INTRODUCED LEAF BEETLES OF THE MARITIME PROVINCES, 6: THE COMMON ASPARAGUS BEETLE, *CRIOCERIS ASPARAGI* (LINNAEUS), AND THE TWELVE-SPOTTED ASPARAGUS BEETLE, *CRIOCERIS DUODECIMPUNCTATA* (LINNAEUS) (COLEOPTERA: CHRYSOMELIDAE)

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Abstract.—The common asparagus beetle, Crioceris asparagi (Linnaeus) and the twelve-spotted asparagus beetle, Crioceris duodecimpunctata (Linnaeus) are introduced Palearctic leaf beetles that feed exclusively on asparagus. The introduction history of these species in North America is reviewed and their dispersal to and distribution in the Maritime Provinces of Canada are described. Both species were first reported in Canada in 1899 in asparagus production areas in Queenston, Ontario, and other parts of the Niagara Peninsula where they caused serious crop damage. However, we discovered that both species were already found around Québec City 22 years earlier. Populations now established in the Maritime Provinces of Canada probably originated from southwestern Ontario where most commercial asparagus production in Canada began and now occurs. Crioceris asparagi and C. duodecimpunctata spread steadily throughout eastern Canada by adult flight dispersal abetted by wind, by the dissemination of seeds by birds, and by commercial movement of root crowns and spears of asparagus. Asparagus escaped from cultivation, growing along transportation corridors (such as railway tracks, power utility right-of-ways and roads) and in vacant lands, which facilitated the spread and establishment of C. asparagi and C. duodecimpunctata throughout North America. Now, both these adventive pest species occur wherever asparagus is grown. Both C. asparagi and C. duodecimpunctata are confirmed to occur in New Brunswick and Nova Scotia, but not Newfoundland and Labrador. However, C. duodecimpunctata is newly recorded from Prince Edward Island. These introduced beetles are not regulated by Canada or by the U.S.A., and they are readily controlled at economically acceptable damage thresholds.

Key Words: Coleoptera, Chrysomelidae, Criocerinae, *Crioceris asparagi, Crioceris duodecimpunctata*, asparagus beetle, twelve-spotted asparagus beetle, Canada, Maritime Provinces, adventive species, pest distribution, quarantine pest, invasive alien species

The common asparagus beetle, Crioceris asparagi (Linnaeus, 1758) and the twelve-spotted asparagus beetle, Crioceris duodecimpunctata (Linnaeus, 1758) are chrysomelid beetles introduced to North America that are monophagous on asparagus (Clark et al. 2004). They generally occur wherever asparagus grows, either cultivated or escaped from cultivation, and both beetles originate from the Mediterranean Sea region (Monro and Small 1997, Fara 2007). Crioceris asparagi and C. duodecimpunctata co-exist throughout North America wherever asparagus is grown because of adaptive differences in their phenological development which enable both to exploit the same single plant species (Capinera 1976, 2001). The major differences are found during the larval stages. While the larvae of C. asparagi feed only on foliage, those of C. duodecimpunctata develop one month later in the berries (Capinera 2001). Damage can be severe, particularly to cold-stressed plants. This is uncommon now because of effective pesticides and quick harvesting of spears upon which beetles normally feed, thereby reducing resource availability. Eulophid parasitoids such as Tetrastichus *coeruleus* Nees (= *T. asparagi* Crawford) are a significant population control in C. asparagi, but not for C. duodecimpunctata (Capinera 2001). Other biological mortality agents and seed scarcity probably limit C. duodecimpunctata populations (Campbell et al. 1989, Capinera 2001).

Most of the available information on *C. asparagi* and *C. duodecimpunctata* in Canada has consisted of reports in Canadian agricultural pest surveys or reports by Canadian entomological societies, either at the provincial or federal government level. Primarily notes, reports, or articles on asparagus beetles from eastern Canada (Ontario, Québec, and the Maritime Provinces) were considered. References from western Ca-

nada are not included here but most of them are found in Beirne (1971). Various United States government documents have provided useful data as well. In this analysis, we provide new verified information obtained directly from voucher specimens of older records, or from new data not previously published.

HISTORICAL REVIEW

Asparagus (Asparagus officinalis Linnaeus) and its many varieties, is a vegetable delicacy known to ancient Egyptians, Romans, and Greeks more than two thousand years ago. In his De Agricultura, Cato the Elder (234–149 B.C.) described techniques of production and cultivation which are still in use today (Dalby 1998, Hutchinson et al. 2006). Asparagus has been used for heart trouble, dropsy, liver and jaundice complaints, bee stings, poor eyesight, and sciatica. Asparagus has been marketed as a good source of folic acid, vitamin C. thiamin, vitamin B6, potassium, and many micronutrients such as glutathione which is thought to protect against cancer, and rutin which strengthens blood vessels (Borris and Brunke 2006).

