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Translocation in Leaf Beetles (Coleoptera: Chrysomelidae)[1]

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Abstract. An overview of leaf beetle translocations, and the possible effects related to endangerment of native leaf beetle species is presented. Translocation is defined as the movement of living organisms from one area to another across natural barriers. In the new area the translocated organism lives free. Translocations can be intentional or accidental. The database of records of translocated leaf beetles is compiled using published records as the main source of information. In this study 126 leaf beetle species have been recorded to have been translocated at least once. Most translocated species occur in the subfamilies Chrysomelinae, Galerucinae, Alticinae, Cassidinae and Hispinae. Most unintentional successful translocations occur in mono- and oligophagous species that develop on cultivated and non-indigenous plant species. At present, no negative effects of translocated Chrysomelidae on biodiversity have been reported. The successful control of imported weeds by introduced Chrysomelidae can be seen as a positive effect to biodiversity since some of these weeds prevent natural processes in ecosystems. Historical distribution patterns of Chrysomelidae are discussed in relation to the translocations.

Keywords. Coleoptera, Chrysomelidae, invasive species, bioinvasion, alien species, translocation, introduction

1. INTRODUCTION

One of the major threats to native biological diversity is now acknowledged by scientists and governments to be biological invasions caused by alien invasive species (IUCN 2000, UNION OF CONCERNED SCIENTISTS 2001). This is not a new item: the threat of invasive species for the conservation of biodiversity was already pointed out by ELTON in 1933 (cf. SIMBERLOFF's foreword in ELTON 2000). Meanwhile it is supposed that every year a wide range of alien species are imported into many countries through international trade both intentionally as trade products (horticulture, pets, etc.) or unintentionally (for example by hitch-hiking on legitimate products). Little is known about the number of leaf beetles (Coleoptera, Chrysomelidae) that are translocated in this way or about their impact on biological diversity.

Translocated species can be a threat in the way that a native leaf beetle is displaced by an alien leaf beetle species. On the other hand translocated species can reduce indigenous plant species and thus affect the native herbivores depending on it. In this study we restrict consideration to leaf beetle translocations and their effects on native leaf beetle populations caused by competition.

Interspecific competition is any interaction between two or more species populations which adversely affects their growth and survival (ODUM 1971). The importance of interspecific competition is not clear (STEWART 1996) but evidence for competition among phytophagous species (including Chrysomelidae) exists (e.g., GONZÁLES-MEGÍAS & GÓMEZ (2003)).

When a population of a non-indigenous species out competes a population of a native species, the invasive species must have reached a population level in which its competition can be effective. When the population level is too low, it is unlikely that there will be a large effect on the population of the indigenous species. COLAUTTI & MACISAAC (2004) developed a framework for defining different stages during invasions. After the new species is established a non-indigenous species may be localised and rare (a), widespread but rare (b) or widespread and dominant (c). In this last mentioned stage, out competing of indigenous species may be the result.

Therefore, for our purpose, we need to know whether translocated Chrysomelidae have become established. That is the first step. Subsequently we would like to know the status of the established species. The aim of this study is to get an overview of leaf beetle introductions, and the possible effects related to endangerment of native leaf beetle species.

Natural range expansion of a species, as for example recorded for *Chaetocnema major* Jacquelin-Duval by DÖBERL (1994a), is not treated here. Here we consider all transport across natural barriers as translocation. Both intentionally (e.g., in biological control programs) as unintentionally. The IUCN (1987) defines translocation more strictly and restricts to "introductions", "re-introductions" and "re-stocking". Introductions can be effective tools in the management of natural and man made environments. Re-introduction and re-stocking as an aim in nature management has not been used with

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Chrysomelidae species. Thus, for this purpose we do not have to include the IUCN-restrictions.

Here we define translocation as the movement of living organisms from one area to another across natural barriers. In the new area the translocated organism lives free. Translocations can be intentional or accidental. The role of man is not always clear in cases of translocation.

2. METHODS

The database of records of intentionally or non-intentionally introduced leaf beetles is compiled using published records as the main source of information. Because not all published information was available for this study there is a chance that information is lacking; this is believed to be compensated by other publications in which similar information is available.

Only the traditional leaf beetles have been studied, i.e. exclusive the Bruchidae. Subfamily names used in this study are the traditional as have been used by SEENO & WILCOX (1982). All species group names of Chrysomelidae in Appendix 1 are scientific names complete with author. In the text they are without author names, except for those species that are not listed in Appendix 1.

A translocation event is defined as a translocation from an area where the species is indigenous to an area where the species previously did not occur. In this respect the translocation of *Chrysolina hyperici* from England to Australia in 1930 and from France to Australia in 1980 are considered as two different translocation events. In the case of biocontrol, translocations with different targets (host plants) are considered as different translocation events.

Excluded from the database are natural expansions. However we have to admit that it is not always clear to discriminate between natural range expansion and transport across natural barriers. This might be the case in species that are still in the phase of post-glacial expansion.

Also accidental translocations that have resulted in establishment in artificial environments as in greenhouses are not included in this research. In the Netherlands for example the alticine *Acrocrypta purpurea* Baly has established in a greenhouse where during several generations it damaged orchids (DÖBERL 1994b). *Acrocrypta purpurea* originates from South East Asia and it is unlikely that it will survive in the Netherlands outside (green)houses.

Sometimes it is difficult to define the exact moment of establishment. *Leptinotarsa decemlineata*, for example, was discovered in the Rocky Mountains and described in 1824. Suddenly, in 1859, it began devastating potato crops 100 miles west of Omaha, Nebraska, USA. Over the next few years, the beetle spread eastward to the Atlantic coast, which it reached in 1874. *Leptinotarsa decemlineata* became established in Europe following its introduction from the USA to Bordeaux, France in 1922 (after several unsuccessful attempts from 1876). The beetle spread rapidly in Europe despite intensive operations to control it. It was first reported in Belgium and Spain in 1935, Luxembourg in 1936, the Netherlands and Switzerland in 1937, Austria in 1941, Hungary and the former Czechoslovakia in 1945, Poland and Romania in 1947, and Turkey in 1949 (CAB-CPC 2003). In Appendix 1 the year 1922 is taken as the moment of establishment in Europe although it has been found earlier in France and established many years later in some European countries.

On the other hand a species may not have established in all parts of the country to which it is translocated. For example: all attempts to establish *L. jacobaeae* in Ontario, New Brunswick and Prince Edward Island were unsuccessful. In Canada it is at present established only in British Columbia. In the United States it is currently known from California and Oregon (LESAGE 1988).

3. RESULTS

In this study 126 leaf beetle species have been recorded to have been translocated at least once. They are listed in Appendix 1. Because many species have been translocated more than once, a total number of 230 translocation events in Chrysomelidae is listed (Appendix 1). Of each event information is given on place of origin of the leaf beetle, place where it is translocated to, moment of translocation, degree of success, host plant and source (reference). In Figure 1 the length of each bar represents the total number of species of each subfamily. Most translocated species occur in the subfamilies Chrysomelinae, Galerucinae, Alticinae, Cassidinae and Hispinae. In Figure 2 the length of the bar represents the number of translocations of each subfamily. The bar for the subfamily Hispinae is much larger than in Figure 1, indicating that some species have been translocated several times.

Translocations can be intentional or unintentional. The number of intentional translocations exceeds the number of unintentional translocations (Table 1). This is not surprising. Unintentional translocations are hard to detect; they mostly have not been published. Publications on species that have been unintentionally translocated mostly will deal with species that have become established in the newly inhabited land. When established they are more likely to be observed. Of the unintentional translocated species 81 % (70 out of 86) have become established against 63 % (91 out of 144) of the intentionally translocated species. The successes of intentional translocations that are part of a biological control program are monitored. This means that not only information on successful translocations are available but also of the unsuccessful releases. On the other hand the intentional translocations mostly take place only after intensive study. In biological control programs the success (and the risk) of the introduction is carefully studied before release. In that respect it is surprising to notice that 27 % (39 out of 144) of the intentionally translocated species have not become established.

