Biogeography of the *Jaera albifrons* superspecies (Isopoda, Asellota) on the Atlantic coast of Canada

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The biogeographical study of the four Canadian forms of the *Jaera albifrons* superspecies leads to a division into two groups. *J. (a.) albifrons*, *J. (a.) ischiosetosa*, and *J. (a.) praehirsuta* are spread along the whole Atlantic coast, from cold to temperate shores but, as in Europe, salinity and exposure affect their relative abundance. *J. (a.) posthirsuta* occurs only in the warm shallow waters protected from arctic currents. The presumably postglacial origin of its disjunct distribution is discussed.

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L'étude biogéographique des quatre formes canadiennes de la super-espèce *Jaera albifrons* amène à y distinguer deux groupes. Les espèces *J. (a.) albifrons*, *J. (a.) ischiosetosa* et *J. (a.) praehirsuta* colonisent tout le littoral atlantique, des côtes froides aux rivages tempérés, mais comme en Europe, la salinité et l'exposition influencent leur abondance respective. L'espèce *J. (a.) posthirsuta* ne se trouve que dans les eaux plus chaudes et peu profondes des rivages protégés de l'influence des eaux arctiques. L'origine vraisemblablement post-glaciaire de son aire de répartition disjointe est discutée.

Introduction

Although the superspecies *Jaera albifrons* is a common component of the shore fauna of eastern Canada, very little is known about the distribution of its various forms in this large area. The identification from the Gaspé Peninsula of three samples belonging to the species *albifrons*, *ischiosetosa*, and *praehirsuta* by Forsman (Brunel 1970*a*) and the study by Steele and Steele (1972) of a natural population of *ischiosetosa* from Newfoundland are the only reports for this area.

The Atlantic coast of Canada is a very heterogenous biogeographical region, and systematic investigations were required to establish the distribution of these species according to environmental conditions. A second problem was provided by the species *posthirsuta*, known until now only in Massachussets, where it was described by Forsman (1949) and Bocquet and Prunus (1963); the northern limit of the range of this species remained unknown.

In addition to the collections made by the author, data were supplied by loans from the Smithsonian Institution, the Marine Biology Station of Grande Rivière, and by extensive collections of the National Museum of Natural Sciences of Ottawa.

Main Features of the Region

This survey deals with the Estuary and Gulf of St. Lawrence, the southern coast of Newfoundland, Nova Scotia, and the Bay of Fundy. From a biogeographical point of view, it is a part of the subarctic boreal region, which is cooled by the Labrador current and extends south to the Gulf of Maine. Cold deep layers of seawater enter the St. Lawrence through the Laurentian Channel as far as the Saguenay Fjord and their effects are felt in the main part of the estuary. The stirring effect of the tides of the Bay of Fundy lowers the surface temperatures of this other sea arm.

Some shallow waters remain protected from boreal waters: the southwestern Gulf of St. Lawrence and the Minas Basin have warm waters in summer, with relatively low salinities, contrasting with the boreal euhaline areas (Lauzier *et al.* 1951; Bousfield 1962). Otherwise, the outflow of the St. Lawrence River gives the estuary a decreasing salinity from seawater landwards to freshwater, mainly south from the Saguenay Fjord, and with an abrupt change between baie St. Paul and Rivière du Loup (Lavoie and Beaulieu 1971). South of this last limit is a low-salinity brackish subregion that is also warmed in summer (Bousfield 1955).