Asparagus was brought to North America by early colonists from Europe. According to Lescarbot (1612), asparagus was grown at Port Royal (Nova Scotia). The earliest archaeological evidence found by Erskine (1975) was from 1770 in surficial remains at the Minas settlement (Nova Scotia). In their survey of the colonial garden plants, Favretti and DeWolf (1971) cited Parkinson (1629) who recommended asparagus as a delicacy which was also good for treatment of urinary and kidney problems. Boucher (1664) mentioned that, like parsnip (Pastinaca sativa L.), it had escaped from cultivation and was found wild on islands around Hochelaga (Montréal Island). It was reported to thrive well in Massachusetts in 1672 and was growing in every colony along the Atlantic Coast by 1776 (Haughton 1978). During his travels in North America in 1750, the Finn, Pehr Kalm, noticed that some asparagus grew wild on the shores of the Hudson River (Benson 1966, Rousseau et al. 1977), which means that the plant must have been grown in gardens for many years previously.

The establishment of the asparagus beetle, C. asparagi, and the twelvespotted asparagus beetle, C. duodecimpunctata, came much later. Fitch (1862) was the first entomologist to report C. asparagi in North America from Albany (New York). Three years later, he mentioned that a Mr. John Quin had already noticed C. asparagi at Astoria, New York, in 1859 (Fitch 1865). Chittenden (1908) believed that the beetle was introduced there about 1856 but he did not explain on what he based his assumption. In a footnote, he added: "The capture of this species was recorded early in the past century in Pennsylvania - presumably near Hanover - and again in the vicinity of Chicago and Rock Island, Illinois, about ten years after the discovery on Long Island; but, as the insect did not obtain a permanent foothold, but died out in these localities, these importations can not be considered introductions."

Beetles probably entered the USA during the commercial production of that period as adults or pupae in root crowns or with soil (Chittenden 1917, Caesar 1938). However, there were probably sporadic introductions earlier that were never noticed because of low numbers or failure to establish due to winter mortality or asynchronous host conditions. Various life stages, most likely including eggs, may have been transported with the movement of spears or asparagus stems. A few such cases have been documented, but without clear reference to the life stage. Crioceris sp. was intercepted in Hawaii in 1983 on

asparagus spears for consumption originating in Japan (USDA 1984), and in Massachusetts and New York in 1981 originating in Italy and the former Yugoslavia (USDA 1982).

Even though *Crioceris asparagi* and *C. duodecimpunctata* co-occur, they were detected in the U.S.A. about 25 years apart. *Crioceris duodecimpunctata* was first found near Baltimore, Maryland about 1881 (Chittenden 1908, 1917).

Both beetles caused severe damage in asparagus crops and were established several years prior to their detection at outbreak population levels. Fortunately, a primary parasitoid of *C. asparagi*, *T. coeruleus* Nees, was found in asparagus beetle populations about 1863 (Walsh and Riley 1868; Johnston 1915; Capinera and Lilly 1975a, 1975b).

Crioceris asparagi spread steadily throughout eastern U.S.A. at an estimated rate of 32 km/year, primarily by human-mediated pathways such as movement of root crowns of asparagus, or by "hitch-hiking" accidentally along transportation corridors (road, train, boat, etc.), but also by water along various waterways (Chittenden 1917).

Crioceris duodecimpunctata probably spread similarly after its detection in Baltimore, Maryland in 1881 (Chittenden 1917). Escaped plants from cultivated asparagus beds facilitated the spread and establishment of C. asparagi and C. *duodecimpunctata* throughout North America, and both these species now occur wherever asparagus is grown commercially or as a volunteer crop (White 1993, Capinera 2001). By 1898, C. asparagi was reported to occur in Buffalo, New York, and Berrien County, Michigan (Chittenden 1898b), and along parts of the Niagara River just across from Canada (Kilman 1899).

Both *C. asparagi* and *C. duodecimpunctata* are usually considered to have been officially recognized as present in Canada for the first time in 1899, with both species causing serious damage in asparagus production areas in Queenston and other parts of the Niagara Peninsula in Ontario (Fletcher 1900a, 1900b; Webster 1900; Chittenden 1907a, 1917). However, Provancher (1877) had already collected *C. asparagi* from the Québec City area 22 years before, but this occurrence has been overlooked by many authors.

By the end of 1899 both asparagus beetles had reached St. Catharines, Lincoln. and Welland Counties in Ontario (Lochhead 1900). By 1900 they were near Hamilton, and by 1901 both beetles had reached Guelph where it was noted that C. duodecimpunctata was more damaging (Fletcher 1902, 1904). By 1902 this species was first recorded from London (Balkwill 1903). Meanwhile, C. asparagi had spread further east to Bracondale near Toronto (Fletcher 1904). In 1904 it continued to do some damage in the Niagara and St. Catharines districts (Fletcher 1905). It was reported in large numbers in western Québec in 1903 (Kilman 1904). Beirne (1971) stated that the asparagus beetle was found in Québec City in 1917, and in British Columbia in 1962.