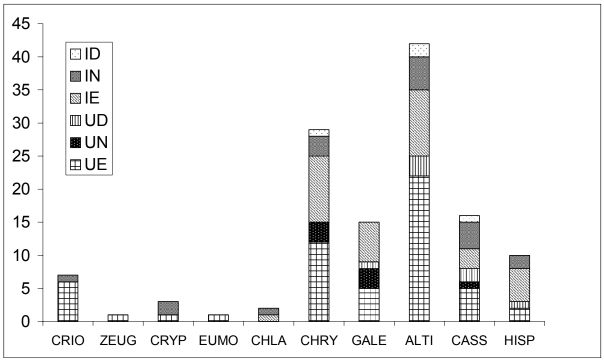

Fig. 1. Results of translocations in Chrysomelidae. Number of translocated species per subfamily. Subfamily abbreviations: CRIO = Criocerinae; ZEUG = Zeugophorinae; CRYP = Cryptocephalinae; EUMO = Eumolpinae; CHLA = Chlamisinae; CHRY = Chrysomelinae; GALE = Galerucinae; ALTI = Alticinae; CASS = Cassidinae; HISP = Hispinae. Results: UE = unintentional translocation followed by establishment; UN = unintentional, not established; UD = unintentional, establishment doubtful; IE = intentional and established; IN = intentional and not established; ID = intentional and doubtful.

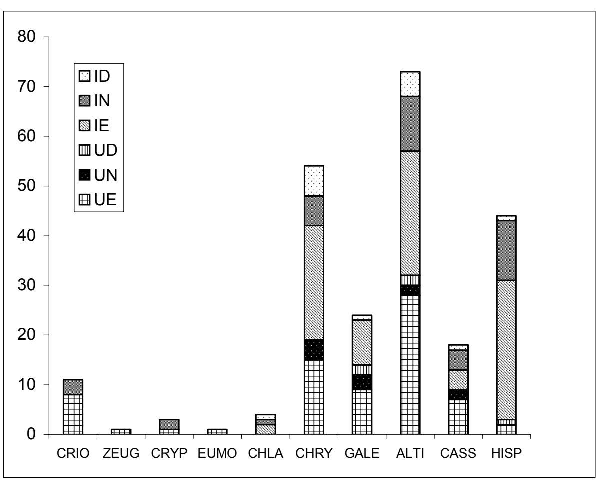

Fig. 2. Results of translocations in Chrysomelidae. Events per subfamily. Subfamily abbreviations as in Figure 1. Results: UE = unintentional translocation followed by establishment; UN = unintentional, not established; UD = unintentional, establishment doubtful; IE = intentional and established; IN = intentional and not established; ID = intentional and doubtful.

Intentionally translocated species mostly have very restricted food preference. The chances that they become a problem as a result of feeding on non-target species is lowest in monophagous species. We analysed the food preference of the unintentionally translocated species. In Figure 3 the number of species is presented for the next groups of phytophages: monophages – species that develop on a single plant species or genus; oligophages – species that develop on more than one plant genus of a single plant family; polyphages – species that develop on plant species of more than one family. It shows that most of these successful translocated species are mono- or oligophagous; they develop on plant species within a single genus or within a single plant family. This more or less implies that, because of the food restriction of most leaf beetles, host plants from the same genus or family have to be available in the new country.

It is interesting to find out what types of plants these successfully unintended translocated species feed on. Four categories of plants species have been distinguished: cultivated plant species, non-indigenous “wild” plants, indigenous “wild plants” and a last category of which information was insufficient (Fig. 4). It is evident that the majority of unintended successful translocation of leaf beetles occurred on cultivated plants and on non-indigenous (introduced plant species). Only a minority occurs on plants that are indigenous.

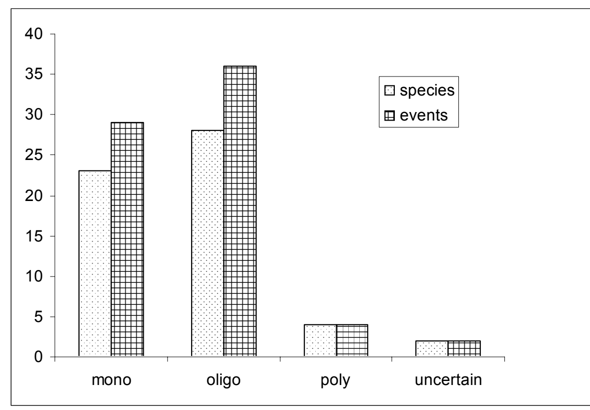

Fig. 3. Number of unintentionally translocated leaf beetles that have established per categories of food plants. Mono = monophagous, oligo = oligophagous, poly = polyphagous. Species = number of translocated species, events = number of translocation events.

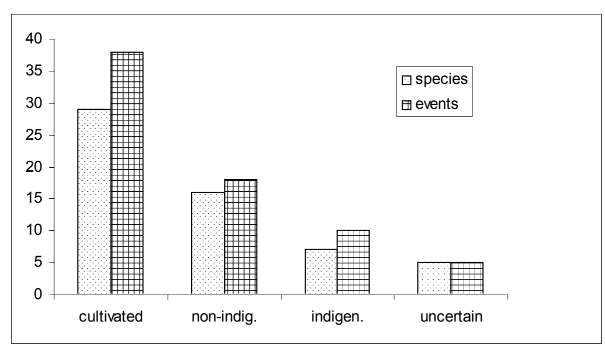

Fig. 4. Number of unintentionally translocated leaf beetles that have established per plant category: cultivated plants, non-indigenous plants, indigenous plants and plants of which this information is not available.

4. MISCELLANEOUS RESULTS

Apart from the results described above, interesting information became available on a variety of subjects. An extract of this is presented in this section. The following subjects are presented: description of species based on translocated specimens; unused biological control agents; the use of indigenous species in biological control; anecdotal information on the ways unintentional translocations have taken place and finally non-target effects.

4.1. Description of species based on translocated specimens

Some species description were based on displaced specimens: *Falsoplatyxantha diversicornis* Pic, *Luperus marginalis* Allard and *Aulacophora pannonica* Csiki (= *Hoplasoma unicolor* Ill.) (all Galerucinae). The type specimen(s) of *Falsoplatyxantha diversicornis* were from Turkey, but the author already stated that the species most probably originally came from the Indies ("Acquis comme provenant d'Asie Mineure, mais originaire vraisemblablement des Indes") (PIC 1931). Of *Hoplasoma unicolor* a single specimen was collected in Hungary and described as *Aulacophora pannonica* by CSIKI (1953). SILFVERBERG (1978) studied the type specimen of *A. pannonica* and reduced it to a junior synonym of *H. unicolor*. The type specimen of *A. pannonica* was probably imported from the Oriental region. Although there always remains the possibility of mislabelled specimens (see MOHAMEDSAID 2001). *Luperus marginalis* was described by ALLARD (1890) from the Falkland archipelago and according JOLIVET & VERMA (2002) evidently imported there in historical times. Apart from *L. marginalis* no Chrysomelidae have been mentioned from the Falkland archipelago.

