# Îles-de-la-Madeleine (Magdalen Is.): a glacial refugium for short-horned bugs (*Homoptera: Auchenorrhyncha*)?

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***Isolé dans le golfe Saint-Laurent, l'archipel des îles de la Madeleine présente, par ses aspects géologique et biologique, un intérêt particulier. L'étude des dernières glaciations, de sa flore et de sa faune indique que l'archipel aurait été la seule partie du territoire qui n'aurait pas été recouverte par les glaces dans le sud-est du Canada. Quelques espèces de plantes et d'insectes se trouvent uniquement sur ces îles. L'étude des 42 espèces de Cicadelles (Homoptera : Auchenorrhyncha), insectes piqueurs phytophages, capturées aux Îles-de-la-Madeleine, montre que la faune de l'archipel est caractéristique et se distingue des régions avoisinantes. Sept espèces sont d'origine européenne, tandis que les 35 autres sont nord-américaines, dont 22 espèces sont largement réparties sur le continent, 12 sont endémiques aux îles et huit sont trouvées seulement à l'île du Havre-Aubert. Cette étude démontre que l'archipel aurait été un refuge pour plusieurs espèces au cours des dernières glaciations et que sa faune renfermerait plusieurs formes de cicadelles trouvées uniquement sur les iles. L'île de l'âge glaciaire, beaucoup plus grande que l'actuel archipel, aurait été suffisamment grande pour maintenir une forêt boréale d'arbres décidus offrant une niche favorable à cette partie de la faune.***

## Introduction

The most isolated part of Québec is Îles-de-la-Madeleine (or Magdalen Islands), an archipelago of small islands (figure 1), isolated rocks and shoals that lies 90 km north of Prince Edward Island and 150 km south of Île Anticosti in the Gulf of St. Lawrence. Despite their tiny size and remote location they are of particular geological and biological interest. They may have been the only unglaciated land in southeastern Canada. On these islands live one species of plant, *Bidens heterodoxa* Fernald, and one grasshopper, *Melanoplus madeleineae* V. & K., found nowhere else on earth (Alexandre, 1935; Vickery and Kevan, 1985). Also, the endemic Gulf of St. Lawrence aster, *Aster laurentianus* Fernald, is probably native to these islands (Houle and Haber, 1990). Its seeds may have been spread both by wind and water to adjacent coasts of New Brunswick and Prince Edward Island (figure 2, NB, PEI). It is the purpose of this paper to consider the geological and biological evidence for or against the theory of a glacial-age refugium on the Îles-de-la-Madeleine. If this theory is confirmed, finding evidence for the kind of glacial-age ecosystem that evolved on the islands is a supplementary objective.

### *Geography*

Îles-de-la-Madeleine comprise some 25 shoals, rocky islets, and heavily eroded islands. Seven of the ten largest of these islands, each 1-8 km wide, are connected by extensive sand bars (tombolos, figure 3) into a C-shaped chain 65 km in length (figure 4) from the southernmost island, Île du Havre-Aubert (Amherst Is.), to the northernmost, Île de l'Est (East Cape, often included in Grosse-Île), with the chain terminating at Île de la Grande Entrée (Coffin Is.) and tiny Île Boudreau, which together lie just south of Île de l'Est. An eighth island (Île d'Entrée) lies just off a major sand spit to the southeast. The ninth (Île Brion) is an isolated islet 2 km wide that lies 15 km to the north of Île de l'Est. The tenth, Le Corps Mort (Dead Man's Is.) is found 15 km to the west of the southernmost island. Shoals and rocky islets are mostly on the east and northeastern side of the archipelago where erosion has been most severe.

### *Erosion*

The soft, red sandstone which composes most of the bulk of Îles-de-la-Madeleine is readily eroded (figure 5). Steep sea cliffs are found along all coasts and also behind

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K. G. ANDREW HAMILTON

**Figure 1. Île du Havre-aux-Maisons with Île d'Entrée on the horizon, showing the almost treeless condition of much of the islands at present.**

sand dunes; and inland, differential erosion has left harder sedimentary rocks and volcanic intrusions forming prominent hills (buttes) which reach as much as 170 m. Sandstone uplands are not flattened by glaciation but are shaped by precipitation and freeze-thaw cycles into dome-shaped or conical mounds (demoiselles). Some of these mounds are cut almost to the centre by sea cliffs (e.g., Big Hill on Île d'Entrée and East Cape on Île de l'Est), eloquent testimony to the erosive power of waves. The largest cliffs are east-facing (figure 6) although 35 times as many storms come from the north as from the east. It is, however, the storms from the southeast that are by far the most powerful. These affect the bottom to a depth exceeding 11 m off Île d'Entrée and as deep as 7 m in the comparatively sheltered Baie de Plaisance, compared to less than 4.5 m for northerly storms (CSSA Consultants, 1986).

Sand and gravel from these cliffs has been swept by wave action mostly in a northeasterly direction, forming sand bars and multiple dunes such as "Les Sillons" to the north of Île du Havre-aux-Maisons (Alright Island), and most of Île de l'Est. Such redeposition is probably effected mostly by storms as there is little tidal action around the islands. Due to the shape of the Gulf of St. Lawrence, the twice-daily (lunar) tides propagate around the Gulf in a counter-clockwise direction with their axis just off the NW coast of the Madeleines. The tides are therefore highest at the entrance to the Gulf off Cape Breton Island (CBI), off northern Newfoundland (NFLD), and along the Québec mainland shore, but zero at the axis. A much weaker daily (lunisolar) tidal component has its axis SE of Nova Scotia

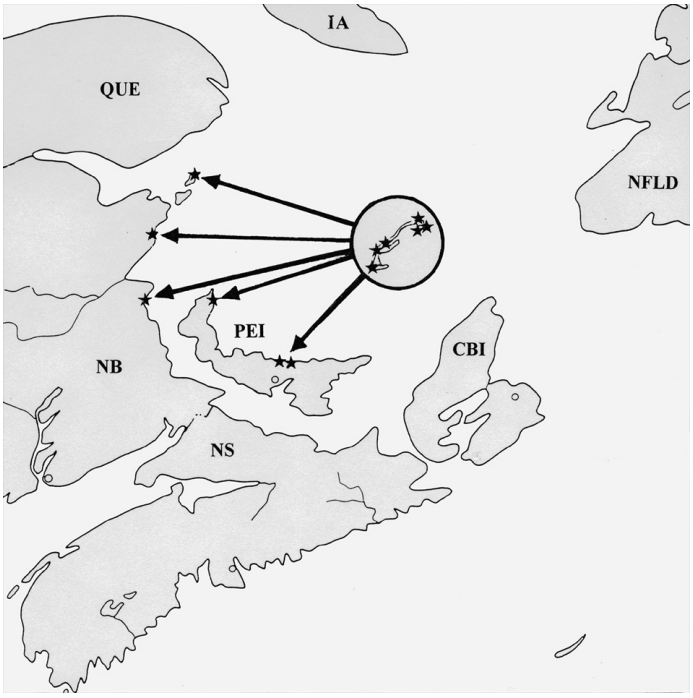


**Figure 2. Dispersal of the endemic Gulf of St. Lawrence aster, *Aster laurentianus* (stars) from its Pleistocene refugium on the ice-free Îles-de-la-Madeleine (circled) to adjacent deglaciated coasts of New Brunswick (NB) and Prince Edward Island (PEI). The aster is not found on adjacent Cape Breton Island (CBI), mainland Nova Scotia (NS), Newfoundland (NFLD), Île Antocosti (IA) or the Gaspé Peninsula of Québec (QUE).**

