q. glauca</i> Thunberg,			An <i>et al.</i> 1985, Chen <i>et al.</i> 1986 (illustr.), Gressitt and Kimoto 1963, Hayashi 1986 <i>et al.</i> 1986 (illustr.), Nakane 1955 (illustr.)

<i>D. sumatrana</i> Weise	Java	<i>Q. mongolica</i> Fischer ex Turczaninow ( var. <i>grosseserrata</i> Rehd and Wilson, <i>Q. serrata</i> Thunberg, <i>Q. variabilis</i> Blume (Fagaceae)	Kalshoven 1957
<i>D. vestita</i> Maulik	India	<i>Saccharum officinarum</i> Linné (Poaceae)	Maulik 1937
<i>D. vethi</i> Gestro	Java	<i>Prunus</i> sp. (Rosaceae), 'almond leaf'	Kalshoven 1957
		<i>Plectronia horrida</i> (Blume) Bentham and Hooker f. <i>ex</i> Kurz (Rubiaceae) larvae, 'tauluan' (Rubiaceae?) larvae	
<i>Dactylispa</i> sp.	Old World	<i>Semecarpus</i> sp. (Anacardiaceae), <i>Phoenix</i> sp. (Arecaceae), <i>Carpinus</i> sp. (Betulaceae), <i>Ceiba</i> sp., <i>Durio</i> sp. (Bombacaceae), <i>Lobelia</i> sp. (Campanulaceae), <i>Commelina</i> sp. (Commelinaceae), <i>Artemisia</i> sp., <i>Petasites</i> sp. (Asteraceae), <i>Phyllostachis</i> sp., <i>Scleria</i> sp. (Cyperaceae), <i>Croton</i> sp., <i>Hevea</i> sp. (Euphorbiaceae), <i>Castanea</i> sp., <i>Castanopsis</i> sp., <i>Quercus</i> sp. (Fagaceae), <i>Isodon</i> sp., <i>Plectranthus</i> sp., <i>Prunella</i> sp. (Lamiaceae), <i>Dalbergia</i> sp., <i>Desmodium</i> sp., <i>Piliostigma</i> sp., <i>Phaseolus</i> sp. (Leguminosae), <i>Jussiaea</i> sp. (Onagraceae), <i>Andropogon</i> sp., <i>Anthrascon</i> sp., <i>Arundinaria</i> sp., <i>Bambusa</i> sp., <i>Cynodon</i> sp., <i>Callipedium</i> sp., <i>Dactyloctenium</i> sp., <i>Digitaria</i> sp., <i>Eleusine</i> sp., <i>Echinochloa</i> sp., <i>Hymenachne</i> sp., <i>Hyparrhenia</i> sp., <i>Imperata</i> sp., <i>Leersia</i> sp., <i>Leptochloa</i> sp., <i>Lignania</i> sp., <i>Loudetia</i> sp., <i>Melinis</i> sp., <i>Mnesithea</i> sp., <i>Oplismenus</i> sp., <i>Oryza</i> sp., <i>Panicum</i> sp., <i>Paspalum</i> sp., <i>Pennisetum</i> sp., <i>Rottboellia</i> sp., <i>Saccharum</i> sp., <i>Setaria</i> sp., <i>Sinobambusa</i> sp., <i>Sporobolus</i> sp., <i>Triticum</i> sp., <i>Urelytrum</i> sp., <i>Vetiveria</i> sp., <i>Vossia</i> sp., <i>Zea</i> sp., <i>Zizania</i> sp. (Poaceae), <i>Filipendula</i> sp., <i>Leucosidea</i> sp., <i>Malus</i> sp., <i>Prunus</i> sp. <i>Rosa</i> sp., <i>Rubus</i> sp. (Rosaceae) <i>Canthium</i> sp., <i>Cinchona</i> sp., <i>Coffea</i> sp., <i>Gardenia</i> sp., <i>Plectronia</i> sp., <i>Nertera</i> sp. (Rubiaceae), <i>Helicteres</i> sp., <i>Sterculia</i> sp., <i>Theobroma</i> sp. (Sterculiaceae) <i>Callicarpa</i> sp. (Verbenaceae), <i>Guaiacum</i> (Zygophyllaceae). Apparently, also in some Acanthaceae, Malvaceae, and Marantaceae chichona, kapok, coffee, and maize	Banwo <i>et al.</i> 2001b, Collart 1934, De and Konar 1954, Jolivet 1989a, Staines 2003b, Uhmman 1953
<i>Dicladispa armigera</i> (Olivier)	Pakistan, India, Nepal, Burma (or Myanmar), Thailand, Laos, Vietnam, China, Taiwan, Malaya, Sumatra, Java, Indonesia	<i>Cyperus rotundus</i> Linné (Cyperaceae), <i>Digitaria ciliaris</i> Persoon, <i>D. setigera</i> Roth, <i>Echinochloa colona</i> (Linné) Link, <i>E. crusgalli</i> (Linné) Beauvois, <i>Eleusine indica</i> Gaertner, <i>Leersia hexandra</i> Swartz, <i>Oryza sativa</i> Linné (larvae),	Abdullah and Qureshi 1969; An <i>et al.</i> 1985; Chen <i>et al.</i> 1986 (illustr.); Cox 1996 (illustr.); Kalshoven 1957, 1981 (illustr.); Kimoto 1999 (illustr.); Maulik 1919 (illustr.), 1931, 1937; Rawat and Singh 1980; Razzaque and Karim 1989; Zaka-ur-Rab 1991

Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<i>D. alternata</i> (Chapuis)	Java	<i>Saccharum officinarum</i> Linné (larvae), <i>Zea mays</i> Linné and other Poaceae, 'paddy'			Kalshoven 1957
<i>D. cyanipennis</i> (Motschulsky)	India	<i>Saccharum spontaneum</i> Linné (Poaceae) adults			Anand 1989
<i>D. dama</i> (Chapuis)	India (including Assam region on east), Burma (or Myanmar)	<i>Sorghum</i> sp. 'sorghum' (Poaceae)			Maulik 1937
<i>D. fabricii</i> (Guérin-Méneville)	New Guinea, New Britain, Bougainville	<i>Oplismenus</i> sp. 'and other grasses' (Poaceae)			Gressitt 1960a, 1963
<i>D. kapauku</i> Gressitt	New Guinea	'grasses'			Gressitt 1957, 1960a
<i>D. linnei</i> (Weise)	New Guinea	<i>Paspalum</i> sp. (Poaceae) larvae, 'grass', <i>Aralia?</i> sp. (Araliaceae), <i>Costus?</i> sp. (Zingiberaceae)			Gressitt 1957 (illustr.), 1960a, 1963 (illustr.); Staines 2003b
<i>D. occator</i> (Brullé)	Canary Islands (Spain)	<i>Cistus</i> sp. (Cistaceae)			Hering 1957
<i>D. striaticollis</i> (Gestro)	east Africa	<i>Zea mays</i> Linné (Poaceae)			Abdullah and Qureshi 1969, Maulik 1937
<i>D. testacea</i> (Linné)	southern Europe, Canary Islands, Algeria, northern Africa, Turkey, Syria	<i>Cistus albidus</i> Linné, <i>C. monspeliensis</i> Linné, <i>C. salvifolius</i> Linné, <i>Cistus</i> sp. (Cistaceae)			Bordy 2000 (illustr.); Buhr 1955; Cox 1996 (illustr.); Grandi 1959 (illustr.); Hering 1957 (illustr.); Maulik 1919, 1937; Needham <i>et al.</i> 1928
<i>D. vicinalis</i> (Péringuey)	southwest Africa	<i>Crotalaria</i> sp. (Leguminosae)			Uhmann 1953
<i>Di cladispa</i> sp.	Old World	<i>Aralia</i> sp. (Araliaceae), <i>Petasites</i> sp. (Asteraceae), <i>Cistus</i> sp. (Cistaceae), <i>Lobelia</i> sp. (Lobeliaceae), <i>Crotalaria</i> sp., <i>Dalbergia</i> sp., <i>Rhynchosia</i> sp. (Leguminosae), <i>Malvastrum</i> sp. (Malvaceae), <i>Callipedium</i> sp., <i>Cynodon</i> sp., <i>Dactyloctenium</i> sp., <i>Digitaria</i> sp., <i>Echinochloa</i> sp., <i>Eleusine</i> sp., <i>Leersia</i> sp., <i>Leptochloa</i> sp., <i>Mnesithea</i> sp., <i>Oryza</i> sp., <i>Panicum</i> sp., <i>Paspalum</i> sp., <i>Saccharum</i> sp., <i>Vetiveria</i> sp., <i>Vossia</i> sp., <i>Zizania</i> sp. (Poaceae), <i>Leucosidea</i> sp. (Rosaceae), <i>Grewia</i> sp. (Tiliaceae), <i>Costus</i> sp. (Zingiberaceae)			Jolivet 1989a, Staines 2003b, Uhmann 1953
<i>Dorcathispa</i> sp. [prob. <i>D. bellicosa</i> (Guérin-Méneville)]	Africa	<i>Oryza</i> sp., <i>Pennisetum</i> sp., <i>Sorghum</i> sp., <i>Zea</i> sp. (Poaceae)			Jolivet 1989a
<i>Downesia bambusae</i> Maulik	Java	'bamboo' <i>Bambusa</i> sp. (Poaceae) larvae			Maulik 1937, Kalshoven 1957
<i>D. javana</i> Weise	Java	'bamboo' <i>Bambusa</i> sp. (Poaceae) larvae			Kalshoven 1957
<i>D. marginicollis</i> Weise	China	<i>Sinocalamus</i> sp. (Poaceae) larvae			Kalshoven 1957
<i>D. pernicioso</i> Spaeth	Java	bamboo (Arecaceae) larvae			Maulik 1937, Kalshoven 1957
<i>D. sumatrana</i> Gestro	Java, Sumatra	bamboo (Arecaceae) larvae			Maulik 1937, Kalshoven 1957
<i>D. vandykei</i> Gressitt	China, Vietnam	bamboo ( <i>Bambusa</i> sp.) Poaceae			Yu 1993
<i>Downesia</i> sp. (some species are miners)	Indo-Australian region	<i>Bambusa</i> sp., <i>Saccharum</i> sp., <i>Sinocalamus</i> sp. (Arecaceae)			Chen <i>et al.</i> 1986 (illustr.), Cox 1996 (illustr.), Jolivet 1989a
<i>Enischnispa calamivora</i> Gressitt (includes two subspecies listed in Gressitt and Samuelson 1988)	Bismark Archipelago, New Ireland (New Guinea)	<i>Calamus</i> sp., <i>Daemonorops</i> sp., 'palms' (Arecaceae)			Gressitt 1957 (illustr.), 1960a (illustr.), 1963 (illustr.); Gressitt and Samuelson 1988 (illustr.)

<i>E. daemonoropa</i> Gressitt	New Guinea	<i>Daemonorops</i> sp. (Arecaceae)	Gressitt 1963 (illustr.)
<i>E. palmicola</i> Gressitt	New Guinea	'small palm'	Gressitt 1963 (illustr.)
<i>E. rattana</i> Gressitt	New Guinea	<i>Calamus</i> sp., <i>Daemonorops</i> sp., 'rattan with slender pinnae' (Arecaceae)	Gressitt 1960a (illustr.)
<i>Enischnispa</i> sp.	New Guinea	<i>Calamus</i> sp., <i>Daemonorops</i> sp. (Arecaceae)	Jolivet 1989a
<i>Euprionota gebieni</i> Uhmann	Central America	<i>Vernonia</i> sp. (Asteraceae) larvae	Maulik 1937, Uhmann 1934
<i>Euprionota</i> sp.	Mexico to Colombia	<i>Vernonia</i> sp. (Asteraceae)	Staines 2002b
<i>Freycinetispa collinsi</i> Gressitt	Solomon Islands	<i>Freycinetia</i> sp. (Pandanaeae) larvae	Gressitt 1960a (illustr.)
<i>Freycinetispa</i> sp.	Asia, Indo-Australian region	small <i>Freycinetia</i> sp. (Pandanaeae) larvae	Cox 1996 (illustr.)
<i>Gestronella</i> sp.	Madagascar, Mascareignes-Reunion	<i>Acanthophoenix</i> sp., <i>Cocos</i> sp., <i>Dictyosperma</i> sp. (Arecaceae)	Jolivet 1989a
<i>Glyphuroplata nigella</i> (Weise)	Arizona (United States)	<i>Glycine max</i> Merrill, <i>Mimosa?</i> sp. (Leguminosae), <i>Eriochloa gracilis</i> (Fournier) Hitchcock (adults), <i>Valota</i> sp., unidentified poacean (larvae) (Poaceae)	Hespenheide and Dang 1999, Riley 1985
<i>G. pluto</i> (Newman)	eastern United States	<i>Panicum capillare</i> Linné (Poaceae) (larvae) and possibly other members of the Poaceae	Ford and Cavey 1985, Needham <i>et al.</i> 1928, Riley 1985 (illustr.)
<i>G. uniformis</i> (Smith)	southern and western United States, Mexico	a species of Bombacaceae, <i>Mimosa laxiflora</i> Benth. <i>Mimosa</i> sp. (Leguminosae), <i>Digitaria sanguinalis</i> Scopoli, <i>Digitaria</i> spp. (Poaceae), <i>Celtis pallida</i> Torrey (Ulmaceae)	Riley 1985 (illustr.), Noguera 1988
<i>Glyphuroplata</i> sp. (Only reported genus of the Uroplatini reported to mine grasses and not broad leaf plants)	United States to Costa Rica	<i>Digitaria</i> sp., <i>Eriochloa</i> sp., <i>Panicum</i> sp., and <i>Valota</i> sp. (Poaceae)	Jolivet 1989a, Riley 1985, Staines 2002b
<i>Gonophora biakana</i> Gressitt	Biak island (New Guinea)	? <i>Alpinia</i> sp. (Zingiberaceae)	Gressitt 1963 (illustr.)
<i>G. bicolor</i> (Gestro)	Java	<i>Metroxylon</i> sp. (Arecaceae)	Kalshoven 1981
<i>G. bowringii</i> Baly	Java	<i>Curcuma</i> sp., <i>Zingiber cassumunar</i> Roxburgh (Zingiberaceae) larvae	Kalshoven 1957, Staines 2003b
<i>G. cubicularis</i> Gressitt	New Guinea	'smooth-leaved ginger, possibly <i>Alpinia</i> ' sp. (Zingiberaceae)	Gressitt 1963 (illustr.)
<i>G. cyperaceae</i> Gressitt	Admiralty Islands (New Guinea)	'small sedge, near <i>Scleria</i> (?)' (Cyperaceae) larvae	Gressitt 1960a (illustr.)
<i>G. donaxiae</i> Gressitt	New Guinea	<i>Donax caniniformis</i> Schumann (Marantaceae) larvae	Gressitt 1963 (illustr.)
<i>G. haemorrhoidalis</i> Weber	Sumatra, Sunda Islands, Moluccas	<i>Amomum</i> sp. (Zingiberaceae) larvae	Gressitt 1957, Kalshoven 1957, Staines 2003b
<i>G. integra</i> Baly	Java	probably <i>Amomum</i> sp. larvae, <i>Nicolaia</i> sp., <i>Zingiber</i> sp. (Zingiberaceae)	Kalshoven 1957, Staines 2003b, Uhmann 1955 (illustr.)
<i>G. maai</i> Gressitt	New Guinea	<i>Alpinia</i> sp. (Zingiberaceae)	Gressitt 1963 (illustr.)
<i>G. musae</i> Gressitt	New Guinea	<i>Musa</i> sp. (Musaceae), <i>Costus</i> sp. (Zingiberaceae)	Gressitt 1963 (illustr.)
<i>G. pellucida</i> Gressitt	New Guinea	<i>Alpinia</i> sp. (Zingiberaceae)	Gressitt 1963 (illustr.)
<i>G. puncticollis</i> Gressitt	New Guinea	<i>Alpinia</i> sp. (Zingiberaceae)	Gressitt 1963 (illustr.)
<i>G. scleriae</i> Gressitt	New Guinea	<i>Scleria</i> ? sp. (Cyperaceae)	Gressitt 1963 (illustr.)
<i>G. semiviridis</i> Gressitt	New Guinea	? <i>Alpinia</i> sp. (Zingiberaceae)	Gressitt 1963 (illustr.)
<i>G. sinuicosta</i> Gressitt	New Guinea	<i>Alpinia</i> sp. and other gingers (Zingiberaceae)	Gressitt 1963 (illustr.)
<i>G. taylorii</i> Spaeth	Java	Orchidaceae, and probably <i>Amomum</i> sp. (Zingiberaceae) larvae	Kalshoven 1957, Maulik 1937

Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<i>G. xanthomela</i> (Wiedemann)	Sumatra, Java, Borneo	<i>Musa</i> sp. (Musaceae), <i>Arundina</i> sp., <i>Phalaenopsis amabilis</i> (Linné) Blume, <i>Spathoglottis</i> sp., <i>Vanda coerulea</i> Griffith ex Lindley, <i>V. tricolor</i> Hooker, <i>Vanda</i> sp. (Orchidiaceae), <i>Amomum</i> sp., <i>Nicolaia</i> sp., <i>Elatteria</i> sp. (Zingiberaceae) all larvae			Maulik 1937; Kalshoven 1957, 1981 (illustr.); Staines (2003b); Uhmann 1955 (illustr.)
<i>Gonophora</i> sp.	Asia, Indo-Australian region	<i>Arundina</i> sp., <i>Dendrobium</i> sp., <i>Phalaenopsis</i> sp., <i>Spathoglottis</i> sp., <i>Vanda</i> sp. (Orchidiaceae), <i>Donax</i> sp., <i>Setaria</i> sp. (Poaceae), <i>Alpinia</i> sp., <i>Amomum</i> sp., <i>Curcuma</i> sp., <i>Elettaria</i> sp., <i>Nicolaia</i> sp. (Zingiberaceae)			Jolivet 1989a
<i>Heptispa limbata</i> (Baly)	Central America	<i>Cassia fruticosa</i> Miller (Leguminosae), <i>C. grandis</i> Linné (larvae), <i>Cassia</i> sp., <i>Inga edulis</i> Martinez, <i>Inga</i> sp. (larvae), <i>Machaerium</i> sp., <i>Mimosa</i> sp., (Leguminosae) larvae, <i>Serjania</i> sp. (Sapindaceae) larvae (record of <i>Serjania</i> is questioned by Hespenheide and Dang 1999)			Hespenheide and Dang 1999, Maes 1998, Maulik 1937, Uhmann 1934 (illustr.), 1937 (illustr.)
<i>Heptispa</i> sp.	Mexico to Brazil	<i>Cassia</i> sp., <i>Inga</i> sp., <i>Machaerium</i> sp., <i>Mimosa</i> sp. (Leguminosae), <i>Serjania</i> sp. (Sapindaceae)			Staines 2002b
<i>Heterispa costipennis</i> (Bohemann)	Paraguay, Uruguay, Argentina	<i>Althaea</i> sp., <i>Malvastrum coromandelinus</i> (Linné) Gracke, <i>Sida rhombifolia</i> Linné, <i>Sphaeralcea bonariensis</i> (Cavanilles) Grisebach (Malvaceae), <i>Panicum</i> sp. (Poaceae)			Maulik 1919, Monrós and Viana 1947 (illustr.)
<i>H. vinula</i> (Erichson)	Mexico, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia	<i>Indigofera</i> sp. (Leguminosae), <i>Sida rhombifolia</i> Linné (larvae), <i>Sida</i> sp. (Malvaceae), <i>Guazuma ulmifolia</i> Linné (larvae), <i>Guazuma</i> sp. (Sterculiaceae), <i>Apeiba membranacea</i> Spruce ex Bentham <i>Triumfetta josefina</i> Polak. (larvae), <i>Triumfetta</i> sp. (Tiliaceae)			Hespenheide and Dang 1999; Maes 1998; Maes and Staines 1991; Maulik 1937; Noguera 1988; Staines 1996; Uhmann 1934 (illustr.), 1937
<i>Heterispa</i> sp.	Mexico to Argentina	<i>Althaea</i> sp., <i>Malvastrum</i> sp., <i>Sida</i> sp., <i>Sphaeralcea</i> sp. (Malvaceae), <i>Panicum</i> sp., <i>Stenotaphrum</i> sp. (Poaceae), <i>Guazuma</i> sp. (Sterculiaceae), <i>Apeiba</i> sp., <i>Triumfetta</i> sp. (Tiliaceae)			Jolivet 1989a, Staines 2002b
<i>Hispa andrewesi</i> Weise <i>H. atra</i> Linné	China northern Africa, Europe, Asia	'narrow leaved grass' (larvae) <i>Agropyron repens</i> Beauvois, <i>Agropyron repens</i> Beauvois, <i>Agropyron</i> sp., <i>Agrostis</i> sp., <i>Avena</i> sp., <i>Elymus repens</i> (Linné) Gould, <i>Helicotrichon</i> sp., <i>Phleum</i> sp., <i>Poa compressa</i> Linné, <i>Poa</i> spp., <i>Triticum</i> sp. (Poaceae) 'beetles seen on cereals'			Gressitt and Kimoto 1963 (illustr.), Kalshoven 1957 Bordy 2000 (illustr.), Chen <i>et al.</i> 1986 (illustr.), Collart 1928, Grandi 1959 (illustr.), Gressitt and Kimoto 1963, Hering 1957, Kaszab 1962, Koch 1992, Lopatin 1984, Maulik 1937, Medvedev and Zaitzev 1978
<i>H. ramosa</i> Gyllenhal	United Provinces (India), Sri Lanka	'cholum' <i>Sorghum</i> sp. (Poaceae)			Maulik 1937
<i>H. stygia</i> Chapuis <i>H. viridicyanea</i> Kraatz	India Congo	<i>Sorghum</i> sp. (Poaceae) <i>Vossia</i> sp. (Poaceae)			Maulik 1937 Collart 1934

<i>Hispa</i> sp.	Palaearctic, Turkey, and Indonesia	<i>Cistus</i> sp. (Cistaceae), <i>Aegopodium</i> sp., <i>Agropyrum</i> sp., <i>Dactylis</i> sp., <i>Digitaria</i> sp., <i>Poa</i> sp., <i>Saccharum</i> sp., <i>Sorghum</i> sp., <i>Triticum</i> sp., <i>Zea</i> sp., <i>Zizania</i> sp. (Poaceae), <i>Malus</i> sp. (Rosaceae), <i>Robinia</i> sp. (Leguminosae), <i>Zizyphus</i> sp. (Rhamnaceae), <i>Physalis</i> sp. (Solanaceae), <i>Lantana</i> sp. (Verbenaceae)	Jolivet 1989a
<i>Hispellinus albertisii</i> (Gestro) <i>H. callicanthus</i> (Bates)	Australia, New Guinea Sri Lanka, India, Burma (or Myanmar), Thailand, Laos, Cambodia, Vietnam, China, Taiwan, Malaysia, Indonesia, Sumatra, Nias, Borneo, Philippine Islands, Indonesia	wild <i>Saccharum</i> sp. (Poaceae) larvae <i>Centothea</i> sp. ('suan-me-mang' genus), <i>Imperata</i> sp. ('bai-mao' genus), <i>Oryza sativa</i> Linné (larvae), <i>Saccharum</i> sp. (sugarcane), <i>Zizania</i> sp., 'bamboo' ( <i>Bambusa</i> sp.) (Poaceae)	Gressitt 1957, 1960a, 1963; Kalshoven 1957 Abdullah and Qureshi 1969; Chen <i>et al.</i> 1986 (illustr.); Kalshoven 1957; Kimoto 1999 (illustr.); Maulik 1919, 1937; Tan 1993 (illustr.)
<i>H. coarctatus</i> (Chapuis) <i>H. csikii</i> (Gestro)	Australia, New Guinea New Guinea	'grasses' <i>Themeda</i> sp., <i>Imperata</i> sp., <i>Saccharum spontaneum</i> Linné (Poaceae) <i>Miscanthus</i> sp. (Poaceae)	Gressitt 1963 Gressitt 1957 (illustr.), 1960a, 1963
<i>H. moerens</i> (Baly)	eastern China, Korea, Japan, Taiwan, Siberia		An <i>et al.</i> 1985, Chen <i>et al.</i> 1986 (illustr.), Gressitt and Kimoto 1963
<i>H. moestus</i> (Baly)	Burma, India, south eastern Asia, Philippine Islands, southern China, Hainan Island, Malaya	'bamboo', <i>Saccharum officinarum</i> Linné, grass leaf (Poaceae)	Cox 1996 (illustr.), Gressitt and Kimoto 1963 (illustr.), Kalshoven 1957
<i>H. multispinosus</i> (Germar)	Australia, Papua-New Guinea (?), Buru (?)	<i>Themeda</i> sp., <i>Imperata</i> sp., <i>Saccharum spontaneum</i> Linné 'grasses', (Poaceae)	Gressitt 1957, 1960a, 1963
<i>Hispellinus</i> sp.	Old World	<i>Imperata</i> sp., <i>Heteropogon</i> sp., <i>Miscanthus</i> sp., <i>Oryza</i> sp., <i>Panicum</i> sp., <i>Paspalum</i> sp., <i>Saccharum</i> sp., <i>Sorghum</i> sp., <i>Themeda</i> sp., <i>Zea</i> sp., <i>Zizania</i> sp. (Poaceae)	Jolivet 1989a
<i>Hispoleptis diluta</i> (Guérin-Ménéville)	French Guiana	<i>Elaeis guineensis</i> Jacquin (Arecaceae)	Mariau 2001
<i>H. ollagnieri</i> Berti and Desmier de Chenon	Colombia	<i>Elaeis guineensis</i> Jacquin (Arecaceae)	Mariau 2001
<i>H. subfasciata</i> Pic <sup>5</sup>	Latin America, especially Ecuador, Colombia, and Amazon region	<i>Elaeis guineensis</i> Jacquin (Arecaceae)	Mariau 1988, 2001
<i>Hispoleptis</i> sp.	French Guyana to Brazil	<i>Elaeis</i> sp., <i>Cocos</i> sp. (Arecaceae)	Jolivet 1989a, Staines 2002b
<i>Javeta arecae</i> Uhmman	Sumatra	<i>Areca</i> sp. (Arecaceae) larvae	Kalshoven 1957, 1981
<i>J. corporaali</i> Uhmman	Java	<i>Pinanga kuhlii</i> Blume (Arecaceae) larvae	Kalshoven 1957
<i>J. thoracica</i> Uhmman	Java	<i>Metroxylon</i> sp. (Arecaceae) larvae	Kalshoven 1957
<i>Javeta</i> sp.	Indonesia: Java and Sumatra, Hainan Island	<i>Areca</i> sp., <i>Metroxylon</i> sp., <i>Pinanga</i> sp. (Arecaceae)	Jolivet 1989a
<i>Klitispa opacula</i> (Spaeth)	Java	<i>Bambusa</i> sp. (Poaceae) larvae	Kalshoven 1957, Maulik 1937
<i>Klitispa</i> sp.	Java	bamboo (Poaceae) larvae	Jolivet 1989a, Kalshoven 1957
<i>Metaxycera subapicalis</i> Bondar	Brazil	<i>Cecropia</i> sp.	Jolivet 1989a, 1989b
<i>Micrispa alpiniae</i> (Gressitt)	New Guinea	<i>Alpinia</i> sp. (Zingiberaceae)	Gressitt 1957 (illustr.), 1960a, 1963 (illustr.); Staines 2003b