4.2. Unused biological control agents

Some species have been selected to be used as a biological control agent but have not been used yet: *Ageniosa electoralis* Vogel (Chrysomelinae) was selected to be introduced in Australia to control *Chrysanthemoides monilifera* (JOLIVET 2001). *Charidotes pygmaea* Klug (Cassidinae) was selected to be released in Australia to control species of *Lantana* (JOLIVET 2001). *Homichloda barkeri* Jacoby (Alticinae) from Kenya was selected to control *Acacia nilotica* in Queensland (JOLIVET 2001). *Trachyaphthona sordida* (Baly) (Alticinae) a specialist herbivore on *Paederia foetida* (Skunk Vine) in China and Japan, which is a very invasive weed in Florida spreading in other parts of the Southern Unites States. *Trachyaphthona sordida* is of special interest to be be used as a biological agent (PEMBERTON & PRATT 2002).

Several species have been selected for the control of invasive plants but finally introduction has been abandoned because the species proved to be not selective enough in their food choice. This is the case for example for *Platyphora biforis* (Germar), *P.conviva* (Stål), *P. nigronotata* (Stål) and *P. paraguana* (Jacoby) for the control of Solanaceae (JOLIVET 2001).

4.3. The use of indigenous species in biological control

Very rarely indigenous species are successful in controlling nuisance herbs. Both *Chelymorpha cassidea* (F.) (Cassidinae) and *Chirida guttata* (Olivier) (Cassidinae) have been collected in 1979 in Saskatchewan and released in Alberta in an attempt to extend their ranges for the control of *Convolvulus arvensis*, where they did not establish (JULIEN 1992). In order to control *Calystegia sepium*, native organism of *Chirida guttata* have been collected in Ontario in 1971 and released in British Columbia. They did not establish either (JULIEN 1992). The same holds true for *Metriona purpurata* native organism collected in 1979 in Saskatchewan and released in Alberta in an attempt to extend its range and control *Convolvulus arvensis* (JULIEN 1992). However, *Altica foveicollis* Jacoby (Alticinae) a native species of Thailand was used in this country to control *Ludwigia adscendens*. It caused considerable damage with satisfactory degree of control (JULIEN 1992). *Gastrophysa atrocyanea* a native species introduced in Noto Peninsula (Japan) to control *Rumex obtusifolius* quickly established, increased its population and spread rapidly. Population of the beetle reached satisfactory levels within four years of release (JULIEN 1992). *Metriona bicolor*, a native organism collected in 1971 in Ontario and released in British Columbia in order to control *Calystegia sepium*, established. In 1985 it was found 14 km from the release site (JULIEN 1992).

Both *Leptinotarsa defecta* and *L. texana* are indigenous in the USA (Texas) and have been proposed as a biological control agent against three invasive *Solanum* species. The results of the study suggest that of the invasive *Solanum* species, *S. torvum* may be included in the potential host range of *L. texana*. It is suggested that this "new association" approach might result in a substantial control of one of Florida's most invasive solanaceous weeds with acceptable ecological risks (CUDA et al. 2002).

Native biological control agents offer potential advantages over non-native agents, because they may have little impact on non-target native species that have coexisted with the control agent (SHELDON et al. 1995).

4.4. Registered unintentional translocations

Very rarely aspects of unintentional translocations have been registered. In a few cases they can however be reconstructed. Sometimes unintentional introductions have been the result of intentional introduction during a biological control program. *Aphthona nigriscutis* was accidentally released in Canada in 1982 together with *Aphthona cyparissiae*. The release site was treated with herbicide and insecticide in order to eradicate this species (JULIEN 1992). And *Chrysolina hyperici* is believed to have been introduced accidentally in Hawaii together with *C. quadrigemina* in 1965. It was discovered in 1970 (JULIEN 1992) and JOLIVET (2001) assumes this species is established in Hawaii. In 1979 a *Longitarsus* species referred to as *L. jacobaeae* has been released in Australia from France. This species more closely resembles *L. flavicornis*. It is established and spreading, causing high reduction in weed density at some sites (JULIEN 1992).

Longitarsus ganglbaueri, a European species, is recently found in Oregon. LESAGE (1988) assumed it to be accidentally introduced with those of *L. jacobaeae* imported from Italy and introduced in Oregon.

Xanthogaleruca luteola was accidentally introduced into Britain from Bolzano (Italy) in July 1986. Several specimens had accidentally been transported in camping equipment (SMITH 1990). The single specimen recorded by STERRENBURG (1989) for the Netherlands may also have been based on a displaced specimen. This species has been recorded for the Netherlands only from the very south of the country (BEENEN 1998)

4.5. Non-target effects

Zygogramma bicolorata is an efficient biocontrol agent that can have significant negative impact on the growth and reproduction of *Parthenium hysterophorus* (DHILEEPAN et al. 2000). *Zygogramma bicolorata* breeds in India on small scale on *Xanthium strumarium* and feeds on *Helianthus annuus*. Feeding on *H. annuus* is regarded unwanted non-target feeding. *Parthenium* pollen, which contains parthenin, when deposited on *Helianthus annuus*, makes the latter attractive to beetles in absence of *Parthenium*. Continuous feeding on *Helianthus annuus* retards ovarian development and thus affects fecundity (VIRAKTAMATH et al. 2004).

JULIEN (1992) mentioned the case of *Chrysolina hyperici* that was introduced in New Zealand in 1947 from England to control *Hypericum perforatum* but attacked *Hypericum androsaemum*. Despite some early damage the insect has not persisted on *H. androsaemum* and has not established. In this case the non-target effect did not persist. *Galerucella calmariensis* and *Galerucella pusilla* have been introduced to North America in 1992 as a biological control agent for *Lythrum salicariae* and are now established in many US states and Canadian provinces. At some sites short-term attack on *Rosa multiflora*, *Potentilla anserina* and *Decodon verticillatus* has been observed. This "spillover" does not constitute a host shift since the beetles are unable to complete development on these non-target plants (BLOSSEY et al. 2001).

5. DISCUSSION

It is difficult to give an explanation of the observed relative high number of species from the subfamilies Chrysomelinae, Galerucinae, Alticinae, Cassidinae and Hispinae that have been translocated. It cannot be explained from the representation of these subfamilies within Chrysomelidae. Eumolpinae for example is a large subfamily and is represented in our database by only one species. Although JOLIVET (2001) attributed this to the endogenic life of the larvae of Eumolpinae, this can only be part of the explanation. KIMOTO (1988) showed remarkable differences in the geographical representation of subfamilies in Chrysomelidae. The translocated species originate from all biogeographical regions (Palearctic [47 %], Neotropical [20 %], Nearctic [16 %], Australasian [12 %] and Afrotropical Region [2 %]). The observed representation of subfamilies among the translocated species seems to be a mix of the subfamily representations in these biogeographical regions. For exampled, in the Palearctic Eumolpinae are represented by a low number of species.

It is most likely that the number of unintentional translocations is highly underestimated. Unintentional translocations that did not result in establishment are rarely detected and rarely published. However, unintentional translocations that resulted in establishment and showed negative effects are likely to have been noticed. Such translocations are of importance for our main question, namely the impact of translocations on the biodiversity.

Sometimes the reason why an introduced species has not established is clear. *Altica carduorum* was introduced in Canada in 1963 from Switzerland and France to control *Cirsium arvense*. It did not establish in Alberta, British Colombia, Nova Scotia or Ontario. Slow development in cool summers exposed larvae to high predation (JULIEN 1992). It was also introduced to Great Britain in 1969 and 1970 from France. Several thousands of specimens were released at Silkwood Park, Ascot, Berkshire and at three sites west of Cardiff, Glamorganshire, South Wales (BAKER et al. 1972, COX 2000). They survived the winter in cages only. The climate is too cold and wet to allow survival, except locally (JULIEN 1992). *Chrysolina varians* was introduced in Australia from England in 1930 to control *Hypericum perforatum* and did not establish. It is considered to have suffered from heavy predation and unfavourable climate (JULIEN 1992). It was introduced in Canada from Sweden in 1957 to control *Hypericum perforatum* and did not establish in British Columbia. Release sites were too dry during summer (JULIEN 1992). Adults of the alticinae *Disonycha glabrata* (F.) have been released to control *Amaranthus retroflexus* from Massachusetts (U.S.A.) in Red River Valley, North Dakota in 1979 and 1980 but failed to overwinter (JULIEN 1992). *Longitarsus albineus* was introduced in Australia in 1979 and 1981 from Greece and France to control *Heliotropium europaeum*. Establishment failed due to drought, which eliminated the host (JULIEN 1992). *Physonota alutacea* was introduced in Mauritius from Trinidad in 1947 to control *Cordia curassavica.* It did not establish due to interference by ants (JULIEN 1992).