K. G. ANDREW HAMILTON

**Figure 3. An extensive sandbar connecting Île du Havre-Aubert to Île du Cap-aux-Meules.**

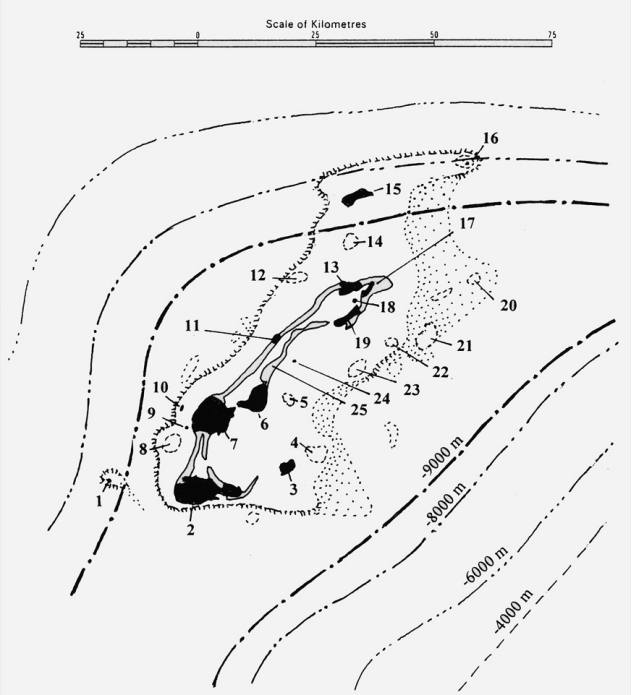


**Figure 4. Îles-de-la-Madeleine (black), tombolos (solid lines) and reefs (doted lines) in relation to basal syncline (dashed lines) and submarine platform: submerged cliffs, 12-14 fathoms (22-25.6 m below sea level) indicated by hatch lines; gradual slopes in this depth range stippled. 1, Le Corps Mort; 2, Île du Havre-Aubert; 3, Île d'Entrée; 4, Pearl Reef; 5, Alright Reef; 6, Île du Havre-aux-Maisons; 7, Île du Cap-aux-Meules; 8, White Horse Reef; 9, Île aux Goélands; 10, Pierre de Gros Cap; 11, Île aux Loups; 12, Glawson Patch [reef]; 13, Grosse-Île; 14, [unnamed] shoals; 15, Île Brion; 16, Rochers-aux- Oiseaux; 17, Île de l'Est; 18, Île aux Loups marins; 19, Île de la Grande Entrée; 20, Doyle Reef; 21, Clark Shoal; 22, Les Colombines [shoal]; 23, Goodwin Shoal; 24, Île Shag; 25, Les Sillons [dunes]. Redrawn from Howie and Barss (1975).**

(NS), and this gives 12 cm of tides to the islands (Farquharson, 1962) for a total tide averaging only 58 cm (Pereira, 1992).

Underwater sediments around the archipelago are sorted by bottom currents (Loring and Nota, 1973). Fine sand is deposited on the southeast side, leaving only gravel caps to north and south (figure 7). This redeposited sand conceals bottom features such as submerged sea cliffs and leaves the southeast side of the archipelago vulnerable to wave action during storms. Erosion during storms probably resulted in the deep embayment of Baie de Plaisance on this side of the archipelago, the very high cliffs of Île du Havre-aux-Maisons and Île d'Entrée along this coast, plus the many reefs marking the location of foundered islets.

### *Glacial history*

The archipelago lies on the underwater Magdalen shelf which is defined by three broad submarine troughs with depths exceeding 200 m. These emanate from the St. Lawrence River and both ends of Northumberland Strait (which lies between PEI and NS). The Laurentian Channel (500 m below sea level only 60 km due east of Rochers-aux-Oiseaux) extends from the St. Lawrence River and passes just north of Île Brion. The much smaller Cape Breton Trough lies well to the southeast along the edge of CBI and the Shediac Trough runs northwest paralleling the coast of NB to converge with a trough emanating from the Baie des Chaleurs. Such submarine troughs are formed by glacial erosion of the continental shelf. This particular pattern suggests a pre-existing (Pliocene) river drainage basin of emergent land (Nota and Loring, 1964). Flooding of the Gulf by seawater may have been the outcome of hundreds of millennia of ice burden, resulting in a continuously sinking sea plain.

During the height of the Pleistocene glaciation (Illinoian age, which ended about 124 000 years ago), continental glaciers covered the islands and probably extended as far as the continental shelf. During the Sangamon interglacial period (ending about 80 000 years ago) temperatures were warmer than today: fossil peat from Île du Havre-Aubert, dated younger than 97 000 years, contains pollen of temperate-zone trees including beech, elm, hickory and holly (Dredge *et al.*, 1992). This warm period was followed by the Wisconsinan glaciation that produced glacier tongues extending at least as far as St. Pierre et Miquelon (Josenhans and Lehman, 1999).

A boreal flora including birch and spruce had reestablished itself on the southernmost part of the Îles-de-la-Madeleine at least 11 000 years ago (Dredge *et al.*, 1992), by the time NS was ice-free and forested (Stea and Mott, 1998). Postglacial weather patterns probably have been stable for


**Figure 5. Île d'Entrée showing the archipelago's characteristic rounded hills and strongly eroded cliffs.**

the last 8000 years. No sign of postglacial (Hypsithermal) warming above current temperatures has been found further east than southern Ontario (Anderson, 1985). Present-day weather around Îles-de-la-Madeleine is cool-temperate (summer temperatures are similar to those at sea level on the Gaspé peninsula) with a delayed onset of winter weather and a late spring. Pack ice becomes heavy only in late January, but does not break up until May as it is transported by surface currents southwards from colder parts of the Gulf (Loring and Nota, 1973). Thereafter, shallow coastal seas warm rapidly.

### *Flora*

Today, much of the islands have been cleared of native vegetation (figure 8) and planted for pasture or converted to house lots. Virtually all of Île d'Entrée and much of Île du Havre-aux-Maisons are devoid of trees and shrubs, while tiny Île aux Loups has almost disappeared under housing. Development of the rest of the islands for tourism and cottages (figure 9) is increasing the destruction of what is left. Still, much native vegetation may be found. What remains, chiefly on Île de la Grande Entrée and Île du Havre-Aubert, is reminiscent of the ecology of windswept clifftops at the extremities of PEI: dense coniferous forests interrupted by extensive boggy areas and low sand ridges. Balsam fir, *Abies balsamea* (L.) Mill., and spruces, *Picea* spp. are dominant although often dwarfed and twisted by the wind into "elfinwoods" (Bourque *et al.*, 1994). Shrubs such as green alder, *Alnus crispa* (Ait.) Pursh, and dogwood, *Cornus* spp., edge the woods on sandy or boggy ground where tamarack, *Larix laricina* (DuRoi) K. Koch, or juniper, *Juniperus communis* L. may grow intermingled with bayberry and sweet gale, *Myrica* spp. (Myricaceae), chokeberry, *Aronia* spp. (Rosaceae) and ericaceous plants such as bearberry, *Arctostaphylos uva-ursi* (L.) Spreng., cranberries, *Vaccinium* spp. and huckleberries, *Gaylussacia* spp. Some plants such as spike rush, *Eleocharis erythropoda* Steud. (Cyperaceae) and woolly hudsonia, *Hudsonia tomentosa* Nutt. (Cistaceae)


**Figure 6. Some of the highest cliffs are on the eastern side of Île du Havre-aux-Maisons facing the Baie de Plaisance.**

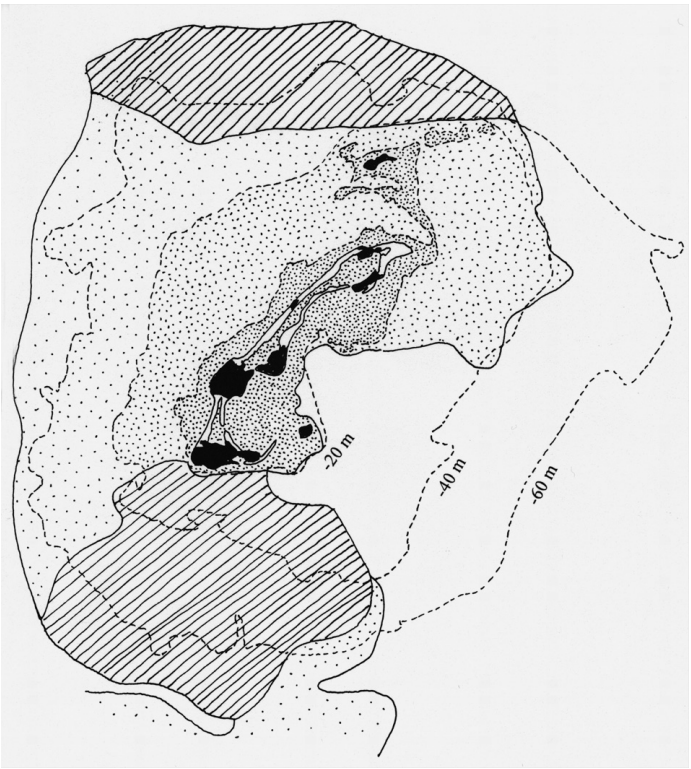


**Figure 7. Îles-de-la-Madeleine and alluvial fan. Hatched: gravel; stippled: coarse sand; white: fine sand. Dotted lines indicated depth below sea level, at intervals of 20 m. Redrawn from Loring and Nota (1973).**

seem confined to the southernmost island, Île du Havre-Aubert and its associated marshes around Lagune du Havre aux Basques (figure 10).