Crioceris asparagi was known to occur in Ottawa in 1906, whereas C. duodecimpunctata was not detected in Ottawa until 1915 (Gibson 1916). Ross and Curran (1917) reported that the egg parasitoid T. coeruleus satisfactorily held in check the beetle at Vineland Station of Agriculture Canada. In his preliminary list of the insects of Québec, Chagnon (1917) reported both species from the Island of Montréal, Île-Jésus, and Saint-Jean-sur-Richelieu. Twenty years later he stated that they both were common on asparagus without additional information on their distribution (Chagnon 1937).

Crioceris asparagi and *C. duodecimpunctata* are characterized by intermittent periods of several years during which populations may go undetected. For some reason, pest activity for both species remained unreported for many years in Canada during the period of both World Wars. In 1948, *C. duodecimpunctata* was first reported in Morden, Manitoba, and it was found to be numerous in Winnipeg in the summer of 1954, but caused little damage (MacNay 1955, Beirne 1971).

Crioceris asparagi was first recorded in the Maritimes in 1950 in Truro, Nova Scotia and subsequently in 1952 from Fredericton, New Brunswick (Pond 1953). Its incursion into the Maritimes coincided with outbreak population levels in southern Ontario, and moderate damage levels in Montréal and Québec City in 1952. Crioceris duodecimpunctata was also first recorded in the Maritimes in 1950 in Truro, Nova Scotia. Both species were present in low numbers in Truro and Kentville, Nova Scotia, in 1952, and shortly thereafter, in 1953, C. duodecimpunctata was also found on Prince Edward Island (Fox and Neary 1953).

In Western Canada, *C. duodecimpunctata* was first detected in British Columbia in 1962 (Beirne 1971, Capinera 2001). *Crioceris asparagi* was reported to be mainly a pest in the Lower Fraser Valley, and sporadic on Vancouver Island and in the southern Okanagan (Banham and Arrand 1978).

Both asparagus beetle species are now widespread across southern Canada, but neither is yet reported from Newfoundland and Labrador (LeSage 1991).

METHODS AND CONVENTIONS

Codens of collections (following Evenhuis 2007) referred to in the text are:

- ACNS Agriculture and Agri-Food Canada, Kentville, Nova Scotia, Canada
- ACPE Agriculture and Agri-Food Canada, Charlottetown, Prince Edward Island, Canada

- CNC Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario
- DHWC David H. Webster Collection, Kentville, Nova Scotia, Canada
- JOC Jeffrey Ogden Collection, Truro, Nova Scotia, Canada
- NSAC Nova Scotia Agricultural College, Bible Hill, Nova Scotia, Canada
- NSMC Nova Scotia Museum Collection, Halifax, Nova Scotia, Canada
- NSNR Nova Scotia Department of Natural Resources, Shubenacadie, Nova Scotia, Canada
- UMNB Université de Moncton, Moncton, New Brunswick, Canada

The number of specimens is indicated in parentheses together with the collection codens.

Nomenclature

In an application to the International Commission of Zoological Nomenclature for a decision regarding the status of the generic name *Corixa* Geoffroy (1762), H.B. Hungerford (1947) raised the much broader question of the validity for nomenclatorial purposes of the whole work of this author, *Histoire abrégée des insectes qui se trouvent aux environs de Paris.* In a first decision, the Commission placed Geoffroy's entire work in the Official Index of Rejected and Invalid Works in Zoological Nomenclature (ICZN 1954, Opinion 228).

In the late sixties, B. J. Selman and R. F. Smith appealed to the Commission in order to clarify the generic status of *Crioceris* Müller, 1764, and *Lema* Fabricius, 1798 (Selman and Smith 1967, 1968). Three years later, the Commission ruled that *Crioceris* Müller was a masculine genus and designated under the plenary powers *Chrysomela asparagi*

Linnaeus, 1758 as the type species (ICZN 1970, Opinion 908).

At the beginning of the nineties, I. M. Kerzhner resubmitted the case of Geoffroy's work to the Commission (Case 2292), but this time for the conservation of most of the genera published by this author (Kerzhner 1991, Tubbs 1992). With respect to the leaf beetle genera Altica, Crioceris, Cryptocephalus, and Galeruca created by Geoffroy, the Commission reverted to the ruling of 1954 and recognized his Histoire abrégée as valid for nomenclatorial purposes, and also recognized the authorship of Geoffroy for many of the genera created in his original work, including the four leaf beetle genera mentioned above (ICZN 1994, Opinion 1754).

Recently, Schmitt (2005) proposed an official correction of the gender of *Crioceris* Geoffroy to feminine (it was recognized as masculine before, ICZN 1954). The case has not yet been ruled by the Commission but the correction will very likely be accepted.