The observed low percentage of polyphagous species (7 %) that have established after unintentional translocations is not surprising. It seems to be the result of the small proportion of polyphagous Chrysomelidae. Of Chrysomelidae (including Bruchidae) in Central Europe only 19 % are polyphagous, whereas monophagous species contribute 21 % and oligophagous species 60 % (SCHÖLLER 1996).

Although we know of some invasive species that cause a lot of harm, for example *Leptinotarsa decemlineata* and *Diabrotica* species, these species had effect on plants that were non-native culture plants. The spread of the potato over the world was followed by the spread of the insect species associated to it. The same holds for *Diabrotica virgifera* and the increasing culture of corn (*Zea mais*) in Europe. The associated insects will follow the crop when environmental conditions are favourable for the leaf beetle species. *Dicladispa armigera* (Olivier) (Hispinae) was recorded as a pest of rice in Bengal and Bangladesh in 1906. It is the most important hispid pest of rice in tropical Asia, and known from Bangladesh, Myanmar, India, Nepal and China, frequently causing extensive losses of rice crops. Although *D. armigera* is widely distributed throughout India, and frequently causes considerable damage to rice crops, it is only considered as a major pest of rice in Andhra Pradesh, Assam, Bihar, Madhya Pradesh, Manipur, Kerala, Orissa, Indian Punjab, Uttar Pradesh and West Bengal. It is only a rice pest in the southern provinces of China and is present in western Iran and Sumatra, Indonesia and Taiwan (CAB-CPC 2003).

Introduced leaf beetle species affecting native plants seem to be rare. The introduced *Plagiodera versicolora*, *Agelastica alni* and *Xanthogaleruca luteola* are known to damage ornamental trees, and they could cause damage to indigenous woody trees such as *Salix*, *Populus*, *Alnus* or *Ulmus* in North America. However this has never been reported. At present, *Epithrix hirtipennis* native to North and Central America occurs in Italy on several Solanaceae, also on the wild and indigenous species (Maurizio Biondi, L'Aquila-Coppito, pers. comm. 2004) but there is no indication that this causes a threat to biodiversity in Italy.

It seems that negative effects of introduced species on nature are barely recognised. However, this does not mean that they may never occur (DOWNIE 2001). SILFVERBERG (1995) listed the exotic beetle species that have colonized Finland and established themselves outdoors. No leaf beetle was included among the 14 species. This might be due to the climatic conditions in Finland. However, among the more than 200 invasive species listed in the internet invasive species database no Chrysomelidae have been listed (IUCN/SSC 2004). This database focuses on invasive species that are believed to be a threat to biodiversity. From the absence of leaf beetles we might conclude that translocated leaf beetles do not threaten biodiversity yet. This is interesting because there are very alarming situations of leaf beetles attacking cultivated plants (*Diabrotica virgifera*, *Leptinotarsa decemlineata*) or species that have been effectively used as control agent against introduced weeds (*Chrysolina hyperici* and *C. quadrigemina*). In these circumstances, where alien leaf beetle species eradicate a population of a host plant, the host plants grow vigorously because of two different situations: one is the cultivated situation in which the environmental (fertilisation, hydration) and ecological conditions (absence of competition, diseases) favour the host plant very much. A monoculture of good growing plants is the result. The other is a situation in which an alien plant is invading a new environment, mostly in absence of natural enemies or diseases and mostly without competitors. Under more natural conditions the herbivorous beetles find less favourable conditions. When a leaf beetle enters an ecosystem it faces a complex of interrelations in which it first has to establish. It has been shown (KOVALEV 2004) in model studies that this process is more likely to occur in situations where host plants are evenly spread. Under natural conditions this situation rarely occurs. ELTON (2000) promoted in his famous work on ecological invasions, ecological stability to resist invading species.

The threats caused by introduced species on native species are larger than can be concluded from this study on Chrysomelidae. Introduced plant species, introduced carnivorous species, introduced plant or animal diseases, may all have their effect on native leaf beetles. Many cases have been listed in which non-native insects (predators or parasitoids) have been released to control non-native pest species (for examples release of *Oomyzus gallerucae* Fonscolombe (Hymenoptera, Eulophidae) in the United States for the control of *Xanthogaleruca luteola* (PUTTLER & BAILEY 2003). The damage of intentionally introduced species to non-target, native species from these biological controls are rarely documented.

No negative effects on biodiversity of translocated Chrysomelidae have, at present, been reported. The successful control of imported weeds by introduced Chrysomelidae can be seen as a positive effect to biodiversity since some of these weeds prevent natural processes in ecosystems. It is generally accepted that only a minority of alien species become abundant. WILLIAMSON & FITTER (1996) concluded that as many as 80 – 90 % of the established non-indigenous species may actually have minimal detectable effects. Apart from that, introduction of non-indigenous species as a biological control agent is preceded by intensive research to predict the effect of these introductions. BYERS et al. (2002), however, indicated that although there has been a lot of research, we still have little information on the effects on the communities and species we are attempting to protect. They propose key research questions to effectively prioritise and manage non-indigenous species.

Although there are no cases known in which biodiversity is threatened by translocated Chrysomelidae this is no guarantee that it will not happen. Accidental translocations must be avoided as much as possible. No intentional translocations should be considered until the factors, which limit its distribution and abundance in its native range, have been understood. The approach suggested by the IUCN (1987, 2000) will minimise the risks.

The Convention on Biological Diversity (Rio de Janeiro 1992) called for prevention of the introduction of, control or eradication of those alien species, which threaten ecosystems, habitats or species. However it proved to be difficult to discriminate between alien species that are likely to be invasive and those that are not. Because post entry control of invasive alien species is much more costly than prevention of invasions, MACK et al. (2000) suggested that national and international quarantine laws should be altered by adopting a "guilty until proven innocent" approach.

A rarely studied risk of alien species is the role of evolutionary processes. KOVALEV (2002) showed changes in the introduced *Zygogramma suturalis* which developed flight ability and morphological differences within five generations. The differences where large enough to attribute the Palearctic population to a new subspecies: *Z. suturalis volutes* KOVALEV. About the risk of hybridisation between native leaf beetle species and alien species nothing is clear. Hybridisations between native and alien plants species or between genetically different populations of alien plants are believed to promote rapid evolution and further invasion as has been observed in *Spartina anglica* (polyploid hybrid of *S. alterniflora* from eastern America and the European *S. maritima*) and *Rhododendron ponticum* (introduced from several different Iberian populations) (PETIT 2004).

Apart from natural processes as the post glacial spread of many species (including spread across barriers as the Alps and Pyrenees in Europe), human-induced translocations may have started as soon as man appeared.