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<i>M. biakana</i> Gressitt	New Guinea	? <i>Alpinia</i> sp. (Zingiberaceae)			Gressitt 1963, Staines 2003b
<i>M. costi</i> Gressitt	New Britain, New Ireland (New Guinea)	<i>Alpinia</i> sp. (adult), <i>Costus</i> sp. (larvae) (Zingiberaceae) adults			Gressitt 1957 (illustr.), 1960a; Staines 2003b
<i>M. cubicularis</i> Gressitt	New Guinea	'a smooth-leaved ginger', ? <i>Alpinia</i> sp. (Zingiberaceae)			Gressitt 1963, Staines 2003b
<i>M. donaxiae</i> Gressitt	New Guinea	<i>Donax cunniformis</i> Rolfe, ? <i>Heliconia</i> sp. (Heliconiaceae), ? <i>Costus</i> sp. (Zingiberaceae)			Gressitt 1963 (illustr.), Staines 2003b
<i>M. maai</i> Gressitt	New Guinea	<i>Alpinia</i> sp. (Zingiberaceae)			Gressitt 1963, Staines 2003b
<i>M. musae</i> Gressitt	New Guinea	<i>Musa</i> sp. (Musaceae), <i>Costus</i> sp. (Zingiberaceae)			Gressitt 1963, Staines 2003b
<i>M. pellucida</i> Gressitt	New Guinea	<i>Alpinia</i> sp. (Zingiberaceae)			Gressitt 1963, Staines 2003b
<i>M. puncticollis</i> Gressitt	New Guinea	<i>Alpinia</i> sp. (Zingiberaceae)			Gressitt 1963, Staines 2003b
<i>M. semiviridis</i> Gressitt	New Guinea	<i>Alpinia</i> sp. (Zingiberaceae) larvae			Gressitt 1963, Staines 2003b
<i>M. sinuicosta</i> Gressitt	New Guinea	<i>Alpinia</i> sp. and other gingers (Zingiberaceae)			Gressitt 1963, Staines 2003b
<i>M. zinzibarisis</i> (Motschulsky)	Sri-Lanka, Java	'ginger' (Zingiberaceae) larvae			Kalshoven 1957, Staines 2003b
<i>Micrispa</i> sp.	southeastern Asia	<i>Maranta</i> sp. (Marantaceae) larvae			Cox 1996 (illustr.), Jolivet 1989a, Kalshoven 1957, Kimoto 1999
<i>Microrhopala cyanea</i> (Say)	southern Canada, United States	<i>Solidago drummondii</i> Torrey and A.Gray , <i>Solidago</i> sp. (Asteraceae)			Riley and Enns 1979, Staines to Santiago-Blay, pers. comm., July 2003
<i>M. erebus</i> (Newman)	Florida (United States) and Mexico	<i>Solidago</i> sp. (Asteraceae)			Clark 1983, Noguera 1988
<i>M. excavata</i> (Olivier) (including data for subspecies recognized by Clark 1983)	southern Canada and United States	<i>Doellingeria umbellata</i> Nees, <i>Helianthus</i> sp., and <i>Solidago</i> sp. (Asteraceae)			Clark 1983, Hilgendorf and Goeden 1981
<i>M. floridana</i> Schwarz	eastern and southeastern United States	<i>Chrysopsis</i> (Michaux) Elliott or <i>Pityopsis graminifolia</i> (Michaux) Nutall (Asteraceae), <i>Lupinus diffusus</i> Nuttall (Leguminosae; according to Clark, a questionable host plant record)			Chittenden 1902, Clark 1983, Maulik 1937, McCauley 1938, Needham <i>et al.</i> 1928
<i>M. perforata</i> Baly	Guatemala to Colombia	<i>Salvia costaricensis</i> Oersted (larvae), <i>Salvia</i> sp. (Lamiaceae) adults			Maes 1998, Staines 1996
<i>M. pulchella</i> Baly	Mexico, Honduras, Nicaragua, Costa Rica	<i>Gossypium</i> sp., <i>Sida acuta</i> N. L. Burman (Malvaceae) adults, <i>Zea</i> sp. (Poaceae)			Gillett <i>et al.</i> 1991, Maes 1998, Maes and Staines 1991
<i>M. rileyi</i> Clark	southeastern United States	<i>Helkianthus</i> sp. (Asteraceae)			Clark 1983
<i>M. rubrolineata</i> (Mannherheim) (including data subspecies recognized by Clark 1983)	western United States and Mexico	<i>Ambrosia chenopodiifolia</i> (Bentham) Payne (larvae), <i>A. confertifolia</i> DeCandolle (adults), <i>A. dumosa</i> (Gray) Payne (adults), <i>Brickelia vernica</i> Robinson (adults), <i>Encelia californica</i> Nuttall, <i>E. farinosa</i> A. Gray <i>ex</i> Torrey, <i>E. halimifolia</i> Cavanilles (adults), <i>Flourensia cernua</i> DeCandolle (larvae), <i>Franseria acanthicarpa</i> (Hooker) Coville, <i>F. ambrosioides</i> Cavanilles, <i>F. confertiflora</i> (DeCandolle) Rydberg, <i>Franseria</i> sp., <i>Haplopappus squarrosus</i> Hooker and Arnold, <i>H. venetus</i> S.F. Blake, <i>Helianthus hirsutus</i> Rafinesque, <i>Helianthus</i> sp., <i>Heterotheca</i>			Clark 1983; Goeden and Ricker 1975, 1976a, 1976b; Jones and Brisley 1925, McCauley 1938, Moldenke 1971, Richerson and Boldt 1995, Riley and Enns 1979

<i>M. vittata</i> (Fabricius)	United States and southwestern Canada	<i>grandiflora</i> Nuttall, <i>Solidago californica</i> Nuttall (larvae), <i>Solidago</i> sp. (Asteraceae) <i>Seriocarpus</i> sp., <i>Silphium laciniatum</i> Linné, <i>S. perfoliatum</i> Linné, <i>Silphium</i> sp., <i>Solidago altissima</i> Linné, <i>S. canadensis</i> Linné, <i>S. graminifolia</i> (Linné) Salisbury, <i>S. juncea</i> Aiton, <i>S. laevigata</i> Aiton, <i>S. lanceolata</i> Burman f., <i>S. missouriensis</i> Nuttall, <i>S. mollis</i> Bartling, <i>S. nemoralis</i> Aiton, <i>S. sempervirens</i> Linné, <i>Solidago</i> spp. (Asteraceae)	Byes 2002 (illustr.); Cappucino 1991; Chittenden 1902; Clark 1983, 2000; Damman (1994); Ford and Cavey 1985 (illustr.); Lawson 1991; Maulik 1919; McCauley 1938; Needham <i>et al.</i> 1928; Riley and Enns 1979
<i>M. xerene</i> (Newman)	United States and southern Canada	<i>Ambrosia chamissonis</i> (Lessing) Greene, <i>Aster chilensis</i> Nees, <i>A. cordifolius</i> Linné, <i>A. novae-angliae</i> Linné, <i>A. patens</i> Aiton, <i>A. paternus</i> Cronquist, <i>A. psilostachya</i> DeCandolle (larvae), <i>A. puniceus</i> Linné (larvae), <i>A. simplex</i> Willdenow (larvae), <i>Boltonia asteroides</i> (Linné) L'Her, <i>Aster</i> sp., <i>Boltonia</i> sp., <i>Seriocarpus asteroides</i> (Linné) BSP, <i>Seriocarpus</i> sp., <i>Solidago caesia</i> Linné, <i>S. canadensis</i> Linné, <i>S. juncea</i> Aiton, <i>Solidago</i> sp., (Asteraceae), <i>Setaria viridis</i> (Linné) Beauvois (Poaceae), 'boneset', 'bottle brush grass', 'box elder', 'boxwood' 'service berry', 'shad bush'	Chittenden 1902; Clark 1983, 2000; Ford and Cavey 1985 (illustr.); Goeden and Ricker 1974, 1976c; McCauley 1938; Needham <i>et al.</i> 1928; Riley and Enns 1979; Williams 1989b, 1991
<i>Microrhopala</i> sp.	Canada to Colombia	<i>Ambrosia</i> sp., <i>Aster</i> sp., <i>Boltonia</i> sp., <i>Brickellia</i> sp., <i>Chrysopsis</i> sp., <i>Dicoria canescens</i> Torrey and Gray, <i>Encelia</i> sp., <i>Franseria</i> sp., <i>Helianthus</i> sp., <i>Silphium</i> sp., <i>Sericocarpus</i> sp., <i>Solidago</i> sp. (Asteraceae), <i>Salvia</i> sp. (Lamiaceae)	Goeden and Teerink 1993, Staines 2002b
<i>Nonispa carlosbruchi</i> Maulik	Argentina	<i>Panicum grumosum</i> Nees, <i>Paspalum</i> sp. (Poaceae)	Monrós and Viana 1947 (illustr.)
<i>Ocnosispa humerosa</i> Staines	Costa Rica	'Taken fogging <i>Conceveiba pleiostemona</i> J. Donnell Smith (Euphorbiaceae).'	Staines 2002a (illustr.)
<i>Octhispa bimaculata</i> Uhmman	Costa Rica	<i>Stigmaphyllon lindenianum</i> A. Jussieu (Malpighiaceae) larvae	Hespenheide 2000, Hespenheide and Dang 1999
<i>O. decepta</i> (Baly)	Nicaragua, Costa Rica, Panama	<i>Stigmaphyllon lindenianum</i> A. Jussieu (Malpighiaceae) larvae	Hespenheide 2000, Hespenheide and Dang 1999, Maes 1998
<i>O. elegantula</i> (Baly)	Central America	<i>Pithecoctenium echinatum</i> K. Schumann (Bignoniaceae) larvae, <i>Serjania costaricensis</i> unable to find name (larvae), <i>Serjania</i> sp., <i>Paullinia</i> sp. (Sapindaceae) larvae	Cox 1996 (illustr.), Hespenheide and Dang 1999, Maulik 1937, Uhmman 1937
<i>O. elevata</i> (Baly)	Central America	<i>Pithecoctenium echinatum</i> K. Schumann (Bignoniaceae) larvae, <i>Paullinia costaricensis</i> Radkofer (larvae), <i>Paullinia</i> sp. larvae (Sapindaceae)	Hespenheide and Dang 1999, Maulik 1937, Uhmman 1934 (illustr.)
<i>O. elongatas</i> Chapuis	Argentina	Sapindaceae	Monrós and Viana 1947 (illustr.)
<i>O. gracilis</i> (Weise)	Paraguay, Bolivia, Argentina	<i>Adenocalymma marginata</i> (Chamisso) DeCandolle (Bignoniaceae)	Monrós and Viana 1947 (illustr.)
<i>O. haematopyga</i> (Baly)	Costa Rica	<i>Colubrina spinosa</i> John Donnell Smith (larvae), <i>Colubrina</i> sp. (Rhamnaceae) larvae	Hespenheide 2000, Hespenheide and Dang 1999



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<i>O. loricata</i> Weise	Puerto Rico	<i>Coccoloba uvifera</i> (Linné)	Linné	(Polygonaceae)	Sanderson 1967
<i>O. nervermanni</i> Uhmann	Costa Rica	<i>Ochroma lagopus</i> Swartz		(Bombacaceae)	Hespenheide and Dang 1999, Wilcox 1975
<i>O. spitzii</i> Uhmann	Paraguay, Argentina	Malpighiaceae			Monrós and Viana 1947 (illustr.)
<i>Octhispa</i> sp.	Mexico to Argentina	<i>Ochroma</i> sp. (Bombacaceae), <i>Adenocalymma</i> sp., <i>Paullinia</i> sp., <i>Serjania</i> sp. (Ehretiaceae), <i>Cassia</i> sp., <i>Dioclea</i> sp., <i>Inga</i> sp., <i>Machaerium</i> sp. (Leguminosae), <i>Byrsonima</i> sp., <i>Malpighia</i> sp., <i>Stigmaphyllon</i> sp. (Malpighiaceae), <i>Coccoloba</i> sp. (Polygonaceae), <i>Colubrina</i> sp. (Rhamnaceae), <i>Basanacantha</i> sp. (Rubiaceae)			Staines 2002b
<i>Octotoma championi</i> Baly	Panama, Costa Rica, Honduras, Nicaragua, Guatemala, México, and southern Texas (United States). Introduced into Hawaii and South Africa for biological control of <i>Lantana</i> spp.	<i>Mentha</i> sp., <i>Origanum</i> sp. (Lamiaceae), <i>Sesamum</i> sp. (Pedaliaceae) all previous ones, adults; <i>Lantana camara</i> Linné; <i>L. hispida</i> Kunth; <i>L.</i> <i>urticifolia</i> Miller; <i>Lantana</i> sp. (Verbenaceae)			Broughton 2000, Cilliers 1983, Maes 1998, Maes and Staines 1991, Staines 1996 (illustr.) , Uhmann 1934, 1937
<i>O. gundlachi</i> Suffrian	Cuba	<i>Lantana</i> sp. (Verbenaceae) (larvae)			Krauss 1964, Staines 1989
<i>O. marginicollis</i> Horn	southwestern United States and Mexico	<i>Perezia thurberi</i> Gray (Asteraceae) (larvae), <i>Ocimum basilicum</i> Linné (Lamiaceae), <i>Fraxinus</i> sp. (Oleaceae) (adults)			Jones and Brisley 1925. Needham <i>et al.</i> 1928, Staines 1989 (illustr.)
<i>O. plicatula</i> (Fabricius)	Brazil, Honduras, Cuba, eastern and southern United States	<i>Daucus carota</i> Linné (Apiaceae) (adults), <i>Lactuca</i> sp. (Asteraceae), <i>Campsis radicans</i> (Linné) Seeman ex Bureau (larvae) (Bignoniaceae), <i>Aesculus</i> sp. (larvae? and adults) (Hippocastanaceae), <i>Lespedeza capitata</i> Michaux, <i>Lespedeza</i> sp. (larvae) (Leguminosae), <i>Chionanthus</i> <i>virginica</i> Linné (larvae? and adults), <i>Fraxinus</i> <i>americana</i> Linné, <i>F. pennsylvanica</i> Marshall, <i>Fraxinus</i> sp. (adults), <i>Ligustrum vulgare</i> Linné, <i>Ligustrum</i> sp. (adults) (Oleaceae), <i>Tilia americana</i> Linné (Tiliaceae), <i>Lantana</i> sp. (Verbenaceae) larvae			Balsbaugh and Hays 1972, Broughton 2000, Chittenden 1902, Clark 2000, Ford and Cavey 1985 (illustr.), Krauss 1964, Needham <i>et al.</i> 1928 (illustr.), Riley and Enns 1979, Staines 1989 (illustr.)
<i>O. scabripennis</i> Guérin-Ménéville	Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Hawaii, Australia, South Africa	<i>Eupatorium collinum</i> DeCandolle (Asteraceae) adults, <i>Quercus astriglanis</i> Warburg (Fagaceae) adults, <i>Mentha spicata</i> Linné (adults), <i>M. viridis</i> Linné, <i>Mentha</i> sp. (adults), <i>Origanum</i> sp. (adults), <i>Salvia occidentalis</i> Swartz (adults), <i>Salvia</i> sp. (adults) (Lamiaceae) , <i>Phaseolus vulgaris</i> Linné, <i>Phaseolus</i> sp. (adults), <i>Stizolobium aterrimum</i> Piper and Tracy, <i>Stizolobium</i> sp. (adults), <i>Vigna</i> <i>unguiculata</i> (Linné) Walpers (adults), <i>Vigna</i> sp. (adult) (Leguminosae) (adults), <i>Sesamum</i> <i>orientale</i> Linné (adults), <i>Sesamum</i> sp. (Pedaliaceae), <i>Lantana camara</i> Linné (larvae), <i>L. glandulosissima</i>			Annonymous, no date; Broughton 2000; Cilliers 1977, 1983, 1987a (illustr.), 1987b (illustr.); Harley 1969; Krauss 1964; Maes 1998, Moldenke 1971; Needham <i>et al.</i> 1928; Staines 1989 (illustr.)