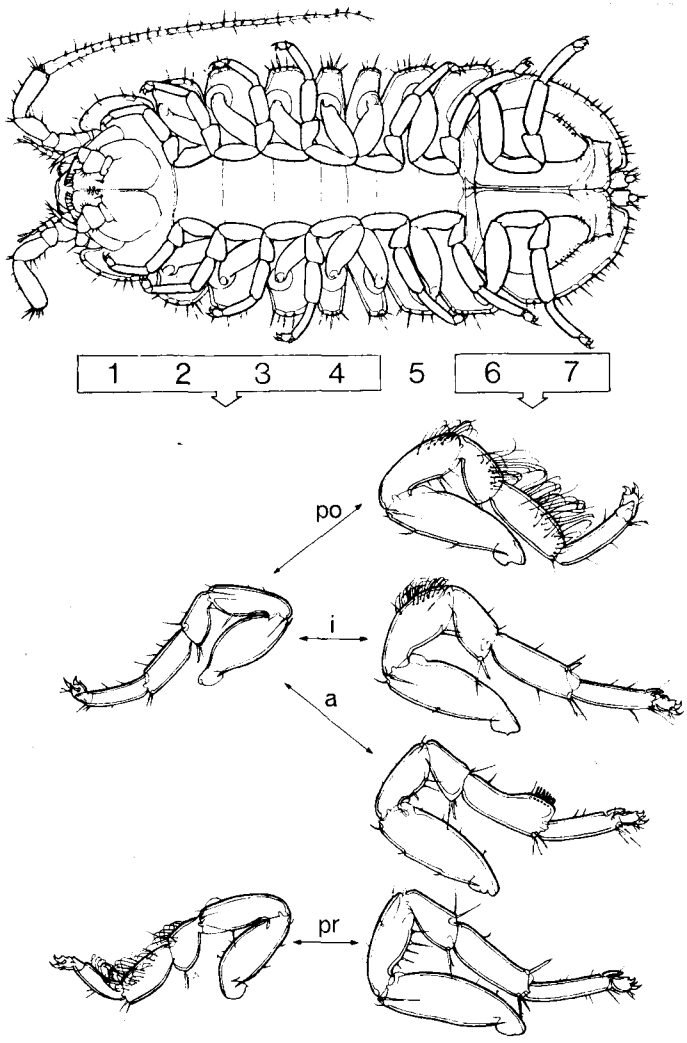

FIG. 1. Key to males of Canadian species of *Jaera*. Top, male in ventral view; 1, 2, 3, 4: four anterior pairs of pereopods; 6, 7: two posterior pairs of pereopods; *po*, *Jaera* (*albifrons*) *posthirsuta*; *i*, *J.* (*a.*) *ischiosetosa*; *a*, *J.* (*a.*) *albifrons*; *pr*, *J.* (*a.*) *praehirsuta*.

Salinity and surface temperature are important factors in the biology of intertidal invertebrates, and all these features divide the coast into subregions with different physical conditions. Since they are close to the boundaries of two biogeographical provinces, the subarctic boreal and the temperate ones, they provide a shelter to animals of various origins and they determine a mosaic of faunal elements superimposed on corresponding heterogenous environmental factors. They may be useful in the study of the main factors that act on the distribution of the littoral species; their effect on the different forms of the *Jaera albifrons* group is obvious.

Canadian Species of Jaera albifrons

Jaera albifrons are minute isopods from 1 to 5 mm in length; they live intertidally beneath stones or on *Fucus*. They show a conspicuous widening of their lateral margins, and their minute biramous uropods seem to emerge posteriorly out of a pleotelson notch (Fig. 1, top). The T-shaped praeoperculum of males is another fairly distinctive feature of the superspecies.

Jaera albifrons (Leach) was split by Forsman (1949) and Bocquet (1953) into five sibling forms, which the latter recognized to be true species. Four of these forms occur on the eastern coast of Canada and show no mor-