There are distinct color variations in *C. asparagi* and *C. duodecimpunctata* with the result that over thirty varieties, aberrations, or forms for each species were named by authors. These color differences have no taxonomic significance (White 1993, Riley et al. 2003).

IDENTIFICATION

Within the family Chrysomelidae, the leaf beetles, members of the subfamily Criocerinae are easily recognizable by lateral slopes of the pronotum that are rounded without a marginal bead, and by their elytral punctures arranged into regular rows (Figs. 1–2). Within the subfamily Criocerinae *Crioceris* Geoffroy, 1762 is characterized by tarsal claws that are broadly divergent from the base and by a pronotum that is not markedly constricted in the middle, as in *Lilioceris* Reitter, 1912.

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Crioceris asparagi

Fig. 1. Habitus of Crioceris asparagi (dorsal view).



Fig. 2. Habitus of Crioceris duodecimpunctata (dorsal view).

Both species are very easy to recognize since their color pattern is unique among the Canadian leaf beetle fauna. Crioceris asparagi is multicoloured (Fig. 1). In most specimens of eastern Canada the appendages are black, the elytra also are black but with metallic bluish reflections. In addition, the elytra bear three pairs of white spots of variable size and the lateral margins vary from yellow to reddish, often with an enlargement at the apex. The pronotum is reddish with a more or less poorly defined dark spot on the disc. C. duodecimpunctata (Fig. 2) is largely bright reddish orange with black antennae, black apex of the femora, and six pairs of small round black spots on the elytra. Both species are treated in Chagnon (1937, 1940), Chagnon and Robert (1962), Swan and Papp (1972), White (1993), Howard et al. (1994), and Downie and Arnett (1996). A field key is found in Metcalf and Flint (1939, 1962).

The eggs of *C. asparagi* were sketched by Walsh and Riley (1868), Wickham (1896), Chittenden (1896, 1908, 1917), Balachowsky and Mesnil (1936), Drake and Harris (1932), and Parrott and Huckett (1944), and a photograph of eggs on spears was provided by Metcalf and Flint (1939, 1962) and by Howard et al. (1994). The eggs of *C. duodecimpunctata* were illustrated by Chittenden (1898a, 1907b) and Drake and Harris (1932). However, the fine structure of the egg chorion of both species is still unknown.

Habitus of *Crioceris* larvae and illustrations of the head, mouthparts and legs are found in Chittenden (1908), Bøving and Craighead (1931), Sailsbury (1943), Peterson (1951), and Lawson (1991). The head is dark brown, the labrum narrowly notched and the body tan in *C. asparagi*, whereas the head is light brown, the labrum broadly notched and the body off-white in *C. duodecimpunctata* (Lawson 1991). A lateral view of the second abdominal segment was provided by Chittenden (1896). Larvae of both species can be keyed out using the key of Sailsbury (1943). The egg bursters are present on a heavily sclerotized tubercle dorsal to the spiracle on abdominal segment I in the first instar larva (Cox 1994). A photograph of a live mature larva is given by Metcalf and Flint (1939, 1962) and by Howard et al. (1994), a lateral view in Drake and Harris (1932) and Hutchinson et al. (2005).

Chittenden (1896, 1908) illustrated the ventral view of the pupa of *C. asparagi*. Fink (1913) gave photographs of the ventral and dorsal views of the pupa of *C. duodecimpunctata*. Unfortunately, these illustrations do not allow for the recognition of species and detailed descriptions of both are still needed.

The complete mitochondrial DNA sequence of *C. duodecimpunctata* is known (Stewart and Beckenbach 2003). Compositions of the mitochondrial genome were reported to be similar to other insects in general. Distinct features of this genome included the substitution of UCU for GCU as the anticodon for tRNASer, an unusual T psi C loop for the tRNAIle gene, and the identification of a putative ATT start codon for cox1 (Stewart and Beckenbach 2003).

BIOLOGY

The asparagus beetles pass the winter in the adult stage, hibernating under sticks, stones, litter, bark, rubbish, or any other suitable shelter. They also may be found in numbers inside the cavity of asparagus stems or other plants (Drake and Harris 1932). Adults of C. asparagi emerge from hibernation in late April or early May when asparagus sprouts start to emerge from the soil. They feed for a few days before mating and ovipositing. Feeding damage and eggs laid on spears make the spears unmarketable (Hutchinson et al. 2005). The eggs are cylindrical, greenish grey to brownish, and about 1-2 mm long; they are always deposited endwise upon the spears or on the foliage either separately or in up to 7 (Chittenden 1908), or 11 eggs per row (Balachowsky and Mesnil 1936). Eggs hatch after about twelve days, the time needed largely depending on local temperatures. Larval development passes through four instars and takes 2–3 weeks to be completed. According to Taylor and Harcourt (1978), the optimum temperatures for eggs and larval instars I and II is 32°C, but 30°C for the larval instars III and IV and the pupa.