<i>O. tessellata</i> Maulik <i>Octotoma</i> sp.	Brazil United States to Brazil	Hayek (larvae), <i>Lantana</i> sp. (larvae), <i>Lippia umbellata</i> Cavanilles (adults), <i>Tectona grandis</i> Linné F. (Verbenaceae) (adults) <i>Canavalia ensiformis</i> DeCandolle (Leguminosae) <i>Eupatorium</i> sp. (Asteraceae), <i>Campsis</i> sp., <i>Tecoma</i> sp. (Bignoniaceae), <i>Mentha</i> sp., <i>Monarda</i> sp., <i>Origanum</i> sp., <i>Salvia</i> sp., <i>Quercus</i> sp. (Fagaceae), (Lamiaceae), <i>Canavalia</i> sp., <i>Cymbosema</i> sp., <i>Dioclea</i> sp., <i>Lespedeza</i> sp. (Leguminosae), <i>Stigmaphyllon</i> sp. (Malpighiaceae), <i>Fraxinus</i> sp. (Oleaceae), <i>Sesamum</i> sp. (Pedaliaceae), <i>Clerodendron</i> sp., <i>Lantana</i> sp., <i>Tectona</i> sp., <i>Verbena</i> sp. (Verbenaceae), <i>Xanthorrhoea</i> sp. (Xanthorrhoeaceae)	Maulik 1929 Jolivet 1989a, Staines 2002b
<i>Octouropata octopustulata</i> (Baly)	Brazil	<i>Senna australis</i> (Vellozo) H.S.Irwin and R.C.Barneby (Leguminosae), <i>Eugenia ovalifolia</i> Cambess. (Myrtaceae), <i>Ouratea cuspidata</i> Tieghen (Ochnaceae)	Teixeira <i>et al.</i> 1999 (illustr.)
<i>Octouropata</i> sp. <i>Odontota arizonicus</i> (Uhmann) <i>O. dorsalis</i> (Thunberg)	French Guyana to Argentina Arizona (United States) southeastern Canada, eastern United States	<i>Senna</i> sp. (Leguminosae) <i>Glycine soja</i> (Linné) (Leguminosae) <i>Acer saccharum</i> Marshall (Aceraceae), <i>Betula alba</i> Linné, <i>Betula</i> sp. adults (Betulaceae), <i>Fagus</i> sp. (adults), <i>Quercus alba</i> Linné, <i>Q. pedunculata</i> Ehrhart, <i>Q. rubra</i> Linné, <i>Q. prinus</i> Linné, <i>Quercus</i> sp. (adults) (Fagaceae), ‘rhododendron’ (Ericaceae), <i>Amorpha fruticosa</i> Linné, <i>Desmodium</i> sp. (adults), <i>Falcata comosa</i> (Linné) Kuntze, <i>Glycine max</i> (Linné) Merrill (larvae), <i>Laburnum</i> spp. (larvae), <i>Malus sylvestris</i> Miller, <i>Pueraria lobata</i> (Willdenow) Owhi (adults), <i>P. montana</i> (Loureiro) Merrill var. <i>lobata</i> (Willdenow) Maesen and S. Almeida, <i>Robinia hispida</i> Linné, <i>R. pseudoacacia</i> Linné, <i>Robinia</i> sp. (larvae in all <i>Robinia</i> ), <i>Sophora japonica</i> Linné (larvae), <i>Wisteria</i> sp. (adults) (Leguminosae), <i>Polygonum perfoliatum</i> Linné (Polygonaceae) adult, <i>Crataegus calpodendron</i> (Ehrhart) Medic, <i>C. coccinea</i> Linné, <i>C. tomentosa</i> Linné (adults), <i>Malus sylvestris</i> Miller (adults), <i>Prunus serotina</i> Ehrhart, ‘some quinces’ (Rosaceae), <i>Ulmus americana</i> Linné (Ulmaceae)	Staines 2002b Butte 1968c (illustr.) Anonymous 2000; Butte 1968c (illustr.); Chittenden 1902 (illustr.); Clark 2000; Ford and Cavey 1985 (illustr.); Hargrove 1986; Hodson 1942; Kirkendall 1984; Kogan and Kogan 1979; Lawson 1991; McPherson and Ravlin 1983; Mullins 1976; Needham <i>et al.</i> 1928 (illustr.); Wheeler 1980 (illustr.), 1987 (illustr.); Wheeler and Mengel 1984; Williams 1989a
<i>O. horni</i> Smith	eastern half of the United States	<i>Amphicarpa bracteata</i> (Linné) Fernald (adults), <i>Desmodium canescens</i> (Linné) DeCandolle, <i>D. illinoense</i> Gray, <i>D. rigidum</i> (Elliott) DeCandolle, <i>Glycine max</i> (Linné) Merrill, <i>Meibonia rigida</i>	Butte 1968c (illustr.), Buntin and Pedigo 1982, Chittenden 1902, Ford and Cavey 1985, Kogan and Kogan 1979 (illustr.), Needham <i>et al.</i> 1928

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<i>O. mundula</i> (Sanderson)	eastern half of the United States	Elliot, <i>Tephrosia virginiana</i> (Linné) Persoon (Leguminosae) <i>Amphicarpaea bracteata</i> (Linné) Fernald (Leguminosae) larvae			Butte 1968c (illustr.), Ford and Cavey 1985 (illustr.), Riley and Enns 1979
<i>O. notata</i> (Olivier)	eastern and southeastern United States	<i>Tephrosia virginiana</i> (Linné) Persoon (Leguminosae)			Butte 1968c (illustr.), Chittenden 1902, Needham <i>et al.</i> 1928
<i>O. scapularis</i> (Olivier)	southeastern Canada and United States	<i>Solidago</i> sp. (adults) (Asteraceae), <i>Alnus serrulata</i> (Aiton) Willdenow (adults), <i>Betula nigra</i> Linné (adults) (Betulaceae), <i>Cornus alternifolia</i> Linné f. (adults) (Cornaceae), <i>Quercus</i> sp. (adults) (Fagaceae), <i>Apios americana</i> Medikus (larvae), <i>A. tuberosa</i> Moench, <i>Desmodium</i> sp. (adults), <i>Glycine apios</i> Linné (Leguminosae), <i>Glyceria nervata</i> (Willd) Trinius (Poaceae), <i>Rubus</i> sp. (adults) (Rosaceae)			Butte 1968c (illustr.), Chittenden 1902, Ford and Cavey 1985, Needham <i>et al.</i> 1928 (illustr.), Riley and Enns 1979
<i>Odontota</i> sp.	North and Central America	<i>Aster</i> sp., <i>Eupatorium</i> sp., <i>Solidago</i> sp. (Asteraceae), <i>Alnus</i> sp., <i>Betula</i> sp., <i>Carpinus</i> sp. (Betulaceae), <i>Cornus</i> sp. (Cornaceae), <i>Rhododendron</i> sp. (Ericaceae), <i>Fagus</i> sp., <i>Quercus</i> sp. (Fagaceae), <i>Acacia</i> sp., <i>Amorpha</i> sp., <i>Amphicarpaea</i> sp., <i>Apios</i> sp., <i>Desmodium</i> sp., <i>Glycine</i> sp., <i>Meibomia</i> sp., <i>Pueraria</i> sp., <i>Robinia</i> sp., <i>Sophora</i> sp., <i>Tephrosia</i> sp. (Leguminosae), <i>Polygonum</i> sp. (Polygonaceae), <i>Amelanchier</i> sp., <i>Crataegus</i> sp., <i>Malus</i> sp., <i>Prunus</i> sp., <i>Pyrus</i> (Rosaceae), <i>Tilia</i> sp. (Tiliaceae), <i>Ulmus</i> sp. (Ulmaceae)			Jolivet 1989a
<i>Oncocephala angulata</i> Gestro	India, Malaysia Archipelago, Java, Sumatra (Indonesia)	<i>Ipomoea</i> sp. (Convolvulaceae), <i>Dioscorea</i> sp. (Dioscoreaceae) larvae, Orchidiaceae (larvae), <i>Curcuma</i> sp. (Zingiberaceae) larvae. Staines (2003b) considers that 'the true host plant of this species appears to be unknown.'			Kalshoven 1957, Maulik 1937, Staines 2003b
<i>O. dorsalis</i> Weise	India, Java	<i>Ipomoea</i> sp. (Convolvulaceae)			Anand 1989
<i>O. tuberculata</i> (Olivier)	India	<i>Ipomoea batatas</i> (Linné) Lamarck larvae, <i>I. sepiaria</i> Koenig ex Roxburgh (larvae) (Convolvulaceae), 'egg plant' (Solanaceae) larvae			Anand 1989, Maulik 1937, Zaka-ur-Rab 1991
<i>Oncocephala</i> sp.	Old World	<i>Ipomoea</i> sp., <i>Mina</i> sp. (Convolvulaceae), <i>Discorea</i> sp. (Dioscoreaceae), <i>Oryza</i> sp. (Poaceae), Orchidiaceae, <i>Curcuma</i> sp. (Zingiberaceae)			Jolivet 1989a, Staines 2003b, Uhmman 1953
<i>Oxychalepus alienus</i> (Baly)	Costa Rica, Nicaragua, Panama	<i>Cassia fruticosa</i> Miller (Leguminosae) larvae			Hespenheide and Dang 1999, Wilcox 1975
<i>O. anchora</i> (Chapuis)	Mexico, Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Ecuador, Brazil, Bolivia, Paraguay, Argentina	<i>Canavalia ensiformis</i> (Linné) DeCandolle, <i>C. spontanea</i> unable to find name, <i>Canavalia</i> sp., <i>Cimbosema</i> sp., <i>Dioclea</i> sp., <i>Phaseolus</i> sp. (Leguminosae), <i>Solanum auriculatum</i> Aiton (Solanaceae) all adults			Maes 1998, Monrós and Viana 1947 (illustr.)

<i>O. posticatus</i> (Baly)	Costa Rica	<i>Cassia fruticosa</i> Miller (Leguminosae)	Hespenheide and Dang 1999, Maes 1998
<i>Oxychalepus</i> sp.	Mexico to Argentina	<i>Pleomele</i> sp. (Agavaceae), <i>Cocos</i> sp. (Arecaceae), <i>Flagellaria</i> sp. (Flagellariaceae), <i>Heliconia</i> sp. (Heliconiaceae), <i>Cassia</i> sp., <i>Canavalis</i> sp., <i>Centrosema</i> sp., <i>Cymbosema</i> sp., <i>Dioclea</i> sp., <i>Inga</i> sp., <i>Mucuna</i> sp., <i>Phaseolus</i> sp. (Leguminosae), <i>Freycinetia</i> sp. <i>Pandanus</i> sp. (Pandanaceae), <i>Solanum</i> sp. (Solanaceae). Staines (2003b) considers the reference to <i>Heliconia</i> sp. as ‘unverified’.	Ramos 1998, Flowers and Janzen 1997, Staines 2002b
<i>Oxyroplata bellicosa</i> (Baly)	Central America	<i>Banisteria argentea</i> Sprengel (Malpighiaceae) larvae	Maulik 1937, Uhmman 1937
<i>O. nr. bellicosa</i> (Baly)	Costa Rica	unidentified host plant (larvae)	Hespenheide and Dang 1999
<i>Pentispa collaris</i> (Thunberg)	Jamaica	<i>Bunchosia</i> sp. (Malpighiaceae)	Sanderson 1967
<i>P. explanata</i> (Chapuis)	Mexico, Guatemala, Nicaragua, Costa Rica, Panama, Colombia	<i>Pithecoctenium</i> sp. (Bignoniaceae) adults	Hespenheide and Dang 1999, Maes 1998, Maes and Staines 1991
<i>P. fairmairei</i> (Chapuis)	Mexico to Panama	<i>Calea axillaris</i> DeCandolle, <i>C. urticifolia</i> DeCandolle, <i>Calea</i> sp., <i>Clibadium</i> sp. (larvae), <i>Elephantopus spicatus</i> Aublet (larvae), <i>Elephantopus</i> sp., <i>Eupatorium populifolium</i> Hooker and Arnold (larvae), <i>Eupatorium</i> sp., <i>Verbesina costaricensis</i> B. L. Robinson (larvae), <i>Verbesina</i> sp. (larvae), <i>Vernonia mollis</i> Humboldt, Bonpland and Kunth, <i>Vernonia</i> sp. (larvae) (Asteraceae), <i>Indigofera</i> sp. (Leguminosae), <i>Malpighia glabra</i> Linné, <i>Malpighia</i> sp. (Malpighiaceae), <i>Chusquea</i> sp. (Poaceae), <i>Serjania</i> sp. (Sapindaceae) adults	Hespenheide and Dang 1999, Maes 1998, Maes and Staines 1991, Staines 1996 (illustr.), Uhmman 1937 (illustr.)
<i>P. morio</i> (Fabricius)	Mexico	<i>Benthalthanthea mollis</i> (Humboldt, Bonpland, and Kunth) Alefeld, <i>Desmodium lindheimeri</i> Vail (Leguminosae) both adults	Moldenke 1971
<i>P. suturalis</i> (Baly)	southwestern United States	<i>Baccharis bigelovii</i> Gray (Asteraceae)	Boldt and Staines 1993 (illustr.), Cox 1996 (illustr.)
<i>Pentispa</i> sp.	southern United States to Peru	<i>Baccharis</i> sp., <i>Clibodium</i> sp., <i>Elephantopus</i> sp., <i>Eupatorium</i> sp., <i>Verbesina</i> sp., <i>Vernonia</i> sp. (Asteraceae), <i>Colea</i> sp., <i>Pithecoctenium</i> sp. (Bignoniaceae), <i>Malpighia</i> sp. (Malpighiaceae), <i>Chusquea</i> sp. (Poaceae), <i>Paullinia</i> sp., <i>Serjania</i> sp. (Sapindaceae)	Jolivet 1989a, Staines 2002b
<i>Pharangispa alpiniae</i> Samuelson (includes four subspecies listed in Gressitt and Samuelson 1988)	Solomon Islands (Malaita, Santa Isabel, New Georgia Group, Florida Group)	‘coconut palm’ (Arecaceae), <i>Heliconia</i> sp. (Heliconiaceae), ‘banana’ (Musaceae), ‘karo’ (Pittosporaceae), <i>Alpinia</i> sp. (larvae), <i>Freycinetia</i> sp., <i>Pandanus</i> sp. (Pandanaceae), ‘ginger’ (Zingiberaceae)	Gressitt and Samuelson 1988 (illustr.), Staines 2003b
<i>P. cristobala</i> Gressitt	Solomon Islands (San Cristobal, Malaita)	‘rattan’ (Arecaceae), <i>Heliconia</i> sp. (Heliconiaceae), ‘banana’ (Musaceae), Zingiberaceae	Gressitt and Samuelson 1988 (illustr.), Staines 2003b
<i>P. heliconiae</i> Gressitt	Solomon Islands (Santa Isabel)	<i>Heliconia</i> sp. (Heliconiaceae)	Gressitt and Samuelson 1988 (illustr.)