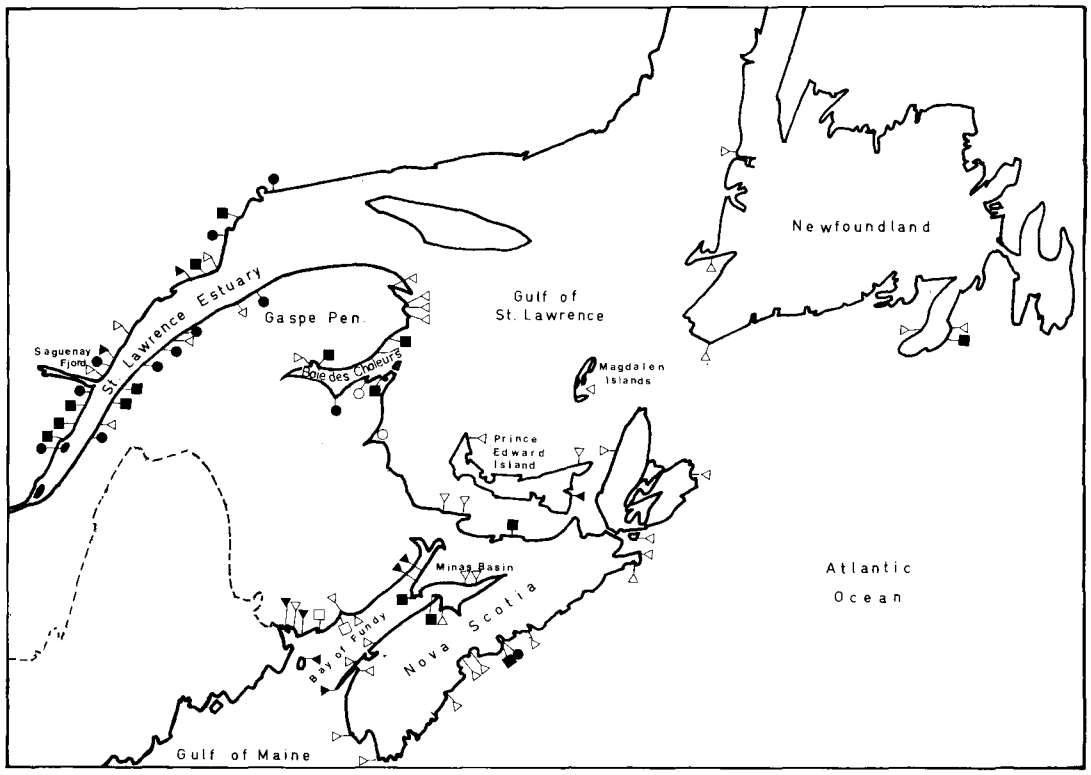

FIG. 2. Distribution of *Jaera (albifrons) ischiosetosa*. △▲ stations with one recorded species of *Jaera albifrons*; □■ stations with two sympatric species; ○● stations with three sympatric species; ▲■● stations of *ischiosetosa*.

phological difference from previously described populations. They may be identified by the secondary sexual characters of the pereopods (Fig. 1) in the males.

In species lacking anterior differentiations, the sixth and seventh pairs of pereopods bear long setae from ischiopodite to carpopodite (*Jaera* (*a.*) *posthirsuta*), or a brush of long curved setae on a distally broadened ischiopodite (*Jaera* (*a.*) *ischiosetosa*), or a distal lobe with a comb of short setae on the carpopodites (*Jaera* (*a.*) *albifrons*). The only species with anterior differentiations (*Jaera* (*a.*) *praehirsuta*) possesses long curved setae on pereopods 1 through 4 (except in young males) and a stout distal spine on the two last pairs of carpopodites.

Variations occur among Canadian populations in the expression of these characters, without affecting the certainty of their determination (e.g. graduations in the length of the lobe in *albifrons*, and in the number of setae in *praehirsuta*, and extension, in large specimens, of the secondary sexual characters to other legs). Such variations were previously reported from European and American representatives of these species, and appear to be expressions of a natural intraspecific variability within each form (see Bocquet 1953; Bocquet and Veuille 1973; Prunus 1966, 1968; Solignac 1967).

Only one F_1 hybrid, *albifrons* × *ischiosetosa*, was found at the Pilot Station (Quebec North Shore).

Jaera albifrons is widespread throughout the eastern coast of Canada, and 157 different stations were recorded, but it is misleading to look at a mixing of species as a whole, and the 124 stations that are known to the species level (*ischiosetosa* (36), *albifrons* (34), *praehirsuta* (41), and *posthirsuta* (13)) are a good illustration of this.

