

## The ground beetles (Coleoptera: Carabidae) of the Maritime Provinces of Canada: review of collecting, new records, and observations on composition, zoogeography, and historical origins

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## Abstract

The Carabidae of Nova Scotia and New Brunswick are surveyed. The collecting history of the family in the region is reviewed. New records of 20 species are reported, 6 from New Brunswick and 15 from Nova Scotia. Six species are newly recorded in the Maritime Provinces (New Brunswick, Nova Scotia, and Prince Edward Island) as a whole. Six species are removed from the faunal list of Nova Scotia and one from the faunal list of New Brunswick. Consequently, 282 species of Carabidae are now known from Nova Scotia, 273 species from New Brunswick, and 329 from the Maritime Provinces as a whole. A new and earlier timeline (1942) is reported for the introduced Palearctic carabid, *Bembidion properans* (Stephens), in North America. The status of *Stenolophus carbo* Bousquet in the region is reviewed and its presence in Nova Scotia is considered doubtful. The historical origins of the Maritime fauna are discussed based on studies of post-glacial Coleoptera. These indicate at least three colonization phases, some elements of which are still apparent in the contemporary fauna. Elements of the native Nova Scotia fauna not found in New Brunswick (26 species), may represent colonization from New England across post-glacial land bridges and island chains. Elements of the native fauna found in New Brunswick and not Nova Scotia (31 species), may represent species that have reached the eastward limit of their distribution for climatic or environmental reasons; or that have found the Northumberland Strait and/or the isthmus of Chignecto an obstacle to geographical dispersal; or represent widely distributed boreal species (6 species) that should be sought in Nova Scotia. Eighteen species of Nova Scotia carabids have been recorded only from Cape Breton Island, two of which are known in Atlantic Canada solely from there. Although Cape Breton is separated from the mainland by the 1.5 km wide Strait of Canso, the number of flightless, native carabids present is proportionally greater than that in Nova Scotia overall, or the Maritime Provinces as a whole. Despite differences in land mass and distance to the neighbouring mainland, the faunas of Cape Breton, Prince Edward Island, and insular Newfoundland, exhibit similarities in size and composition, although Newfoundland's fauna has twice the proportion of Holarctic species. Cape Breton's carabid fauna is diminished compared to the neighbouring mainland, having only 57% of the native species. This may represent an island-associated diminution, the paucity of collecting, or a combination of both, although in comparison with other groups of Coleoptera the Carabidae appear relatively well represented. Within Atlantic Canada, New Brunswick has the lowest proportion (8.8%) of introduced carabids and the highest proportion (83.2%) of native, Nearctic species. Given the potential utility of carabids as bioindicators, and the wide range of disturbance to which the environment of the Maritime Provinces has been subjected, further research on this diverse group of beetles would be desirable.

**Key words:** Coleoptera, Adephaga, Carabidae, New Brunswick, Nova Scotia, Maritime Provinces, Canada, biodiversity, biogeography

## Introduction

The family Carabidae (ground beetles) represents a species-rich lineage of Coleoptera second only to the Staphylinidae (rove beetles) in terms of their representation in Atlantic Canada. Investigators commencing with W. Kirby (1837) have reported them from the region, and many carabid specialists including C.H. Lindroth, A. Laroche, H. Goulet, and Y. Bousquet have contributed to an understanding of the region's fauna. Although Lindroth (1963a) analyzed the composition, zoogeography, and origins of the Newfoundland Carabidae in great detail, the fauna of the Maritime Provinces (New Brunswick, Nova Scotia, and Prince Edward Island) has not been subject to the same scrutiny. In that spirit, the intent of the present paper is to take a step in that direction, adding new species records and contributing insights toward an understanding of the composition, zoogeography, and origins of the region's carabid fauna. In this paper, new records are reported from New Brunswick and Nova Scotia. (Majka et al. in press) have similarly treated the fauna of Prince Edward

Island), and the composition, zoogeography, and historical origins of the Maritime Provinces fauna as a whole are examined.

### Historical review

Among the early authors who reported Carabidae from Nova Scotia were W. Kirby (1837) (*Cicindela longilabris longilabris* Say and *Pterostichus adstrictus* Eschscholtz), M. Jones (1869) (16 species), W.H. Harrington (1892) (*Agonum muelleri* (Herbst)), and J.D. Evans (1899) (20 species). William J. Brown, an entomologist with the Department of Agriculture in Ottawa, Ontario collected Coleoptera in the Maritime Provinces from the 1930's to the 1960's and published several papers (Brown 1940, 1950, 1967) which provided records of 25, principally adventive, species of Carabidae. The first compilation of carabid records from the province (186 species) was published by Carl H. Lindroth (1954), who collected in Nova Scotia in 1951 and compiled other records from the province. Later, in his authoritative treatment of the Carabidae of Canada and Alaska, Lindroth (1961, 1963b, 1966, 1968, 1969a, 1969b) provided records of 197 species from Nova Scotia.

A major contribution to the knowledge of carabids of the province was the research program reported by Lafontaine *et al.* (1987) conducted in 1983–1984 in Cape Breton Highlands National Park. One hundred and fifty species of Carabidae were collected as part of this initiative. Bousquet (1987) then provided records of seven additional species from Nova Scotia. Another major contribution to the knowledge of the province's carabid fauna was the collecting expedition of André Larochelle and Marie-Claude Larivière who visited the province in 1987 and found over 100 species. As a consequence of this research 244 species were listed as occurring in Nova Scotia by Bousquet (1991). The number had increased to 260 in Bousquet & Larochelle (1993), and to 263 in Goulet & Bousquet (2004).

Although Lindroth examined the material in the Nova Scotia Museum (principally collected by D.C. Ferguson), the historical collections at the Atlantic Food and Horticulture Research Centre in Kentville, Nova Scotia and at the Nova Scotia Agricultural College in Bible Hill, Nova Scotia were not seen by him. These contain additional specimens and records of Carabidae. Substantial collections of Carabidae have been gathered by the Nova Scotia Department of Natural Resources and by researchers at Cape Breton and Dalhousie universities. In a series of studies of fossil Coleoptera (primarily in Nova Scotia) done during the 1990's, R.F. Miller of the New Brunswick Museum has made important contributions to an understanding of the pre-historical development of the region's beetle fauna, including that of the Carabidae.

In recent years a number of studies including Bousquet (1987, 1992), Pearsall & Walde (1994), McCorquodale (2000), Majka & Klimaszewski (2004), D'Orsay (2005), Majka (2005), Majka *et al.* (2006), Aikens (2006), and Ewing (2006) have contributed to the knowledge of Carabidae in Nova Scotia, and other investigators such as J. Ogden, T. Rossolimo, D.H. Webster, and S. Westby have collected specimens and conducted research on the Carabidae.

In New Brunswick the earliest collections of Carabidae are from 1891 by W.H. Harrington who collected *Carabus granulatus hibernicus* Lindroth and *Carabus nemoralis* Müller in Saint John (Harrington 1892). Between 1898–1907 W. McIntosh, P.R. McIntosh, and A.G. Leavitt of the New Brunswick Natural History Society in Saint John made extensive collections of insects which included 72 species of Carabidae including early records of adventive species such as *Bembidion tetracolum* Say and *Harpalus affinis* (Schrank). This collection is now included in the New Brunswick Museum collection where D.F. McAlpine and R.F. Miller have continued to collect specimens. In the 1930s and 1940s W.J. Brown made a number of trips to New Brunswick where he collected adventive species such as *Clivina fossor* (Linnaeus), *Amara familiaris* (Duftschmid), *Pterostichus melanarius* (Illiger), *Harpalus rubripes* (Duftschmid), and *Paranichus albipes* (Fabricius) (Brown 1940, 1950). Lindroth (1961, 1963b, 1966, 1968, 1969a, 1969b), drawing in large measure on specimens at the Canadian National Collection (CNC) collected by Brown, reported 101 species of Carabidae from New Brunswick.

In 1977–1978 a major initiative of the Biosystematic Research Center of Agriculture Canada brought several entomologists to Kouchibouguac National Park where Coleoptera, including Carabidae, were collected. Unfortunately the results of this work were not published, however that material was subsequently integrated into the CNC. Larochelle, Larivière, and Bousquet subsequently visited the province in 1987 and 1988 collecting over 110 species of Carabidae. As a result of these investigations Bousquet (1991) was able to report 243 species of carabids from the province, Bousquet & Larochelle (1993) reported 254, and Goulet & Bousquet (2004) reported 258.

Since the early 1970s students at the Université de Moncton have collected insects and have found almost 50 species of Carabidae, primarily from eastern portions of the province. Boiteau *et al.* (2000) collected 57 species of Carabidae in a study of agricultural fields in Fredericton in 1992–1995, including three species, (*Mioptachys flavicauda* (Say), *Poecilus chalcites* (Say), and *Platynus opaculus* LeConte), that were not previously recorded for the province (see below). Apigian & Wheelwright (2000) found 16 species of carabids on Kent Island including *Calathus opaculus* LeConte, a species newly recorded from the province (see below). A.-S. Bertrand conducted research on Carabidae in northwestern NB in 2003 where she found 55 (erroneously reported as 54) species of carabids (Bertrand 2005). She reported three species, *Harpalus solitaris* Dejean, *Patrobis foveocollis* (Eschscholtz), and *Trechus crassiscapus* Lindroth, as new for New Brunswick, but failed to mention *Platynus mannerheimii* (Dejean) as new for the province (see below). C.G. Majka has focused on Albert County where he has recorded 80 species of carabids since the late 1960's. Bousquet (1987, 1992), Bousquet & Webster (2004, 2006), Majka (2005), and Majka *et al.* (2006) have all contributed knowledge with respect to the carabid fauna of the province. In recent years R.P. Webster has worked extensively on the Carabidae of the province and has found many additional species. These records will be published separately.

## Methods and conventions

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

ACNS	Agriculture and Agri-Food Canada, Kentville, Nova Scotia
CGMC	Christopher G. Majka collection, Halifax, Nova Scotia
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario
NBM	New Brunswick Museum, Saint John, New Brunswick
NSMC	Nova Scotia Museum collection, Halifax, Nova Scotia
NSNR	Nova Scotia Department of Natural Resources, Shubenacadie, Nova Scotia
UMNB	Université de Moncton, Moncton, New Brunswick

The number of specimens is indicated in parentheses with the collection coden. The systematics follow Ball and Bousquet (2000). For the purposes of this treatment, northeastern North America is considered to consist of the following jurisdictions: Connecticut (CT), Labrador (LB), Massachusetts (MA), Maine (ME), New Brunswick (NB), Newfoundland (NF), New Hampshire (NH), Nova Scotia (NS), New York (NY), Ontario (ON), Prince Edward Island (PE), Québec (QC), Rhode Island (RI), Saint-Pierre et Miquelon (PM), and Vermont (VT).

## Results

New records of 20 species of Carabidae (all Nearctic taxa) are reported (Table 1). Six are newly recorded for New Brunswick and 15 for Nova Scotia. Six of these are newly recorded in the Maritime Provinces as a

whole. Six species, *Cicindela purpurea purpurea* Olivier, *Dyschirius larochei* Bousquet, *Dyschirius setosus* LeConte, *Bembidion basicorne* Notman, *Myas cyanescens* Dejean, and *Amara lacustris* LeConte are removed from the faunal list of Nova Scotia and one species, *A. lacustris*, is removed from the faunal list of New Brunswick. The status of *Stenolophus carbo* Bousquet in the region is reviewed and its presence in Nova Scotia is designated as doubtful. Furthermore three species of carabids previously reported from New Brunswick, but not noted as additions to the provincial fauna list, are discussed. Additionally, a new and earlier timeline (1942) is reported for the introduced Palearctic carabid, *Bembidion properans* (Stephens), in North America. Specific details follow.