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<i>P. purpureipennis</i> Maulik	Solomon Islands, (Guadalcanal, Malaita, Santa Isabel), New Georgia	<i>Heliconia</i> sp. (Heliconiaceae), <i>Alpinia</i> sp., <i>Costus</i> sp. 'ginger in bush' (Zingiberaceae) larvae			Maulik 1929, 1937; Gressitt 1957 (illustr.), 1960a; Gressitt and Samuelson 1988; Staines 2003b
<i>Pharangispa</i> sp. <i>Phidodonta modesta</i> Weise	Solomon Islands Pakistan, India	<i>Costus</i> sp., <i>Zingiber</i> sp. (Zingiberaceae) <i>Andropogon sorghum</i> (Linné) Brotero (larvae), <i>Avena sativa</i> Linné, <i>Oryza sativa</i> Linné, <i>Saccharum officinale</i> Linné (larvae), <i>Sorghum vulgare</i> Persoon (Poaceae), 'wild grass' <i>Andropogon</i> sp., <i>Saccharum</i> sp., <i>Zea</i> sp. (Poaceae)			Jolivet 1989a Abdullah and Qureshi 1969, Anand 1989, Kalshoven 1957, Maulik 1919, Zaka-ur-Rab 1991
<i>Phidodonta</i> sp.	East Indies (Malasyian Archipelago and, more broadly SE Asia)				Jolivet 1989a
<i>Physocoryna expansa</i> Pic	southern Central America and northern South America	<i>Stigmaphyllon</i> sp. (Malpighiaceae) larvae			Hespenheide 2000
<i>P. scabra</i> Guérin-Ménéville	Colombia, Brazil, Paraguay, Peru, Argentina	<i>Canavalia ensiformis</i> (Linné) DeCandolle, <i>Canavalia</i> sp., <i>Cymbosema</i> sp., <i>Dioclea</i> sp., <i>Phaseolus</i> sp (Leguminosae), <i>Stigmaphyllon</i> sp. (Malpighiaceae) larvae			Monrós and Viana 1947, Staines 1998, Staines 2002b (illustr.)
<i>Physocoryna</i> sp.	Nicaragua to Argentina	<i>Canavalia</i> sp., <i>Cymbasema</i> sp., <i>Dioclea</i> sp., <i>Mucuna</i> sp., <i>Phaseolus</i> sp. (Leguminosae), <i>Stigmaphyllon</i> sp. (Malpighiaceae)			Jolivet 1989a, Staines 2002b
<i>Pistosia</i> sp. (some species are miners ) <i>Platochispa championi</i> (Baly) ' <i>Platochispa</i> sp. 1' <i>Platochispa</i> sp.	Indo-Australian region Mexico, Costa Rica, Panama Costa Rica southern United States to Peru	<i>Areca</i> sp., <i>Phoenix</i> sp. (Arecaceae) <i>Calathea</i> sp. (Marantaceae), <i>Piper</i> sp. (Piperaceae) <i>Ochroma lagopus</i> Swartz (Bombacaceae) <i>Ochroma</i> sp. (Bombacaceae), <i>Cassia</i> sp. (Leguminosae), <i>Calathea</i> sp. (Marantaceae), <i>Piper</i> sp. (Piperaceae), <i>Costus</i> sp. (Zingiberaceae)			Jolivet 1989a Hespenheide and Dang 1999, Staines 2003b, Wilcox 1975 Hespenheide and Dang 1999 Staines 2002b
<i>Platypria andrewesi</i> Weise	India, Sri Lanka	<i>Saccharum officinarum</i> Linné (Poaceae), <i>Erythrina</i> sp. (Leguminosae), <i>Zizyphus jujuba</i> Lamarck (larvae), <i>Z. mauritiana</i> Lamarck (Rhamnaceae)			Abdullah and Qureshi 1969; Anand 1989; Kalshoven 1957; Maulik 1919, 1937; Zaka-ur-Rab 1991
<i>P. coronata</i> (Guérin-Ménéville)	Africa	<i>Pueraria phaseoloides</i> (Roxburgh) Bentham (Leguminosae)			Bernon and Graves 1979
<i>P. echidna</i> (Guérin-Ménéville)	India, Sri Lanka, Burma (or Myanmar), Thailand, Vietnam	<i>Erythrina indica</i> Lamarck, <i>E. lithosperma</i> Blume ex. Miquel (larvae) (Leguminosae)			Chen <i>et al.</i> 1986 (illustr.), Kimoto 1999 (illustr.), Zaka-ur-Rab 1991
<i>P. echinogale</i> Gestro	Java, Sumatra	<i>Cajanus indicus</i> Sprengel, <i>Erythrina</i> sp., <i>Tephrosia candida</i> DeCandolle, 'katjangen' (Leguminosae) all larvae, <i>Uncaria gambier</i> Roxburgh (Rubiaceae)			Gressitt 1957, Kalshoven 1957
<i>P. erinaeus</i> (Fabricius)	India, Sri Lanka, Burma (or Myanmar), Vietnam, Borneo, Sumatra, Java, Sulawesi (= Celebes Islands), Philippines, Guinea (Principe Island, St. Thome Is.)	<i>Zizyphus</i> sp. (Rhamnaceae), 'paddy'			Anand 1989, Maulik 1937

<i>P. hystrix</i> (Fabricius)	India, Sri-Lanka Nepal, Burma (or Myanmar), Thailand, Laos, Vietnam, China, Sumatra, Indonesia, Java, Sulawesi (= Celebes Islands)	<i>Dolichos lablab</i> Linné (larvae), <i>Erythrina indica</i> Lamarck, <i>E. lithosperma</i> Blume ex. Miquel, <i>Erythrina</i> spp. (larvae), <i>Sesbania aculeata</i> (Willdenow) Poiret, <i>S. grandiflora</i> (Linné) Persoon (larvae) (Leguminosae), <i>Myrica</i> sp. (Myricaceae) larvae, <i>Rubus ellipticus</i> Smith (Rosaceae) larvae	Abdullah and Qureshi 1969, Chen <i>et al.</i> 1986 (illustr.), Gressitt and Kimoto 1963, Kalshoven 1957, Kimoto 1999 (illustr.), Maulik 1937, Zaka-ur-Rab 1991
<i>Platypria</i> sp.	Old World	<i>Quercus</i> sp. (Fagaceae), <i>Cajanus</i> sp., <i>Desmodium</i> sp., <i>Dolichos</i> sp., <i>Erythrina</i> sp., <i>Mucuna</i> sp., <i>Phaseolus</i> sp., <i>Pueraria</i> sp., <i>Sesbania</i> sp. (Leguminosae), <i>Myrica</i> sp. (Myricaceae), <i>Ziziphus</i> sp. (Rhamnaceae), <i>Pyrus</i> sp., <i>Rubus</i> sp. (Rosaceae), <i>Uncaria</i> sp. (Rubiaceae)	Chen <i>et al.</i> 1986 (illustr.), Jolivet 1989a
<i>Plesispa cocotis</i> Maulik	New Caledonia	<i>Cocos nucifera</i> Linné (Arecaceae)	Lepesme 1947 (illustr.)
<i>P. hagenensis</i> Gressitt	New Guinea	<i>Heterospathe</i> ? (Arecaceae)	Gressitt 1960a (illustr.)
<i>P. korthalsiae</i> Gressitt	New Guinea	<i>Calamus</i> sp., <i>Korthalsia</i> sp., palm similar to <i>Heterospathe</i> sp. (Arecaceae) all larvae	Gressitt 1963 (illustr.)
<i>P. montana</i> Gressitt	New Guinea	<i>Saccharum officinarum</i> Linné (Poaceae) larvae	Gressitt 1960a (illustr.)
<i>P. nipae</i> Maulik	Malaysian Peninsula, Java	<i>Areca catechu</i> Linné, <i>Cocos</i> sp., <i>Metroxylon sagu</i> Rottbóll, <i>Nypa fruticans</i> Thunberg, <i>Oncosperma</i> sp. (Arecaceae)	Kalshoven 1981 (illustr.), Lepesme 1947, Maulik 1937
<i>P. palmarum</i> Gressitt	New Guinea	possibly <i>Rhopaloblaste</i> sp. (Arecaceae) larvae	Gressitt 1960a (illustr.)
<i>P. palmella</i> Gressitt	New Guinea	<i>Archontophoenix</i> sp., <i>Areca</i> sp., <i>Korthalsia</i> sp., <i>Metroxylon</i> sp., <i>Phoenix</i> sp. (Arecaceae) all larvae	Gressitt 1963 (illustr.)
<i>P. reichei</i> Chapuis	Thailand, Malaysia, Indonesia, Philippines, New Guinea, (New Britain, Cape York Peninsula, Malacca), Malaysian Peninsula, Sumatra, Java, Sulawesi (= Celebes Islands) Indonesia, Bismark Archipelago, Samoa, Australia	<i>Adonidia merrilli</i> Beccari (larvae), <i>Archontophoenix</i> sp., <i>Areca catechu</i> Linné, <i>Areca</i> sp., <i>A. pinnata</i> (Wurmb) Merrill, <i>Arenga</i> sp., <i>Borreria flabellifer</i> Linné (larvae), <i>Calamus</i> spp., <i>Caryota cumingii</i> Loddiges ex Martinez (larvae), <i>Cocos nucifera</i> Linné (larvae), <i>Corypha elata</i> Roxburgh, <i>Cyrtostachys renda</i> Blume <i>Daemonorops</i> sp., <i>Korthalsia</i> sp., <i>Metroxylon sagu</i> Rottbóll, <i>Metroxylon</i> sp., <i>Nypa fruticans</i> Thunberg, <i>Oreodoxa regia</i> Kunth (Arecaceae), <i>Flagellaria indica</i> Linné, <i>Flagellaria</i> sp. (Flagellariaceae), <i>Leptochloa chinensis</i> (Roth) Nees (Poaceae)	Gallego and Abad 1985; Howard <i>et al.</i> 2001; Maulik 1937; Gressitt 1957 (illustr.), 1960a, 1963; Kalshoven 1981 (illustr.); Lepesme 1947; Panggoy and Pedro 1982 (illustr.)
<i>P. ruficollis</i> Spaeth	New Caledonia	<i>Cocos nucifera</i> Linné (Arecaceae)	Lepesme 1947
<i>P. saccharivora</i> Gressitt	New Guinea	<i>Saccharum officinarum</i> Linné (Poaceae) larvae	Cox 1996 (illustr.); Gressitt 1957 (illustr.), 1960a
<i>Plesispa</i> sp.	Indo-Australian region	<i>Archontophoenix</i> sp., <i>Areca</i> sp., <i>Arenga</i> sp., <i>Calamus</i> sp., <i>Cocos</i> sp., <i>Cyrtostachys</i> sp., <i>Daemonorops</i> sp., <i>Heterospathe</i> sp., <i>Korthalsia</i> sp., <i>Metroxylon</i> sp., <i>Nypa</i> sp., <i>Oncosperma</i> sp., <i>Oreodoxa</i> sp., <i>Phoenix</i> sp., <i>Rhopaloblaste</i> sp. (Arecaceae), <i>Flagellaria</i> sp. (Flagellariaceae), <i>Saccharum</i> sp. (Poaceae)	Cox 1996 (illustr.), Jolivet 1989a

Taxon Author	Geographical Distribution	Reported Host Plants	Author	Family	Selected References
<i>Polyconia</i> sp.	Africa	<i>Oryza</i> sp., <i>Pennisetum</i> sp., <i>Sorghum</i> sp., <i>Zea</i> sp.		(Poaceae)	Jolivet and Hawkeswood 1995
<i>Prionispa fulvicolis</i> Guérin-Méneville	Java	<i>Polliia thyrsiflora</i> Endl <i>ex</i> Hasskarl		(Commelinaceae) larvae	Kalshoven 1957
<i>Prionispa</i> sp.	India to New Guinea	Zingiberaceae (questionable)	Staines 2003b		Gressitt 1982, Staines 2003b
<i>Probaenia armigera</i> (Baly)	Costa Rica, Nicaragua	<i>Piptocarpha chontalensis</i> Baker		(Asteraceae)	Hespenheide and Dang 1999
<i>P. atricornis</i> Pic	Argentina	<i>Vernonia mollisima</i> Don		(Asteraceae) larvae	Cox 1996 (illustr.)
<i>P. crenulata</i> Uhmann	Costa Rica	unidentified plant (larvae)			Uhmann 1934 (illustr.)
<i>P. pici</i> Uhmann	Costa Rica	<i>Mikania guaco</i> Humboldt and Bonpland		(Asteraceae)	Hespenheide and Dang 1999
' <i>Probaenia</i> sp. 1'	Costa Rica	<i>Arrabidaea chica</i> Verlot		(Bignoniaceae)	Hespenheide and Dang 1999
<i>Probaenia</i> sp.	Nicaragua to Argentina	<i>Rolandra</i> sp., <i>Mikania</i> sp., <i>Piptocarpha</i> sp., <i>Verbesina</i> sp., <i>Vernonia</i> sp. (Asteraceae), <i>Arrabidaea</i> sp. (Bignoniaceae), <i>Inga</i> sp. (Leguminosae), <i>Verbena</i> sp. (Verbenaceae)			Hespenheide and Dang 1999, Staines 2002b
<i>Promecothea alpiniae</i> Malik (including two subspecies listed in Gressitt 1960a)	Solomon Islands (Malaita)	<i>Heliconia</i> sp. (Heliconiaceae) larvae, <i>Alpinia</i> sp. (Zingiberaceae) larvae			Gressitt 1957 (illustr.), 1960a (illustr.); Maulik 1937; Kalshoven 1957
<i>P. antiqua</i> Weise	New Guinea, Solomon Islands	<i>Cocos</i> sp., <i>Elaeis guineensis</i> Jacquin		(Arecaceae)	Abdullah and Qureshi 1969, Maulik 1937
<i>P. bicolor</i> Maulik	Fiji	<i>Arecaceae</i> sp. and <i>Flagellaria</i> sp.		(Flagellariaceae)	Gressitt 1957, Lepesme 1947
<i>P. bryantiae</i> Gressitt	Solomon Islands	<i>Pandanus (Bryantia)</i> sp.		(Pandanaceae) larvae	Gressitt 1960a (illustr.)
<i>P. callosa</i> Baly (including two subspecies mentioned in Gressitt 1963)	Australia (Cape York Peninsula), New Guinea	<i>Cocos nucifera</i> Linné, <i>Cocos</i> sp., 'unidentified native palms' (Arecaceae), <i>Pandanus</i> sp. (Pandanaceae) larvae			Gressitt 1957, 1960a, 1963; Howard <i>et al.</i> 2001; Kalshoven 1957; Lepesme 1947; Mariau 2001
<i>P. caeruleipennis</i> Blanchard	southeast Asia and many Pacific islands, Philippine Islands, Solomon Islands, Tonga, Fiji, Samoa	<i>Cocos nucifera</i> Linné (larvae), <i>Livistona</i> sp. <i>Pritchardia pacifica</i> Seeman and H. Wendland, <i>Pritchardia</i> sp. (larvae), and other Arecaceae			Dharmadhikari <i>et al.</i> 1977; Howard <i>et al.</i> 2001; Kalshoven 1957; Lepesme 1947; Mariau 2001; Maulik 1931, 1937
<i>P. cumingii</i> Baly	Sri-Lanka, southeast Asia including Java, Singapore, Malayan Archipelago, Philippines, Borneo, other Pacific islands, Australia	<i>Areca catechu</i> Linné, <i>Caryota</i> sp., <i>Cocos nucifera</i> Linné, <i>Elaeis guineensis</i> Jacquin, <i>Metroxylon sagu</i> Rottbóll, <i>Nypa fruticans</i> Thunberg (larvae), <i>Oreodoxa regia</i> Kunth (Arecaceae)			Abdullah and Qureshi 1969, Cox 1996 (illustr.); Dharmadhikari <i>et al.</i> 1977; Gallego <i>et al.</i> 1983; Howard <i>et al.</i> 2001; Kalshoven 1957, 1981 (illustr.); Lepesme 1947; Maulik 1919, 1929 (illustr.), 1931, 1937; Mariau 2001; Zaka-ur-Rab 1991
<i>P. cyanipes</i> (Erichson)	Philippine Islands	<i>Cocos</i> sp. (Arecaceae) larvae			Gressitt and Kimoto 1963, Kalshoven 1957
<i>P. freycinetiae</i> Gressitt	Biak Island (New Guinea)	<i>Freycinetia</i> sp. (large species) (Pandanaceae) larvae			Gressitt 1960a (illustr.), 1963
<i>P. guadala</i> Maulik	Solomon Islands	<i>Balaka (Ptychosperma)</i> sp. (Arecaceae) larvae			Gressitt 1957 (illustr.), 1960a; Howard <i>et al.</i> 2001; Kalshoven 1957; Lepesme 1947; Maulik 1937
<i>P. kolombangara</i> Maulik	Solomon Islands (Kolombangara)	<i>Balaka (Ptychosperma)</i> sp.			Gressitt 1957 (illustr.), 1960a
<i>P. leverii</i> Spaeth (includes two species listed in Gressitt 1960a)	Solomon Islands	<i>Areca</i> sp., <i>Balaka</i> sp., <i>Calamus</i> sp. (Arecaceae)			Gressitt 1957 (illustr.), 1960a, Howard <i>et al.</i> 2001
<i>P. lindingeri</i> Aulmann	Samoa	<i>Cocos</i> sp. (Arecaceae)			Lepesme 1947, Mariau 2001
<i>P. nuciferae</i> Maulik	Sulawesi (= Celebes Island), Indonesia	<i>Cocos nucifera</i> Linné (Arecaceae) larvae			Chen <i>et al.</i> 1986 (illustr.), Cox 1996 (illustr.); Gressitt 1959; Lepesme 1947 (illustr.); Mariau 2001; Maulik 1929 (illustr.), 1937