Jaera (albifrons) ischiosetosa (Fig. 2)

This form is found all over the coast with abundance varying according to the subregion. Most of the samples come from the St. Lawrence Estuary (19 out of 36). Numerous popula-

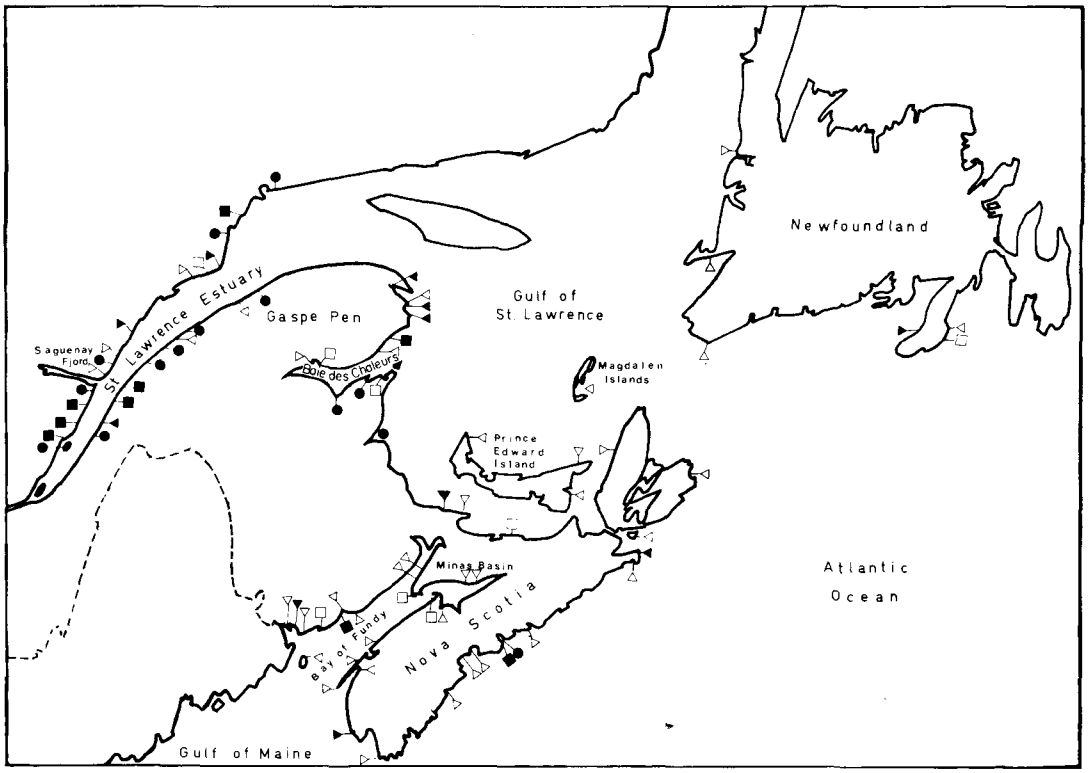

FIG. 3. Distribution of *Jaera (albifrons) albifrons*. △▲ stations with one recorded species of *Jaera albifrons*; □■ stations with two sympatric species; ○● stations with three sympatric species; ▲■● stations of *albifrons*.

tions have also settled in the Bay of Fundy and la baie des Chaleurs. These are sheltered areas with variable temperatures and salinities (down to 10‰ in the southern Estuary of St. Lawrence, at Ile aux Coudres).

In contrast, very few *ischiosetosa* were collected on exposed shores, such as the southern coast of Nova Scotia. The two populations known from this subregion were found in the estuary of Halifax harbour and in an isolated rock pool. Both stations are presumably refuges for this organism, and since such places occur in a scattered way along the shore, they may lead to an underestimation of its true abundance in exposed areas.