**TABLE 1.** New records of Nova Scotia and New Brunswick Carabidae.

Species	Bionomics <sup>1</sup>				Distribution in Northeastern North America <sup>2</sup>
	D/N	Wing	Flight	Runner	
<b>Nebrinae</b>					
<i>Notiophilus semistriatus</i> Say	D	WD	–	Fast	CT, MA, NB, NH, NS, NY, ON, QC
<b>Carabinae</b>					
<i>Calosoma scrutator</i> (Fabricius)	N	M	F	Mod	CT, MA, NH, NS, NY, ON, QC, RI
<b>Trechinae</b>					
<i>Bembidion punctatostriatum</i> Say	D	M	F	Fast	CT, MA, NB, NH, NS, NY, ON, QC, VT
<i>Bembidion cheyennense</i> Casey	N	M	F	Fast	NH, NS, ON, QC, VT
<i>Bembidion properans</i> (Stephens)	D&N	M	F	Fast	ME, NB, NF, NS, PE, QC
<i>Bembidion sulcipenne prasinoides</i> Lindroth	N	M	F	Mod	LB, NB, NF, NS, QC
<i>Bembidion nigripes</i> (Kirby)	N	M	F	Mod	LB, ME, NB, NF, NS, NY, ON, PE, PM, QC
<i>Bembidion rapidum</i> (LeConte)	N	M	F	Mod	CT, MA, ME, NB, NH, NS, NY, ON, QC, VT
<i>Elaphropus vernicatus</i> (Casey)	D	M	–	Fast	CT, MA, ME, NB, NH, NS, NY, ON, QC, RI, VT
<b>Harpalinae</b>					
<i>Poecilus chalcites</i> (Say)	N	M	F	Mod	CT, MA, NB, NH, NY, ON, QC, VT
<i>Pterostichus corvinus</i> (Dejean)	N	M	O	Mod	MA, ME, NB, NH, NS, NY, ON, PE, QC, RI, VT
<i>Amara convexa</i> LeConte	N	M	F	Mod	CT, MA, ME, NH, NS, NY, ON, QC, VT
<i>Amara neoscotica</i> Casey	D	WD	F	Mod	NB, NS, ON, QC, VT
<i>Amara rubrica</i> Haldeman	D	M	F	Mod	CT, MA, ME, NH, NS, NY, ON, QC, VT
<i>Bradycellus congener</i> (LeConte)	N	M	F	Mod	MA, NH, NS, NY, ON, QC, VT
<i>Bradycellus semipubescens</i> Lindroth	N	M	F	Mod	CT, MA, ME, NB, NH, NS, NY, ON, QC, VT
<i>Harpalus solitaris</i> Dejean	N	M	O	Mod	LB, ME, NB, NF, NH, ON, PE, PM, QC
<i>Diplocheila striatopunctata</i> (LeConte)	N	M	F	Mod	NB, NH, NS, NY, ON, QC, VT
<i>Lachnocrepis parallela</i> (Say)	D&N	M	F	Mod	CT, MA, ME, NH, NS, NY, ON, QC, VT
<i>Calathus opaculus</i> LeConte	N	M	O	Fast	CT, MA, ME, NB, NH, NY, ON, QC, RI, VT

to be continued.

TABLE 1. (continued)

Species	Bionomics <sup>1</sup>				Distribution in Northeastern North America <sup>2</sup>
	D/N	Wing	Flight	Runner	
<i>Agonum crenistriatum</i> (LeConte)	N	M	–	Mod	CT, MA, ME, NB, NH, NS, NY, ON, PE, QC, RI, VT
<i>Platynus indecentis</i> Liebherr & Will	N	M	–	–	CT, MA, ME, NS, NY, ON, VT
<i>Platynus mannerheimii</i> (Dejean)	N	sM	I	Mod	CT, LB, ME, NB, NF, NH, NS, NY, ON, PE, PM, QC, VT
<i>Cymindis limbatus</i> Dejean	N	WD	F	Mod	CT, MA, ME, NB, NH, NS, NY, ON, QC, RI, VT
<i>Lebia tricolor</i> Say	D	M	F	Mod	CT, MA, NB, NH, NS, NY, ON, QC, VT

**Notes:** new, species newly recorded; D/N, diurnal/nocturnal; Wing, wing condition; Flight, flight ability; Runner, running ability; D, diurnal; N, nocturnal; M, macropterous; sM, sub-macropterous; WD, wing dimorphic; F, frequent; O, occasional; I, incapable; Mod, moderate; –, information unavailable.

<sup>1</sup>Larochelle & Larivière (2003); <sup>2</sup>Bousquet & Larochelle (1993)

### *Notiophilus semistriatus* Say, 1823

**NEW BRUNSWICK: Albert Co.:** 3 km north of Fundy National Park, 4.viii.1994, black spruce plantation, J. Julian, pitfall trap, (6, NSMC).

Newly recorded in New Brunswick. These specimens were collected incidentally in the course of research on amphibians published by Waldick *et al.* (1999). In Nova Scotia the species is recorded only from Cape Breton Island (C.G. Majka, unpublished data). Found in a large variety of environments on open or half-shaded ground (Larochelle & Larivière 2003). Adults and larvae of *Notiophilus* prey on Collembola (Ball & Bousquet 2000).

### *Calosoma scrutator* (Fabricius, 1775)

**NOVA SCOTIA: Shelburne Co.:** Cape Sable Island: The Hawk, 19.ix.2002, G. Milroy, coastal meadow: under board, (1, NSMC).

Newly recorded in Nova Scotia and in the Maritime Provinces as a whole. The discovery of this specimen on Cape Sable Island, in the extreme southwest of Nova Scotia, is surprising given the absence of records elsewhere in the Maritimes. Although it is unlikely that the species is a permanent resident, it is possible that the mild climate of Cape Sable Island allows a population to persist. Alternatively, the individual may represent a wind-blown stray from New England where this adept flyer occurs. The location of the island (the outermost projection of land into the northern Gulf of Maine) annually attracts many migrant and wind-blown stray birds. *Calosoma scrutator* is found in a large variety of environments on shaded ground; nocturnal and predaceous on Lepidoptera caterpillars and other insects (Larochelle & Larivière 2003).

### *Cicindela purpurea purpurea* Olivier, 1790

There has long been confusion with regard to the presence of this species in Nova Scotia. It was listed as occurring in Nova Scotia by Bousquet (1991), Bousquet & Larochelle (1993), Leonard & Bell (1999), Acorn (2001), Goulet & Bousquet (2004), and Pearson *et al.* (2006), but not by Wallis (1961) or Freitag (1999).

Maps in Pearson *et al.* (2006) show it as occurring in southern New Brunswick and throughout Nova Scotia. There are, however, no published records or voucher specimens that would substantiate its presence in the region. In the range map for the species in Leonard and Bell (1999, p. 127) a spot in south-central Nova Scotia is indicated. However, J. Leonard (pers. comm.) reports that he never examined a specimen from the province and cannot recall the source of this information. There are specimens of *Cicindela limbalis* in the CNC that were misidentified as *C. purpurea* and there is a dark specimen of *Cicindela duodecimguttata* in the NSMC (collected by D.C. Ferguson in Armdale, Nova Scotia in 1952) that was misidentified as *C. purpurea* by A.E. Brower (a lepidopterist). There are no specimens of this species from Nova Scotia in any collection in the Maritime Provinces or at the CNC. Neil (2004) found no evidence of the occurrence of the species in the province. Accordingly we conclude that past reports of this species occurring in Nova Scotia have been in error and it is removed from the faunal list of the province.

### ***Dyschirius larochelei* Bousquet, 1988**

Bousquet (1988) described *D. larochelei* from specimens collected in the United States noting that the range of the species *probably* (emphasis added) extends north to Newfoundland since the specimens reported by Lindroth (1955) from there as *D. erythrocerus* LeConte almost certainly referred to this new species. Subsequently Bousquet and Larochelle collected the species in New Brunswick in 1988 (CNC) and it was included in the faunal lists of both New Brunswick and Nova Scotia by Bousquet (1991), Bousquet & Larochelle (1993), and Goulet & Bousquet (2004). However, no specimens from Nova Scotia have actually been collected. Accordingly we remove this species from the faunal list of Nova Scotia.

### ***Dyschirius setosus* LeConte, 1857**

There are specimens of *D. setosus* from both New Brunswick and Prince Edward Island in the CNC and the species was included in the faunal lists of New Brunswick, Nova Scotia, and Prince Edward Island by Bousquet (1991), Bousquet & Larochelle (1993), and Goulet & Bousquet (2004). However, there are no voucher specimens from Nova Scotia in any collection. Accordingly we remove this species from the faunal list of Nova Scotia.

### ***Bembidion cheyennense* Casey, 1918**

**NOVA SCOTIA: Kings Co.:** Sheffield Mills, 3.vii.2000, K. Neil, light-trap, (1, ACNS).

Newly recorded in Nova Scotia and in the Maritime Provinces as a whole. Found at the edges of ponds, reservoirs, water holes, riverbanks, and lakeshores; also close to water in cultivated fields and meadows on open or sparsely vegetated ground (Larochelle & Larivière 2003).

### ***Bembidion properans* (Stephens, 1828)**

**NOVA SCOTIA: Halifax Co.:** Halifax, 1.vii.1942, M. Mosher, carrot row, (4, ACNS); **Kings Co.:** Kentville, 27.v–7.vi.1949 and 28.vi.1949, C.R. MacLellan, insecticide plots, (2, ACNS); **Lunenburg Co.:** Lunenburg, 16.ix.1954, C.J.S. Fox, (1, ACNS).

This species was first reported in North America by Lindroth (1954) on the basis of a single specimen collected by W.J. Brown in 1947 in Dartmouth and subsequent specimens collected by C.H. Lindroth in 1951 in Halifax, Riversdale, and Crescent Beach, Nova Scotia, and D.C. Ferguson in 1952 in Halifax (NSMC). The above specimens, collected in 1942 in Halifax, establish a new and earlier timeline for this species on the continent. It is also noteworthy that specimens were collected so soon afterwards in Kings (1949) and Lunenburg (1954) counties, indicating either rapid dispersal or multiple points of entry. The species is found in vacant

lots, edges of fields, roadsides, sand pits, and open forests; primarily on open, moderately moist soil (Larochelle & Larivière 2003).

***Bembidion basicorne* Notman, 1920**

This species is listed as occurring in Nova Scotia by Bousquet (1991), Bousquet & Larochelle (1993), and Goulet & Bousquet (2004). The only Canadian specimens, however, are from Québec (CNC). Accordingly we remove this species from the faunal list of Nova Scotia.

***Bembidion punctatostriatum* Say, 1823**

**NOVA SCOTIA: Kings Co.:** Perea Beach, 9.ix.2003, S. Westby, (1, ACNS).

Newly recorded in Nova Scotia. Found on moist, bare soil along the banks of rivers and the shores of lakes (Larochelle & Larivière 2003).

***Bembidion sulcipenne prasinoides* Lindroth, 1963**

**NOVA SCOTIA: Colchester Co.:** Portapique, 19.vii.1987, A. Larochelle & M.–C. Larivière, (15, NSMC).

Newly recorded in Nova Scotia. Gregarious, found on moist, bare, or gravelly soil along the banks of swift rivers and brooks; nocturnal (Larochelle & Larivière 2003).

***Bembidion nigripes* (Kirby, 1837)**

**NOVA SCOTIA: Halifax Co.:** Petpeswick, 23.vi.1971, B. Wright, (1, NSMC).

Newly recorded in Nova Scotia. Found on seashores, salt meadows, and margins of marshes, lakes, and slow brooks and rivers on open, moist or wet, clay soil; nocturnal (Larochelle & Larivière 2003).

***Bembidion rapidum* (LeConte, 1848)**

**NOVA SCOTIA: Halifax Co.:** Sable Island, 26.vii.1976, B. Wright, (1, NSMC).

Newly recorded in Nova Scotia. This specimen, a teneral one, was reported by Wright (1989) as *Bembidion* sp. nr. *castor* Lindroth. Its presence on Sable Island, a 45 kilometre long sand bar located near the edge of the continental shelf, and 160 km from the nearest point of land, is noteworthy, given that it has not been otherwise recorded in Nova Scotia. Further research at this site is required to determine its status. Found in a large variety of environments on open, wet, clayish or sandy soil. A synanthropic species (Larochelle & Larivière 2003).

***Elaphropus vernicatus* (Casey, 1918)**

**NOVA SCOTIA: Annapolis Co.:** Moshelle, 26.v.2005, K. MacKenzie, pitfall trap, (1, ACNS).

Newly recorded in Nova Scotia. Found on the banks and shores of rivers and brooks; also along lakes, ponds and marshes, roadsides, sand pits, vacant lots, and cultivated fields; adults feed on plants in the Brassicaceae (Larochelle & Larivière 2003). Some species of *Elaphropus* are myrmecophilous (Ball & Bousquet 2000).

***Myas cyanescens* Dejean, 1828**

This species was listed as occurring in Nova Scotia by Bousquet & Larochelle (1993), and Goulet & Bousquet (2004). However, there is only one specimen from the Maritime Provinces, collected in Saint



Andrews, New Brunswick (CNC). Accordingly we remove this species from the faunal list of Nova Scotia.

***Poecilus chalcites* (Say)**

Deserving of attention is the record of *Poecilus chalcites* reported from Fredericton, NB (1992–1995) by Boiteau *et al.* (2000). This species was not included in the compendium of New Brunswick carabid fauna compiled by Goulet & Bousquet (2004). Found in cultivated fields planted with many crops, rangelands, pastures, meadows, lawns, vacant lots, gravel pits, roadsides, orchards, open forests, and near water on open moist ground. Adults feed on Lepidoptera caterpillars, flies, wasps, other insects, fungi, and vegetable material (Larochelle & Larivière 2003).