In Europe the invasion of alien species started in ancient times. The original landscape most probably was a mosaic of forest and open areas. When man arrived large areas were cleared for agriculture. Plant and animal species from deserts and steppes invaded the European region when new, cultivated, habitats appeared. Already at the time of Columbus the coastland of Western Europe was almost devoid of forests and transformed into an artificial steppe inhabited by man's constant followers among plants and animals, invited or self-invited (LINDROTH 1957). Part of theses species have simply expanded their range but it is very likely that part of them were actively transported with seeds or with the transport of livestock (both plants and animals). It is very likely that leaf beetle species associated with crops or the herbs that grow between them have taken the same route as herbs associated with cereals. They are supposed to have arrived in Europe from the Near East (PINHASI *et al*. 2005). This process is still going on. HAMMOND (1974) assumed that some of the relative recent immigrants to the British Isles may represent delayed movements of the same kind. An example of such a species combination may be *Buglossoides* (= *Lithospermum*) *arvensis* and *Longitarsus fuscoaeneaus* REDTENBACHER. Both species are nowadays indigenous in Europe. It is believed that *B. arvensis* originated in southwest-Asia and spreaded with agriculture to large parts of the temperate parts of the Northern Hemisphere. In The Netherlands it already occurred during the Roman times (WEEDA *et al*. 1988). It is likely that *L. fuscoaeneus* spreaded with this herb. FRITZ-KÖHLER (1996) and FRITZLAR (1998) estimate that about 5% of the leaf beetles of the German states Rhineland and Thüringia came along with introduced plants (neophytes and archeophytes).

In America conditions were different when transatlantic trade started. In northeastern North America the tribes were more or less migratory and had hardly progressed beyond the Neolithic stage. Therefore in North America, the chance of native steppe plants invading permanent arable land and transforming into constant weeds was considerably less than in the old world. When the first Europeans arrived and permanent settlements were founded upon which agriculture started, there were few indigenous plants present able to intrude as weeds. This gave free entrance to the corresponding floral elements from Europe. Species introduced from Europe into North America are about ten times as numerous as those transported in the opposite direction (LINDROTH 1957). This is partly explained by the peculiar character of ballast traffic in the 19th century. The small sailing vessels used for commercial traffic needed cargo or ballast to be sailed efficiently. On their way to Northern American ports they often were short in tonnage. The bottom of the lower holds were then filled with material available at the shore of departure: gravel, rocks or even moist sand. On arrival at their destination the ballast was dumped on the coast, including the plants and animals that came along with this material. Examples of leaf beetles that have been transported in this way are *Cassida flaveola*, *Chrysolina staphylea* and *Gastrophysa polygoni* (LINDROTH 1957).

Not all translocations have to be human-induced. CLARKE & ZALUCKI (2004) suggested, based on historical information, that a substantial population of the monarch butterfly (*Danaus plexippus* (L.), Danaidae) was carried to Australia on winds associated with cyclones that hit the Queensland coast in early 1870. The leaf beetle *Chaetocnema confinis*, originally a North American species, has spread to tropical America, Africa, Asia and the Pacific, accidentally introduced in Hawaii and established, it is reported to be transported by a hurricane (JOLIVET 2001). *Stegnaspa trimeni* is common on Tristan da Cunha and originated from Southern Africa, most probably it was accidentally introduced or transported eolic (hurricane ?) (JOLIVET 1998). *Epithrix hirtipennis* from North and Central America was recorded in 1984 from the Azores and Italy (DÖBERL 1994a). Subsequently it spreaded to Greece (1988) and Turkey (1993). Although introduction with cultivated plants is possible, spreading with passatwinds is also suggested as a possibility (DÖBERL 1994a).

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Appendix 1

Table of translocated leaf beetle species with information on the translocation events, the success of the translocation and the host plants. For all records the information source is presented. Status: E = established; N = not established; D = doubtful. Intention: I= intentional; U = unintentional. Subfamily abbreviations: CRIO = Criocerinae; ZEUG = Zeugophorinae; CRYP = Cryptocephalinae; EUMO = Eumolpinae; CHLA = Chlamisinae; CHRY = Chrysomelinae; GALE = Galerucinae; ALTI = Alticinae; CASS = Cassidinae; HISP = Hispinae.

Species	Subfamily	Indigenous	Destination	Status	Date	Host	Reference	Intention
Acalymma vittatum (Fabricius)	ALTI	Central USA	West USA	E	?	Cucumber	CAB-CPC 2003	U
Agasicles hygrophila Selman & Vogt	ALTI	Argentina	USA	E	1964	*Alternanthera philoxeroides*	Julien 1992; Hawkes et al. 1967	I
			Australia	E	1977		Julien 1992	I
			New Zealand	E	1981		Julien 1992	I
			Thailand	E	1982		Julien 1992	I
			P. R. China	?	1986		Julien 1992	I
Agelastica alni (Linnaeus)	GALE	Europe	Northeast USA	E	?	*Alnus glutinosa*	Lindroth 1957	U
Alagoasa parana Samuelson	ALTI	Brazil	Australia	N	1981	*Lantana camara*	Julien 1992	I
			Rep. South Africa	N	1985		Julien 1992	I
Altica carduorum Guérin-Méneville	ALTI	Continental Europe	Canada	N	1963	*Cirsium arvense*	Julien 1992	I
			Great Britain	N	1969, 1970		Julien 1992	I
			New Zealand	?	1999		Julien 1992	I
			USA	N	1966, 1970			I
		P. R. China	USA	?	?		Jolivet 2001	I
Altica foveicollis Jacoby	ALTI	Thailand	Thailand	E	?	*Ludwigia adscendens*	Julien 1992	I
Anacassis fuscata (Klug)	CASS	Australia	Brazil	N	1976	*Baccharis halimifolia*	Julien 1992	I
Anacassis phaeopoda Buzzi	CASS	Australia	Brazil	N	1976	*Baccharis halimifolia*	Julien 1992	I
Aphthona abdominalis (Duftschmid)	ALTI	Europe	USA	E	1993	*Euphorbia esula*	Jolivet 2001; Schroeder & Gassmann 1997	I
Aphthona cyparissiae (Koch)	ALTI	Europe	Canada	E	1982	*Euphorbia cyparissias*	Julien 1992	I
				E	1982	*Euphorbia x pseudovirgata, E. esula*	Julien 1992; Schroeder & Gassmann 1997	I

Aphthona cyparissiae (Koch)			USA		1986	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
Aphthona czwalinai (Weise)	ALTI	Europe	Canada	N	1987	*Euphorbia cyparissias*	JULIEN 1992	I
			Canada	E	1985, 1989, 1990	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
			USA	E	1987	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
Aphthona flava Guillebeau	ALTI	Europe	Canada	N	1982	*Euphorbia cyparissias*	JULIEN 1992	I
				E	1982	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
			USA	E	1985	*Euphorbia x pseudovirgata, E. esula*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
			Canada	E	1990	*Euphorbia esula*	SCHROEDER & GASSMANN 1997	I
			USA	E	1993	*Euphorbia esula*	SCHROEDER & GASSMANN 1997	I
Aphthona nigriscutis Foudras	ALTI	Europe	Canada	N	1982	*Euphorbia cyparissias*	JULIEN 1992	U
				E	1983	*Euphorbia esula, E. cyparissias,*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
				N	1982	*Euphorbia x pseudovirgata*	JULIEN 1992	U
				E	1983		JULIEN 1992; SCHROEDER & GASSMANN 1997	I
			USA	E	1989	*Euphorbia x pseudovirgata*	JULIEN 1992; SCHROEDER & GASSMANN 1997	I
Argopistes gourvesi Samuelson	ALTI	Tahiti	Archipel de Tahiti	E	?	Oleaceae	JOLIVET 2001	U
Aspidimorpha deusta (Fabricius)	CASS	Asia: East of Java	Malaysia	E	?	*Ipomoea pes-caprae*	VELU 2001	U