We conclude that *ischiosetosa* is a eurythermal and euryhaline species, occurring from euhaline to mesohaline waters (according to the 'Venice system') and living in sheltered places. Similar ecological characters are reported from European populations of this species.

Jaera (albifrons) albifrons (Fig. 3)

The distribution of this form is very similar to that of *ischiosetosa*, since there appears to be no exclusion regarding salinity or temperature. *J. (a.) albifrons* is well represented in the St. Lawrence Estuary (19 out of 34 populations) and sparse on the Atlantic coast of Nova Scotia. Nevertheless, it has been recorded in several stations of the eastern coast of the Gaspé Peninsula, and is significantly less common in the Bay of Fundy. This scarcity cannot be explained from the factors analyzed at the very macroscopic level of this survey. The ecological preferences of Canadian populations of *albifrons* with regard to main physical factors are very close to those of European ones.

Jaera (albifrons) prachirsuta (Fig. 4)

The prominent characteristic of this species is its dominance along the exposed shores of southern Nova Scotia and the coasts of New-

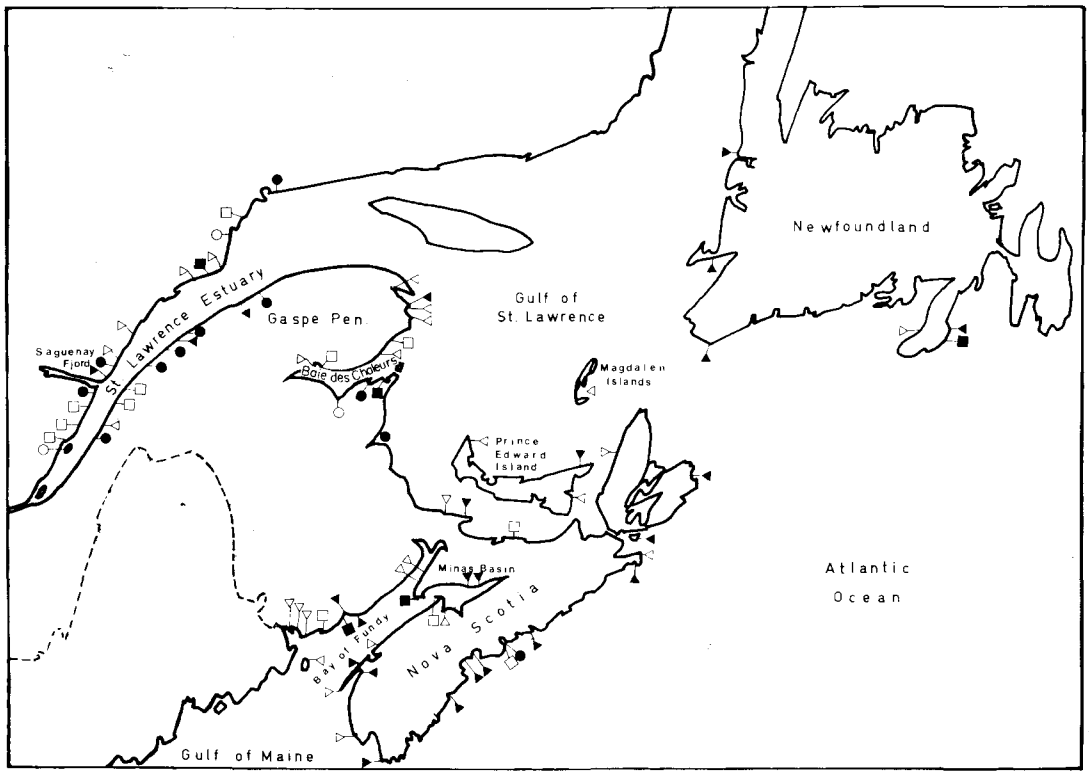

FIG. 4. Distribution of *Jaera (albifrons) praehirsuta*. △▲ stations with one recorded species of *Jaera albifrons*; □■ stations with two sympatric species; ○● stations with three sympatric species; ▲■● stations of *praehirsuta*.