***Pterostichus corvinus* (Dejean, 1828)**

**NOVA SCOTIA: Kings Co.:** Starr's Point, v–xii.1991, I. Pearsall, apple orchard, pitfall trap, (1, NSMC).

Newly recorded in Nova Scotia. This specimen was collected as part of the research done by Pearsall and Walde (1994) but was not correctly identified until recently. Gregarious, found along marsh edges, borders of small ponds and lakes, along slow rivers and brooks, and in swamp forests (Larochelle & Larivière 2003).

***Amara lacustris* LeConte, 1855**

This species was listed as occurring in Nova Scotia by Bousquet (1991), Bousquet & Larochelle (1993), and Goulet & Bousquet (2004), and from New Brunswick by the two latter sources. However, there are Canadian specimens only from Ontario westwards (CNC). Accordingly we remove this species from the faunal lists of Nova Scotia and New Brunswick.

***Amara convexa* LeConte, 1848**

**NOVA SCOTIA: Kings Co.:** Avonport, 29.vii.2003, S. Westby, C. Sheffield, and K. Jansen, (1, ACNS).

Newly recorded in Nova Scotia. Gregarious, found in grasslands, meadows, pastures, cultivated fields, and their borders; feeds on coccinellids. A synanthropic species (Larochelle & Larivière 2003).

***Amara neoscotica* Casey, 1924**

**NEW BRUNSWICK: Albert Co.:** 3 km north of Fundy National Park, 8.vi.1994, black spruce plantation, J. Julian, pitfall trap, (6, NSMC); **Saint John Co.:** Saint John, 13.vii.1904, A.G. Leavitt, (1, NBM); **Westmoreland Co.:** Moncton, 28.x.1978, E. Ouellette, (1,UMNB). **NOVA SCOTIA: Colchester Co.:** Kempton, 18.v.1995, C. Corkum, young deciduous forest, flight-intercept trap, (1, NSMC); **Cumberland Co.:** Harrington River, 17.v.1995, C. Corkum, young deciduous forest, flight-intercept trap, (1, NSMC); **Guysborough Co.:** Borneo, 1995, C. Corkum, young deciduous forest, flight-intercept trap, (1, NSMC).

Newly recorded in New Brunswick. *Amara neoscotica* was originally described from Halifax, Nova Scotia by Casey (1924). It was subsequently synonymized by Lindroth (1954) with *A. cupreolata* Putzeys before being restored as a distinct species by Hieke (2003). Recorded in northeastern North America from Nova Scotia, Ontario, Québec, and Vermont (Hieke 2003).

***Amara rubrica* Haldeman, 1843**

**NOVA SCOTIA: Kings Co.:** Canard, 11.viii.1978, Agriculture Canada, (2, NSMC).

Newly recorded in Nova Scotia. Found in meadows, vacant lots, cultivated fields, and sand and gravel pits

where it feeds on seeds of goldenrods (*Solidago* spp.) and other Compositae (Larochelle & Larivière 2003).

### ***Stenolophus carbo* Bousquet, 1993**

In the context of reviewing the carabid fauna of the region, it is worth drawing attention to this species, which is known in Atlantic Canada solely from a record (as *S. carbonarius* (Dejean)) reported by Lindroth (1954, 1968) on the basis of a specimen observed by him in a cattail (*Typha*) swamp in Waverly (on the outskirts of Halifax), Nova Scotia, in May 1951, which subsequently escaped. Thus, there is no voucher specimen to substantiate the record and there are otherwise no Canadian records of this species east of Ontario. There has been some subsequent collecting of Carabidae in Waverley (D.C. Ferguson and B. Wright, NSMC), and extensive collecting of Carabidae in Halifax and environs, and no further specimens have been found. Bearing this in mind, and pending further fieldwork, *S. carbo* should be regarded as doubtful in Nova Scotia, and consequently the region as a whole.

### ***Bradycellus congener* (LeConte, 1848)**

**NOVA SCOTIA: Kings Co.:** Kentville, 8.vi.1998, S. Rigby, pitfall trap, (1, ACNS).

Newly recorded in Nova Scotia and the Maritime Provinces as a whole. Found in the borders of marshes, ponds, lakes, reservoirs, watering holes, slow rivers and brooks, swamps, pastures, vacant lots, cultivated fields, and roadsides on open, somewhat wet, soil with sparse vegetation; adults feed on coccinellids (Larochelle & Larivière 2003).

### ***Bradycellus semipubescens* Lindroth, 1968**

**NOVA SCOTIA: Guysborough Co.:** Malay Lake, 2–15.vi.1997, D.J. Bishop, red spruce forest, flight-intercept trap, (1, NSMC); **Hants Co.:** Armstrong Lake, 14.v–2.vi.1997, D.J. Bishop, red spruce forest, flight-intercept trap, (1, NSMC); Panuke Lake, 14.v–2.vi.1997, D.J. Bishop, red spruce forest, flight-intercept trap, (1, NSMC).

Newly recorded in Nova Scotia. Found in deciduous woodland swamps, borders of marshes, low forests, wet meadows, and roadside ditches (Larochelle & Larivière 2003).

### ***Harpalus solitaris* Dejean, 1829**

**NEW BRUNSWICK: Albert Co.:** 3 km north of Fundy National Park, 8.vi.1994, 4.vii.1994, and 4.viii.1994, J. Julian, black-spruce plantation, (4, NSMC).

This species was first reported in New Brunswick by Bertrand (2005) from a single specimen collected in the Black Brook District in the northwest of the province in June–July 2003. The above specimens precede the earlier record and establish the presence of the species in the southeast of the province. Found on moraines, meadows, vacant lots, abandoned fields, sand and gravel pits, roadsides, thickets, and open forests (Larochelle & Larivière 2003).

### ***Diplocheila striatopunctata* (LeConte, 1844)**

**NEW BRUNSWICK: Queens Co.:** Gagetown, 2.ix.1999, E. Estabrooks, apple orchard, (1, ACNS); Gagetown, 10.viii.1999, E. Estabrooks, apple orchard, (1, ACNS). **NOVA SCOTIA: Colchester Co.:** Debert, no date or collector specified, (2, NSNR).

Newly recorded in New Brunswick, Nova Scotia, and the Maritime Provinces as a whole. Found on the margins of eutrophic marshes, ponds, lakes, pools, canals, rivers, brooks, swamps, and flood-plain forests;

nocturnal; a good burrower and swimmer (Larochelle & Larivière 2003). One species of *Diplocheila* was observed eating snails (Ball & Bousquet 2000).

***Lachnocrepis parallela* (Say, 1830)**

**NOVA SCOTIA: Cumberland Co.:** Amherst, 22.v.1994, J. Ogden, (1, NSNR).

Newly recorded in Nova Scotia and the Maritime Provinces as a whole. Found on the borders of eutrophic marshes, ponds, lakes, and swamps; diurnal and nocturnal where it feeds on plant seeds (Larochelle & Larivière 2003). Typically found in cattail (*Typha* spp.) marshes (Ball & Bousquet 2000).

***Calathus opaculus* LeConte, 1854**

It is worth drawing attention to the records of this species published by Apigian & Wheelwright (2000) from Kent Island, New Brunswick since this species was not included in Goulet & Bousquet's (2004) compendium of New Brunswick carabid fauna. Apigian and Wheelwright found *C. opaculus* to be one of the two most abundant species on the island. Found in meadows, old fields, pastures, vacant lots, cultivated fields, lawns, hedges, sand hills, orchards, forest edges, and open forests on open or shaded dry, sandy soil (Larochelle & Larivière 2003).

***Agonum crenistriatum* (LeConte, 1863)**

**NEW BRUNSWICK: Westmoreland Co.:** Moncton, 15.x.1982, G. Babin, (1, UMNB).

Newly recorded in New Brunswick. Found on open ground in meadows, abandoned fields, pastures, cultivated fields, vacant lots, sand and gravel pits, and open forest; adults are both carnivorous as well as feeding on seeds (Larochelle & Larivière 2003).

***Platynus indecentis* Liebherr & Will, 1996**

**NOVA SCOTIA: Halifax Co.:** Lake Major, 19.vii.2004, K. Moore, NSNR; **Hants Co.:** South Maitland, Hayes Cave Reserve, 19.vi.1978, B. Wright, (2, NSMC); **Lunenburg Co.:** Upper LaHave, 6.vii.1987, A. Larochelle, and M.-C. Larivière, (1, NSMC).

Newly recorded in Nova Scotia and the Maritime Provinces as a whole. Liebherr & Will (1996) found it associated with *Sphagnum* bog habitats. While the precise collection habitat of the specimens from the Hayes Cave Reserve is unknown (wet areas do exist along a stream), there are no *Sphagnum* bogs in the area, which is characterized by limestone karst geology. In contrast to the flightless and morphologically similar *Platynus decentis*, *P. indecentis* is fully macropterous (Liebherr & Will 1996).

***Platynus mannerheimii* (Dejean, 1828)**

It is worth drawing attention to the records of *Platynus mannerheimii* published by Bertrand (2005) who collected 89 specimens of this species in the Black Brook district of northwestern New Brunswick. Although this Holarctic species was not recorded from New Brunswick by Bousquet (1991), Bousquet & Larochelle (1993) or Goulet & Bousquet (2004), Bertrand failed to note that this species was a new record for New Brunswick. It is found in coniferous forests, thickets bordering lakes, ponds and slow rivers, *Sphagnum* bogs, open *Carex* marshes, open sub-alpine scrubland, and moist alpine meadows, on open or shaded wet soil; adults feed on Coleoptera larvae (Larochelle & Larivière 2003).

### *Cymindis limbatus* Dejean, 1831

**NEW BRUNSWICK: Albert Co.:** Mary's Point, 12.viii.2004, C.G. Majka, seashore, (1, CGMC).

Newly recorded in New Brunswick. Found in deciduous, coniferous, and mixed forests and in orchards (Larochele & Larivière 2003).

### *Lebia tricolor* Say, 1823

**NEW BRUNSWICK: York Co.:** Fredericton, 10.vi.1979, A. Chenard, (1, UMN).

Newly recorded in New Brunswick. Found in open deciduous forests, clearings, thickets, orchards, hedges, meadows, and abandoned fields; active on the foliage of plants, bushes, and trees (Larochele & Larivière 2003). Commonly found on goldenrod (Lindroth 1969). Some species of *Lebia* are known parasitoids on chrysomelids and it is suspected that a parasitic mode of life is common to the whole genus (Ball & Bousquet 2000).

## Discussion

### Origins of the Maritimes' Carabid Fauna

An interesting window on the genesis of the Maritimes' carabid fauna is provided by the research of Miller & Morgan (1991) and Miller (1995, 1996, 1997a, 1997b, 2000) who embarked on a series of studies of the late-glacial Coleoptera of the region. Table 2 shows a compilation of carabid species found in these studies along with approximate  $C^{14}$  and calibrated (cal yr) dates of the deposits that range in age from 12,600 to 10,600 (calibrated) years BP. There are frequently difficulties associated with the identification of fragmented specimens collected from peat deposits, and so some determinations can only be made to generic level or approximately to species. Nonetheless the picture presented by the data in Table 2 is instructive. At least a third (and potentially more) of the species found in these deposits are Holarctic, four times the 8.7% present-day ratio in the Maritime Provinces. Virtually all the species represented are found throughout the sub-arctic and northern boreal zones of the continent (Alaska, Labrador, Newfoundland, Northwest Territories (including Nunavut), and the Yukon), although a few species (*Blethisa julii* LeConte, *Trechus crassiscapus* Lindroth, and *Chlaenius niger* Randall) have a slightly more restricted northern distribution, and 12 species range south into more temperate portions of the northern United States. Two species, the Holarctic *Patrobus septentrionis* Dejean and *Bembidion grapii* Gyllenhal, are found in Greenland (Böcher, 1988). Eleven species no longer occur in the Maritime Provinces and are presently found at more northern latitudes.

Miller & Elias (2000) interpreted changing faunal assemblages at this time as indicative of three temporal "zones" at the Allerød/Younger Dryas transition: 1) a tree-line/tundra assemblage older than 13,760 cal yr BP, which colonized the region following deglaciation and the development of tundra vegetation; 2) a boreal assemblage from 13,760 to 12,730 cal yr BP which colonized the region following climatic warming and the development of forested taiga vegetation; and 3) a northern boreo-montane assemblage younger than 12,730 cal yr BP. They interpreted the third zone as reflecting the Coleoptera response to the climatic deterioration during the Younger Dryas chronozone. After the Younger Dryas period (which lasted  $1,300 \pm 70$  years) climate returned to conditions more closely resembling present-day ones.