The larvae are eruciform, their body grayish, the head and appendages black. Each abdominal segment is provided with a pair of tubercles which, with the aid of the anal prolegs, help in crawling and climbing the plants. Hutt (1900) observed that when approached the larvae had the peculiar habit of raising their heads and excreting a dark viscid fluid. When mature, the larvae drop to the ground. They build a pupal cell by packing and mixing soil particles with their saliva. Only the inside of the cell is covered with a silken secretion. Consequently, the pupal cells are not exactly "cocoons spun by the larvae" as stated by Armand (1949). The pupa is yellow. Adults emerge from the pupal cells in 7-10 days.

The bright coloration of adult C. asparagi is aposematic, and the beetles are commonly avoided by predators (Jones 1932). Lutz (1908) found that, when a normal C. asparagi with three yellow spots on blue-black elytra was crossed with a variety where the upper spot was united with the middle one, the normal form was dominant. According to Capinera (1976), the first defensive behavior of C. asparagi adults is to dodge to the opposite side of stems. With persistent stimulation, beetles will feign death or run to another part of the plant. Crioceris duodecimpunctata adults respond quite differently to stimuli, by taking flight and stridulating; their redblack coloration is avoided by predators and stridulating may protect them by startling the predator and causing it to release its hold (Haskell 1961, Rettenmeyer 1970).

According to Campbell et al. (1989), referring to populations in Canada, C. asparagi is trivoltine with egg-laying peaks in June, early July, and early August. Adults of the third generation overwinter in dead stalks of asparagus, in the ground litter, or any other convenient shelter. No information is available on the exact number of generations in the Maritimes, but there are probably two complete generations and a partial third one as in Massachusetts (Capinera and Lilly 1975a). Chittenden (1917) estimated the time needed from the egg to the emergence of the adult at Long Island, New York as 30 days. The development time for C. asparagi should be of this order in the Maritime Provinces.

The biology of *C. duodecimpunctata* was described by Fink (1913) in New York State and by Beaulne (1935) in the province of Québec. Fink (1913) stated that both asparagus beetle species emerged in early spring at almost the same time, but Beaulne (1935) mentioned that *C. duodecimpunctata* emerged from hibernation a week later. According to our own observations, both species have been collected together in the spring in eastern Canada.

In contrast to *C. asparagi*, the oviposition of *C. duodecimpunctata* occurs much later, not before the berries have begun to form by the middle of June or later (Chittenden 1898a, Fink 1913). Meanwhile, adults attack the sprouting shoots in the same manner as do those of *C. asparagi*. Later, when the shoots have begun to branch out, they feed mainly on stalks and branches, gnawing out large pieces of their epidermis. They will extend their feeding to flowers and berries when these appear. Eggs are not laid in conspicuous rows as in C. asparagi but instead singly, on the side, and hidden among narrow branches, preferably those with berries. Their incubation lasts 7-12 days. After hatching, the young larvae wander about the stems until they find a berry. As soon as one is located, the larvae will bore into it between the two sepals of the calyx. Although up to four berries will be utilized throughout their development until they mature, Fink (1913) never observed more than one larva per berry. The larvae have the ability to discriminate between occupied and unoccupied berries which accounts for their consistent singular distribution amongst asparagus berries (Alphen and Boer 1980). Females of C. duodecimpunctata do not oviposit on or in the asparagus berries in which the larvae feed, and therefore this distribution of a single larva in each berry cannot be the result of ovipositing females (Alphen and Boer 1980). The larvae spend several days inside the berries, eating only the soft juicy pulp. Before leaving for a second berry, the larva molts and the cast skin is found inside the discarded berry. After the second molt a larva can eat an entire berry in less than a day. Berries are mildly poisonous to humans (Plants for a Future 2007).

There are four larval instars as in C. asparagi, although Fink (1913) and Beaulne (1935) erroneously reported only three. The larvae mature in 3-4 weeks, and, like those of C. asparagi, drop to the ground where they make silken cells in which they pupate. Pupation lasts 12-20 days in Ithaca, New York (Fink 1913). Adults overwinter in plant debris or other suitable shelters (Banham and Arrand 1978), and like those of C. asparagi can stridulate by rubbing the tip of the abdomen against the elytra (Dingler 1932, Schmitt 1994). According to Caesar (1938) there are two generations per year in Ontario, and a similar number is expected for the Maritimes. The adults of the first new generation emerge in late July while those of the second generation appear in September (Armand 1949).

PREDATORS

References to avian predation on asparagus beetles are few. House sparrows (*Passer domesticus* (Linnaeus)), and eastern kingbirds (*Tyrannus tyrannus* (Linnaeus)) were reported by Beal (1912) to consume adults, but Capinera (1976) stated that North American birds were probably accidental predators. According to Drake and Harris (1932), chickens and ducks destroy asparagus beetles and may be used under favorable conditions.