Species	Subfamily	Indigenous	Destination	Status	Date	Host	Reference	Intention
Aspidimorpha nigropunctata (Klug)	CASS	Africa	Netherlands	N	1988	?	Beenen, unpubl.	U
Aulacophora indica (Gmelin)	GALE	Asia, Oceania	Canada: Vancouver	N	1964	Cucurbitaceae	Beenen, unpubl.	U
Brontispa chalybeipennis (Zacher)	HISP	?	Hawaii.	E	?	Palms	Jolivet 2001	U
Brontispa longissima Gestro	HISP	Indonesia, Papua New Guinea, Irian Jaya.	Japan: Okinawa	E	1978	Palms	Morimoto & Kiritani 1995	U
Calligrapha pantherina Stål	CHRY	Mexico	Australia	E	1989	*Sida acuta*	Julien 1992	I
				E	1989	*Sida rhombifolia*	Julien 1992	I
Calligrapha polyspila (Germar)	CHRY	Nearctic	Azores	E	?	*Sida rhombifolia*	Jolivet 2001	U
Cassida azurea Fabricius	CASS	Europe	Canada	?E	1989	*Silene vulgaris*	Julien 1992	I
			USA	E	?		Jolivet 2001	I
Cassida circumdata Herbst	CASS	Indomalaysia	Hawaii	E	?	Convolvulaceae	Jolivet 2001	U
Cassida flaveola Thunberg	CASS	Europe	Eastern USA, Canada	E	?	Cariophyllaceae	Lindroth 1957	U
Cassida miliaris Fabricius	CASS	Southeast Asia	St. Helena	N	?	*Ipomoea*, *Convolvulus*	Jolivet 2001	U
Cassida obtusata Boheman	CASS	Southeast Asia	Japan	E	?	Amaranthaceae	Morimoto & Kiritani 1995	U
Cassida rubiginosa Müller	CASS	Europe	Canada	E	prior 1902	*Carduus acanthoides, Carduus nutans*	Julien 1992	U
			USA	E	±1901	*Carduus rthoermeri*, *Cirsium vulgare*	Spring & Kok 1999 Lindroth 1957	U
Chaetocnema concinna (Marsham)	ALTI	Europe	Canada, USA	E	?	*Polygonum persicariae, Sorghum sudanense*	LeSage 1990 Lindroth 1957	U
Chaetocnema confinis Crotch	ALTI	USA	tropical America, Africa, Asia and the Pacific	E	?	*Ipomoea*	Jolivet 1998 Jolivet 2001	U
Chlamisus mimosae Karren	CHLA	Brazil	Australia	E	1985	*Mimosa pigra*	Julien 1992	I
			Thailand	E	1986		Julien 1992	I
			Vietnam	?	1999		Julien 1992	I

Chlamisus gibbosa (Fabricius)	CHLA	U.S.A (Missouri)	Hawaii	N	1969	*Rubus argutus*	Julien 1992	I
Chrysolina bankii (Fabricius)	CHRY	Europe	Azores	E	?	Labiatae	Jolivet 2001	U
Chrysolina brunsvicensis (Gravenhorst)	CHRY	England	Australia	N	1930	*Hypericum perforatum*	Julien 1992	I
Chrysolina gypsophilae Küster	CHRY		USA	E	?	*Linaria genistifolia dalmatica*	Jolivet 2001	I
Chrysolina hyperici (Forster)	CHRY	England	New Zealand	E	1943	*Hypericum perforatum*	Julien 1992; Fields et al. 1988	I
			Australia	E	1930		Julien 1992	I
		France	Australia	?	1980		Julien 1992	I
		England via Australia via U.S.A	Canada	E	1951		Julien 1992; Fields et al. 1988	I
		England via Australia	USA	E	1945		Julien 1992; Fields et al. 1988	I
		England via Australia via USA	Chile	E	1953		Julien 1992	I
		England via Australia	Rep. South Africa	N	1960		Julien 1992	I
		England via Australia via USA via Canada		D	1973		Julien 1992	I
			Hawaii	E	1965		Julien 1992; Jolivet 2001	U
Chrysolina polita (Linnaeus)	CHRY		Lesser Antilles	N	?		Jolivet 2001	U
Chrysolina quadrigemena (Suffrian)	CHRY	France	Australia	E	1939	*Hypericum perforatum*	Julien 1992; Fields et al. 1988	I
		France via Australia via USA	Canada	E	1952		Julien 1992; Fields et al. 1988	I
		France via Australia via USA	Chile	E	1953		Julien 1992	I
		France via Australia via California	Hawaii	E	1965		Julien 1992	I
		France via Australia	New Zealand	E	1963		Julien 1992; Fraser & Emberson 1987	I
		France via Australia	South Africa	E	1961		Julien 1992	I
		France via Australia	USA	E	1946		Julien 1992; Fields et al. 1988	I

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Chrysolina staphylea (Linnaeus)	CHRY	Palearctic	Nova Scotia (Canada)	E	?	*Plantago*	LINDROTH 1957	U
Chrysolina varians (Schaller)	CHRY	England	Australia	N	1930	*Hypericum perforatum*	JULIEN 1992	I
		Sweden	Canada	N	1957			I
		Europe	USA	N	1950		JULIEN 1992	I
Colposcelis signata (Motschulsky)	EUMO	Southeast Asia	Hawaii	E	?	Fabaceae	JOLIVET 2001	U
Crioceris asparagi (Linnaeus)	CRIO		Eastern USA	E		*Asparagus officinalis*	LINDROTH 1957	U
Crioceris decempunctata Linnaeus	CRIO		Eastern USA	E		*Asparagus officinalis*	LINDROTH 1957	U
Diabrotica undecimpunctata Mannerheim	GALE	USA	Hawaii	N	?		JOLIVET 2001	U
Diabrotica virgifera virgifera LeConte	GALE	Central America	North America	E	after 1000	*Zea mais*	GRAY & STEFFEY 1999	U
			Europe	E	1992		GRAY & STEFFEY 1999	U
Diachus auratus (Fabricius)	CRYP	Central America	New Caledonia, Australia, Pacific Region (Hawaii, Tahiti)	E	?	Polyphagous	JOLIVET 2001	U
Diorhabda elongate Brullé	GALE		USA	E	?	*Tamarix ramosissima*	JOLIVET 2001	I
Disonycha argentinensis Jacoby	ALTI	Brazil	Australia	N	1980	*Alternanthera philoxeroides*	JULIEN 1992	I
			New Zealand	N	1982		JULIEN 1992	I
Disonycha glabrata (Fabricius)	ALTI	MS (U.S.A.)	ND (U.S.A.)	N	1979/80	*Amaranthus retroflexus*	JULIEN 1992	I
Epithrix fasciata Blatchely	ALTI	Brazil	Hawaii	E	?	Solanaceae	JOLIVET 2001	U
Epithrix hirtipennis (Melsheimer)	ALTI	North and Central America	Azores and	E	1984	Solanaceae	DÖBERL 1994a	U
			Italy	E	1984		DÖBERL 1994a; SANNINO et al. 1985	U