foundland. It is well represented in the Bay of Fundy, but, in contrast to *albifrons* and *ischiosetosa*, it is poorly established in the St. Lawrence Estuary, where it is confined to the northern part. This limit corresponds to the end of the Laurentian Channel, off the mouth of the Saguenay Fjord, where oceanic waters no longer maintain high-salinity brackish conditions through blending with upper layers. Only one population was recorded in the southern estuary ($20^{o}/_{oo}$ salinity). Although this might have been achieved through competition with other forms, *praehirsuta* is obviously limited to euhaline and polyhaline waters. All these features unite the North American and European representatives of this species.

Jaera (albifrons) posthirsuta (Fig. 5)

There is an obvious difference between the distribution of this form and those of its sister species. It is absent in all the cold boreal waters of the St. Lawrence Estuary, the Gaspé Peninsula, Newfoundland, Nova Scotia, and the Bay of Fundy and occurs only in the Virginian refuges of la baie des Chaleurs, the southwestern Gulf of St. Lawrence, Prince Edward Island, Magdalen Islands, and the Minas Basin. Its presence at Ile aux Coudres, in the southern St. Lawrence Estuary, is in agreement with its limitation to warm shallow waters. There is only one atypical population north of Digby, in the Bay of Fundy. This is the typical disjunct distribution of the relict populations of a temperate thermophilic species.

We may add that it is a euryhaline organism (down to mesohaline waters), yet the brackish and sheltered nature of the Virginian shallow waters of Canada does not tell us whether or not it can live in pure seawater and on an exposed shore.

Discussion

On the basis of the preceding observations, the Canadian species of *Jaera* may be divided