The coccinellid beetles, Coleomegilla maculata (De Geer, 1775) and Hippodamia convergens (Guérin-Méneville, 1842), are efficient predators of eggs and larvae (Chittenden 1896, 1898a, 1908, 1917; Watts 1938). Capinera and Lilly (1975a) interpreted the decrease of C. asparagi eggs during the increase of coccinellid populations as a response of the latter to the diminishing numbers of aphids, their larvae being forced to feed on whatever food is available. Large carabids such as Poecilus lucublandus Say, 1823, Pterostichus melanarius Illiger, 1798, Harpalus pennsylvanicus De Geer, 1774, and Harpalus erraticus Say, 1823 are presumed to consume mature larvae when these drop to the ground to pupate (Capinera and Lilly 1975a). The melyrid beetle, Collops quadrimaculatus (Fabricius, 1798), fed freely on eggs and larvae of Crioceris in confinement (Chittenden 1898a).

Chittenden (1896, 1907b, 1917) reported that the stink bugs (Pentatomidae) *Podisus maculiventris* (Say, 1832) and *Stiretrus anchorago* (Fabricius, 1775) devoured the larvae of *C. asparagi*, but the latter does not occur in Canada (Maw et al. 2000). Drake and Harris (1932) gave a photograph of *P. maculi*- *ventris* piercing the body of an adult *C. asparagi*. The nabid bug, *Nabis rufusculus* Reuter, 1872, was commonly observed to prey on larvae earlier in the season, whereas the reduviid bug, *Sinea diadema* (Fabricius, 1776), was an occasional predator (Capinera and Lilly 1975a).

The vespid wasp, *Polistes fuscatus* (Fabricius, 1793), hovers over infested plants, pounces upon larvae, and carries them away (Chittenden 1917).

Chittenden (1898a) noticed the damselfly, *Ischnura positum* (Hagen, 1861), flying about infested asparagus, seize small larvae and fly off with them. *Ischnura* species are peculiarly adept at picking small insects from foliage (Westfall and May 2006).

The neuropteran chrysopid, *Chrysopa* oculata Say, 1839, is an occasional predator of the larvae (Capinera and Lilly 1975a).

PARASITES

The European hymenopteran eulophid, *T. coeruleus* (Nees, 1834), usually reported in North America as *T. asparagi* was placed in synonymy by Graham (1961, 1991). The "black parasite fly *Chalcis* or *Proctotrupes*" reported by Walsh and Riley (1868) corresponds to *T. coeruleus*. The parasitoid was formally identified for the first time in Canada in 1915 at the Agriculture Canada Vineland Research Station, Ontario, by Ross (1915).

The parasitoid female pierces the egg of the beetle with its ovipositor and deposits therein 3–9 eggs (Beaulne 1935, Van Alphen 1980). She is also able to discriminate between unparasitized and parasitized eggs after checking with antennae or probing with the ovipositor (Van Alphen 1980). The egg of the asparagus beetle host is not visibly affected, hatches and develops into normal larval stages, but when the larva falls to the ground for pupation it develops no further because by this time it has been completely devoured by the parasitic larvae which will pupate within the host pupal cell and later emerge as an adult (Capinera and Lilly 1975b).

The level of egg parasitism or feeding can be very high. The parasitoid females are avid feeders on the beetle eggs and may consume a greater number of eggs than they parasitize. Johnston (1915) found that of 2,097 eggs counted, 71.3% had been destroyed by the feeding by the parasitoid females. According to Capinera and Lilly (1975a), 50% of the eggs of C. asparagi were destroyed by this parasitoid through feeding, and nearly 50% of those not fed upon were parasitized. At L'Assomption, Québec, Hendrickson et al. (1991) observed 39.1% of parasitism in the first generation and 49.2% in the second during the years 1980 to 1987. Tetrastichus coeruleus is a monophagous parasitoid of asparagi and does not accept С. C. duodecimpunctata as a host, whereas T. crioceridis (Graham 1983) feeds and parasitizes exclusively the eggs of *C. duodecimpunctata*. This parasitoid has not yet been recorded in North America.

The hymenopteran ichneumonid, *Lemophagus crioceritor* Aubert, 1986, is probably established in Canada and favored by cooler latitudes. A parasitism level of 8.9% was measured at L'Assomption, Québec, and 15.7–24.8% at the Cambridge Research Station of the University of Guelph, Ontario, where the parasitoid was released in 1987 (Hendrickson et al. 1991). Harmer et al. (1990), also at Guelph, estimated the annual rate of parasitism at 19.5%; that is, 15.7% for the first generation and 24.8% for the second.

In 1939, 9,500 puparia and 17,825 host larvae from France parasitized by the tachinid fly, *Meigenia mutabilis* (Fallén, 1810), were introduced into the United States of America and released at several infestation points in New Jersey. The parasite failed, however, to establish either because it could not survive through the winter or because of the lack of a suitable alternate host (Clausen 1956, 1978). Another tachinid fly, *Myiopharus (Paralispe) infernalis* (Townsend, 1919), a native species, has been reared from larvae of *C. asparagi*, but it is an uncommon parasitoid (Watts 1938, Capinera and Lilly 1975b). It produced only 2.1% parasitism at the Beneficial Insects Research Laboratory, in Saint-Brunode-Mortarville, Québec (Hendrickson et al. 1991).