Epithrix hirtipennis (Melsheimer)			Greece	E	1988		DÖBERL 1994a	U
			Turkey	E	1993		DÖBERL 1994a	U
			Hawaii	E	?		JOLIVET 2001	U
Galeruca rufa Germar	GALE	Europe	USA	E	?	*Convolvuls arvensis, C. sepium*	JOLIVET 2001	I
Galerucella calmariensis (Linnaeus)	GALE	Germany	USA	E	1992	*Lythrum salicariae*	HIGHT et al. 1995	I
			Canada	E	1992		HIGHT et al. 1995	I
Galerucella pusilla (Duftschmid)	GALE	Germany	USA	E	1992	*Lythrum salicariae*	HIGHT et al. 1995	I
			Canada	E	1992		HIGHT et al. 1995	I
Gastrophysa atrocyanea Motschulsky	CHRY	Japan	Noto Peninsula (Japan)	E	?	*Rumex obtusifolius*	JULIEN 1992	I
Gastrophysa polygoni (Linnaeus)	CHRY	Palearctic	USA, Canada	E	?	Polygonaceae	LINDROTH 1957	U
Lema bilineata (Germar)	CRIO	Argentina	South Africa	E	± 1900	Solanaceaea	JOLIVET 2001	U
Lema cyanella (Linnaeus)	CRIO	Switzerland	Canada	N	1978/83	*Cirsium arvense*	JULIEN 1992	I
			New Zealand	N	1983/90		JULIEN 1992	I
			USA	N	?		JOLIVET 2001	I
Lema trilinea White	CRIO	Northern America	Hawaii	E	?	Solanaceae	JOLIVET 2001	U
			South Africa	E	± 1900	Solanaceaea	JOLIVET 2001	U
Leptinotarsa decemlineata Say	CHRY	Rocky Mountains	USA, Canada,	E	1859	Solanaceaea	LINDROTH 1957	U
			Europe	E	1922			
			Lesser Antilles	N	?		JOLIVET 2001	U
Leptinotarsa defecta (Stål)	CHRY	USA	South Africa	E	1992	*Solanum elaeagnifolium*	HOFFMANN et al. 1998, CUDA et al. 2002	I
Leptinotarsa texana (Schaeffer)	CHRY	USA	South Africa	E	1992	*Solanum elaeagnifolium*	HOFFMANN et al. 1998, CUDA et al. 2002	I
Lilioceris lilii Scopoli	CRIO	Palearctic	Montreal (Canada)	E	1945	Liliaceae	LINDROTH 1957	U
			USA	E	1992		UNIVERSITY OF RHODE ISLAND 2002	U
Lioplacis elliptica (Stål)	CHRY	Brazil	Australia	N	1977	*Baccharis halimifolia*	JULIEN 1992	I

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Longitarsus aeneus Kutschera	ALTI	Mediterranean	Australia	?	?	*Echium plantagineum*	Jolivet 2001	I
Longitarsus albineus (Foudras)	ALTI	Greece and France	Australia	N	1979, 1981	*Heliotropium europaeum*	Julien 1992	I
Longitarsus echii (Koch)	ALTI	Palearctic	Australia	?	?	*Echium plantagineum*	Jolivet 2001	I
Longitarsus ferrugineus (Foudras)	ALTI	Europe	USA, Canada	E	?	*Mentha*	Lindroth 1957; LeSage 1988	U
Longitarsus flavicornis (Stephens)	ALTI	Spain	Australia	E	1985	*Senecio jacobaea*	Julien 1992	I
		Britain	Canada	E	1971	*Senecio jacobaea*	Julien 1992	I
Longitarsus ganglbaueri Heikertinger	ALTI	? Italy	Oregon (USA)	E		*Senecio*	LeSage 1988	U
Longitarsus jacobaeae (Waterhouse)	ALTI	Italy	USA	E	1969	*Senecio jacobaea*	Julien 1992; LeSage 1988	I
		Italy via USA	Canada	E	1971		Julien 1992; LeSage 1988	I
		Italy via USA	New Zealand	E	1983		Julien 1992	I
		Italy via USA via New Zealand	Australia	E	1988		Julien 1992	I
Longitarsus luridus (Scopoli)	ALTI	Europe	USA, Canada	E	?	Plantaginaceae	LeSage 1988	U
Longitarsus pellucidus (Foudras)	ALTI	Europe	Ontario (Canada)	?	?	Convolvulaceae	LeSage 1988	U
Longitarsus pratensis (Panzer)	ALTI	Europe	USA, Canada	E	?	Plantaginaceae	LeSage 1988; Jolivet 2001	U
Longitarsus rubiginosus (Foudras)	ALTI	Europe	Canada (Québec, Ontario)	E	?	Convolvulaceae	LeSage 1988	U
Longitarsus succineus (Foudras)	ALTI	Europe	Newfoundland (Canada)	E	?	Asteraceae	Lindroth 1957; LeSage 1988	U
Macrima pallida (Laboissière)	GALE	Himalaya range	Cyprus	?	?		Beenen unpubl.	U
Mantura chrysanthemi Koch	ALTI	Europe	USA (Massachusetts)	?	?	Poylgonaceae	Lindroth 1957; Jolivet 2001	U
Metallactus nigrofasciatus Suffrian	CRYP	Brazil	Australia	N	1982	*Baccharis halimifolia*	Julien 1992	I

Metallactus patagonicus Suffrian	CRYP	Brazil	Australia	N	1974	*Baccharis halimifolia*	JULIEN 1992	I
Metriona bicolor (Fabricius)	CASS	Ontario (Canada)	British Columbia (Canada)	E	1971	*Calystegia sepium*	JULIEN 1992	I
Metriona purpurata (Boheman)	CASS	Saskatchewan (Canada)	Alberta (Canada)	N	1979	*Convolvulus arvensis*	JULIEN 1992	I
Metrogaleruca obscura (Degeer)	GALE	Trinidad	Malaysia	?	1977 ?	*Cordia curassavica*	JULIEN 1992	I
			Mauritius	E	1948		JULIEN 1992	I
		Trinidad via Malaysia	Sri Lanka	E	1948		JULIEN 1992	I
Microtheca ochroloma Stål	CHRY	Argentina and Uruguay	USA	E	?	Brassicaceaea	JOLIVET 2001	U
Microtheca picea (Guérin)	CHRY	Argentina and Uruguay	USA	E	?	Brassicaceae	JOLIVET 2001	U
Monoxia minuta Blake	GALE	USA	Hawaii	E	?	*Chrysothamnus*	JOLIVET 2001	U
Neolochmaea dilatipennis (Jacoby)	GALE	Panama	Miami (USA)	E	?	*Borreria terminalis*	JOLIVET 2001; JOLIVET & HAWKESWOOD 1995	U
Octacoma championi Baly	HISP	Costa Rica	Australia	E	1975	*Lantana camara*	JULIEN 1992	I
			Norfolk island	?	1988		JULIEN 1992	I
		Central America via Australia	Fiji	N	1976		JULIEN 1992	I
		Central America via Australia	South Africa	N	1978		JULIEN 1992	I
Octacoma plicatula (Fabricius)	HISP	?	Hawaii	N	1954	*Lantana camara*	JULIEN 1992	I
Octocoma scabripennis Guérin-Méneville	HISP	Mexico via Hawaii	Australia	E	1966	*Lantana camara*	JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
			Norfolk island	E	1971		JULIEN 1992	I
		El Salvador	Australia	E	1974		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Mexico via Hawaii via Australia	Cook Islands	N	1973		JULIEN 1992	I
		Mexico via Australia	Fiji	N	1971, 1976		JULIEN 1992	I
		Mexico via Hawaii via Australia	Ghana	E	1971, 1973		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Mexico	Hawaii	N	1902		JULIEN 1992	I