On the sheltered northern and eastern slopes of the southernmost island is found the only mixed hardwood forest on Îles-de-la-Madeleine. Pin cherry, *Prunus pensylvanica* L.f. grows in thickets that include smaller quantities of aspen, *Populus tremuloides* Michx. and willows, *Salix* spp. with a few remaining paper birch, *Betula papyrifera* Marsh. and shrubs such as red-berried elder, *Sambucus pubens* Michx. (Caprifoliaceae). Some of these trees are found isolated in forests or along roadsides on Île du Cap-aux-Meules (Grindstone Island) just to the north of Île du Havre-Aubert.

Grasses (Poaceae) are ubiquitous on low ground and even invade forested areas. Dunes support mostly beachgrass, *Ammophila brevigulata* Fern. Extensive tidal flats of cordgrass (*Spartina* spp.) are usually zonated. Smooth cordgrass, *Spartina alterniflora* Loisel occupies the narrow tidal zone along with glasswort, *Salicornia europaea* L. (Chenopodiaceae). Salt hay, *Spartina patens* (Ait.)Muhl. forms extensive beds above these and broad-leaf, *Spartina pectinata* Link takes the drier sandy areas. Sandy ridges well back from the shoreline may have other native grasses such as poverty-grass, *Danthonia spicata* (L.) Beauv. and hair-grass, *Deschampsia flexuosa* (L.) Trin.

Behind dunes, or on lagoon edges where slopes are low and seeps occur, cordgrass gives way to sedges (*Carex* spp.) and rushes (*Juncus* and *Scirpus* spp., Cyperaceae). One of the most common and easily recognized of these is Baltic rush, *Juncus balticus* Willd. which forms extensive swards or grows intermingled with sedges. The low-growing toad-rush, *Juncus bufonius* L. is an important component of marginally wet areas.

## Methods

The target group considered here are the insects belonging to the Homoptera-Auchenorrhyncha (figure 11). These are known as "short-horned bugs" because they usually have very short, bristlelike antennae. They include the large family Cicadellidae (leafhoppers) and the related Membracidae (treehoppers), plus the superfamilies Cercopoidea (spittlebugs), Cicadoidea (cicadas) and Fulgoroidea (planthoppers). There are 1 463 species known from Canada (Maw *et al.*, 2000) of which 602 have been reported from Québec. These are all phytophagous insects representing the next-to-lowest level on the food chain. Many migrate only short distances annually (Hamilton, 1999), making them ideal for biogeographic studies. For example, their distribu-

K.G. ANDREW HAMILTON

**Figure 8. Typical European plants used as pasturage.**

K.G. ANDREW HAMILTON

**Figure 9. "Urban sprawl" on Île du Cap-aux-Meules.**

tion on other islands in the Gulf of St. Lawrence points to a refugium on the Grand Banks of NFLD (Hamilton and Langor, 1987) which were above sea level during the glacial maxima.

The first short-horned bug recorded from Îles-de-la-Madeleine was the leafhopper *Platymetopius magdalensis* Provancher (1890). It was probably collected not far from the earliest ferry port at Havre-Aubert. The original specimens have never been found (Hamilton, 1976). Despite this, the species has been regarded as a senior synonym of the blueberry leafhopper *Scaphytopius vaccinium* DeLong (Hepner, 1947). In 1984, the archipelago was visited by M-C. Larivière who collected a pair of spittlebugs that did not exactly match any known species. The identity of both these species remain unresolved problems.

K.G. ANDREW HAMILTON

**Figure 10. Spike rush marsh between Île du Havre-Aubert and Lagune du Havre-aux-Basques (site #3) where two species of leafhoppers occur that are unknown on Prince Edward Island.**

Sampling was done by sweep-net throughout the conjoined islands during August 1999 and July 2000. This represents most of the summer season, as a long, cool spring in 2000 delayed the onset of the early summer fauna. All habitats were sampled although many of the sites yielded few, if any, native species. The most representative sites (from south to north) were the following 12 (figure 12):

1. 47°14.61'N, 61°59.25'W: 2 km N Bassin at corner of Chemin de la Montagne and Chemin des Buttes, Île de Havre-Aubert. Old growth mixed coniferous-hardwood forest.
2. 47°15.41'N, 61°58.66'W: 3 km N Bassin, 1 km S Pointe-des-Canots, Île de Havre-Aubert. Grassy opening in coniferous forest on sandy soil.
3. 47°15.49'N, 62°00.26'W: 2 km NL'Étang-des-Caps, 5 km NW Bassin, Chemin de la Dune de l'Ouest, Île de Havre-Aubert. Dunes, and sedgy flats with pools beyond old breech in dunes. This is apparently the site visited in August 1984 by M-C. Larivière.
4. 47°15.67'N, 61°54.03'W: 2 km NW Portage-du-Cap, 4 km NW Havre-Aubert, Île de Havre-Aubert. Boggy flats behind dunes, with grasses, bearberry and hudsonia on low sand ridges.
5. 47°18.99'N, 61°56.23'W: 5 km S L'Étang-du-Nord, south of Île du Cap-aux-Meules. Sedgy flats behind dunes.
6. 47°22.25'N, 61°52.90'W: L'Étang-du-Nord, along Chemin Lepré, Île du Cap-aux-Meules. Trees along roadside, mostly planted.

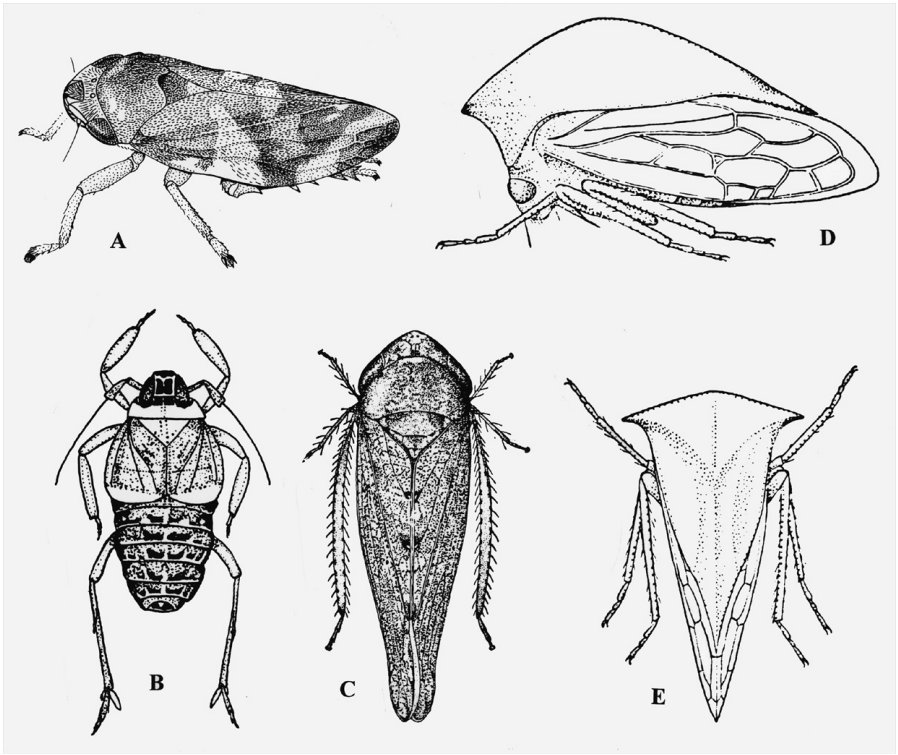


**Figure 11. Families of short-horned bugs represented on Îles-de-la-Madeleine: (A), Cercopidae or spittlebugs (*Philaenus spumarius*, the meadow spittlebug, probably the most common species on the islands); (B) Delphacidae or planthoppers (*Pissonotus* sp.); (C) Cicadellidae, or leafhoppers (*Paraphlepsius irroratus*); (D-E) Membracidae or treehoppes (*Ceresa* sp.).**