Impudentia crioceris Vujanovic is a newly discovered dematiaceous hyphomycetous fungus that is found on *C. asparagi* and *C. duodecimpunctata* from asparagus fields in Quebec, Canada (Vujanovic et al. 2003).

HOST PLANT

Asparagus is a perennial salt-tolerant herbaceous plant that has both wild and domesticated forms. It is believed to be native to the region east of the Mediterranean Sea and the Middle East (Fara 2007). In Canada, the domesticated form escaped from cultivation and can be found as a naturalized plant across southern regions of the country, except Saskatchewan (Monro and Small 1997). It is also found in the waste steppes of southern Poland and Russia (Ohioline 2007). Volunteer plants from seeds serve as a reservoir for asparagus insects and asparagus rust during harvest, after all other asparagus plant material is removed from commercial fields (Hutchinson et al. (2005).

Asparagus consists of thick matted rootstocks from which emerge branched stems, 1-2 m tall, which are produced annually (Hutchinson et al. 2006). The edible parts are the succulent shoots, or spears, as they issue from the crown and emerge above the ground. The later shoots develop into large bushes. The

flowers are dioecious with both male and female plants. Generally, female plants produce larger spears than the male plants (Hutchinson et al. 2006). The flowers are small, greenish yellow, and fixed on jointed pedicels. Honeybees are not needed for pollination in asparagus, but they are very common when the plants are flowering in mid- to late summer (Hutchinson et al. 2005). Of interest for the production of an exclusively male plant is the indirect impact for control of the larvae of C. duodecimpunctata since these develop in berries (produced only by female plants). The filiform so-called "leaves" are actually branchlets, functioning as leaves, clustered in the axils of little scales which are the true leaves (Fernald 1970). The fruits are red round berries produced only by female plants. The propagation of asparagus can be done by seeds or roots. Asparagus which has escaped from cultivation is spread by seeds disseminated by birds (Haughton 1978). Cultivated plants are usually duplicated by splitting older root crowns into smaller bundles. Ornamental varieties are produced in the same manner. Commercial asparagus plantations can be established either by traditional crown planting or by transplanting seedlings (Hutchinson et al. 2006). A well established asparagus bed can be profitable for 15-20 years. The new shoots are sold fresh, frozen, or canned.

Crioceris asparagi and *C. duodecimpunctata* are both monophagous in North America since they feed exclusively on *A. officinalis*, but are oligophagous in the Old World because they develop on other species and varieties as well (see extended bibliography in Clark et al. 2004).

DISTRIBUTION

The distribution of *C. asparagi* and *C. duodecimpunctata* in the Maritime Provinces of Canada is shown in Fig. 3. Both



Fig. 3. Distribution of *Crioceris asparagi* (open circles) and *C. duodecimpunctata* (closed circles) in the Maritime Provinces of Canada.

species are newly recorded in Nova Scotia and *C. duodecimpunctata* is newly recorded on Prince Edward Island since publication of the latest checklist of the beetles of Canada (LeSage 1991).

Crioceris asparagi.—A total of 32 specimens were examined.

NEW BRUNSWICK: *Gloucester Co.*: Tracadie, 2.VIII.1978, S. Poirier, (1, UMNB).

NOVA SCOTIA: Antigonish Co.: Antigonish, 15.VI.2006, M. Workman, (3, NSNR); Colchester Co.: Bible Hill, 28.V.1998, T.D. Smith, (12, NSAC); Truro, 18.VII.1950, V.R. Vickery, (2, NSAC); Truro, 11.VIII.1950, V.R. Vickery, (9, NSAC); Kings Co.: Wolfville, 28.VI.1996, D. de Geus, (1, ACNS); Kentville, 11.VI.1995, D.H. Webster, (1, DHWC).

Crioceris duodecimpunctata.—A total of 117 specimens were examined.

NEW BRUNSWICK: Sunbury Co.: Hoyt, 4.VI.1987, host Asparagus, D.B. Finnamore, (1, CNC); York Co.: Fredericton, 4–30.VII.1955, ex goldenrods with Macrosiphum ambrosiae Thomas, B.C. Smith (8, CNC).

NOVA SCOTIA: Colchester Co.: Shubenacadie, 8.VII.2002, J. Ogden, (1, NSNR); Truro, 1.VII.1950, V.R. Vickery, (3, NSAC); Truro, 18.VII.1950, V.R. Vickery, (16, NSAC); Truro, 11.VIII. 1950, V.R. Vickery, (1, NSAC); Truro, 11.IX.1975, A.M. Bubar, (1, NSAC); Cumberland Co.: Oxford, 2.VIII.1990, J.