In that context, sub-arctic species such as *Miscodera arctica* (Paykull) and *Bembidion grapii* which are presently found in the Maritime Provinces, could be regarded as relicts of the original tree-line/tundra assemblages that colonized the region following deglaciation, while the range of sub-arctic species such as *Diacheila arctica amoena* (Faldermann), *Elaphrus lapponicus* Gyllenhal, *Dyschirius hiemalis* Bousquet, *Bembidion hastii* Sahlberg, *Bembidion sordidum* (Kirby), *Bembidion morulum* LeConte, *Patrobus stygicus* Chaudoir, and *Stereocerus haematopus* (Dejean) – which are no longer present in the region – moved northwards following climatic amelioration.

TABLE 2. Post-glacial Carabidae in the Maritime Provinces.

site localities	MP	R	Nova Scotia, Mainland						Nova Scotia, Cape Breton				New Brunswick	
			Hirtles	Lismore	Lantz	Blomodin	Joggins	Amquadees	Benacadie	Campbell	W. Mabou	Saint John		
approximate C14 yr BP (basal deposit)			12,150	12,000	11,700	11,700	11,800	12,600	12,400	11,250	10,600	10,800		
approximate cal yr BP (basal deposit)			14,200	13,990	13,610	13,610	13,730	14,800	14,500	13,160	12,530	12,730		
<i>Peolophila/Nebria</i>										X			X	
<i>Notiophilus</i> sp.			X					X	X	X			X	X
<i>Carabus</i> sp.			X											
<i>Diacheila arctica amoena</i> (Faldermann) *	A	N	X					X						
<i>Blethisa julii</i> LeConte	P	N	X							X				
<i>Blethisa quadricollis</i> Haldeman	P	N/S			X									
<i>Elaphrus clairvillei</i> Kirby	P	N/S				X		X						
<i>Elaphrus americanus</i> Dejean	P	N/S	X					X						
<i>Elaphrus lapponicus</i> Gyllenhal *	A	N		X				X		X			X	
<i>Elaphrus</i> sp.							X			X				
<i>Dyschirius hienalis</i> Bousquet	A	N						X	X				X	
<i>Dyschirius integer</i> LeConte	P	N/S				X		X						
<i>Dyschirius melancholicus</i> Putzeys *	A	N/S						X						
<i>Dyschirius</i> sp.				X				X						
<i>Miscodera arctica</i> (Paykull) *	P	N							X					
<i>Trechus crassiscapus</i> Lindroth *	P	N	X						X				X	
<i>Bembidion hastii</i> Sahlberg *	A	N						X						
<i>Bembidion grapti</i> Gyllenhal *	P	N	X					X					X	
<i>Bembidion sordidum</i> (Kirby)	A	N						X	X				X	
<i>Bembidion petrosum</i> Gebler *	P	N/S				X								

to be continued.

TABLE 2. (continued)

site localities	MP	R	Nova Scotia, Mainland							Nova Scotia, Cape Breton				New Brunswick	
			Hirtles	Lismore	Lantz	Blomodin	Joggins	Amguadees	Benacadie	Campbell	W. Mabou	Saint John			
approximate C14 yr BP (basal deposit)			12,150	12,000	11,700	11,700	11,800	12,600	12,400	11,250	10,600	10,800			
approximate cal yr BP (basal deposit)			14,200	13,990	13,610	13,610	13,730	14,800	14,500	13,160	12,530	12,730			
<i>Bembidion scopulinum</i> (Kirby) *	P	N/S	X					X	X						
<i>Bembidion morulum</i> LeConte	A	N						X	X						
<i>Bembidion</i> sp.			X	X	X	X	X	X	X	X	X	X			
<i>Patrobis foveocollis</i> (Eschscholtz) *		N/S	X					X	X						
<i>Patrobis septentrionalis</i> Dejean *	A	N/S	X					X	X						
<i>Patrobis stygicus</i> Chaudoir	A	N	X					X							
<i>Patrobis</i> sp.			X				X	X							
<i>Stereocerus haematopus</i> (Dejean) *	A	N			X			X	X			X			
<i>Pterostichus arcticola</i> (Chaudoir)															
<i>P. patruelis</i> (Dejean)	A/P	N										X			
<i>P. adstrictus</i> Eschscholtz *															
<i>P. pennsylvanicus</i> LeConte	P/P	N/S						X	X						
<i>Pterostichus</i> sp.								X							
<i>Anara</i> sp.									X						
<i>Chlaenius niger</i> Randall	P	N/S				X									
<i>Agonum affine</i> Kirby	P	N/S	X												
<i>Agonum</i> sp.					X			X	X						
<i>Cymindis</i> sp.			X					X							

Notes: \*, Holarctic species. MP, Current Distribution in the Maritime Provinces; A, Absent; P, Present. R, Range; N, Northern/Sub-arctic; N/S, northern species ranging south.

There are also carabids found in the Maritime Provinces that have a more temperate distribution and reach the northern limit of their distribution in the region, such as *Omophron labiatum* (Fabricius), *Notiophilus novemstriatus* LeConte, *Calosoma scrutator*, *Cicindela marginipennis* Dejean, *Bembidion postremum* Say, and *Agonum deceptiveum* (LeConte). Although Miller did not find such carabids in his research, he did find the coccinellid *Nephus flavifrons* (Melsheimer) at Amaguadees and Benacadie on Cape Breton Island (Miller 1997a). This is a temperate species found from Texas and Florida north to Iowa and east to southern Quebec and New Hampshire (Gordon 1985). It is not presently found as far north as the Maritime Provinces. Although the paleontological record is fragmentary, it is clear that the carabid fauna of the region developed its present character over time and exhibits the history of that development in the component faunas that comprise it.

### Contemporary Composition and Zoogeography

As a result of the present investigations 282 species of Carabidae have been recorded from Nova Scotia, 273 species from New Brunswick, and 329 from the Maritime Provinces as a whole (Table 9). A complete analysis of the region's carabids remains to be done, but an examination of Table 3 makes apparent certain features of the fauna. Despite the lesser historical attention that New Brunswick has received in terms of collecting, its fauna and that of Nova Scotia appear roughly similar in size. The combined Maritime Provinces fauna is similar to that of the state of Maine (343 species), although substantially smaller than that of Québec (456 species) (Bousquet & Larochelle 1993).

**TABLE 3.** A comparison of the zoogeographic composition of the Atlantic Canadian Carabidae.

	Nearctic	%	Holarctic	%	Native	%	Palaearctic	%	Total	%
Prince Edward Island	126	73.7%	18	10.5%	144	84.2%	27	15.8%	171	100%
Cape Breton Island	146	75.6%	24	12.4%	170	88.1%	23	11.9%	193	100%
Newfoundland	112	65.9%	36	21.2%	148	87.1%	22	12.9%	170	100%
Nova Scotia mainland	209	80.1%	20	7.7%	229	87.7%	32	12.3%	261	100%
Nova Scotia	222	78.7%	26	9.2%	248	87.9%	34	12.1%	282	100%
New Brunswick	228	83.5%	21	7.7%	249	91.2%	24	8.8%	273	100%
Maritime Provinces	266	80.9%	29	8.8%	295	89.7%	34	10.3%	329	100%
Atlantic Canada	278	78.5%	38	10.7%	316	89.3%	38	10.7%	354	100%

**Notes:** Numbers of species in the Maritime Provinces are derived from Bousquet & Larochelle (1993), Majka *et al.* (2006), and C.G. Majka (unpublished data). Numbers of species in Newfoundland are derived from Lindroth (1955, 1963b) and Larson & Langor (1982).

There are 36 species (10.9% of the Maritime fauna) found in Nova Scotia that have not been recorded in New Brunswick (Table 4). Nine of these are introduced and 27 are native species (26 Nearctic and one Holarctic). The nine introduced species largely reflect an introduction history in which the seaports of Nova Scotia played a more prominent role in trans-Atlantic commerce (and associated dry ballast, see below), allowing for more opportunities for the introduction of Palaearctic species there.

Although it is possible that some of these 27 native species occur in New Brunswick but have remained un-detected there, it is also possible that some may have colonized Nova Scotia from New England across post-glacial, emergent land-bridges and island chains that existed between Cape Cod, Georges Bank, and the continental shelf of Nova Scotia from circa 14,500 to 8,000 years BP (King 1996). This mechanism is well established in the case of Nova Scotia's coastal-plain flora (Keddy & Wisheu 1989) and might be applicable to some carabids (see Klimaszewski *et al.* 2006, pp 69–72 for further discussion of this topic). Of the 27 native species, all are found in northern New England (Massachusetts, Maine, New Hampshire, and Vermont), and all but one (*Acupalpus pumilus* Lindroth) are found in Nova Scotia, but are otherwise unrecorded in the rest of

Atlantic Canada. Of these 26, almost all are macropterous and capable of flight with two species (*Notiophilus novemstriatus* LeConte and *Microlestes linearis* (LeConte)) being wing-dimorphic with some individuals capable of flight. Fifteen are categorized as frequent flyers and eight as occasional flyers by Laroche & Larivière (2003) (information is unavailable for three species). Flight ability is not a pre-requisite for dispersal via this pathway (e.g. the flightless, coastal tenebrionid, *Ephalus latimanus* (LeConte), is present on Sable Island (Wright 1989)) but would facilitate dispersal across the ~ 25 km Northeast Channel which once separated the Georges Bank refugium (which remained unglaciated during the Wisconsinian glaciation) from the emergent Brown's Bank, which was connected to the Nova Scotian mainland.

**TABLE 4.** Carabidae reported from Nova Scotia and not from New Brunswick.

Species	Distribution in Northeastern North American	Wing	Flight
<b>Native Species</b>			
<b>Omophroninae</b>			
<i>Omophron labiatum</i> (Fabricius)	CT, MA, NS, NY	M	F
<b>Nebriinae</b>			
<i>Notiophilus novemstriatus</i> LeConte	CT, MA, ME, NH, NS, NY, RI, VT	WD	O
<b>Carabinae</b>			
<i>Calosoma scrutator</i> (Fabricius)	CT, MA, NH, NS, NY, ON, QC, RI	M	F
<b>Cicindelinae</b>			
<i>Cicindela formosa generosa</i> Dejean	CT, MA, ME, NH, NS, NY, ON, QC, RI, VT	M	F
<i>Cicindela marginata</i> Fabricius	CT, MA, ME, NH, NS, RI	M	F
<b>Trechinae</b>			
<i>Bembidion cheyennense</i> Casey	NH, NS, ON, QC, VT	M	F
<i>Elaphropus xanthopus</i> (Dejean)	CT, MA, ME, NH, NS, NY, ON, QC, RI, VT	M	O
<i>Polyderis laevis</i> (Say)	CT, MA, ME, NH, NS, NY, ON, QC, RI, VT	M	F
<b>Harpalinae</b>			
<i>Amara pennsylvanica</i> Hayward	CT, MA, NH, NS, NY, ON, QC	M	O
<i>Amara convexa</i> LeConte	CT, MA, ME, NH, NS, NY, ON, QC, VT	M	F
<i>Stenolophus carbo</i> Bousquet	CT, MA, NH, NS, NY, ON, RI	M	O
<i>Stenolophus humidus</i> Hamilton	CT, MA, ME, NH, NS, ON, QC, RI, VT	M	-
<i>Bradycellus congener</i> (LeConte)	MA, NH, NS, NY, ON, QC, VT	M	F
<i>Acupalpus pumilus</i> Lindroth	MA, ME, NH, NS, NY, ON, PE, QC	M	F
<i>Harpalus compar</i> LeConte	CT, MA, ME, NH, NS, NY, ON, QC, RI, VT	M	F
<i>Harpalus erythropus</i> Dejean	CT, MA, ME, NH, NS, NY, ON, QC, RI, VT	M	F
<i>Harpalus longicollis</i> LeConte	CT, MA, NS, NY, ON, QC, RI, VT	M	O
<i>Harpalus caliginosus</i> (Fabricius)	CT, MA, ME, NH, NS, NY, ON, QC, RI, VT	M	F
<i>Harpalus fuscipalpis</i> Sturm *	NH, NS, ON, QC	M	O
<i>Agonum deceptiveum</i> (LeConte)	MA, ME, NH, NS	M	-
<i>Platynus indecentis</i> Liebherr & Will	CT, MA, ME, NS, NY, ON, VT	M	-
<i>Platynus cincticollis</i> (Say)	CT, MA, NH, NS, NY, ON, QC, RI, VT	M	O
<i>Cymindis limbatus</i> Dejean	CT, MA, ME, NB, NH, NS, NY, ON, QC, RI, VT	M	F

to be continued.