7. 47°27.48'N, 61°54.92'W: 1 km N plage Dune-du-Sud, Île de Havre-aux-Maisons. Elfin spruce woods with shrubby understory in low places.
8. 47°29.89'N, 61°44.66'W: 3 km SW Pointe-aux-Loups, north of Île de Havre-aux-Maisons. Tidal edge of lagoon with glasswort and cordgrass beds.
9. 47°33.92'N, 61°30.32'W: 2 km WSW Old-Harry, Chemin du Bassin Est, Île de la Grande Entrée. Boggy ground with ericaceous cover.
10. 47°34.13'N, 61°30.10'W: 1 km W Old-Harry, Île de la Grande Entrée. Alder thickets in hollow between dunes.
11. 47°34.21'N, 61°38.24'W: 6 km NE Pointe-aux-Loups, 7 km SW Grosse-Île (formerly Leslie). Dunes with bearberry and very low growth of juniper, spruce and bayberry.
12. 47°37.15'N, 61°28.64'W: 3 km E Grosse-Île at East Cape. Extensive cordgrass flats edging lagoon.

These samples were compared to similar samples taken in PEI during the same months. Sites in PEI with native vegetation were identified by the Island Nature Trust. Fifty-seven species new to the PEI fauna were collected during the 1999 season (Hamilton, 2000). These were added to the list for PEI (Maw *et al.*, 2000). Subsequently, the following 18 species were added from the 2000 season:

**CICADELLIDAE** *(14 spp.): Agalliopsis ancistra Oman, Deltocephalus nigriventer Sanders & DeLong, Empoasca copula DeLong, Idiodonus morsei (Osborn), Kyboasca splendida (Gillette), Latalus sayii (Fitch), Macropsis basalis (Van Duzee), Macropsis bifasciata (Van Duzee), Macrosteles fascifrons (Stål), Oncopsis prolixa Hamilton, Oncopsis sobria (Walker), Ribautiana unca (McAtee), Typhlocyba persephone McAtee, and an European species on linden: Pediopsis tiliae (Germar)*

**CIXIIDAE** *(1 sp.): Oliarus quinquelineatus (Say)*

**DELPHACIDAE** *(3 spp.): Delphacodes albocarinata (Stål), Delphacodes lineatipes (Van Duzee), Pissonotus basalis Van Duzee.*

## Results

A total of 42 species of Homoptera-Auchenorrhyncha were collected on Îles-de-la-Madeleine. Of these, 14 (33%) were represented only on, or near, the southernmost island, Île du Havre-Aubert; these are designated by an asterisk (*). Sites where these species were found are indicated by number in the following list.

Seven (18%) are European species that have been introduced into North America by agriculture, and presumably have spread from the mainland to Îles-de-la-Madeleine by the same route. Two of these have been found only on Île du Havre-Aubert.

The remaining 35 species are native to North America. Fully 22 (63%) of these species represent a widespread fauna, 6 of which (25%) have been found only on Île du Havre-Aubert. It is by no means certain that all these widespread species are native to Îles-de-la-Madeleine. In particular, the few species which feed on forbs may represent importations from the mainland. Species that feed only on sedges, beach and heath plants, spruce and alders (15 species) are highly unlikely to have been imported along with their host plants (figure 13).

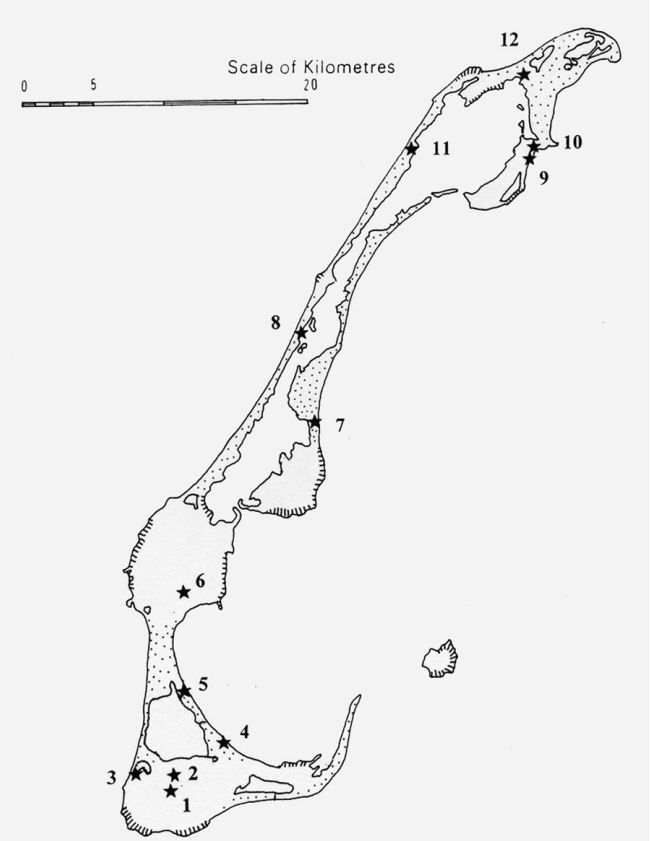


**Figure 12. Collection localities (stars) on Îles-de-la-Madeleine. Numbered sites: see text.**

Twelve other species are either endemic to Îles-de-la-Madeleine, or are absent from PEI and thus judged to be localized in eastern Canada and unlikely to have found their way from the mainland in recent times. Eight of these (67%) are found only on Île du Havre-Aubert.

The one remaining species is represented by an unidentifiable female.

**CERCOPIDAE** *(4 spp., 2 native)*

**Aphrophora gelida (Walker), on spruce: 1, 2 (widespread native species)*

*Neophilaenus lineatus (L.), on grasses and sedges (Carex spp.): 1, 2, 3, 4, 7, 8, 11, 12 (abundant; introduced European species)*

*Philaenarcys spartina Hamilton, on broad-leaf cordgrass: 3, 4, 5, 7 (common;* **endemic subsp.***)*

*Philaenus spumarius (L.), on forbs: 1, 2, 3, 4, 7, 8, 11, 12 (abundant; introduced European species)*