Ogden, (1, JOC); Nappan, 19.XI.1975, D.A. Smith, (2, NSAC); *Halifax Co.:* Dartmouth, 24.VIII.1988, K. McKay, (7, NSMC); Dartmouth, 16.VI.1991, R. Sircom, (3, NSMC); *Kings Co.:* Kentville, 26.VII.1961, C.J.S. Fox, (4, ACNS); Kentville, 5.IX.1961, R.L. Horsbourgh, (71, NSAC); Kentville, 6.IX.1961, R.L. Horsbourgh, (6, NSAC); Kentville, 3.VII.1973, D.H. Webster, (1, DHWC).

PRINCE EDWARD ISLAND: *Queens Co.:* Charlottetown, 10.VII.1953, F.M. Cannon, (1, ACPE).

DISCUSSION

Although both species of Crioceris were reported as occurring in Nova Scotia by Fox and Neary (1953) and MacNay (1955), this information was overlooked by LeSage (1991); thus, the present paper confirms their presence in this province. However, C. duodecimpunctata is newly recorded as occurring on Prince Edward Island from a specimen collected in 1953. Since both species feed exclusively on asparagus, their distribution in the region is limited to places where asparagus is cultivated, or where it has escaped and has been naturalized, primarily in agricultural areas of the region. None of the two beetle species has yet been found in Newfoundland, although asparagus is cultivated there in gardens (D. Larson, S. Pardy, and J. Coombes, personal communication). The earliest documented date of introduction known for C. asparagi in Astoria, New York is 1859 (Fitch 1865), although Chittenden (1908) estimated that it was already present there by 1856.

Both asparagus beetles were probably repeatedly introduced for more than two centuries but did not survive or could not establish before the sixties of the nineteenth century. As Webster (1902) has shown, one of the main lines of migration and spread of insects in North America has been from New York or the North Atlantic States through the open gateway into the interior of the continent past lakes Ontario and Erie. Clearly, both asparagus beetles were able to acclimatize to cold temperatures encountered in North America compared to their native range. Thus, they have been able to survive and spread successfully throughout their new continental environment.

Another possibility is that both species of asparagus beetles survived for decades unnoticed until they could survive the winters in greater numbers. The commercial production initiated soon after 1860 helped in building larger populations. Such pattern of appearance, apparent disappearance, and reappearance in numbers is known for the lily leaf beetle (Lilioceris lilii Scopoli, 1763). This beetle almost disappeared for forty years prior to spreading rapidly from Montréal where it was first discovered in 1943 (LeSage 1983). According to Provancher (1877), C. asparagi was present at Cap-Rouge near Québec City that year. We have examined the voucher specimens preserved in his collection housed at the Université Laval, in Québec. Although not mentioned by Provancher (1877), specimens of C. duodecimpunctata were also preserved in his collection. Consequently, it is evident that both species were thriving 22 years before the official date of introduction into Canada (1889) in a location completely separate from the known infested areas of the United States. We don't know, however, if these early populations disappeared or survived long enough to merge with those originating from southern Ontario and which eventually spread northeastwards. The two asparagus beetle species were rediscovered in Québec City in 1917 (Chittenden 1917, Beirne 1971), and Kilman (1904) reported the occurrence of C. asparagi in abundance in Québec in 1903.

It is well known that a large number of adventive insect and plant species were

introduced to North America in ships' ballast (Lindroth 1957, Sheffield 1990, Buckland et al. 1995). This is true for soil dwelling insects but not likely for adults or larvae of asparagus beetles which thrive on plants. The first vegetables to become of importance in the new colonies appeared to have been the roots. Numerous cargo lists included "roots," and in addition to root-crops commonly found in gardens, settlers were experimenting with asparagus and other vegetables. Asparagus root crowns were probably used regularly because they were easy to dig out (in Europe), transport by ship, and replant in a new environment (in North America). Vegetative propagation produces new spears quickly and is much faster than starting production from seeds. Asparagus beetle adults may have been hiding in the root crowns, and could have crossed the ocean by means of this pathway. Certainly eggs or other life stages attached to transported spears could have been introduced in this way, but interceptions are not well documented. The European obligate endoparasite T. coeruleus was found in 1863, only a few years after the discovery of the asparagus beetles. Its presence in North America can be explained only by the (unintentional) introduction of parasitized eggs. The early introduction of T. coeruleus which established successfully in Canada probably significantly controlled C. asparagi populations, as commercial asparagus farms were being developed in the New World. Now, pesticides with little residual toxicity levels are used to prevent adult egg laying on spears which are harvested daily (Capinera 2001, Wold-Burkness et al. 2007).

Neither *C. asparagi* nor *C. duodecimpunctata* are regulated by Canada or by the U.S.A., and they are readily controlled at economically acceptable damage thresholds.

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