<i>P. opacicollis</i> Gestro	Vanuatu and Solomon Islands (Santa Cruz Island, Banks Island)	<i>Areca catechu</i> Linné, <i>Areca</i> sp. (larvae), <i>Cocos nucifera</i> Linné, <i>Cocos</i> sp. (larvae), <i>Elaeis guineensis</i> Jacquin, <i>Phoenix</i> sp. (larvae), <i>Phytelephas macrocarpa</i> Ruiz et Pavón, <i>Phytelephas</i> sp. (larvae), <i>Ravenala madagascariensis</i> J. F. Gmelin, <i>Ravenala</i> sp. (larvae) (Arecaceae)	Abdullah and Qureshi 1969, Gressitt 1960a, Howard <i>et al.</i> 2001, Kalshoven 1957, Lepesme 1947, Mariau 2001, Maulik 1937
<i>P. palmella</i> Gressitt	Solomon Islands	‘small pinnate palm’	Gressitt 1960a (illustr.)
<i>P. palmivora</i> Gressitt	New Guinea	‘unknown thick-leaved palm’ (larvae)	Gressitt 1960a (illustr.), 1963
<i>P. pandani</i> Gressitt	New Guinea	<i>Pandanus</i> sp. (Pandanaaceae) larvae	Gressitt 1960a (illustr.), 1963 (illustr.)
<i>P. papuana</i> Csiki	New Guinea, Solomon Islands, Australia, Manus, New Britain, Bismark Archipelago	<i>Areca catechu</i> Linné, <i>Cocos nucifera</i> Linné, <i>Cocos</i> sp. (larvae), <i>Elaeis guineensis</i> Jacquin, <i>Elaeis</i> sp. (larvae), <i>Metroxylon sagu</i> Rottbóll, <i>Metroxylon</i> sp. (larvae), <i>Nypa fruticans</i> Thunberg, <i>Nypa</i> sp. (larvae) (Arecaceae)	Gressitt 1957 (illustr.), 1959 (illustr.), 1960a, 1963; Howard <i>et al.</i> 2001; Kalshoven 1957, 1981; Lepesme 1947; Mariau 2001
<i>P. ptychospermae</i> Maulik	Solomon Islands	<i>Balaka (Ptychosperma)</i> sp. (Arecaceae)	Gressitt 1957, 1960a; Howard <i>et al.</i> 2001; Lepesme 1947; Maulik 1937
<i>P. reichei</i> Baly	Philippines, Tonga, Samoa, Fiji, Solomon Islands, Indo-Pacific region	<i>Cocos nucifera</i> Linné, <i>Livistona</i> sp., <i>Pritchardia pacifica</i> Seeman <i>et</i> Wendland, and other Arecaceae	Abdullah and Qureshi 1969, Lepesme 1947, Mariau 1988, Maulik 1937
<i>P. sacchari</i> Gressitt	Solomon Islands (Guadalcanal)	<i>Saccharum</i> spp. (cultivated and wild) or <i>Miscanthus</i> sp. (Poaceae)	Cox 1996 (illustr.); Gressitt 1957 (illustr.), 1960a
<i>P. salomonina</i> Spaeth	Solomon Islands (Guadalcanal)	<i>Balaka (Ptychosperma)</i> sp., <i>Calamus</i> sp. (Arecaceae)	Gressitt 1957 (illustr.), 1960a; Howard <i>et al.</i> 2001
<i>P. soror</i> Maulik	Sulawesi (= Celebes Island), Moluccas Islands, Sula Island (Indonesia)	<i>Cocos nucifera</i> Linné, <i>Cocos</i> sp. (Arecaceae) larvae	Gressitt 1957, 1959; Howard <i>et al.</i> 2001; Kalshoven 1957, 1981; Lepesme 1947; Mariau 2001; Maulik 1929 (illustr.)
<i>P. straminipennis</i> Weise	New Britain, Manus (New Guinea)	<i>Pandanus</i> spp. (Pandanaaceae)	Gressitt 1957 (illustr.), 1959, 1960a, 1963
<i>P. varipes</i> Baly	Australia	<i>Cocos nucifera</i> Linné, <i>Cocos</i> sp. (Arecaceae) larvae and some <i>Pandanus</i> sp. (Pandanaaceae)	Gressitt 1957, 1960a; Howard <i>et al.</i> 2001; Kalshoven 1957; Lepesme 1947
<i>P. violacea</i> Uhmman	Solomon Islands (Bougainville, Ysabel, New Georgia)	<i>Ptychosperma</i> sp. (Arecaceae) larvae, <i>Pandanus</i> sp. (Pandanaaceae)	Cox 1996 (illustr.); Gressitt 1957 (illustr.), 1959; Kalshoven 1957
<i>Promecotheca</i> sp.	Africa, Asia, Indo-Australia, Oceania	<i>Areca</i> sp., <i>Balaka</i> sp., <i>Calamus</i> sp., <i>Caryota</i> sp., <i>Cocos nucifera</i> Linné, <i>Metroxylon</i> sp., <i>Elaeis</i> sp., <i>Livingstonia</i> sp., <i>Nypa</i> sp., <i>Phoenix</i> sp., <i>Phychosperma</i> sp., <i>Phytelephas</i> sp. (Arecaceae), <i>Flagellaria</i> sp. (Flagellariaceae), <i>Heliconia</i> sp. (Heliconiaceae), <i>Ravenala</i> sp. (Musaceae), <i>Freycinetia</i> sp., <i>Pandanus</i> sp. (Pandanaaceae), <i>Mischanthus</i> sp., <i>Saccharum</i> sp. (Poaceae), <i>Alpinia</i> sp. (Zingiberaceae)	Cocheraeu 1972, Gressitt 1959 (illustr.), Jolivet 1989a, Kalshoven 1981, Würmli 1975
<i>Prosopodonta corallina</i> Weise	Colombia	Arecaceae	Lespesme 1947 (illustr.), Maulik 1931 (illustr.), 1937
<i>P. cordillera</i> Maulik	Colombia	Arecaceae	Chen <i>et al.</i> 1986 (illustr.), Cox 1996 (illustr.), Lespesme 1947 (illustr.), Maulik 1931 (illustr.)



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<i>P. interrupta</i> Weise	Colombia	Arecaceae			Lepesme 1947 (illustr.), Maulik 1937
<i>P. intercepta</i> Weise	Colombia	Arecaceae			Maulik 1937
<i>P. quinquelineata</i> Weise	[Colombia], St. Antonio, Río Vitaco	Arecaceae			Lepesme 1947 (illustr.); Maulik 1931 (illustr.), 1937
<i>P. sulphuricollis</i> Weise	Colombia	Arecaceae			Maulik 1931 (illustr.), 1937
<i>Prosopodonta</i> sp.	tropical America	Arecaceae and Heliconiaceae ( <i>Heliconia</i> sp.). Staines 2003b casts serious doubts on the association of <i>Prosopodonta</i> leaf-miners and <i>Heliconia</i> host plants.			Jolivet 1989a, Jolivet and Hawkeswood 1995, Staines 2002b
<i>Rhabdotohispa scotti</i> Maulik	Seychelles Islands	<i>Phoenicophorium</i> sp., <i>Roscheria</i> sp., <i>Stevensonia</i> sp. (Arecaceae)			Lepesme 1947 (illustr.), Maulik 1937
<i>Rhabdotohispa</i> sp.	Seychelles Islands (Pacific Ocean)	<i>Phoenicophorium</i> sp., <i>Stevensonia</i> sp. (Arecaceae)			Jolivet 1989a
<i>Rhadinosa fleutiauxi</i> (Baly)	Thailand, Laos, Vietnam, China, Hainan Island, Malaya	'wild grasses' (larvae)			Gressitt and Kimoto 1963, Kalshoven 1957, Kimoto 1999 (illustr.)
<i>R. lebongensis</i> Maulik	India	<i>Oryza sativa</i> Linné 'rice', <i>Saccharum officinarum</i> Linné 'sugarcane' (Poaceae)			Anand 1989
<i>R. nigrocyanea</i> (Motschulsky)	Korea, Japan, China, Siberia	<i>Arundinella</i> sp. ('ye-gu-cao' genus), <i>Digitaria</i> <i>glabra</i> Beauvois, <i>Digitaria</i> sp. ('ma-tang' genus), <i>Miscanthus</i> sp. ('di' genus), <i>Oryza sativa</i> Linné (larvae) Poaceae			An <i>et al.</i> 1985, Kalshoven 1957, Tan 1993
<i>R. parvula</i> (Motschulsky)	Sumatra, Java	<i>Imperata</i> sp. (larvae), <i>Oryza sativa</i> Linné (larvae), <i>Saccharum officinarum</i> Linné (larvae), <i>Zea mays</i> Linné (larvae), 'wild grasses' (larvae) Poaceae			Kalshoven 1957, Maulik 1937
<i>Rhadinosa</i> sp.	Asia	<i>Digitaria</i> sp., <i>Miscanthus</i> sp., <i>Oryza</i> sp., <i>Saccharum</i> sp., <i>Triticum</i> sp., <i>Zea</i> sp. (Poaceae)			Jolivet 1989a
<i>Sceloenopla bicolorata</i> Staines	Costa Rica	<i>Sterculia recordiana papyracea</i> E. Taylor (Sterculiaceae) adults			Staines 2002a (illustr.)
<i>S. af. bidens</i> (Fabricus)	Brazil	<i>Philodendron renauxii</i> Reitz (Araceae)			Costa <i>et al.</i> 1988 (illustr.), Cox 1996 (illustr.)
<i>S. erudita</i> (Baly)	Mexico to Panama	<i>Anthurium</i> sp. (Araceae) adults, <i>Cuspania</i> sp. (Sapindaceae) larvae			Hespenheide and Dang 1999, Maes 1998, Maes and Staines 1991, Staines 1996
<i>S. godmani</i> (Baly)	Nicaragua, Costa Rica, Panama	<i>Clusia flava</i> Jacquin (Clusiaceae) larvae			Hespenheide and Dang 1999, Maes 1998
<i>S. lampyridiformis</i> Staines	Costa Rica	unidentified species of Visaceae (larvae)			Staines 2002a (illustr.)
<i>S. longula</i> (Baly)	Costa Rica, Panama	unidentified Araceae (larvae)			Hespenheide and Dang 1999, Wilcox 1975
<i>S. maculata</i> (Olivier)	Brazil	<i>Cecropia lyratiloba</i> var. <i>nana</i> Andrade and Carauta, <i>Cecropia</i> sp., <i>Pourouma</i> sp. (Cecropiaceae)			Andrade 1984 (illustr.), Jolivet 1989b
<i>S. mantecada</i> Sanderson	Puerto Rico	<i>Rapanea ferruginea</i> (Ruiz <i>et</i> Pavón) Mez. Myristicaceae			Sanderson 1967 (illustr.), Virkki and Santiago-Blay 1998
<i>S. nigropicta</i> Staines	Costa Rica	'Collected fossing <i>Virola koschnyi</i> ' Warburg (Myristicaceae) adults			Staines 2002a (illustr.)
<i>S. obscurovitatta</i> (Baly)	Costa Rica, Nicaragua	<i>Philodendron radiatum</i> var. <i>radiatum</i> Schott (Araceae) larvae			Hespenheide and Dang 1999
<i>S. pretiosa</i> Baly	Brazil, Paraguay, and Argentina	<i>Philodendron</i> sp. (Araceae), <i>Esenbeckia febrifuga</i> (A. St.-Hil.) A. Jussieu <i>ex</i> Martínez (Rutaceae)			Monrós and Viana 1947