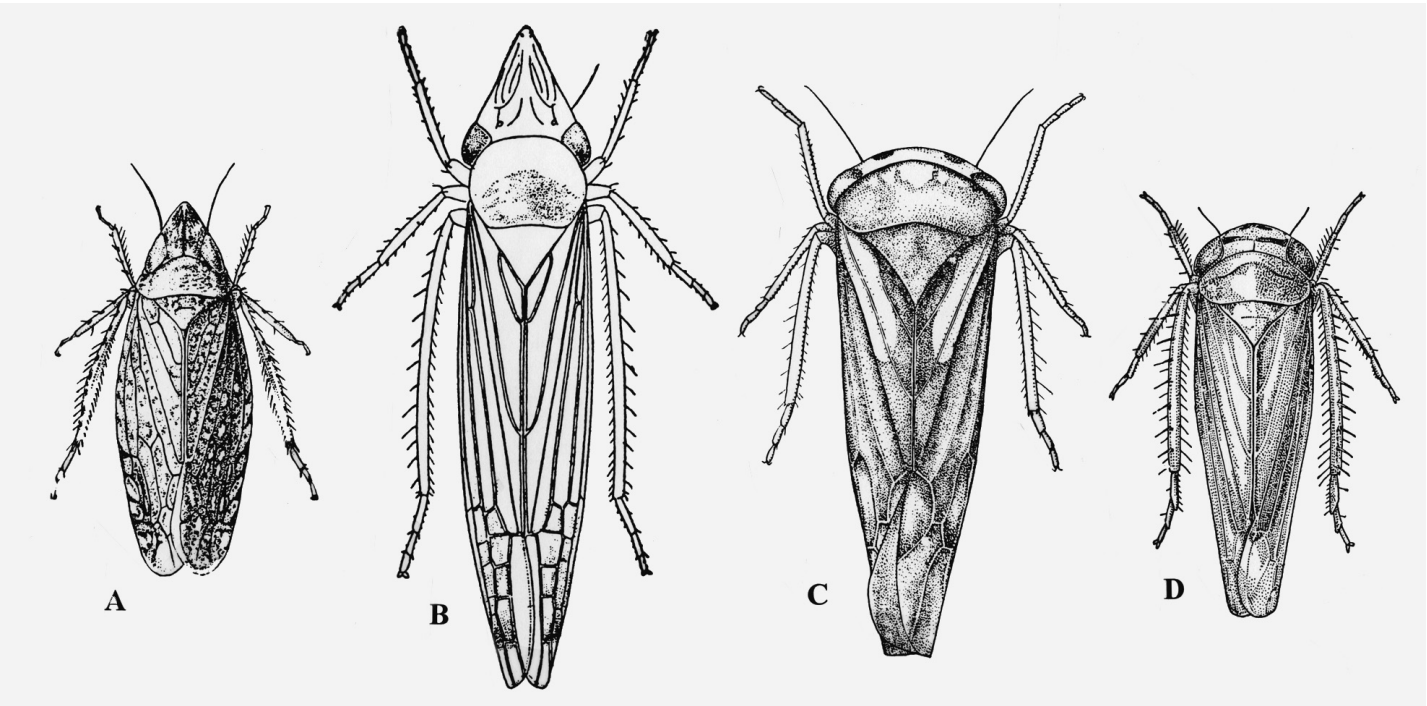


**Figure 13. Representative leafhoppers that feed on sedges and heath plants, and hence are probably native to Îles-de-la-Madeleine: (A) *Scaphytopius* sp., (B), *Draeculacephala* sp.; (C) *Balcanocerus provancheri*; (D) *Limotettix* sp.**

**CICADELLIDAE** *(31 spp., 26 native)*

*Anoscopus flavostriatus (Donovan), on forbs: 8 (introduced European species)*

**Aphrodes bicinctus (Schrank), on forbs: 3 (introduced European species)*

*Athysanus argentarius Metcalf, on grasses: 2, 3, 5, 10 (abundant; introduced European species)*

*Balcanocerus provancheri (Van Duzee), on chokeberry [nymphs]: 9 (native species not on PEI)*

*Cicadula subcupraea (Provancher), on sedges (Carex spp.): 3, 5 (abundant; widespread native species)*

*Doratura stylata (Boheman), on grasses: 2, 4 and on Île du Cap-aux-Meules (common; introduced European species)*

*Draeculacephala angulifera (Walker), on sedges (Carex spp.): 3, 5 (common;* **endemic race***)*

**Draeculacephala zeae Hamilton, on grasses: 1 (***endemic race***)*

**Elymana sulphurella (Zetterstedt), on grasses: 3 (introduced European species)*

**Hecalus montanus (Ball), on grasses: 2 (native species not on PEI)*

*Helochara communis Fitch, on toad-rush: 5, 9 (common; widespread native species)*

*Idiodonus morsei (Osborn), on heath plants: 9 (widespread native species)*

**Kyboasca trilobata (DeLong), on bayberry and sweet gale: 3, 4 (common; widespread native species)*

**Latalus personatus Beirne, on grasses: 4 (possibly introduced; widespread native species)*

*Limotettix ferganensis Dubovsky, on spike-rush: 3 (common; widespread native species)*

**Limotettix parallelus (Van Duzee), on spike-rush: 3 (abundant; native species not on PEI)*

*Macrosteles fascifrons (Stål), on toad-rush: 3, 5, 10, 12 (abundant; widespread native species)*

**Macrosteles galeae Hamilton, on sweet gale: 4 (native species not on PEI)*

*Macrosteles quadrilineatus (Forbes), on forbs: 2 (possibly introduced; widespread native species)*

**Neohecalus lineatus (Uhler), on broad-leaf cordgrass: 2 (widespread native species)*

*Oncopsis crispae Hamilton, on alder: 1, 4, 8, 10 (abundant; widespread native species)*

*Oncopsis minor (Fitch), on paper birch: 6 (possibly introduced; widespread native species)*

*Oncopsis quebecensis Hamilton, on paper birch: 1, 6 (common; native species not on PEI)*

**Paluda gladiola (Ball), on dune grasses: 3 (widespread native species)*

*Paraphlepsius irroratus (Say), on forbs: 3, 4, 5, 8, 11 (common; possibly introduced; widespread native species)*

*Pasaremus concentricus (Van Duzee), on baltic rush: 3, 4, 5 (common; widespread native species)*

*Psammotettix lividellus (Zetterstedt), on grasses: 3, 5 (possibly introduced; widespread native species)*

*Ribautiana unca (McAtee), on alder: 4, 8 (widespread native species)*

**Rosenus acutus (Beamer), on hair-grass: 4 (***not found elsewhere in eastern Canada***)*

*Scaphytopius acutus (Say) [= S. magdalensis (Provancher),* **new synonymy**[1] *], on forbs and ericaceous plants: 3, 4, 5 (possibly introduced; widespread native species)*

**Typhlocyba ariadne McAtee, on alder: 1, 3, 4 (abundant; native species not on PEI)*

**DELPHACIDAE** *(6 native spp.)*

**Delphacodes ?kilmani (Van Duzee), on sedges (Scirpus spp.): 3 (native species not on PEI)*

**Delphacodes sp.nov., on hair-grass: 4 (common;* **endemic?***)*

**Delphacodes sp. [unidentified female]: 3 (host and origin unknown)*

*Megamelus metzaria Crawford, on broad-leaf cordgrass: 3, 12 (locally common; widespread native species)*

*Prokelisia crocea (Van Duzee), on broad-leaf cordgrass: 11 (widespread native species)*

*Prokelisia dolus Wilson [PEI nov.], on smooth cordgrass: 12 (abundant; widespread native species)*

**MEMBRACIDAE** *(1 native sp.)*

*Ceresa basalis Walker, on forbs: 3, 4, 8 (possibly introduced; widespread native species)*

## Discussion

### *(A). Biological evidence.*

The total short-horned bug fauna of Îles-de-la-Madeleine (42 species) is far smaller than that of PEI (141 species). The latter, however, is also much smaller than the mainland fauna (271 species in NB, 299 in NS). Evidently, even a comparatively narrow water channel such as the 15 km-wide strait that separates PEI from NB can strongly limit an insular fauna. The fauna of Îles-de-la-Madeleine is also restricted by the much more depauperate floral diversity as compared to that of PEI.

What is much more significant than the overall numbers of species is the species composition. For example, seven species (17%) are exotics, imported from Europe. This number may prove to be an underestimation, as sampling was most intensive in areas of natural vegetation and tended to avoid plants of European origin. By contrast, 19 species on PEI (14%) are exotics, most commonly on trees planted on city streets. Îles-de-la-Madeleine has no European bugs that feed on trees. By contrast, it has 70% of the imported bug fauna of PEI that feed on grasses and forbs.

The 35 native species on Îles-de-la-Madeleine are represented by no fewer than 12 species or races (34%) that are *not* represented on PEI. This number may be still higher, as additional specimens of some species that were poorly represented in the samples (e.g. *Delphacodes ?kilmani*) may show them to belong to undescribed taxa.

One of these 12 localized species is an undescribed Delphacid quite distinct from its closest relative, *Delphacodes campestris* (Van Duzee) which is a common, transcontinental species of agricultural areas. One other species represents an undescribed subspecies of the spittlebug *Philaenarcys spartina*, superficially resembling instead *P. bilineata* (Say) in having straighter, less convex front wings (figure 14). It has male genitalia of the *P. spartina* type (Hamilton, 1979, figure 11). Two other species may be endemic races: *Draeculacephala* spp. from Îles-de-la-Madeleine differ from mainland populations in their body length. *Draeculacephala angulifera* from Îles-de-la-Madeleine is intermediate in size between the typical mainland race of that species and the related *D. manitobiana* Ball (Hamilton, 1985*a*, figures 26-28), while *D. zeae* from Îles-de-la-Madeleine at 6.6-7.0 mm (males) and 8.0-9.3 mm (females) is smaller than either mainland race (Hamilton, 1985*a*, figures 67-72).