TABLE 4. (continued)

Species	Distribution in		Wing	Flight
	Northeastern North American			
<i>Apristus latens</i> (LeConte)	MA, NH, NS, ON, QC, VT		M	F
<i>Microlestes linearis</i> (LeConte)	CT, MA, ME, NH, NS, ON, QC, VT		WD	O
<i>Lebia solea</i> Hentz	CT, MA, NH, NS, NY, ON, QC, RI, VT		M	F
<i>Lebia vittata</i> (Fabricius)	CT, MA, ME, NH, NS, NY, ON, QC, RI, VT		M	F
<b>Introduced Species</b>				
<b>Nebrinae</b>				
<i>Notiophilus palustris</i> (Duftschmid)	NS, PE		M	–
<b>Trechinae</b>				
<i>Brosicus cephalotes cephalotes</i> (Linnaeus)	NS, PE		M	I
<i>Trechus quadristriatus</i> (Schrank)	NS, ON, QC		M	F
<b>Harpalinae</b>				
<i>Stomis pumicatus</i> (Panzer)	NS, PE		B	I
<i>Abax parallelepidus</i> (Piller & Mitterpacher)	NF, NS		B	I
<i>Amara ovata</i> (Fabricius)	CT, NS, NY, ON, QC, RI		M	F
<i>Ophonus puncticeps</i> Stephens	CT, MA, ME, NH, NS, NY, ON, PE, QC, VT		M	F
<i>Perigona nigriceps</i> (Dejean)	MA, ME, NH, NS, ON, QC, VT		M	F
<i>Dromius fenestratus</i> (Fabricius)	NF, NS		M	F

**Notes:** \*, Holarctic species. M, Macropterous; B, Brachypterous; WD, Wing Dimorphic; F, Frequent; O, Occasional; I, Incapable.

Four of these 27 species (*Harpalus erythropus* Dejean, *Harpalus longicollis* LeConte, *Omophron labiatum* (Fabricius), and *Platynus cincticollis* (Say)) are found on Sable Island, Nova Scotia, a location where it has been proposed that a substantial portion of the native fauna (~ 15%) derives from Pleistocene glacial refugia (see Howden *et al.* (1970, pp. 22–28) and Wright (1989, pp. 82–85) for a discussion of this topic), and indeed three of them (the exception being *H. erythropus*) are restricted in Nova Scotia (and Atlantic Canada) solely to Sable Island. Although other possible mechanisms of dispersal and colonization are not excluded, these 27 species (10.9% of the province's native fauna) are plausible candidates for consideration as having colonized the province via this mechanism.

There are 40 species (13.5% of the native Maritime fauna) that have been recorded in New Brunswick but which have not been found in Nova Scotia (Table 5). Thirty-seven of these are Nearctic and three, *Patrobis foveocollis*, *Harpalus solitaris*, and *Agonum nigriceps* LeConte, are Holarctic species. In terms of their distribution, these species can be placed in the following categories:

1) Those which have a wide distribution in central Canada and northern New England (31 species) but have otherwise not been found elsewhere in Atlantic Canada. These are candidates for species that have, for various climatic or environmental reasons, reached the limit of their distribution in New Brunswick; or which have found the Northumberland Strait and/or the isthmus of Chignecto an obstacle to their geographical dispersal. Some may, of course, occur in Nova Scotia but have remained un-detected there to date.

2) Those with a generally more "boreal" distribution (6 species) which have been found in other parts of Atlantic Canada. These include the three Holarctic species (above) as well as *Bembidion carinula* Chaudoir, *Patrobis lecontei* Chaudoir, and *Agonum superioris* Lindroth. Given their known distribution, they are prime candidates to be sought in Nova Scotia, since on geographical grounds, and in terms of climatic tolerances, one might well expect them to be present.

TABLE 5. Carabidae reported from New Brunswick and not from Nova Scotia.

Native Species	Distribution in		
	Northeastern North American	Wing	Flight
<b>Nebrinae</b>			
<i>Nebria lacustris</i> Casey	CT, MA, ME, NB, NH, NY, ON, QC, VT	M	–
<b>Cicindelinae</b>			
<i>Cicindela marginipennis</i> Dejean	NH, NY, VT	M	F
<i>Cicindela punctulata punctulata</i> Olivier	CT, MA, ME, NB, NH, NY, ON, QC, RI, VT	M	F
<b>Scaritinae</b>			
<i>Schizogenius sulcifrons</i> Putzeys	MA, ME, NB, NH, NY, ON, QC, VT	M	O
<i>Dyschirius larochellei</i> Bousquet		M	–
<i>Dyschirius setosus</i> LeConte		M	O
<b>Trechinae</b>			
<i>Bembidion carinula</i> Chaudoir §	CT, LB, MA, ME, NB, NF, NH, NY, ON, QC, VT	M	F
<i>Bembidion confusum</i> Hayward	CT, MA, ME, NB, NH, NY, ON, QC, VT	M	F
<i>Bembidion postremum</i> Say	MA, ME, NB, NH, NY, QC, VT	M	–
<i>Bembidion iridipenne</i> Bousquet & Webster	NB, NH, QC, VT	M	–
<i>Bembidion variegatum</i> Say	CT, MA, ME, NB, NH, NY, ON, QC, RI, VT	M	O
<i>Bembidion versutum</i> LeConte	CT, MA, ME, NB, NH, NY, ON, QC, VT	M	O
<i>Bembidion oberthueri</i> Hayward	CT, MA, ME, NB, NH, NY, ON, QC, VT	M	F
<i>Bembidion impotens</i> Casey	CT, NB, ON, VT	M	F
<i>Bembidion nigrivestis</i> Bousquet	ME, NB, NH, ON, QC	WD(M)	“C
<i>Bembidion praticola</i> Lindroth	ME, NB, NH, ON, QC	WD(B)	“C
<i>Paratachys scitulus</i> (LeConte)	CT, MA, ME, NB, NH, NY, ON, QC, VT	M	F
<i>Patrobis foveocollis</i> (Eschscholtz) * §	LB, ME, NB, NF, NH, NY, ON, QC, VT	WD(B)	O
<i>Patrobis lecontei</i> Chaudoir §	NB, NF, PM, QC	WD	O
<i>Platypatrobis lacustris</i> Darlington	ME, NB, NH, ON, QC, VT	M	F
<b>Harpalinae</b>			
<i>Myas cyanescens</i> Dejean	CT, MA, ME, NB, NH, NY, ON, QC, VT	B	I
<i>Pterostichus corrusculus</i> LeConte	CT, MA, ME, NB, NH, NY, ON, QC	B	I
<i>Pterostichus femoralis</i> (Kirby)	CT, MA, NB, NH, NY, ON, QC, VT	WD(B)	O
<i>Pterostichus lachrymosus</i> (Newman)	CT, MA, ME, NB, NH, NY, ON, QC, VT	B	I
<i>Pterostichus rostratus</i> (Newman)	CT, MA, ME, NB, NH, NY, ON, QC, VT	B	I
<i>Amara angustata</i> (Say)	CT, MA, NH, NY, ON, QC, VT	M	F
<i>Amara angustatoides</i> Hieke	CT, MA, ME, NB, NH, NY, ON, QC, VT	M	–
<i>Anisodactylus discoideus</i> Dejean	CT, MA, ME, NB, NH, NY, ON, QC, RI, VT	M	F
<i>Bradycellus atrimediis</i> (Say)	ME, NB, NH, NY, ON, QC, RI, VT	M	F
<i>Selenophorus gagatinus</i> Dejean	CT, MA, ME, NB, NH, NY, ON, QC, RI, VT	M	O
<i>Harpalus solitarius</i> Dejean * §	LB, ME, NB, NF, NH, ON, PE, PM, QC	M	O
<i>Chlaenius cordicollis</i> Kirby	CT, MA, ME, NB, NH, NY, ON, QC, VT	M	F
<i>Calathus opaculus</i> LeConte	CT, MA, ME, NB, NH, NY, ON, QC, RI, VT	M	O
<i>Atronus pubescens</i> (Dejean)	CT, MA, ME, NB, NH, NY, ON, QC, VT	M	–
<i>Agonum superioris</i> Lindroth	ME, NB, NH, ON, PE, QC, VT	sM	I

to be continued.

TABLE 5. (continued)

Native Species	Distribution in		
	Northeastern North American	Wing	Flight
<i>Agonum nigriceps</i> LeConte * §	ME, NB, NF, NH, NY, ON, PE, QC	WD	O
<i>Agonum cupreum</i> Dejean §	NB, ON, QC	WD	O
<i>Agonum excavatum</i> Dejean	CT, MA, NB, NH, NY, ON, QC, VT	M	O
<b>Brachininae</b>			
<i>Brachinus cordicollis</i> Dejean	CT, MA, NB, NH, NY, ON, QC, RI, VT	M	O
<i>Brachinus cyanipennis</i> Say	CT, MA, ME, NB, NH, NY, ON, QC, RI, VT	M	O

**Notes:** \*, Holarctic species; §, boreal distribution. M, Macropterous; B, Brachypterous; WD, Wing Dimorphic; WD(M), Wing Dimorphic, primarily Macropterous; WD(B), Wing Dimorphic, primarily Brachypterous; sM, sub-Macropterous; F, Frequent; O, Occasional; I, Incapable.

3) Three other species with varied distributions including *Cicindela marginipennis* which has a relict distribution in eastern North America, *Bembidion impotens* Casey which has a sparse and scattered distribution in the northeast, and *Agonum cupreum* Dejean which has a transcontinental distribution in Canada and the northern USA, but which is absent from New England.

While the native species found in Nova Scotia but not New Brunswick are all macropterous, and the majority (59%) are categorized as frequent flyers (Larochelle & Larivière 2003), a significant number (8 of 40 species) found in New Brunswick but not Nova Scotia are brachypterous, sub-macropterous, or wing-dimorphic (preponderantly brachypterous) species. Five species (13%) are incapable of flight and only 12 species (30%) are categorized as frequent flyers. This would appear to indicate that there has been greater colonization of New Brunswick by Carabidae via terrestrial pathways.

Eighteen species of carabids found in Nova Scotia have been recorded solely from Cape Breton Island and have not been found on the Nova Scotia mainland (Table 6). All but one of these (*Abax parallelepidus* (Piller and Mitterpacher)) are native species. Twelve are Nearctic species and five (*Blethisa multipunctata aurata* Fisher von Waldheim, *Trechus crassiscapus* Lindroth, *Bembidion grapii* Gyllenhal, *Harpalus laevipes* Zetterstedt, and *Sericoda quadripunctata* (DeGeer)) are Holarctic species. Most of the native species are widely distributed in northeastern North America, although two, *Notiophilus semistriatus* Say and *Apristus latens* (LeConte), are known in Atlantic Canada solely from records on Cape Breton.

A noteworthy feature of the Cape Breton carabid fauna is the relatively high proportion of flightless, native species found on the island. Fifteen such brachypterous or sub-macropterous species have been found on the island (Table 7) including *Sphaeroderus canadensis canadensis* Chaudoir, *S. nitidicollis brevoorti* LeConte, *S. stenostomus lecontei* Dejean, *Scaphinotus bilobus* (Say), *Trechus crassiscapus*, *Bembidion semicinctum* Notman, *B. wingatei* Bland, *Pterostichus coracinus* (Newman), *P. punctatissimus* (Randall), *P. adoxus* (Say), *P. tristis* (Dejean), *Amara flebilis* (Casey), *Oxypselaphus pusillus* (LeConte), *Platynus decentis* (Say), and *P. mannerheimii* (Dejean). Being an island, one might expect that the proportion of flightless, native species would be reduced. However, an examination of Table 7 shows that is 8.8%, greater than the 6.5% of such species found in Nova Scotia as a whole, and the 7.1% found in the Maritime Provinces. It would appear that the Strait of Canso, which is only 1.5 km wide, has not proved to be a significant obstacle for colonization by flightless species.

Moreover, four of these species, *S. bilobus*, *T. crassiscapus*, *P. punctatissimus*, and *A. flebilis*, have not been recorded from the Nova Scotia mainland although they are present in New Brunswick. A possible colonization scenario might have been across emergent land in the Gulf of St. Lawrence between 10,000–8,000 years B.P. At that time, deglaciation, changing sea levels, and isostatic rebound contributed to major portions of the Gulf being above sea level for some 2,000 years (Shaw & Gareau 2002). This extensive area of emer-

gent land connected the present-day eastern shore of New Brunswick and the northern shore of Nova Scotia, encompassing all of Prince Edward Island, and extending to the western coast of Cape Breton Island. Conversely, they might be present but undetected on the Nova Scotia mainland.