<i>S. scherzeri</i> (Baly)	Nicaragua, Costa Rica, Panama	<i>Davilla nitida</i> (Vahl) Kubitzki (Dilleniaceae) larvae	Hespenheide and Dang 1999, Wilcox 1975
<i>S. sheppardi</i> (Baly)	Brazil	<i>Cecropia</i> sp., <i>Pourouma</i> sp. (Cecropiaceae)	Jolivet 1989b
<i>S. unicosata</i> Staines	Costa Rica	Unidentified species of Visaceae (larvae)	Staines 2002a
' <i>Sceloenopla</i> sp. 3'	Costa Rica	<i>Sterculia recordiana</i> Standley var. <i>papyracea</i> (Sterculiaceae) larvae	Hespenheide and Dang 1999
<i>Sceloenopla</i> sp.	Central, South America, and Caribbean	<i>Anthurium</i> sp., <i>Philodendron</i> sp., and others (Araceae), <i>Cocos</i> sp. (Arecaceae), <i>Cecropia</i> sp., <i>Pourouma</i> sp. (Cecropiaceae), <i>Clusia</i> sp. (Clusiaceae), Cyclanthaceae, <i>Davilla</i> sp. (Dilleniaceae), <i>Lonchocarpus</i> (Leguminosae), <i>Persea</i> sp. (Lauraceae), <i>Rapanea</i> sp. (Myrsinaceae), Rubiaceae, <i>Esenbeckia</i> sp. (Rutaceae), Rubiaceae, <i>Cupania</i> sp. (Sapindaceae), <i>Chrysophyllum</i> sp. (Sapotaceae), <i>Sterculia</i> sp. (Sterculiaceae)	Jolivet 1989b, Jolivet and Hawkeswood 1995, Staines 2002b (illustr.)
<i>Spilispa</i> sp.[monotypic, <i>S. imperalis</i> (Baly)]	Indonesia	Unknown	Jolivet 1989b
<i>Stenopodius flavidus</i> Horn	southwestern United States and Mexico	<i>Spinacia oleracea</i> L. (Chenopodiaceae), <i>Sphaeralcea grossulariaefolia</i> Ryds. (larvae), <i>Sphaeralcea</i> sp. (Malvaceae)	Jones and Brisley 1925, Needham <i>et al.</i> 1928, Maulik 1937
<i>S. lateralis</i> (Schaeffer)	western United States	<i>Sphaeralcea emoryi</i> J. Torr. (Malvaceae)	Staines 1986b
<i>S. texanus</i> Schaeffer	western United States	<i>Sphaeralcea emoryi</i> J. Torr. (Malvaceae)	Staines 1986b
<i>Stenopodius</i> sp.	North and Central America	<i>Althaea</i> sp., <i>Malva</i> sp., <i>Sphaeralcea</i> sp. (adults) (Malvaceae)	Jolivet 1989a, Moldenke 1971
<i>Stenostena laeta</i> Weise	Peru, Uruguay	<i>Paspalum quadrifarium</i> Lamarck (Poaceae) and other grasses	Cox 1996 (illustr.), Maulik 1937, Monrós and Viana 1947
<i>Sternostena</i> sp.	Costa Rica to Argentina	<i>Paspalum</i> sp. (Poaceae)	Jolivet 1989a, Staines 2002b
<i>Stethispa crenulata</i> Uhmann	Paraguay	<i>Arustolochia</i> sp. (Aristolochiaceae), <i>Ruprechtia latifolia</i> Huber (Polygonaceae)	Monrós and Viana 1947
<i>Stethispa</i> sp. [prob. <i>S. rudgeana</i> Uhmann]	Costa Rica to Argentina	<i>Aristolochia</i> sp. (Aristolochiaceae), <i>Ruprechtia</i> sp., <i>Coccoloba</i> sp. (Polygonaceae)	Jolivet 1989a
<i>Sumitrosis amica</i> (Baly)	Costa Rica and Panama	<i>Heliconia</i> spp. (Heliconiaceae) larvae	Hespenheide and Dang 1999, Staines 2003b
<i>S. ancoroides</i> (Schaeffer)	eastern and southern United States	<i>Strophostyles helvola</i> (Linné) Elliott, <i>S. umbellata</i> Britton (Leguminosae)	Butte 1969 (illustr.), Cavey 1994, Ford and Cavey 1985 (illustr.)
<i>S. arnetti</i> Butte	Arizona (United States)	<i>Baccharis</i> sp., <i>Zexmenia</i> sp. (Asteraceae)	Butte 1969 (illustr.)
<i>S. canavaliae</i> Maulik	Brazil	<i>Canavalia ensiformis</i> DeCandolle (Leguminosae) larvae	Maulik 1929 (illustr.)
<i>S. fryi</i> (Baly)	Central America	<i>Eupatorium populifolium</i> Hooker and Arnold (Asteraceae) larvae	Maulik 1937, Uhmann 1937
<i>S. fuscicornis</i> (Weise)	Brazil, Colombia	<i>Canavalia ensiformis</i> DeCandolle, <i>Phaseolus</i> sp. (Leguminosae)	Maulik 1937
<i>S. heringi</i> (Uhmann)	Central America	<i>Bambusa</i> sp. (Poaceae) 'bamboo' (larvae)	Cox 1996 (illustr.) Maulik 1937, Uhmann 1934 (illustr.)
<i>S. inaequalis</i> (Weber)	North and Central America	<i>Aster divaricatus</i> Linné, <i>A. novae-angliae</i> Linné, <i>A. paniculatus</i> Lamarck, <i>A. sagitifolius</i> Ell., <i>A. simplex</i> Willdenow, <i>Eupatorium agerateroides</i> Linné f., <i>E. maculatum</i> Linné (adults), <i>E.</i>	Balsbaugh and Hays 1972; Butte 1969 (illustr.); Ford and Cavey 1985 (illustr.); Frost 1924; Maulik 1919, 1937; Needham <i>et al.</i> 1928; Noguera 1988; Wheeler and Snook 1986 (illustr.); Wilcox 1954

Taxon Author	Geographical Distribution	Reported Host Plants Author Family	Selected References
<i>S. pallescens</i> (Baly)	United States to Panama	<i>perfoliatum</i> Linné (adults), <i>E. rugosum</i> Houttuyn, <i>E. urticaefolium</i> Richard, <i>E. urticifolium</i> Banks, <i>Eupatorium</i> sp., <i>Helianthus hirsutus</i> Rafinesque (adults), <i>Rudbeckia triloba</i> Linné (adults), <i>Solidago canadensis</i> Linné, <i>S. gigantea</i> Aiton (adults), <i>S. graminifolia</i> (Linné) Salis., <i>S. ulmifolia</i> Muehlenberg (adults), <i>Solidago</i> sp., <i>Vernonia novaboracensis</i> (Linné) Willdenow (Asteraceae), <i>Arabis laevigata</i> (Muehlenberg) Poiret, <i>Radicula</i> sp. (Brassicaceae), <i>Cornus asperifolia</i> Michaux, <i>C. rugosa</i> Lamarck, <i>Cornus</i> sp. (Cornaceae), <i>Quercus alba</i> Linné (= 'white oak', Fagaceae), <i>Cassia nictitans</i> Linné, <i>Robinia neomexicana</i> (Wootton and Standley) W.C. Martins and Hutchins, <i>R. pseudoacacia</i> Linné, <i>Robinia</i> sp. (Leguminosae), <i>Oenothera</i> sp. (Onagraceae), <i>Malus malus</i> Linné, <i>Pyrus malus</i> Linné, <i>Rosa virginiana</i> Miller (Rosaceae), <i>Solanum dulcamara</i> Linné (Solanaceae), <i>Urtica gracilis</i> Aiton (Urticaceae), 'everlasting' <i>Cassia fasciculata</i> Michaux (larvae), <i>C. nistitans</i> Linné (Leguminosae) adults	Butte 1969 (illustr.), Cavey 1994, Hespenheide and Dang 1999, Maes 1998, Staines 1996 Balsbaugh and Hays 1972, Buntin and Pedigo 1982 (identification error, corrected by Ruesink 1984), Butte 1969 (illustr.), Clark 2000, Ford and Cavey 1985 (illustr.), Noguera 1988
<i>S. rosea</i> (Weber)	Canada, eastern United States and Mexico	<i>Chenopodium album</i> Linné (Chenopodiaceae, probably an error according to Ford and Cavey 1985), <i>Cyrilla racemiflora</i> Linné (Cyrillaceae) adults, <i>Amphicarpaea bracteata</i> (Linné) adults, <i>Amorpha fruticosa</i> Linné (adults), <i>Desmodium glutinosum</i> (Muehlenberg) Wood (adults), <i>D. paniculatum</i> (Linné) DeCandolle (adults), <i>Desmodium</i> sp., <i>Glycine max</i> (Linné) Merrill, <i>Lespedeza intermedia</i> (S. Watts) Britton, <i>Robinia pseudoacacia</i> Linné (adults) (Leguminosae), <i>Malus malus</i> Linné (Rosaceae), <i>Laportea canadensis</i> (Linné) Weddell (adults) (Urticaceae), unidentified Urticaceae	Hespenheide and Dang 1999, Wilcox 1975 Jolivet 1989a; Staines 2002b, 2003b
<i>S. terminata</i> (Baly) <i>Sumitrosis</i> sp.	Mexico, Costa Rica, Panama Canada to Argentina	'unidentified Fabaceae' (larvae) <i>Aster</i> sp., <i>Eupatorium</i> sp., <i>Helianthus</i> sp., <i>Rudbeckia</i> sp., <i>Solidago</i> sp., <i>Vernonia</i> sp., <i>Wedelia</i> sp. (Asteraceae), <i>Celastrus</i> sp. (Celastraceae), <i>Chenopodium</i> sp. (Chenopodiaceae), <i>Cyrilla</i> sp. (Cyrillaceae), <i>Quercus</i> sp. (Fagaceae), <i>Amorpha</i> sp., <i>Amphicarpaea</i> sp., <i>Cajanus</i> sp., <i>Canavalia</i> sp., <i>Cassia</i> sp., <i>Desmodium</i> sp., <i>Dolichos</i>	Hespenheide and Dang 1999, Wilcox 1975 Jolivet 1989a; Staines 2002b, 2003b

		sp., <i>Glycine</i> sp., <i>Lespedeza</i> sp., <i>Meibonia</i> sp., <i>Phaseolus</i> sp., <i>Pueraria</i> sp., <i>Robinia</i> sp., <i>Strophostyles</i> sp. (Leguminosae), <i>Heliconia</i> sp. (Heliconiaceae), <i>Bambusa</i> sp., <i>Chusquea</i> sp., <i>Lasiacis</i> sp. (Poaceae), <i>Potentilla</i> sp. (Rosaceae), <i>Guazuma</i> sp. (Sterculiaceae), <i>Laportea</i> sp. (Urticaceae)	
<i>Temnochalepus insolitus</i> Uhmann	Brazil to Argentina	<i>Commelina</i> sp. (Commelinaceae), <i>Panicum</i> sp., <i>Pharus</i> sp. (Poaceae) (all adults)	Monrós and Viana 1947 (illustr.), Jolivet and Hawkeswood 1995, Staines 2002b
<i>Trichispa feae</i> Gestro <i>T. sericea</i> (Guérin-Méneville)	Sao Thome Is., Zaire Tanzania, Madagascar	Unknown <i>Acroceras</i> sp., <i>Echinochloa</i> sp., <i>Oryza</i> sp., <i>Paspalum</i> sp., <i>Setaria</i> sp. (Poaceae)	Collart 1928, Uhmann 1964 Banwo <i>et al.</i> 2001a, Jolivet 1989a, Ravelojaona 1970
<i>Uroplata annonicola</i> (Maulik) <i>U. atricornis</i> (Pic) <i>U. bilineata</i> Chapuis	Brazil Argentina Bolivia, Paraguay, Argentina, South Africa?	<i>Annona squamosa</i> Linné, <i>Annona</i> sp. (Annonaceae) <i>Vernonia molissima</i> D. Don (Asteraceae) <i>Macfadyena unguis-cati</i> (Linné) Gentry (Bignoniaceae), <i>Caesaria silo</i> unable to find name, Leguminosae, <i>Lantana camara</i> Linné, <i>Lippia urticoides</i> Steudel, <i>Verbena trifolia</i> unable to find name, and other verbenaceans (Verbenaceae)	Maulik 1937, Peña <i>et al.</i> 1995 Maulik 1937 Cilliers 1983, Monrós and Viana 1947 (illustr.)
<i>U. bipuncticollis</i> Chapuis <i>U. coarctata</i> Weise	Argentina Brazil, Paraguay, Argentina	<i>Aristolochia fimbriata</i> Cham. (Aristolochiaceae) <i>Anona squamosa</i> Linné, <i>Rollinia longifolia</i> A.St.Hil. (Anonaceae), <i>Arrabidaea coleocalyx</i> Bureau and K. Schumann (Bignoniaceae)	Monrós and Viana 1947 (illustr.) Monrós and Viana 1947 (illustr.)
<i>U. daguerrei</i> (Pic) <i>U. fulvopustulata</i> Baly	Argentina Brazil, Venezuela, Panama, Costa Rica, Guatemala, Mexico	<i>Verbena bonariensis</i> Linné (Verbenaceae) <i>Calea</i> sp. (Asteraceae) larvae, <i>Pithecoctenium</i> <i>echinatum</i> K. Schumann (Bignoniaceae), <i>Lantana</i> <i>camara</i> Linné, <i>L. urticifolia</i> Miller, <i>Lantana</i> sp. <i>Lippia myriocephala</i> Schlecht. and Cham., <i>Lippia</i> sp. (Verbenaceae), larvae on Verbenaceae	Cox 1996 (illustr.), Monrós and Viana 1947 (illustr.) Broughton 2000, Krauss 1964, Uhmann 1934 (illustr.)
<i>U. fusca</i> Chapuis	Nicaragua to Brazil	<i>Pithecoctenium echinatum</i> K. Schumann larvae, <i>Pithecoctenium</i> sp., unidentified bignanean, (Bignoniaceae), <i>Malpighia glabra</i> Linné (larvae), <i>Malpighia</i> sp. (Malpighiaceae)	Hespenheide and Dang 1999, Maes 1998, Staines 1996, Uhmann 1934
<i>U. girardi</i> Pic	Brazil, Paraguay, Argentina, Hawaii, Australia, South Africa	<i>Sesamum orientale</i> Linné (Pedaliaceae), <i>Clerodendron thomsonae</i> Baif., <i>Lantana camara</i> Linné, <i>L. glutinosa</i> Poeppig, <i>L. trifolia</i> Linné, <i>L.</i> <i>tiliaefolia</i> Schlechtendal <i>et</i> Chamisseau, <i>L.</i> <i>montevicensis</i> (Sprengel) Briquet, <i>Lantana</i> sp. (larvae), <i>Lippia alba</i> (Miller) N. E. Britton, and Wilson, <i>L. micromera</i> Schau., <i>Tectona grandis</i> Linné f. (Verbenaceae)	Anonymous, no date; Broughton 2000; Cilliers 1977, 1983, 1987a (illustr.), 1987b (illustr.); Harley 1969; Krauss 1964; Winder and Harley 1982
<i>U. jucunda</i> Chapuis <i>U. lantanae</i> Buzzi and Winder	Uruguay, Argentina Brazil, Mexico	<i>Vernonia mollissima</i> Sch. Bip. (Asteraceae) <i>Lantana glutinosa</i> Poeppig, <i>L. tiliaefolia</i> Schlechtendal <i>et</i> Cham., <i>Lantana</i> sp. (Verbenaceae)	Monrós and Viana 1947(illustr.) Broughton 2000, Winder and Harley 1982
<i>U. mucronata</i> (Olivier)	'Guiana', Brazil	<i>Rolandra argentea</i> Rottbóll, <i>Wedelia paludosa</i> DeCandolle (Asteraceae)	Maulik 1937