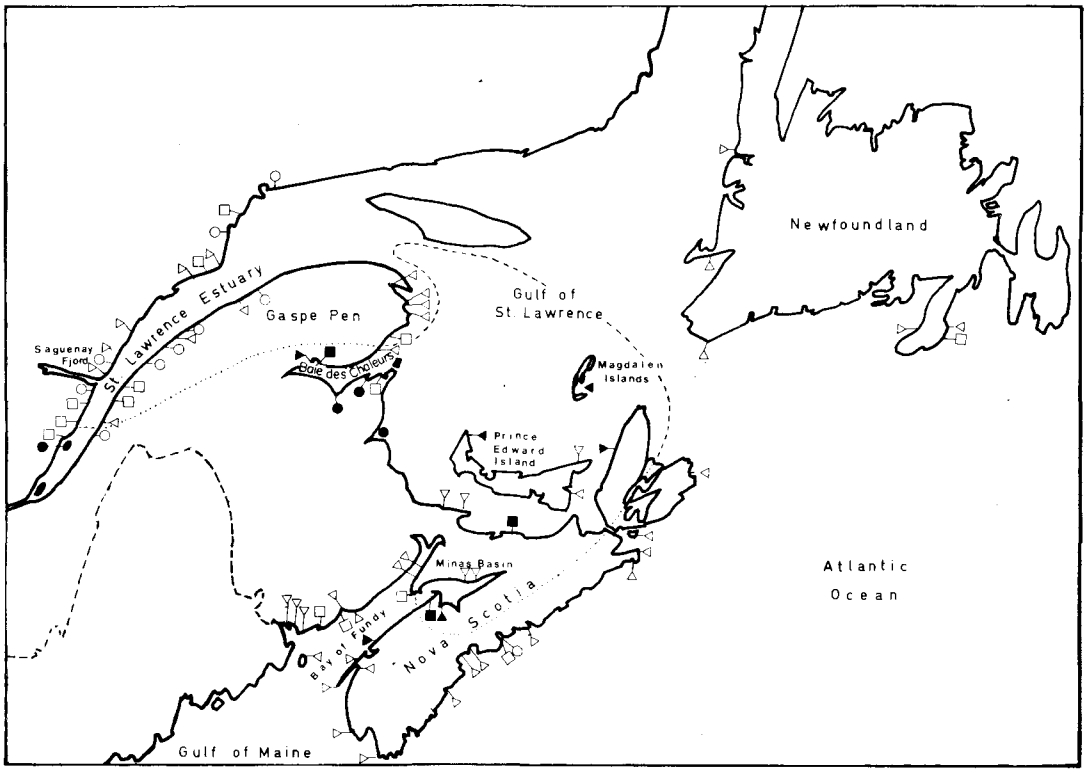

FIG. 5. Distribution of *Jaera (a.) posthirsuta*. △▲ stations with one recorded species of *Jaera albifrons*; □■ stations with two sympatric species; ○● stations with three sympatric species; ▼■● stations of *posthirsuta*; · · · limit of warm surface temperature in summer (arbitrarily set at 15 °C in August).

into two groups: (1) *ischiosetosa*, *albifrons*, and *prachirsuta*; and (2) *posthirsuta*.

J. (a.) ischiosetosa, *albifrons*, and *praehirsuta* are amphi-Atlantic species, well acclimatized to boreal and temperate waters of both sides of the ocean, and of Greenland, Iceland, and the British Isles. The ecological preferences they show on the oceanic coasts of France and Great Britain are consistent with their distribution along the shore of Canada. The decreasing euryhalinity from *ischiosetosa* and *albifrons* to *praehirsuta* is noted by Bocquet (1953) and Naylor (1972) and emphasized by physiological experiments carried out by Jones (1972*a*, 1972*b*). Their distribution regarding exposure agrees with observations made by Bocquet in Brittany and, on the whole, it is noteworthy that the rough inventory on a large scale is in agreement with the careful study of their microhabitat.

On the basis of these few characteristics and from morphological data, we can conclude that no striking differentiation or speciation occurred between European and North American representatives of these species. Furthermore, Canadian forms show even more similarity to oceanic European populations than do those inhabiting the Baltic Sea, where, for instance, *praehirsuta* withstands the very dilute seawater of the Bothnian Bay (Haahtela 1965) or of the Bay of Puck (Jazdzewski 1969).

In contrast, *posthirsuta* is a temperate American endemic species. It lives more or less sympatrically with each of its sibling species all along its range, and does not extend further south (according to observations made by Hoestlandt in the United States), but it is strikingly limited northward. Its situation appears to parallel that of *Jaera (a.) forsmani*, which is known only from Brittany (Bocquet 1953) and from the British Isles (Jones and Naylor 1971).

The main feature of this organism is a clear-cut division of its range into two groups of populations of nearly similar extent. The former inhabits the coast of New England northward to the southern Gulf of Maine (the National Museum of Natural Sciences owns samples

from Cape Neddick and Magnolia Beach, and Bocquet and Prunus (1963) report it from south of Boston). The other group lives in the warm pockets of Acadia, and gives rise to an interesting problem, since it cannot have settled there before the melting of the North American ice cap of the 'classical Wisconsin,' about 15 000 years ago.

A consideration of the flora (Fassett 1928) and of the invertebrate fauna (Ganong 1890; Bousfield and Laubitz 1972), of the Gulf of St. Lawrence also poses this problem, to which Fassett (1928) and Bousfield (1962) have contributed to give an attractive solution. According to them, a postglacial transgression submerged the Isthmus of Chignecto, separating the Bay of Fundy from the Northumberland Strait, during the warm thermal optimum, 10 000 – 6000 years ago. The diversion of the Labrador current by the presumably raised banks of the continental shelf offered temperate species a sheltered way northward (Bousfield 1973) and the spreading of *posthirsuta* populations out of their previous range is likely to have happened at that time; the subsequent isostatic rise of the Isthmus of Chignecto cut off this way, while the uplift of the sea level submerged the banks, opening the way to cold currents into the Gulf of Maine. This sequence of events leads to the cohabitation of two faunas, a situation that occurs within the superspecies *Jaera albifrons*.

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