**TABLE 6.** Nova Scotia Carabidae reported only from Cape Breton Island.

Species	Distribution in Northeastern North American	Wing	Flight
<b>Native Species</b>			
<b>Nebriinae</b>			
<i>Notiophilus semistriatus</i> Say	CT, MA, NH, NS, NY, ON, QC	WD	–
<b>Cicindelinae</b>			
<i>Cicindela limbalis limbalis</i> Klug	CT, MA, ME, NB, NF, NH, NS, NY, ON, QC, RI, VT	M	F
<b>Elaphrinae</b>			
<i>Blethisa julii</i> LeConte	ME, NB, NF, NH, NS, NY, ON, QC, VT	M	–
<i>Blethisa multipunctata aurata</i> von Waldheim *	LB, MA, ME, NB, NF, NH, NS, NY, ON, PE, PM, QC, VT	M	F
<b>Trechinae</b>			
<i>Trechus crassiscapus</i> Lindroth *	LB, MA, ME, NB, NF, NH, NS, NY, ON, QC, VT	B	I
<i>Bembidion planatum</i> (LeConte)	NB, NF, NS, ON, QC	M	F
<i>Bembidion grapii</i> Gyllenhal *	LB, MA, ME, NF, NH, NS, NY, ON, PM, QC, VT	WD	F
<i>Bembidion fortetrium</i> (Motschulsky)	CT, MA, ME, NB, NF, NH, NS, NY, ON, PE, QC, VT	M	O
<b>Harpalinae</b>			
<i>Pterostichus punctatissimus</i> (Randall)	LB, MA, ME, NB, NF, NH, NS, NY, ON, QC, VT	B	I
<i>Amara gibba</i> (LeConte)	NF, NS, NY, ON, QC	M	O
<i>Amara flebilis</i> (Casey)	CT, MA, ME, NB, NH, NS, NY, ON, QC	B	I
<i>Harpalus laevipes</i> Zetterstedt *	LB, ME, NF, NH, NS, NY, ON, PE, QC	M	F
<i>Badister grandiceps</i> Casey	CT, MA, NH, NS, NY, ON, PE, QC, VT	M	F
<i>Calathus gregarius</i> (Say)	CT, MA, ME, NB, NH, NS, NY, ON, PE, QC, RI, VT	WD(B)	O
<i>Sericoda quadripunctata</i> (DeGeer) *	LB, MA, ME, NB, NF, NH, NS, NY, ON, QC, VT	M	F
<i>Cymindis borealis</i> LeConte	CT, ME, NB, NF, NH, NS, NY, ON, QC, VT	WD(B)	O
<i>Apristus latens</i> (LeConte)	MA, NH, NS, ON, QC, VT	M	F
<b>Introduced Species</b>			
<i>Abax parallelepidus</i> (Piller & Mitterpacher)	NF, NS	B	I

**Notes:** \*, Holarctic species; M, Macropterous; B, Brachypterous; WD, Wing Dimorphic; WD(B), Wing Dimorphic, primarily Brachypterous; F, Frequent; O, Occasional; I, Incapable.

A noteworthy feature of the information presented in Table 3 is the relatively similar size of the carabid faunas of Cape Breton Island (with a land area of 10,311 km<sup>2</sup> and 1.5 km from the mainland), Prince Edward Island (with a land area of 5,660 km<sup>2</sup> and 13 km from the mainland), and insular Newfoundland (including Saint-Pierre et Miquelon) (with a land area of 111,390 km<sup>2</sup>, 18 km distant from Labrador and 110 km from Cape Breton Island) despite different land areas and distances to the neighbouring continental mainland. The total number of species is roughly equivalent, as is the number of introduced Palearctic species. Newfound-

land differs from the other two islands in having twice the proportion of Holarctic species, probably reflecting its greater proximity to circumboreal environments and landmasses such as Labrador, Greenland, and Iceland.

**TABLE 7.** Wing State and Flying Frequency of native Atlantic Canada Carabidae.

	PEI	%	NS	%	CB	%	MP	%	NF	%
<b>Wing State</b>	112	77.8%	193	77.8%	123	72.4%	227	76.9%	102	68.9%
Macropterous										
Wing-Dimorphic	9	6.3%	14	5.6%	11	6.5%	18	6.1%	12	8.1%
Wing-Dimorphic (M)	1	0.7%	4	1.6%	3	1.8%	5	1.7%	3	2.0%
Wing-Dimorphic (B)	16	11.1%	19	7.7%	18	10.6%	22	7.5%	19	12.8%
sub-Macropterous	4	2.8%	3	1.2%	2	1.2%	4	1.4%	2	1.4%
Brachypterous	2	1.4%	15	6.0%	13	7.6%	19	6.4%	10	6.8%
Total	144	100.0%	248	100.0%	170	100.0%	295	100.0%	148	100.0%
<b>Frequency of Flight</b>										
Frequent	79	54.9%	137	55.2%	92	54.1%	156	52.9%	70	47.3%
Occasional	52	36.1%	76	30.6%	54	31.8%	91	30.8%	49	33.1%
Incapable	7	4.9%	16	6.5%	15	8.8%	21	7.1%	12	8.1%
Unknown	6	4.2%	19	7.7%	9	5.3%	27	9.2%	17	11.5%
Total	144	100.0%	248	100.0%	170	100.0%	295	100.0%	148	100.0%

**Notes:** PEI, Prince Edward Island; NS, Nova Scotia; CB, Cape Breton; MP, Maritime Provinces; NF, insular Newfoundland. WD(M), Wing Dimorphic, primarily Macropterous; WD(B), Wing Dimorphic, primarily Brachypterous.

**TABLE 8.** Date of first detection of introduced Carabidae in the Maritime Provinces.

Species	NB	NS	PEI	North America	Lindroth <sup>1</sup>	Bionomics <sup>2</sup>
<i>Notiophilus biguttatus</i> (Fabricius)	1978	1976	2002	1923/NF	4	synanthropic
<i>Notiophilus palustris</i> (Duftschmid)		1967	1987	1967/NS	1	synanthropic ?
<i>Carabus granulatus hibernicus</i> Lindroth	1890	1910	1987	1890/NB		synanthropic
<i>Carabus nemoralis</i> Müller	1870	1924	1970	1870/NB		synanthropic
<i>Clivina fossor</i> (Linnaeus)	1926	1922	1953	1915/QC		synanthropic
<i>Broscus cephalotes cephalotes</i> (Linnaeus)		1987	1987	1987/NS & PE	1	coastal
<i>Trechus quadristriatus</i> (Schrank)		2000		1965/ON?	2	synanthropic
<i>Trechus rubens</i> (Fabricius)	1987	<1875	1988	<1875/NS		synanthropic
<i>Blemus discus</i> (Fabricius)	1977	1970	1988	1933/QC		synanthropic
<i>Bembidion properans</i> (Stephens)	1977	1942	1970	1942/NS	3	synanthropic
<i>Bembidion obtusum</i> Audinet-Serville			2004	1956/ON?		synanthropic
<i>Bembidion stephensii</i> Crotch	1987	1980	1988	1891/ON		synanthropic
<i>Bembidion bruxellense</i> Wesmael	1926	1910	1987	1907/NF		synanthropic
<i>Bembidion femoratum</i> Sturm	1988	1967		1967/NS		synanthropic ?
<i>Bembidion tetracolum</i> Say	1902	1951	<1991	1823/?	1	synanthropic

to be continued.

TABLE 8. (continued)

Species	NB	NS	PEI	North America	Lindroth <sup>1</sup>	Bionomics <sup>2</sup>
<i>Porotachys bisulcatus</i> (Nicolai)	1928	1992		<1900/ MA		synanthropic
<i>Stomis pumicatus</i> (Panzer)		1984	<1993	1984/NS	1	synanthropic
<i>Pterostichus melanarius</i> (Illiger)	1947	1926	1981	1926/NS		synanthropic
<i>Abax parallelepidus</i> (Piller & Mitterpacher)		1965		1965/NS	1	forests
<i>Amara aulica</i> (Panzer)	1982	1929	1987	1929/NS	1	synanthropic
<i>Amara apricaria</i> (Paykull)	1928	1899	1970	1875/?		synanthropic
<i>Amara aenea</i> (DeGeer)	1976	1947	1983	1828/?	6	synanthropic
<i>Amara bifrons</i> (Gyllenhal)	1978	1929	1987	1929/NS		synanthropic
<i>Amara communis</i> (Panzer)	1988	1991	2001	1988/NB	1	synanthropic ?
<i>Amara familiaris</i> (Duftschmid)	1929	1945	1957	1915/NY	3	synanthropic
<i>Amara ovata</i> (Fabricius)		1991		1928/ON	3	synanthropic ?
<i>Ophonus puncticeps</i> Stephens		1986	2002	1954/NY	3	synanthropic
<i>Harpalus rufipes</i> (DeGeer)	1939	1938	1937	1937/PE	4	synanthropic
<i>Harpalus affinis</i> (Schrank)	1904	1899	1970	1798/?	5	synanthropic
<i>Harpalus rubripes</i> (Duftschmid)		1997	2004	1981/NH	4	synanthropic
<i>Laemostenus terricola</i> (Herbst)	1900	<1894	unknown	<1894/NS		synanthropic
<i>Paranchus albipes</i> (Fabricius)	1890	1859		<1840/NF		coastal
<i>Agonum muelleri</i> (Herbst)	1975	1890	1920	1840/NF	2	synanthropic
<i>Perigona nigriceps</i> (Dejean)		1989		<1853/?		synanthropic
<i>Dromius fenestratus</i> (Fabricius)		1968		1968/NS		forests
mean date of first detection	1945	1947	1981	1916		

**Notes:** NB, New Brunswick; NS, Nova Scotia; PEI, Prince Edward Island; MA, Massachusetts; NF, Newfoundland; NH, New Hampshire; NY, New York; ON, Ontario; QC, Québec. <sup>1</sup>The number of ballast quarries in southwestern England in which the species was recorded by Lindroth (1957). <sup>2</sup>Bionomic information derived from Larochelle & Larivière (2003).

As is typically the case with islands, the carabid fauna of Cape Breton Island is diminished in comparison with that of the neighbouring mainland. The native fauna is only 58% that of the combined Maritime Provinces fauna. This may represent an island-associated diminution, a paucity of collecting, or a combination of both. Majka & McCorquodale (2006) found that Cape Breton Island had 41% of the Maritime Provinces fauna of native Coccinellidae, and Majka and Jackman (2006) found the same proportion (41%) of native Mordellidae. In examining the saproxylic Tetratomidae, Melandryidae, Synchronidae, and Scaptiidae, Majka & Pollock (2006) found 32% of the native Maritime species on Cape Breton, while Majka (2006) examining another grouping of saproxylic families, the Mycteridae, Boridae, Pythidae, Pyrochroidae, and Salpingidae, found 53% of the Maritime Provinces species on Cape Breton. On that basis, the Carabidae would appear comparatively well represented on Cape Breton, perhaps an indication of a more thorough collecting effort for this group.

Within Atlantic Canada, New Brunswick has the lowest proportion (8.8%) of introduced carabids and the highest proportion (83.5%) of native, Nearctic species (Table 3). These findings may reflect the greater historical importance of seaports such as St. John's, Newfoundland, Charlottetown, Prince Edward Island, and Sydney and Halifax, Nova Scotia in the trans-Atlantic shipping trade that resulted in many dry-ballast

introductions of Coleoptera in those provinces (Brown 1940, 1950; Lindroth 1957). There are 35 species of introduced Carabidae found in the Maritime Provinces. Of these 34 occur in Nova Scotia, 24 in New Brunswick, and 27 on Prince Edward Island (Table 8). Although 40% more introduced species have been found in Nova Scotia than New Brunswick, the mean date of first detection in both provinces is very similar (1947 vs. 1945). Although these dates are both substantially earlier than 1981, the mean date of first detection on Prince Edward Island, this difference is likely indicative of the paucity of early collecting on the island. Twenty-six introduced species have first been found in Nova Scotia, five in New Brunswick, and three on Prince Edward Island.

Of these 35 species, all but four, *Broscus cephalotes cephalotes* (Linnaeus), *Abax parallelepidus*, *Paranichus albipes*, and *Dromius fenestratus* (Fabricius) can be characterized as synanthropic species, and two (*i.e.* *B. c. cephalotes*, and *P. albipes*) are coastal species. Brown (1950) and Lindroth (1957) developed the theory that ships' dry ballast was a probable source of entry of many adventive, ground-dwelling Coleoptera. Brown (1950) noted that large quantities of dry ballast were unloaded at Atlantic ports during the Napoleonic Wars (1799–1815) by British vessels in search of timber when Baltic ports were closed to Britain. Of the 35 introduced species found in the Maritimes, 18 (51%) were found by Lindroth (1957) in quarries in south–western England where dry-ballast destined for Atlantic Canada originated (Table 8), a suggestive indication that many may have been introduced to the region via this mechanism. Indeed, except for *Carabus granulatus hibernicus* and *Dromius fenestratus*, all other introduced carabids (94%) present in the region are found in England.