Most of the remaining species on Îles-de-la-Madeleine that are not found on PEI are boreal species represented in the Gaspé Peninsula of mainland Québec or adjacent NB. One species of leafhopper, *Oncopsis quebecensis*, has a distribution pattern reminiscent of the Gulf of St. Lawrence aster, but more widespread to the east. It is found most commonly on the islands, with isolated mainland populations on the Gaspé Peninsula, coastal NB, on CBI, and with another

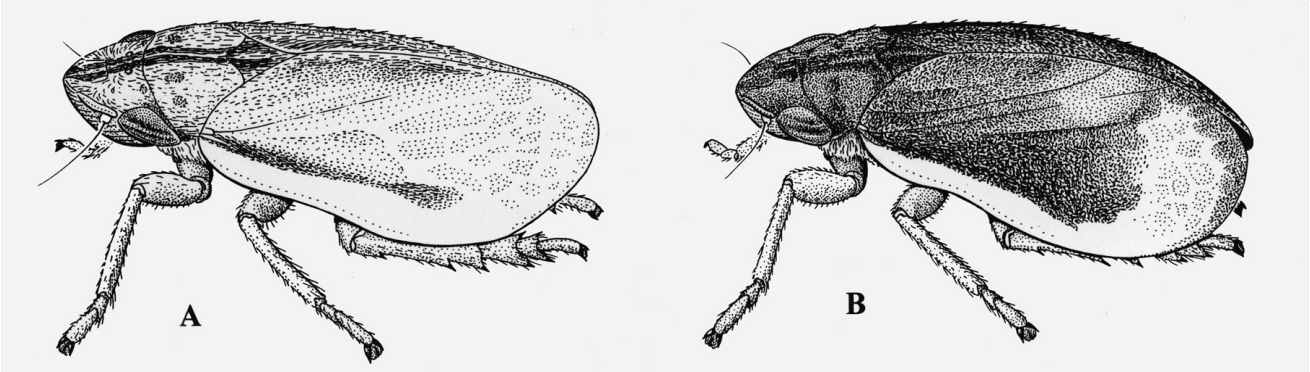


**Figure. 14. Two forms of the spittlebug *Philaenarcys spartina*: (A) from Îles-de-la-Madeleine; (B) from mainland sites, where its wings are more convex.**

population on western NFLD as well (Hamilton and Langor, 1987, figure 31).

One species has a notably disjunct distribution. *Rosenus acutus* is a western species, ranging from northern British Columbia to northern Manitoba. Its presence on Îles-de-la-Madeleine is clearly the result of a range split into eastern and western components by Pleistocene glaciation.

Within the islands, all but seven species (82%) were found on four sites on the southernmost island, but only 12 (34%) were found on the four northernmost sites. This imbalance is still more striking when considering only the smallest leafhoppers (subfamily Typhlocybinae, including *Kyboasca, Ribautiana* and *Typhlocyba*). These wind-transported insects are common to abundant on the southernmost island, while only a single specimen was found in any of the other sites.

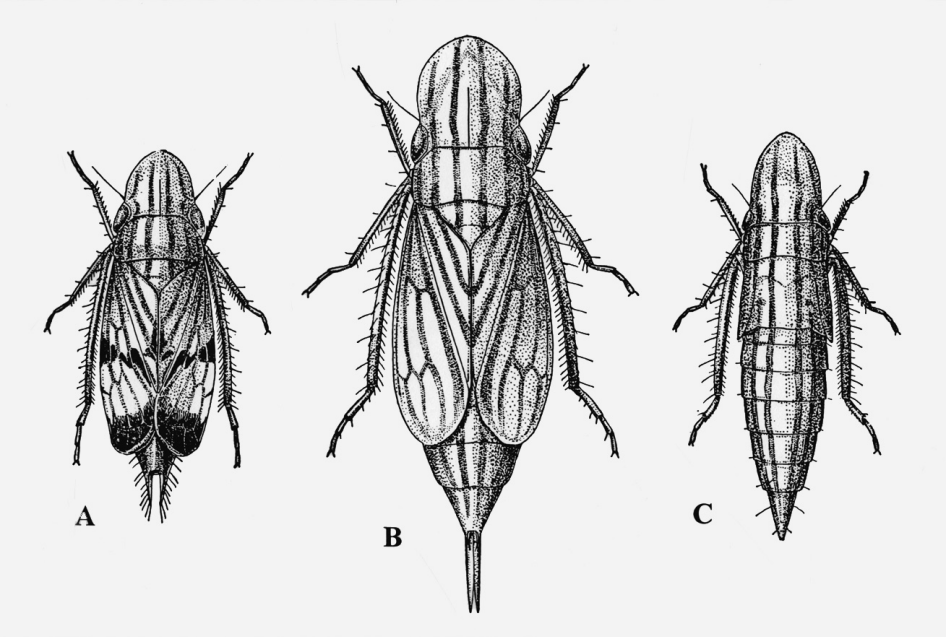


**Figure 15.** ***Neohecalus lineatus*** **is distinctively striped in all forms: (A) male, (B) female and (C) nymph. Males have not yet been, and are needed before it can be determined whether the species found on Îles-de-la-Madeleine is conspecific with the mainland populations.**

A third of native Îles-de-la-Madeleine bugs (12 species) feed on grasses. Half of these are coastal, mostly on cordgrasses: *Philaenarcys spartina, Neohecalus lineatus* (figure 15), *Megamelus metzaria* and *Prokelisia crocea* feed on broad-leaf cordgrass, while *Prokelisia dolus* attacks smooth cordgrass. It is interesting to note, in passing, that *Philaenarcys spartina* does not occur here on salt hay, its preferred host on mainland sites. In fact, none of the specialists on salt hay are found on Îles-de-la-Madeleine although the grass forms extensive beds. Another host shift has occurred in *Paluda gladiola* which is found on dune grasses here, as in other coastal situations in eastern Canada; further west, *P. gladiola* is usually on blue-joint, *Calamagrostis canadensis* (Michx.)Nutt. In total, this sedge and grass-feeding coastal fauna amounts to 67% of that of the coast of PEI. The latter fauna has in addition only the planthopper *Delphacodes detecta* (Van Duzee) on various cordgrasses, and the leafhoppers *Amplicephalus simplarius* (Osborn & Ball) and *Destria crocea* Beirne on salt hay.

Eight other species are associated with back-dune localities, feeding on sedges and rushes: *Cicadula subcupraea* and *Draeculacephala angulifera* on *Carex* spp., *Delphacodes kilmani* on *Scirpus* spp., *Helochara communis* and *Macrosteles fascifrons* on toad-rush, *Limotettix ferganensis* and *Limotettix parallelus* on spike-rush, and *Pasaremus concentricus* on Baltic rush. Sweet gale and northern bayberry, often coastal plants, are the hosts for two more leafhoppers, *Kyboasca trilobata* and *Macrosteles galeae*, making the total coastal fauna amount to 16 species or 45% of the total Îles-de-la-Madeleine bug fauna.

Many of the species of the coastal flora are also found in boggy areas, so their leafhopper faunas also overlap. *Idiodonus morsei* on Ericaceae and nymphs of *Balcanocerus provancheri* on chokeberry were both taken in a single bog on Île de la Grande Entrée, but should prove to be more widespread with additional collecting in other boggy areas.

Coniferous forests are species-poor in Homoptera-Auchenorrhyncha. Consequently, it is not surprising that only the spruce-feeding spittlebug *Aphrophora gelida* should be found there. Green alder thickets, also common on the islands, have three leafhopper species: *Oncopsis crispae, Ribautiana unca,* and *Typhlocyba ariadne*. Only two other leafhoppers are known from this host in eastern Canada: *Kyboasca splendida* and *Typhlocyba latifasciata* (Christian), both of which occur in PEI. Another two species are known from trees in the islands: *Oncopsis minor* and *Oncopsis quebecensis*, both from paper birch. This is only a small portion of the 11 eastern species known from this host (Hamilton, 1985*b*). Many of the other species emerge as adults in spring instead of during midsummer. Perhaps the long, cool spring on the islands is not suitable for such species.