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<i>U. nigritarsis</i> Weise <i>U. sculptilis</i> Chapuis	Paraguay, Argentina Mexico to Panama	<i>Lippia geminata</i> Kunth (Verbenaceae) <i>Clibadium aspersum</i> DeCandolle (adults), <i>Clibadium</i> sp., <i>Synedrella nodiflora</i> Gaertner larvae (Asteraceae), <i>Inga edulis</i> Martinez (Leguminosae) larvae			Monrós and Viana 1947 (illustr.) Hespenheide and Dang 1999; Maes 1998; Staines 1996; Uhmman 1934, 1937
<i>U. sulcifrons</i> Jacoby <i>U. uniformis</i> (Smith) <i>Uroplata</i> sp.	Mexico United States Central and South America	<i>Melanthera nivea</i> Smith (Asteraceae) adults <i>Digitaria</i> sp. (Poaceae) Acanthaceae, <i>Annona</i> sp., <i>Rollinia</i> sp. (Annonaceae), <i>Aristolochia</i> sp. (Aristolochiaceae), <i>Baccharis</i> sp., <i>Clibadium</i> sp., <i>Elephantopus</i> sp., <i>Eupatorium</i> sp., <i>Melanthera</i> sp., <i>Rolandra</i> sp., <i>Vernonia</i> sp., <i>Wedelia</i> sp. (Asteraceae), <i>Arrabidaea</i> sp., <i>Bignonia</i> sp., <i>Colea</i> sp., <i>Pithecoctenium</i> sp. (Bignoniaceae), <i>Ocothea</i> sp. (Lauraceae), <i>Calopogonium</i> sp., <i>Inga</i> sp. (Leguminosae), <i>Banisteria</i> sp., <i>Byrsonima</i> sp. <i>Malpighia</i> sp. (Malpighiaceae), <i>Althaea</i> sp., <i>Sida</i> sp. (Malvaceae), <i>Panicum</i> sp. (Poaceae), <i>Gouania</i> sp. (Rhamnaceae), <i>Lantana</i> sp., <i>Lippia</i> sp., <i>Verbena</i> sp. (Verbenaceae), <i>Caesarea</i> sp. (Vivianaceae) 'undetermined Fabaceae' (larvae)			Moldenke 1971 Thomas and Werner 1981 Cox 1996 (illustr.), Flowers and Janzen 1997, Jolivet 1989a, Jolivet and Hawkeswood 1995, Maulik 1932, Staines 2002b, Winder and Harley 1982
<i>Xenochalepus amplipennis</i> (Baly) <i>X. ater</i> (Weise)	Costa Rica and Panama southern United States and Mexico	<i>Glycyne max</i> (Linné) Merrill, <i>Phaseolus vulgaris</i> Linné, <i>Phaseolus</i> sp., <i>Robinia</i> sp. (Leguminosae)			Hespenheide and Dang 1999 Butte 1968a (illustr.), Jones and Brisley 1925, Kogan and Kogan 1979, Needham <i>et al.</i> 1928
<i>X. bajulus</i> Uhmman	Bolivia, Brazil, Paraguay	<i>Schubertia</i> sp. (Asclepiadaceae), <i>Urera</i> sp. (Urticaceae) both adults			Monrós and Viana 1947
<i>X. bicostatus fasciatus</i> Weise <i>X. chapuisi</i> (Baly)	Paraguay, Argentina Mexico and Central America	<i>Celtis tala</i> Gill. ex Planch (Ulmaceae) adults <i>Nissolia fruticosa</i> Jacquin (larvae), <i>Nissolia</i> sp. (Leguminosae)			Monrós and Viana 1947 (illustr.) Maes 1998, Maulik 1937, Uhmman 1934 (illustr.)
<i>X. contubernalis</i> (Baly) <i>X. erythroderus</i> (Chapuis)	Mexico to Costa Rica Costa Rica, Panama, South America	<i>Nissolia</i> sp. (Leguminosae) adults <i>Cecropia insignis</i> Liebmann, <i>Coussapoa</i> <i>nymphaeifolia</i> Standley, <i>C. villosa</i> Poeppig and Endlicher., <i>Pourouma bicolor</i> Martinez (Cecropiaceae) all larvae			Maes and Staines 1991, Staines 1996 Hespenheide and Dang 1999, Wilcox 1975
<i>X. faustus</i> ab. <i>laetificus</i> Weise	Paraguay, Argentina	<i>Ipomoea heterophylla</i> Ortega (Convolvulaceae) adults			Monrós and Viana 1947 (illustr.)
<i>X. guerini</i> ab. <i>congruus</i> Pic	Brazil, Peru, Bolivia, Paraguay, Argentina	<i>Olyra</i> sp., <i>Oryza</i> sp. (Poaceae) both adults			Monrós and Viana 1947
<i>X. haroldi</i> (Chapuis) <i>X. hespenheidi</i> Staines <i>X. medius</i> (Chapuis)	Bolivia, Argentina Costa Rica Brazil, Paraguay, Uruguay, Argentina	<i>Phaseolus vulgaris</i> Linné (Leguminosae) larvae <i>Cecropia</i> sp. (Cecropiaceae) larvae <i>Inga affinis</i> DeCandolle, <i>Phaseolus</i> sp., <i>Robinia</i> <i>pseudoacacia</i> Linné (larvae), <i>Wisteria chinensis</i> (Sims) DeCandolle (Leguminosae), others adults			Cox 1996 (illustr.), Monrós and Viana 1947 (illustr.) Staines 2000 (illustr.) Cox 1996 (illustr.), Maulik 1919, Monrós and Viana 1947 (illustr.)
<i>X. mucunae</i> Maulik	Brazil	<i>Mucuna pluricostata</i> Barb. (Leguminosae)			Maulik 1937

<i>X. omoerus</i> (Crotch)	southwestern United States to Costa Rica	<i>Benthamantha mollis</i> (Humboldt, Bonpland, and Kunth) Alefeld, <i>Centrosema macrocarpum</i> Bentham, 'species of Fagaceae' (Leguminosae), 'wild bean vine' (Vitaceae) all adults	Butte 1968a (illustr.); Flowers and Janzen 1997; Maes 1998; Maulik 1937; Moldenke 1971; Staines 1996; Uhmman 1934 (illustr.), 1937 (illustr.)
<i>X. phaseoli</i> Uhmman	Argentina	<i>Phaseolus</i> sp. (Leguminosae)	Monrós and Viana 1947 (illustr.)
<i>X. potomacus</i> Butte	eastern United States	<i>Phaseolus polystachios</i> (Linné) Britton, Sterns and Poggenberg (Leguminosae) larvae	Butte 1968a (illustr.), Ford and Cavey 1985
<i>X. robiniae</i> Butte	Arizona (United States)	<i>Robinia neomexicana</i> Gray (Leguminosae)	Butte 1968a (illustr.)
<i>X. signaticollis</i> (Baly)	Honduras	'repollo' (Brassicaceae), 'frijol' (Leguminosae)	Passoa 1983
<i>X. viridiceps</i> Pic	Argentina	<i>Phaseolus</i> sp. (Leguminosae) adults	Monrós and Viana 1947 (illustr.)
<i>X. tandilensis</i> Bruch	Argentina	<i>Lathyrus pubescens</i> Hooker and Arnott (Leguminosae) larvae	Monrós and Viana 1947 (illustr.)
<i>X. trilineatus</i> (Chapuis)	Argentina	<i>Mucuna pluricostata</i> Barbosa Rodrigues (Leguminosae)	Monrós and Viana 1947 (illustr.)
<i>Xenochalepus</i> sp.	New World	<i>Anthurium</i> sp. (Araceae) larvae, <i>Ipomea</i> sp. (Convolvulaceae), <i>Bauhinia</i> sp., <i>Canavalia</i> sp., <i>Cymbosema</i> sp., <i>Dioclea</i> sp., <i>Dolichos</i> sp., <i>Faba</i> sp., <i>Glycine</i> sp., <i>Inga</i> sp., <i>Lathyrus</i> sp., <i>Mucuna</i> sp., <i>Nissolia</i> sp., <i>Phaseolus</i> sp., <i>Robinia</i> sp., <i>Vigna</i> sp., <i>Wisteria</i> sp. (Leguminosae), <i>Schubertia</i> sp. (Malvaceae), <i>Bambusa</i> sp., <i>Olyra</i> sp., <i>Oryza</i> sp., <i>Panicum</i> sp., <i>Saccharum</i> sp., <i>Zea</i> sp. (Poaceae), <i>Prunus</i> sp. (Rosaceae), <i>Theobroma</i> sp. (Sterculiaceae), <i>Celtis</i> sp. (Ulmaceae), <i>Urera</i> sp. (Urticaceae)	Hespenheide and Dang 1999, Jolivet 1989a, Staines 2002b
<i>Wallacispa javanica</i> Gestro	Sulawesi (= Celebes Island)	<i>Metroxylon</i> sp. (Arecaceae) larvae	Kalshoven 1957
<i>Wallacispa</i> sp. (some species appear to be leaf-miners)	Indonesia	<i>Metroxylon</i> sp. (Arecaceae)	Jolivet 1989a
<i>Wallaceana apicalis</i> Gestro	Singapore	<i>Areca catechu</i> Linné, <i>A. triandra</i> Roxburgh, <i>Metroxylon</i> sp., <i>Nypa fruticans</i> Thunberg, <i>Phoenix roebelinii</i> O'Brien, ornamental palms (Arecaceae)	Kalshoven 1981 (illustr.), Lepesme 1947
<i>W. dactyliferae</i> (Maulik)	Pakistan, India	<i>Phoenix</i> sp., 'date palm' (Arecaceae)	Abdullah and Qureshi 1969; Anand 1989; Kalshoven 1957; Lepesme 1947 (illustr.); Maulik 1919 (illustr.), 1937
<i>W. phoenicia</i> Maulik	Malaysian Peninsula, Carey Island	<i>Oncosperma figillaria</i> Ridley, <i>O. filamentosa</i> Bl., <i>Oncosperma</i> sp., <i>Phoenix</i> sp. <i>Zalacca conferta</i> Griffith (Arecaceae)	Kalshoven 1957, 1981; Lepesme 1947, Maulik 1937
<b>CASSIDINAE</b>			
<i>Nothosacantha</i> <sup>9</sup> <i>dorsalis</i> (Waterhouse)	Australia	<i>Acacia crassa</i> ssp. <i>crassa</i> Pedley	Borowiec 1999, Monteith 1991 (illustr.)
<i>N. laticollis</i> (Boheman)	South Africa, Tanzania	<i>Canthium inerme</i> Kuntze (Rubiaceae)	Borowiec 1999
<i>N. nepalensis</i> Borowiec and Takizawa	Nepal	<i>Cleyera japonica</i> Thun. (Theaceae)	Borowiec and Takizawa 1991, Monteith 1991
<i>N. severini</i> (Spaeth)	India	<i>Carissa</i> sp. (Apocynaceae)	Borowiec 1999
<i>N. siamensis</i> Spaeth	Socialist Republic of Vietnam	<i>Phyllanthus emblica</i> Linné (Euphorbiaceae)	Medvedev and Eroshkina 1988 (illustr.)
<i>N. vicaria</i> (Spaeth)	India, Sri Lanka	<i>Carallia brachiata</i> (Loureiro) Merrill (Rhizophoriaceae)	Rane <i>et al.</i> 2000 (illustr.)

1. This site contains the names accumulated in three important indices: Index Kewensis, Gray Card Index, and Australian Plant Name Index. However, there are problems with each of these indexes. Firstly, Index Kewensis (IK) did not include parenthetical author citations until recently. Relying on it can cause a user to have incomplete author citations, such as missing the parenthetical author of a basionym. Secondly, the Gray Card Index (GCI) begins after the first issue of Index Kewensis, names published after 1893. Although it has full, parenthetical author citations of New World taxa names, it does not account for names published before 1893. The GCI is the best tool for names of plants from the New World. Thirdly, the Australian Plant Name Index (APNI) begins with Linnaeus and incorporates full author citations. Essentially, if the plant needs to be accounted for (*e.g.*, invasive weed), it will have updated the full author parenthetical author citation. A little web 'tutorial' on standard reference botanical works (*etc.*) can be found in <http://persoon.si.edu/botlinks/dhntyp.htm>.
2. I am using the more traditional, yet artificial, separation of the Alticinae and the Galerucinae. The problematic phylogenetic distinction of these two taxa has been repeatedly pointed out by numerous workers (*e.g.*, Böving, 1927; Duckett *et al.*, 2003; Kim *et al.*, 2003). 'Trichostomes' (Jacoby) has been used for Alticinae + Galerucinae (Schmitt to Santiago-Blay, personal communication, June 2003).
3. Most students of *Monoxia* believe that all the species in the genus are leaf miners. However, I have collected *Monoxia* larvae in old inflorescences and fruitlets or Chenopodiaceae.
4. Hespeneheide 1991 refers to about 40 other leaf mining taxa in this subfamily in Mesoamerica. They have not been entered in this table as detailed data, including identification, were not provided in that paper.
5. About ten described species inhabit western Africa (Mariau 1988).
6. About 30 more described species inhabit Madagascar (Mariau 1988).
7. About four species inhabit northwestern South America (Mariau 1988).
8. About ten described species inhabit southeastern Asia and the Pacific islands (Mariau 1988).
9. This genus was placed in the Hispinae by Medvedev and Eroshkina (1988) but in the Cassidinae by Borowiec (1995, 1999) and Staines (2002b). See Crowson (1955), Gressitt and Kimoto 1963, Staines (2002b), and references therein, for a discussion on various placements of the hispines and cassidines.