Although the Maritime Provinces have not been surveyed as thoroughly as Newfoundland was by Lindroth (1955), and additional species remain to be discovered and reported, it is apparent that a substantial baseline of information on the region's ground-beetle fauna has been established. In recent years considerable attention has been focused on the potential utility of ground beetles as bioindicators of environmental change. Frequently the numbers of large, poorly dispersing carabid species decrease with increasing disturbance, whereas small generalist species with good dispersal ability increase (Rainio & Niemelä 2003). In a survey of many ecological studies, Rainio & Niemelä (2003) concluded that carabids are useful bioindicators. Given the long history and large range of disturbances to which the environment of the Maritime Provinces has been subjected, it would be worthwhile to continue developing our knowledge of this diverse group of beetles and to monitor their populations.

## Acknowledgments

Thanks are extended to S. Lemoine and S. Bondrup-Nielsen (Acadia University), C. Noronha, M.E. Smith, and C. Sheffield (Agriculture and Agri-food Canada), K. Aikens, C. D'Orsay, and D.B. McCorquodale (Cape Breton University), J. Cook (Carleton University), P. Dollin, R. Ewing, H. Love, T. Rossolimo, and S. Walde (Dalhousie University), D. Sabine (New Brunswick Department of Natural Resources), D.F. McAlpine (New Brunswick Museum), D.J. Bishop (North Mt. Old Forest Society), J.P. Le Blanc (Nova Scotia Agricultural College), J. Ogden (Nova Scotia Department of Natural Resources), C. Cormier (Saint Mary's University), R. Lauff (St. Francis Xavier University), P. Duerr (Université de Moncton), D. Giberson (University of Prince Edward Island), J. Edsall, K. Neil, G. Selig, and D.H. Webster for making specimens, records, and information available. We also thank G. Ball (University of Alberta, Edmonton) and F. Hieke (Museum für Naturkunde, Berlin, Germany) for their assistance. Many thanks to Robert Davidson (Carnegie Museum of Natural History) who read an earlier version of the manuscript and made many constructive suggestions, and to Ignacio Ribera (Museo Nacional de Ciencias Naturales, Madrid, Spain) for his editorial assistance. The senior author thanks D. Christianson, C. Ewing, and A. Hebda (Nova Scotia Museum) for continuing support and encouragement. This work has been assisted by the Board of Governors of the Nova Scotia Museum.

TABLE 9. Checklist of Maritime Provinces Carabidae.

Species	NS	NB	PEI
<b>Omophroninae</b>			
Omophronini			
<i>Omophron americanum</i> Dejean	1	1	1
<i>Omophron labiatum</i> (Fabricius)	1		
<i>Omophron tessellatum</i> Say	1	1	1
<b>Nebrinae</b>			
Nebrini			
<i>Nebria lacustris</i> Casey		1	
<i>Nebria pallipes</i> Say	1	1	1
Notiophilini			
<i>Notiophilus aeneus</i> (Herbst)	1	1	1
<i>Notiophilus aquaticus</i> (Linnaeus) *	1	1	
<i>Notiophilus biguttatus</i> (Fabricius) †	1	1	1
<i>Notiophilus novemstriatus</i> LeConte	1		
<i>Notiophilus palustris</i> (Duftschmid) †	1		1
<i>Notiophilus semistriatus</i> Say	1	1	
<b>Carabinae</b>			
Carabini			
<i>Calosoma frigidum</i> Kirby	1	1	1
<i>Calosoma scrutator</i> (Fabricius)	1		
<i>Calosoma calidum</i> (Fabricius)	1	1	
<i>Carabus granulatus hibernicus</i> Lindroth †	1	1	1
<i>Carabus nemoralis</i> Müller †	1	1	1
<i>Carabus serratus</i> Say	1	1	1
<i>Carabus maeander</i> Fischer von Waldheim *	1	1	1
Cychrini			
<i>Sphaeroderus canadensis canadensis</i> Chaudoir	1	1	
<i>Sphaeroderus nitidicollis brevoorti</i> LeConte	1	1	
<i>Sphaeroderus stenostomus lecontei</i> Dejean	1	1	1
<i>Scaphinotus viduus</i> (Dejean)	1	1	
<i>Scaphinotus bilobus</i> (Say)	1	1	
<b>Cicindelinae</b>			
Cicindelini			
<i>Cicindela duodecimguttata</i> Dejean	1	1	1
<i>Cicindela formosa generosa</i> Dejean	1		
<i>Cicindela hirticollis rhodensis</i> Calder	1	1	1

to be continued.



TABLE 9. (continued)

Species	NS	NB	PEI
<i>Cicindela limbalis limbalis</i> Klug	1	1	
<i>Cicindela longilabris longilabris</i> Say	1	1	1
<i>Cicindela repanda repanda</i> Dejean	1	1	1
<i>Cicindela sexguttata sexguttata</i> Fabricius	1	1	
<i>Cicindela tranquebarica tranquebarica</i> Herbst	1	1	1
<i>Cicindela marginipennis</i> Dejean		1	
<i>Cicindela punctulata punctulata</i> Olivier		1	
<i>Cicindela marginata</i> Fabricius	1		
<b>Loricerinae</b>			
Loricerini			
<i>Loricera pilicornis pilicornis</i> (Fabricius) *	1	1	1
<b>Elaphrinae</b>			
Elaphrini			
<i>Blethisa julii</i> LeConte	1	1	
<i>Blethisa multipunctata aurata</i> Fisher von Waldheim *	1	1	1
<i>Blethisa quadricollis</i> Haldeman	1	1	1
<i>Elaphrus clairvillei</i> Kirby	1	1	1
<i>Elaphrus olivaceus</i> LeConte	1	1	1
<i>Elaphrus americanus americanus</i> Dejean	1	1	1
<i>Elaphrus californicus</i> Mannerheim	1	1	1
<b>Scaritinae</b>			
Clivinini			
<i>Schizogenius sulcifrons</i> Putzeys		1	
<i>Clivina fossor</i> (Linnaeus) †	1	1	1
<i>Clivina americana</i> Dejean	1	1	
<i>Dyschirius larochei</i> Bousquet		1	
<i>Dyschirius sphaericollis</i> (Say)	1	1	1
<i>Dyschirius sellatus</i> LeConte	1	1	1
<i>Dyschirius setosus</i> LeConte		1	1
<i>Dyschirius globulosus</i> (Say)	1	1	1
<i>Dyschirius integer</i> LeConte	1	1	1
<b>Trechinae</b>			
Broscini			
<i>Broscus cephalotes cephalotes</i> (Linnaeus) †	1		1
<i>Miscodera arctica</i> (Paykull) *	1	1	

to be continued.

TABLE 9. (continued)

Species	NS	NB	PEI
Trechini			
<i>Trechus apicalis</i> Motschulsky *	1	1	
<i>Trechus crassiscapus</i> Lindroth *	1	1	
<i>Trechus quadristriatus</i> (Schrank) †	1		
<i>Trechus rubens</i> (Fabricius) †	1	1	1
<i>Blemus discus</i> (Fabricius) †	1	1	1
Bembidiini			
<i>Bembidion inaequale inaequale</i> Say	1	1	1
<i>Bembidion levettei</i> Casey	1	1	
<i>Bembidion punctatostriatum</i> Say	1	1	
<i>Bembidion antiquum</i> Dejean	1		
<i>Bembidion carinula</i> Chaudoir		1	
<i>Bembidion confusum</i> Hayward		1	
<i>Bembidion chalceum</i> Dejean	1	1	
<i>Bembidion honestum</i> Say	1	1	
<i>Bembidion</i> species 1 undescribed <sup>1</sup>	1		
<i>Bembidion</i> species 2 undescribed <sup>1</sup>	1		
<i>Bembidion cheyennense</i> Casey	1		
<i>Bembidion nitidum</i> (Kirby)			1
<i>Bembidion properans</i> (Stephens) †	1	1	1
<i>Bembidion obtusum</i> Audinet-Serville †			1
<i>Bembidion occultator</i> Notman	1	1	
<i>Bembidion carolinense</i> Casey	1	1	
<i>Bembidion planatum</i> (LeConte)	1	1	
<i>Bembidion rusticum rusticum</i> Casey	1	1	
<i>Bembidion sulcipenne prasinoides</i> Lindroth	1	1	
<i>Bembidion planum</i> (Haldeman)	1	1	
<i>Bembidion rolandi</i> Fall	1	1	
<i>Bembidion concolor</i> (Kirby)	1	1	
<i>Bembidion nigrum</i> Say	1	1	1
<i>Bembidion salebratum</i> (LeConte)	1	1	
<i>Bembidion quadratum</i> Notman	1	1	
<i>Bembidion semistriatum</i> (Haldeman)	1		
<i>Bembidion grapii</i> Gyllenhal *	1	1	
<i>Bembidion postremum</i> Say		1	
<i>Bembidion stephensii</i> Crotch †	1	1	1
<i>Bembidion bruxellense</i> Wesmael †	1	1	1
<i>Bembidion femoratum</i> Sturm †	1	1	
<i>Bembidion obscurellum</i> (Motschulsky) *	1	1	1
<i>Bembidion petrosum petrosum</i> Gebler *	1	1	1
<i>Bembidion sejunctum sejunctum</i> Casey	1	1	1

to be continued.

TABLE 9. (continued)

Species	NS	NB	PEI
<i>Bembidion tetracolum</i> Say †	1	1	1
<i>Bembidion transversale</i> Dejean	1	1	
<i>Bembidion scopulinum</i> (Kirby) *	1	1	1
<i>Bembidion graciliforme</i> Hayward	1	1	
<i>Bembidion immaturum</i> Lindroth	1	1	
<i>Bembidion incrematum</i> LeConte	1	1	1
<i>Bembidion iridipenne</i> Bousquet & Webster		1	
<i>Bembidion castor</i> Lindroth	1	1	
<i>Bembidion nigripes</i> (Kirby) *	1	1	1
<i>Bembidion patruelle</i> Dejean	1	1	1
<i>Bembidion rapidum</i> (LeConte)	1	1	
<i>Bembidion variegatum</i> Say		1	
<i>Bembidion versutum</i> LeConte		1	
<i>Bembidion constrictum</i> (LeConte)	1	1	1
<i>Bembidion contractum</i> Say	1	1	1
<i>Bembidion oberthueri</i> Hayward		1	
<i>Bembidion impotens</i> Casey		1	
<i>Bembidion minus</i> Hayward	1	1	1
<i>Bembidion versicolor</i> (LeConte)	1	1	1
<i>Bembidion mutatum</i> Gemminger & Harold	1		
<i>Bembidion quadrimaculatum oppositum</i> Say	1	1	1
<i>Bembidion nigrivestis</i> Bousquet		1	
<i>Bembidion muscicola</i> Hayward	1	1	1
<i>Bembidion praticola</i> Lindroth		1	
<i>Bembidion semicinctum</i> Notman	1	1	
<i>Bembidion transparens</i> (Gebler) *	1	1	1
<i>Bembidion concretum</i> Casey	1	1	1
<i>Bembidion fortestriatum</i> (Motschulsky)	1	1	1
<i>Bembidion frontale</i> (LeConte)	1	1	1
<i>Bembidion wingatei</i> Bland	1	1	
<i>Mioptachys flavicauda</i> (Say)	1	1	
<i>Tachyta angulata</i> Casey	1	1	
<i>Elaphropus anceps</i> (LeConte)	1	1	
<i>Elaphropus granarius</i> (Dejean)	1	1	
<i>Elaphropus incurvus</i> (Say)	1	1	1
<i>Elaphropus saturatus</i> (Casey)	1	1	
<i>Elaphropus tripunctatus</i> (Say)	1	1	
<i>Elaphropus vernicatus</i> (Casey)	1	1	
<i>Elaphropus xanthopus</i> (Dejean)	1		
<i>Porotachys bisulcatus</i> (Nicolai) †	1	1	
<i>Polyderis laevis</i> (Say)	1		

to be continued.