The most surprising elements missing from the bug fauna of the archipelago are the willow and aspen feeders. These insects are both speciose and common across Canada and include species that disperse readily, such as *Idiocerus pallidus* Fitch. Willows formed an important part of the flora of Île d'Entrée as recently as 11 100 years ago (Dredge *et al.*, 1992). Perhaps the species that were common during the cold period called the "Younger Dryas" (10-11 000 years ago) have all died out, and their insect fauna with them.

### *(B). Geological evidence*

Key biological questions remain that rely on detailed geological evidence. Could an endemic flora and fauna of Sangamon age have weathered the vicissitudes of the Wisconsinan glacial period? Even if glaciation of this period wiped out all life, could the flora and fauna have become re-established in some interstadial time? Could the Îles-de-la-Madeleine once have been closer to the mainland than at present due to erosion or changes of sea level?

Whether the Îles-de-la-Madeleine were submerged in ice during the Wisconsinan remains debatable. Glacial deposits on top of dated Sangamon peat have been found on the southernmost islands of the archipelago (Dredge *et al.*, 1992), but superficially similar deposits on the northern islands cannot be dated and may be remnants of Illinoian glacial moraines. That the northern islands of the archipelago were not glaciated since the Sangamon is suggested by the absence of linear erosional features. Glacial boulders are few and present only where water-distributed gravel indicates they were ice rafted into areas once depressed below modern sea level (Dubois, 1992), probably following an earlier glaciation (Dredge *et al.*, 1992) as there is no evidence for postglacial sea level on the archipelago higher than the present level.

The extent of the most recent glaciation in the Gulf can be measured by submarine sediment deposits. These show that the Laurentian Channel was last ice-filled 14 300 years ago and the other two channels were most recently glaciated at 13 500 and again at 13 200 years ago (Josenhans and Lehman, 1999). Smaller but sharply defined submarine channels which left no appreciable sediments extend across the Magdalen shelf between PEI and the archipelago. These are thought to have been meltwater channels beneath receding glacial ice sheets (Nota and Loring, 1964). Thus, Wisconsinan ice once extended as far as Îles-de-la-Madeleine but possibly no farther. But whether or not they were fully glaciated during the Wisconsinan, the islands would surely have been too cold during the height of the glaciation for persistence of a boreo-temperate fauna and flora.

Wisconsinan glaciation in eastern Canada appears to have been a composite of a number of glacial advances from different ice centres. Glaciation may have been divided into three or more stadia (Matthews, 1979) with warmer periods at approximately 75 000 (St. Pierre interstadial), 50 000 (Port Talbot interstadial) and 25 000 (Plum Point or Farmdalian interstadial) years ago. The last of these (Stea *et al.*, 1998) seems to have followed retreat of Appalachian-based glaciers 32 000 years ago and persisted until the readvance of Laurentide ice from northern Québec 22 000 years ago. It was mildest and longest on CBI and may well have brought boreal conditions to the Magdalen shelf that lasted until 20 000 years ago. Later, following retreat of Laurentide ice 14 300-13 700 years ago (Josenhans and Lehman, 1999),

there may have been two brief interstadials before other ice centres around the Gulf produced short-lived local glaciers as recently as 13 200 years ago. Thus, despite a chequered career, glaciers dominated the region of the Magdalen shelf until nearly the beginning of the Holocene.

All the archipelago except Le Corps Mort now lie on a single submerged plateau surrounded by shallow, sun-warmed water which gives the islands a long, mild summer for their latitude. This plateau is a weakly sloped mound resembling a huge alluvial fan 130 by 150 km; but it is in fact covered by a rather thin layer of sediments of modern origin as all sediments older than 20 000 years have been removed from the Magdalen shelf (Loring and Nota, 1973). The plateau's convex shape is formed by a "salt dome" of ancient origin. The basal sedimentary rocks of Îles-de-la-Madeleine rest on the middle of the Fundy Epieugeosyncline, a deep Palaeozoic trough extending from the Bay of Fundy across PEI and northern CBI to a narrow slot across NFLD from St. George's Bay to White Bay (Howie and Barss, 1975, figure 1). The deepest part of this trough lies under eastern PEI and Îles-de-la-Madeleine (figure 4). During the Upper Carboniferous (Mississippian) era, ca. 350-320 million years ago, this trough filled with Windsor formation evaporites, mainly salt, to a depth of 2 km (SOQUEM, undated). Subsequent deposition of Permian red sandstone 3-4 km deep deformed the soft evaporite beds and probably initiated local uplift. When the Gulf of St. Lawrence later filled with glaciers and eventually sea water, the weight further pressed the salt upwards. This created columnar salt intrusions with anhydrite caps extending to sea level under each of the major islands and reefs (SOQUEM, undated). The sandstone islands so created have gypsum as isolated "lenses" (Tiphane, 1970) and deformed mixtures of sedimentary rocks with volcanic intrusions (Maillet, 1992). The "salt dome" continued to significantly affect the elevation of the islands during the Wisconsinan and Holocene. Îles-de-la-Madeleine shore lines of Sangamonian age now lie 8-20 m higher than on mainland sites (Grant, 1980) indicating that some of the islands have risen at least 20 m over the last 80 000 years.

By the nature of salt domes, erosion of upper level rock would allow further upwelling of the salt layer and elevation of still more of the capping sandstone layers to replace what had been worn away. This would only happen where the salt is deepest, and in fact all the extant islands and reefs lie within the Epieugeosyncline where basal rocks are 8-9 km below sea level compared to 4 km or less in surrounding areas (figure 4). This deep area in turn corresponds roughly to the area of sea floor elevated at least to 40 m below sea level (figure 7). Such a continuously generating island, during glacial periods when sea levels were depressed, may have been as much as 70 km wide and 100 km long, judging by the size of the Epieugeosyncline basin they rest upon. This covers an area of 7 000 km$^2$ which is somewhat greater than present-day PEI (5 657 km$^2$). Much of this original island has been

eaten away by cliff erosion, leaving only shoals and isolated rocks behind. One might say that present-day Îles-de-la-Madeleine are PEI whittled down to a toothpick!

Around the island archipelago, submarine sediments reveal a series of terraces. The uppermost lies below 36 m (Sanschagrin, 1964), and another is between 51-62 m (Loring and Nota, 1973). Further out on the Magdalen shelf where it dips into the Laurentian Channel, there are other terraces at –110 and –160 m (Josenhans and Lehman, 1999). The lowermost of these may represent sea level during the height of Wisconsinan glaciation (Woodfordian, 18 000 years ago) when ice tongues were stable in channels 200-500 m deep. The other 3 probably correspond (in order of depth) to sea level stadia during the Younger Dryas (10-11 000 years ago), the Chignecto phase advance at 12 500-13 000 years ago (Stea *et al.*, 1998) and the Scotian phase at 13 500-15 000 years ago (Josenhans and Lehman, 1999). The Chignecto and Scotian glaciers extended well into the Gulf instead of calving just offshore, as they would have if the water were deep at that time. Therefore the entire Magdalen shelf was emergent from the sea (although possibly ice-covered) during the greater part of the last ice age, and these terraces show that the archipelago formed a single large island in a shallow sea from 15 000 until at least 8 000 years ago when glacial melting was nearly complete on the mainland.