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Octocoma scabripennis Guérin-Méneville		Mexico	Hawaii	E	1954		JULIEN 1992	I
		Mexico via Hawaii via Australia	India	E	1921		JULIEN 1992	I
		from Mexico via Hawaii	Mariana Islands	N	1971		JULIEN 1992	I
		Mexico via Hawaii via Australia	New Caledonia	E	1977		JULIEN 1992	I
		Mexico via Hawaii via Australia	South Africa	E	1971, 1974		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
Ophraella communa LeSage	GALE	North America	Honshu (Japan)	E	1996	*Ambrosia artemisiifolia, A. trifida*	SUZUKI & NAKAMURA 1999; WATANABE & HIRAI 2004	U
			Taiwan	E	1996		WANG & CHIANG 1998	U
			China	E	2004		ZHANG et al. 2005	U
Oulema melanopus (Linnaeus)	CRIO	Palearctic	USA	E	?	Gramineae	JOLIVET 2001	U
Paropsis charybdis Stål	CHRY	Australia	South Africa	E	?	*Eucalyptus*	JOLIVET 2001	U
			New Zealand	E	?		JOLIVET 2001	U
Pentispa suturalis Baly	HISP	?	USA	E	?	*Baccharis bigelovii*	JOLIVET 2001	I
Phaedon armoraciae L. (identification needs confirmation !)	CHRY	Palearctic	Canada	E	?	*Veronica beccabunga*	LINDROTH 1957	U
Phaedon cochleariae Fabricius (identification needs confirmation !)	CHRY	Palearctic	USA, Canada	E	?	Brassicaceae	LINDROTH 1957	U
Phyllocharis undulata (Linnaeus)	CHRY	Vietnam	Thailand	E	1990	*Clerodendrum philippinum*	JULIEN 1992	I
Phyllotreta aerea Allard	ALTI	Palearctic	Northeast USA	E	?	Brassicaceae	LINDROTH 1957	U
Phyllotreta armoraciae Koch	ALTI	Palearctic	Northeast USA, Eastern Canada	E	?	*Armoracia rusticana*	LINDROTH 1957; DILLON & DILLON 1972	U
Phyllotreta cruciferae (Goeze)	ALTI	Eurasian	North America	E	± 1920	Cruciferae (crops)	CAB-CPC	U

Phyllotreta undulata Kutschera	ALTI	Palearctic	Maryland	E	?	Brassicaceae	LINDROTH 1957	U
Phyllotreta vittata Fabricius	ALTI	Palearctic	North America	E	?	Brassicaceae	CAB-CPC 2003	U
			South Africa	E	?		CAB-CPC 2003	U
Physonota alutacea Boheman	CASS	Trinidad	Mauritius	N	1947	*Cordia curassavica*	JULIEN 1992	I
Plagiodera versicolora Laicharting	CHRY	Palearctic	Northeastern USA, Eastern Canada	E	1911	*Salix* and *Populus*	LINDROTH 1957; ELTON 2000; JOLIVET 2001	U
Promecotheca papuana Csiki	HISP		Queensland (Australia)	D	?	Coconut	CAB-CPC 2003	U
Pseudolampsis guttata (LeConte)	ALTI	Argentina and Uruguay	USA	E	?	*Azolla*	JOLIVET 2001; JOLIVET & HAWKESWOOD 1995	U
Pseudorupilia ruficollis (Fabricius)	GALE	South African	Sainte Hélène	N	?	Restionaceae, Proteaceae, Asteraceae	JOLIVET 2001	U
Psylliodes chalcomerus (Illiger)	ALTI		USA	E	?	*Carduus nutans*	JOLIVET 2001	I
Psylliodes chrysocephalus Linnaeus	ALTI		Newfoundland (Canada)	E	?	Brassicaceae	LINDROTH 1957	U
Psylliodes cucullatus Illiger	ALTI	Palearctic	Eastern Canada	E	?	?	LINDROTH 1957	U
Psylliodes picina (Marsham)	ALTI		USA	E	?	*Lythrum, Lysimachia*	LINDROTH 1957	U
Silana farinosa (Boheman)	CASS	Sri Lanka	Malaysia	E	?	Curry leaves	VELU 2001	U
Stegnaspa trimeni Baly	ALTI	Southern Africa	Tristan da Cunha	E	?	?	JOLIVET 2001	U
Stolas fuscata (Klug)	CASS	Argentina	USA	E	?	*Baccharis salicifolia*	JOLIVET 2001	I
Stolas ingrata (Boheman)	CASS	Argentina	USA	E	?	*Gutierrezia* spp.	JOLIVET 2001	I
Systena blanda Melsheimer	ALTI	USA	Hawaii	E	?	polyphagous	JOLIVET 2001	U
Timarcha goettingensis-complex	CHRY	Europe	Gran Canaria (Islas Canarias)	N	?	*Galium*	JOLIVET & VERMA 2002	U
Trachymela tincticollis (Blackburn)	CHRY	Australia	South Africa	E	?	*Eucalyptus*	JOLIVET 2001	U
Trirhabda baccharidis (Weber)	GALE	USA	Australia	E	1969	*Baccharis halimifolia*	JULIEN 1992	I

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Uroplata girardi Pic	HISP	Brazil via Hawaii	Australia	E	1966	*Lantana camara*	JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
			Norfolk Island	E	1971		JULIEN 1992	I
		Brazil via Hawaii	Caroline Islands	E	1963, 1974		JULIEN 1992	I
		Brazil via Hawaii via Australia via Fiji	Cook Island	E	1969		JULIEN 1992	I
		Brazil via Hawaii via Australia via India	Cook Island	E	1976		JULIEN 1992	I
		Brazil via Hawaii	Fiji	E	1969		JULIEN 1992	I
		Brazil via Hawaii	Ghana	E	1971		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Brazil	Hawaii	E	1961		JULIEN 1992	I
		Brazil via Hawaii	India	E	1972		JULIEN 1992	I
		Brazil via Hawaii	Mariana Islands	E	1963/1967		JULIEN 1992	I
		Trinidad	Mauritius	E	1967		JULIEN 1992	I
		Brazil via Hawaii via Australia	New Caledonia	E	1977		JULIEN 1992	I
		Brazil via Hawaii via Australia	Papua New Guinea	E	1972		JULIEN 1992	I
		Brazil via Hawaii via Fiji	Philippines	E	1985		JULIEN 1992; BEENEN, unpubl.	I
		Argentina, Brazil, Paraguay via Hawaii via Australia	South Africa	E	1974, 1981		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Trinidad via Mauritius	South Africa	E	1984		JULIEN 1992; JOLIVET & HAWKESWOOD 1995	I
		Brazil via Trinidad	Tanzania	N	1967		JULIEN 1992	I
		Brazil via Hawaii via Australia via Fiji	Tonga Islands	E	1969		JULIEN 1992	I
Uroplata lantanae Buzzi & Winder	HISP	Brazil	Australia	N	1977	*Lantana camara*	JULIEN 1992	I
		Brazil via Australia	South Africa	N	1984		JULIEN 1992	I
Uroplata sp. near *bilineata* Chapuis	HISP	Brazil	Australia	E	1976	*Lantana camara*	JULIEN 1992	I
		Central America	Fiji	N	1976	*Lantana camara*	JULIEN 1992	I

Uroplata sp. near *bilineata* Chapuis		Costa Rica via Australia	South Africa	N	1978	*Lantana camara*	Julien 1992	I
Xanthogaleruca luteola (Müller)	GALE	Europe	North America	E	± 1834	*Ulmus*	Clark pers. comm.; Krafsur & Nariboli 1995	U
		?	Morocco	E	?		Jolivet 1967	U
		Bolzano (Italy)	Britain	?	1986		Smith 1990	U
			Australia	E	1980		Jolivet 2001	U
Zeugophora scutellaris Suffrian (Identification needs confirmation !	ZEUG	Palearctic	USA	E	?	*Populus nigra*	Lindroth 1957	U
Zygogramma bicolorata Pallister	CHRY	Mexico	Australia	E	1980	*Parthenium hysterophorus*	Julien 1992; Dhileepan et al. 2000	I
		Mexico	India	E	1984		Julien 1992; Dhileepan et al. 2000	I
Zygogramma disrupta Rogers	CHRY	USA	the North Caucasus	?	1990	*Ambrosia artemisiifolia*	Julien 1992	I
Zygogramma suturalis Fabricius	CHRY	USA and Canada	Peoples Republic of China	?	1978	*Ambrosia artemisiifolia*	Julien 1992	I
		USA and Canada	Union of Soviet Republics	E	1978		Julien 1992	I
		Canada	Union of Soviet Republics	E	1979	*Ambrosia maritima.*	Julien 1992	I
		USA and Canada	Australia	?	1990		Julien 1992	I
		USA and Union of Soviet Republics	Yugoslavia	?	?		Julien 1992	I