TABLE 9. (continued)

Species	NS	NB	PEI
<i>Paratachys scitulus</i> (LeConte)		1	
<b>Patrobini</b>			
<i>Patrobus longicornis</i> (Say)	1	1	1
<i>Patrobus foveocollis</i> (Eschscholtz) *		1	
<i>Patrobus lecontei</i> Chaudoir		1	
<i>Platypatrobus lacustris</i> Darlington		1	
<i>Diplous rugicollis</i> (Randall)	1	1	
<b>Harpalinae</b>			
<b>Pterostichini</b>			
<i>Poecilus chalcites</i> (Say)		1	
<i>Poecilus lucublandus lucublandus</i> (Say)	1	1	1
<i>Gastrellarius honestus</i> (Say)	1	1	
<i>Stomis pumicatus</i> (Panzer) †	1		1
<i>Myas cyanescens</i> Dejean		1	
<i>Pterostichus commutabilis</i> (Motshulsky)	1	1	1
<i>Pterostichus corrusculus</i> LeConte		1	
<i>Pterostichus femoralis</i> (Kirby)		1	
<i>Pterostichus patruelis</i> (Dejean)	1	1	1
<i>Pterostichus adstrictus</i> Eschscholtz *	1	1	1
<i>Pterostichus mutus</i> (Say)	1	1	1
<i>Pterostichus pensylvanicus</i> LeConte	1	1	1
<i>Pterostichus corvinus</i> (Dejean)	1	1	1
<i>Pterostichus luctuosus</i> (Dejean)	1	1	1
<i>Pterostichus tenuis</i> (Casey)	1	1	1
<i>Pterostichus coracinus</i> (Newman)	1	1	1
<i>Pterostichus lachrymosus</i> (Newman)		1	
<i>Pterostichus melanarius</i> (Illiger) †	1	1	1
<i>Pterostichus punctatissimus</i> (Randall)	1	1	
<i>Pterostichus rostratus</i> (Newman)		1	
<i>Pterostichus adoxus</i> (Say)	1	1	
<i>Pterostichus tristis</i> (Dejean)	1	1	1
<i>Abax parallelepidus</i> (Piller & Mitterpacher) †	1		
<b>Zabrini</b>			
<i>Amara aulica</i> (Panzer) †	1	1	1
<i>Amara pennsylvanica</i> Hayward	1		
<i>Amara torrida</i> (Panzer) *	1	1	1
<i>Amara apricaria</i> (Paykull) †	1	1	1
<i>Amara avida</i> (Say)	1	1	1

to be continued.

TABLE 9. (continued)

Species	NS	NB	PEI
<i>Amara fulva</i> (Müller)	1	1	1
<i>Amara latior</i> (Kirby)	1	1	1
<i>Amara obesa</i> (Say)	1	1	1
<i>Amara aenea</i> (DeGeer) †	1	1	1
<i>Amara aeneopolita</i> Casey		1	
<i>Amara bifrons</i> (Gyllenhal) †	1	1	1
<i>Amara communis</i> (Panzer) †	1	1	1
<i>Amara convexa</i> LeConte	1		
<i>Amara cupreolata</i> Putzeys	1	1	1
<i>Amara familiaris</i> (Duftschmid) †	1	1	1
<i>Amara gibba</i> (LeConte)	1		
<i>Amara laevipennis</i> Kirby	1	1	1
<i>Amara littoralis</i> Mannerheim	1	1	1
<i>Amara lunicollis</i> Schi?de *	1	1	1
<i>Amara musculus</i> (Say)	1		
<i>Amara neoscotica</i> Casey	1	1	
<i>Amara otiosa</i> Casey	1	1	1
<i>Amara ovata</i> (Fabricius) †	1		
<i>Amara patruelis</i> Dejean *	1	1	1
<i>Amara quenseli</i> (Sch?nherr) *	1	1	1
<i>Amara rubrica</i> Haldeman	1		
<i>Amara sinuosa</i> (Casey)		1	1
<i>Amara angustata</i> (Say)		1	1
<i>Amara angustatoides</i> Hieke		1	
<i>Amara flebilis</i> (Casey)	1	1	
<i>Amara pallipes</i> Kirby	1	1	
<i>Pseudamara arenaria</i> (LeConte)	1	1	1
Harpalini			
<i>Notiobia terminata</i> (Say)	1	1	1
<i>Xestonotus lugubris</i> (Dejean)	1	1	1
<i>Anisodactylus discoideus</i> Dejean		1	
<i>Anisodactylus harrisii</i> LeConte	1		
<i>Anisodactylus kirbyi</i> Lindroth	1	1	1
<i>Anisodactylus nigerrimus</i> (Dejean)	1	1	
<i>Anisodactylus nigrata</i> Dejean	1	1	1
<i>Anisodactylus rusticus</i> (Say)	1	1	1
<i>Anisodactylus sanctaecrucis</i> (Fabricius)	1	1	1
<i>Stenolophus carbo</i> Bousquet	1		
<i>Stenolophus fuliginosus</i> Dejean	1	1	1
<i>Stenolophus humidus</i> Hamilton	1		

to be continued.

TABLE 9. (continued)

Species	NS	NB	PEI
<i>Stenolophus ochropezus</i> (Say)	1	1	
<i>Stenolophus comma</i> (Fabricius)	1	1	1
<i>Stenolophus lineola</i> (Fabricius)			1
<i>Stenolophus conjunctus</i> (Say)	1	1	1
<i>Bradycellus lecontei</i> Csiki	1	1	1
<i>Bradycellus congener</i> (LeConte)	1		
<i>Bradycellus neglectus</i> (LeConte)	1	1	1
<i>Bradycellus nigriceps</i> LeConte		1	
<i>Bradycellus rupestris</i> (Say)	1	1	
<i>Bradycellus nigrinus</i> (Dejean)	1	1	1
<i>Bradycellus semipubescens</i> Lindroth	1	1	
<i>Bradycellus atrimediis</i> (Say)		1	
<i>Bradycellus lugubris</i> (LeConte)	1	1	1
<i>Dicheirotichus cognatus</i> (Gyllenhal) *	1	1	1
<i>Acupalpus canadensis</i> Casey	1	1	1
<i>Acupalpus carus</i> (LeConte)	1	1	1
<i>Acupalpus nanellus</i> Casey	1	1	
<i>Acupalpus pumilus</i> Lindroth	1		1
<i>Acupalpus pauperculus</i> Dejean	1	1	1
<i>Selenophorus gagatinus</i> Dejean		1	
<i>Ophonus puncticeps</i> Stephens †	1		1
<i>Harpalus compar</i> LeConte	1		
<i>Harpalus erythropus</i> Dejean	1		
<i>Harpalus longicollis</i> LeConte	1		
<i>Harpalus pensylvanicus</i> (DeGeer)	1	1	1
<i>Harpalus rufipes</i> (DeGeer) †	1	1	1
<i>Harpalus affinis</i> (Schrank) †	1	1	1
<i>Harpalus rubripes</i> (Duftschmid) †	1	1	1
<i>Harpalus fulvilabris</i> Mannerheim	1	1	1
<i>Harpalus indigenus</i> Casey	1	1	
<i>Harpalus laevipes</i> Zetterstedt *	1		1
<i>Harpalus laticeps</i> LeConte	1	1	
<i>Harpalus lewisii</i> LeConte	1	1	
<i>Harpalus nigratarsis</i> Sahlberg	1	1	
<i>Harpalus caliginosus</i> (Fabricius)	1		
<i>Harpalus plenalis</i> Casey	1	1	1
<i>Harpalus herbivagus</i> Say	1	1	1
<i>Harpalus solitarius</i> Dejean *		1	1
<i>Harpalus somnulentus</i> Dejean	1	1	1
<i>Harpalus fuscipalpis</i> Sturm *	1		

to be continued.

TABLE 9. (continued)

Species	NS	NB	PEI
Licinini			
<i>Diplocheila striatopunctata</i> (LeConte)	1	1	
<i>Diplocheila obtusa</i> (LeConte)	1	1	1
<i>Badister neopulchellus</i> Lindroth	1		1
<i>Badister obtusus</i> LeConte	1		
<i>Badister grandiceps</i> Casey	1		1
<i>Badister ocularis</i> Casey	1	1	1
Chlaeniini			
<i>Chlaenius emarginatus</i> Say	1	1	
<i>Chlaenius cordicollis</i> Kirby		1	
<i>Chlaenius sericeus sericeus</i> (Forster)	1	1	1
<i>Chlaenius pennsylvanicus pennsylvanicus</i> Say	1	1	1
<i>Chlaenius tricolor</i> Dejean	1		
<i>Chlaenius lithophilus lithophilus</i> Say	1	1	1
<i>Chlaenius alternatus</i> Horn	1	1	
<i>Chlaenius niger</i> Randall	1	1	1
Oodini			
<i>Lachnocrepis parallela</i> (Say)	1		
Platnyini			
<i>Calathus gregarius</i> (Say)	1	1	1
<i>Calathus ingratus</i> Dejean	1	1	1
<i>Calathus opaculus</i> LeConte		1	
<i>Laemostenus terricola</i> (Herbst) †	1	1	1
<i>Synuchus impunctatus</i> (Say)	1	1	1
<i>Olisthopus parmatus</i> (Say)	1		
<i>Sericoda obsoleta</i> (Say)	1	1	
<i>Sericoda quadripunctata</i> (DeGeer) *	1	1	
<i>Atranus pubescens</i> (Dejean)		1	
<i>Paranchus albipes</i> (Fabricius) †	1	1	
<i>Oxypselaphus pusillus</i> (LeConte)	1		1
<i>Agonum anchomenoides</i> Randall	1	1	1
<i>Agonum canadense</i> Goulet	1	1	1
<i>Agonum consimile</i> (Gyllenhal) *	1	1	
<i>Agonum darlingtoni</i> Lindroth	1	1	
<i>Agonum gratiosum</i> (Mannerheim)	1	1	1
<i>Agonum lutulentum</i> (LeConte)	1	1	1
<i>Agonum picicornoides</i> Lindroth	1	1	1
<i>Agonum retractum</i> LeConte	1	1	1

to be continued.

TABLE 9. (continued)

Species	NS	NB	PEI
<i>Agonum sordens</i> Kirby	1	1	1
<i>Agonum superioris</i> Lindroth		1	1
<i>Agonum thoreyi</i> Dejean *	1	1	1
<i>Agonum nigriceps</i> LeConte *		1	1
<i>Agonum affine</i> Kirby	1	1	1
<i>Agonum cupreum</i> Dejean		1	
<i>Agonum cupripenne</i> (Say)	1	1	1
<i>Agonum deceptivum</i> (LeConte)	1		
<i>Agonum excavatum</i> Dejean		1	
<i>Agonum fidele</i> Casey	1	1	1
<i>Agonum harrisii</i> LeConte	1	1	1
<i>Agonum melanarium</i> Dejean	1	1	1
<i>Agonum metallescens</i> (LeConte)	1	1	1
<i>Agonum muelleri</i> (Herbst)	1	1	1
<i>Agonum octopunctatum</i> (Fabricius)	1	1	1
<i>Agonum placidum</i> (Say)	1	1	1
<i>Agonum propinquum</i> (Gemminger & Harold)	1	1	1
<i>Agonum tenue</i> (LeConte)	1	1	1
<i>Agonum trigeminum</i> Lindroth	1	1	1
<i>Agonum mutatum</i> (Gemminger & Harold)	1	1	1
<i>Agonum aeruginosum</i> Dejean	1	1	
<i>Agonum crenistriatum</i> (LeConte) †	1	1	1
<i>Agonum extensicolle</i> (Say)	1	1	
<i>Platynus cincticollis</i> (Say)	1		
<i>Platynus decentis</i> (Say)	1	1	1
<i>Platynus indecentis</i> Liebherr & Will	1		
<i>Platynus opaculus</i> LeConte		1	
<i>Platynus tenuicollis</i> (LeConte)	1	1	1
<i>Platynus mannerheimii</i> (Dejean) *	1	1	1
Perigonini			
<i>Perigona nigriceps</i> (Dejean) §	1		
Lebiini			
<i>Cymindis borealis</i> LeConte	1	1	
<i>Cymindis cribricollis</i> Dejean	1	1	1
<i>Cymindis neglectus</i> Haldeman	1	1	
<i>Cymindis limbatus</i> Dejean	1		
<i>Apristus latens</i> (LeConte)	1		
<i>Apristus subsulcatus</i> (Dejean)	1	1	
<i>Syntomus americanus</i> (Dejean)	1	1	1

to be continued.



TABLE 9. (continued)

Species	NS	NB	PEI
<i>Dromius piceus</i> Dejean	1	1	1
<i>Dromius fenestratus</i> (Fabricius) †	1		
<i>Microlestes linearis</i> (LeConte)	1		
<i>Lebia tricolor</i> Say	1		
<i>Lebia fuscata</i> Dejean	1	1	1
<i>Lebia moesta</i> LeConte	1	1	1
<i>Lebia ornata</i> Say	1	1	
<i>Lebia pumila</i> Dejean	1	1	1
<i>Lebia solea</i> Hentz	1		
<i>Lebia viridis</i> Say	1	1	1
<i>Lebia vittata</i> (Fabricius)	1		
<b>Brachininae</b>			
<b>Brachinini</b>			
<i>Brachinus cordicollis</i> Dejean		1	
<i>Brachinus cyanipennis</i> Say		1	
Total	282	273	171

**Notes:** NS, Nova Scotia; NB, New Brunswick; PEI, Prince Edward Island. \*, Holarctic species; † Palearctic species; § Oriental species. <sup>1</sup> being described by David Maddisou.

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