## Conclusions

Although sampling was neither exhaustive nor carried out over many years, nevertheless a clear picture emerges of the short-horned bug fauna of Îles-de-la-Madeleine. Where floral communities are extensive and frequently represented (sand dunes, boggy areas, heaths and coniferous woodlands) enough of the fauna is now known that many of its distinctive characteristics are apparent. Three definite conclusions may be drawn from this data, and a fourth is indicated by the bulk of available data:

1) ***Refugium is verified.*** The short-horned bug fauna of the archipelago is not nearly as depauperate as expected considering the small size of the islands, their low elevation and distance from the mainland.
2) ***Endemism is verified.*** The fauna of the archipelago also has a large proportion of forms not yet discovered on PEI or on mainland Québec. Formerly we knew of one endemic grasshopper and one endemic plant species, plus one Gulf coast plant species; now we have an endemic planthopper *Delphacodes* near *campestris*, a Gulf coast leafhopper *Oncopsis quebecensis*, a widely disjunct leafhopper *Rosenus acutus*, and at least three endemic subspecies or races of the spittlebug *Philaenarcys spartina* and the leafhoppers *Draeculacephala angulifera* and *D. zeae*.
3) ***The glacial-age island was larger than at present.*** The fauna of the southernmost island, and in particular its northern and east-facing slopes (figure 16), are comparatively rich in species. Both introduced and endemic species are most numerous there. These areas have representatives of most of the native island fauna, all but one of the localized species, and 100% of the collections of endemic species and widely disjunct species. In addition, most of the species that are sensitive to wind dispersal were best represented there. Significantly, this is also the only area on the islands that supports a forest with deciduous trees. This area is the most sheltered part of the archipelago, furthest inland from southeasterly gales. It is also the most in need of conservation.

If the most sheltered part of the archipelago contains all of the endemic fauna, this probably indicates that the Pleistocene refugium they lived in was similarly sheltered, and its land area was probably larger and less vulnerable to inclement weather than on the present Île du Havre-Aubert. There is clear geological evidence for such a refugium. Terraces of glacial age indicate that, for much of the Wisconsinan, Îles-de-la-Madeleine formed a single island at least 20-35 km wide and 100 km long and possibly as much as 70 by 150 km. Such an island could have been sufficiently wide to maintain a boreal deciduous forest in the interior even under lowered average summer temperatures.

K.G. ANDREW HAMILTON

**Figure 16. The northern side of Île du Havre-Aubert (site #2 show here) supports a mixed forest including shrubs and deciduous trees. The tall grass growing along the roadside is cordgrass, supporting the only known population of *Neohecalus lineatus* on the archipelago.**

4) ***Influx of fauna and flora was postglacial.*** A continuous boreal fauna is ruled out by nearby glacial centres active in NB and NS until the end of the Chignecto phase 12 500 years ago. The entire Gulf was unsuitable for boreal and temperate-zone insects even when global temperatures were rising. But perhaps temperatures rose sufficiently as these glaciers retreated to allow boreal species to invade the deglaciated Magdalen shelf? A lengthy period of isolation is indicated by the degree of endemism, and a large, emergent island mass close to the mainland would have been needed to accrete the present-day fauna.

Environmental conditions on this postglacial island are debatable. Two sources of problems are found that hinder the interpretation of the present-day fauna and flora. Could their present distributions be artifacts of chance, or evidence of speciation? Secondly, do their present ecological characteristics reflect ice-age conditions, or merely postglacial sources of these populations?

The insular fauna shows both temperate and boreal species. Among the species that are not widespread, a boreal fauna is more in evidence: *Draeculacephala angulifera*, *Hecalus montanus*, *Limotettix parallelus*, *Macrosteles galeae*, *Oncopsis quebecensis, Rosenus acutus, Typhlocyba ariadne* McAtee (Cicadellidae), and *Delphacodes kilmani* (Delphacidae) are characteristic of boreal areas. *Delphacodes* sp.nov. is unknown outside the archipelago although an undescribed species from northern British Columbia may be related. Temperate faunas are represented only by *Philaenarcys spartina* (Cercopidae), *Balcanocerus provancheri* and *Draeculacephala zeae* (Cicadellidae). Of the temperate fauna, only *Philaenarcys spartina* shows modification of its biology (elimination of salt hay from its host range) suggestive of adaptation to a situation where that host died out, while the other two species may have been recent in origin.

Further evidence for glacial-era conditions on the islands comes from two endemic plants:

1) *Aster laurentianus* produces flowers after two or three months' growth, as contrasted to its continental relatives *A. brachyactis* Blake and *A. frondosus* (Nutt.) T. & G. which each take six to eight months to mature (Houle and Haber, 1990). This suggests that the endemic aster became adapted to short summers when it weathered the last Wisconsinan glaciation near the ice front.
2) *Bidens heterodoxa* grows best along edges of lagoons during dry summers when the seeds are not waterlogged (Plante et Gervais, 1995). Together with the entomological evidence, these data suggest that these plants lived under a short, dry and comparatively warm summer near a glacier front. Dry, comparatively mild boreal conditions are similar to those postulated to have been associated with glacial ice fronts across eastern North America (Hamilton, 1994). These conditions may be due to a stationary high pressure system that extended well beyond the chilling effect of the glaciers. Such species may have evolved on mainland sites and subsequently come to the Îles-de-la-Madeleine where conditions most closely mimic boreal ice-front habitats.

The known endemics may represent fragments of once-extensive ranges that were truncated by glaciation, like that of *Rosenus acutus*. But since all of them are close relatives of mainland species, allopatric speciation is more probable. The two endemic plants *Aster laurentianus* and *Bidens heterodoxa*, the native grasshopper *Melanoplus madeleineae*, the planthopper *Delphacodes* near *campestris* and the leafhopper *Oncopsis quebecensis* clearly evolved near ice fronts, but whether on the islands or on the mainland remains uncertain. The short-horned bugs *Philaenarcys spartina*, *Draeculacephala angulifera* and *D. zeae* retain, on Îles-de-la-Madeleine, an ancestral (plesiomorphic) morphology which appears to have been modified in related mainland populations. In the case of *Philaenarcys spartina* and *Draeculacephala angulifera* character displacement has differentiated sibling species where they come in contact on the mainland. In the case of *D. zeae*, northern (island) and southern (mainland) races appear to have hybridized, resulting in an intermediate-sized form in northern, mainland populations. Thus, it is noteworthy that the mainland populations seem to have changed from the ancestral form, rather than the insular populations. This suggests that the insular fauna has remained in a relatively stable environment for a short time, while the mainland populations have had to contend with changing environments and sibling rivalries.

The problem of timing can be addressed by studies of shelf bottoms. The presence of melt-water channels south of the archipelago suggests that the ice sheet there began to collapse before sea levels had risen sufficiently to overtop the Magdalen shelf. Silts indicative of shallow water (to 30 m deep) were laid down there 11 600 years ago (Josenhans and Lehman, 1999) during the Younger Dryas when willows and other boreal flora had invaded the island. Thus there was a lengthy postglacial period when world temperatures were comparatively mild and the emergent Îles-de-la-Madeleine were still a single, comparatively large land mass close to the mainland. Boreal insects could come to the islands first, and most easily, as the water gap would be narrowest when the climate was coldest.

The way the mainland fauna invaded is best shown by the high proportion of coastal insects on Îles-de-la-Madeleine compared to the few in forests and boggy areas. Trees, shrubs and their insects would have had to invade the island by wind transport. Floating mats of sea shore vegetation and their accompanying insect eggs would have been washed ashore comparatively frequently. However, salt hay is probably a fairly recent immigrant to the archipelago, since none of the bugs that specialize on it are represented there, and one generalist (*Philaenarcys spartina*) no longer feeds of salt hay on the archipelago.

Thus, all the current evidence suggests an insular fauna and flora accreted during the last 12 000 years, principally during the waning days of the Wisconsinan glaciation. ◂

1. It is possible to state with a fair degree of confidence that the blueberry leafhopper is not present on the island. *Scaphytopius vacciniu*m, formerly a synonym of *S. magdalensis*, therefore becomes the correct name for the blueberry leafhopper. *Scaphytopius magdalensis* becomes a junior synonym of *Scaphytopius acutus*. The location of the types are unknown. The original description of "*Platymetopius magdalensis*" states, "Fond jaunâtre arrosé de brun ... Dessous noir ou brun foncé." The blueberry leafhopper has a face and venter as dark brown as the dorsum, whereas males of *S. acutus* have a yellow face contrasting with the dark venter and paler brown dorsum. Females of *S. acutus* have a paler venter and a longer head, corresponding to Provancher's "*Platymetopius acutus*".

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