AN ALASKAN LEAFHOPPER THAT LIVES NORMALLY BENEATH ICY TIDAL SUBMERGENCE^{1, 2, 3}

DWIGHT M. DELONG

The Ohio State University

ABSTRACT

A leafhopper of the Macrosteles fascifrons (Stal) complex lives on an alkali grass, Puccinellia nutkaënsis (Presl) Fern. & Weath., on the tidal flats of Muir Inlet in Glacier Bay, Alaska. The tidal water, with icebergs and a temperature of approximately 1° C, covers the grass twice daily and the leafhoppers in all stages—egg, nymph, and adult—survive beneath the water for extended periods of time. The winged adults do not attempt to leave the plants when the tidal water begins to submerge them and none were obtained from vegetation surrounding the tidal flats either before or after submergence.

Two publications have discussed insects of the "between tide zone". Arndt, in 1914, made observations on a fulgorid, *Megamelus marginatus* Van Duzee, which he inadvertently called a leafhopper.

Metcalf and Osborn, in 1920, studied the insects of the tidal zone at Wrightville Beach in North Carolina, and observed certain of the Homoptera, especially *Deltocephalus marinus* Met. and Osborn, feeding on grasses at low tide, which vegetation was normally covered by the high tide twice daily. They made no specific observations, but concluded that "there is every reason to assume that the whole life cycle is associated with the grass and although we have not had opportunity to determine as to place of egg deposition or the development of the young, we are confident that all these stages will be found associated with this plant when the necessary observations can be made" (Metcalf and Osborn 1920, p. 111).

During the summer of 1965, an opportunity was presented to work with The Ohio State University Institute of Polar Studies in Muir Inlet, Glacier Bay, Alaska. The Muir Glacier has been retreating rapidly, and accurate data regarding the rate of retreat have been recorded over the past seventy-seven years. Consequently this area offers an unparalleled opportunity for studies of soil development, repopulation by plants and animals, and the succession of biologic associations.

The field study covered some thirty-two kilometers of Muir Inlet, extending

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DWIGHT M. DELONG

Vol. 70

north from approximately the junction of Adams and Muir Inlets to the present glaciers and representing the land newly deglaciated during the last seventy-five years. At its southern end are the ruins of Muir cabin, which was at the base of the Muir Glacier in 1892. The writer was responsible for studying both the insects present in this recently deglaciated area and the succession of insect associations which occurred during this seventy-five years of recession. The summary of this work was published as an Ohio State University Research Foundation report (DeLong, 1966).

During the period of field study and observations, while attempting to observe and secure samples of insect populations in all of the habitats represented, I came upon Goose Cove, a small but prominent cove of Muir Inlet, not far from the gull rookery known as Sealer's Island. At low tide, Goose Cove has a long, gradually

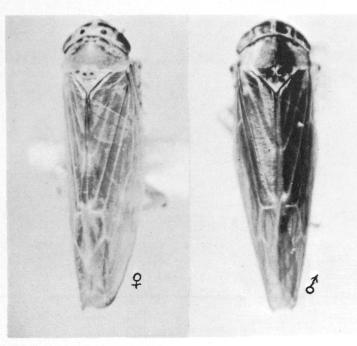


FIGURE 1. Dorsal view of \mathcal{Q} (left) and \mathcal{O} (right) of *Macrosteles fascifrons* (Stal.). (Photomicrographs by Alvah Peterson).

sloping tidal flat, well covered with a rather dense carpet of an alkali grass, *Puccinellia nutkaënsis* (Presl) Fern & Weath. A high high tide of some eighteen feet covers this grass almost completely, while a low high tide submerges a large percentage of this area. Living upon this mat of grass was found an abundant population of leafhoppers of the *Macrosteles fascifrons* (Stal) complex. Adults of both sexes were found in abundance and all stages of the nymphs were observed and collected. Two other members of the party, Dr. E. E. Good and Mr. Don Frickie, who were responsible for observations on the birds and mammals, were with me at the time this tidal flat was first discovered and assisted me in observing what transpired when the high tide submerged this area a few hours later. To our surprise, the adult leafhoppers did not attempt to escape the submergence of the icy tidal waters and remained stationary upon the vegetation. The water contained numerous icebergs, large and small, many of which remained on the

grass as the tide receded, as shown by the accompanying illustration (fig. 2); the temperature of the water was approximately 1° C.

The following day this area was revisited just before the predicted time of the high tide submergence and a number of white cloths were spread upon the grass surrounding several clumps of grass which contained rather heavy populations of leafhoppers. During careful observations made from stations in the water, no leafhoppers appeared to leave these plants as they were submerged. In addition, vigorous collecting on all the vegetation surrounding the tidal flat during the period of submergence produced no specimens of these leafhoppers. At the time of tidal recession, we walked out to the submerged plants, remained until the water had receded and immediately collected active leafhoppers from the grass. Similar observations were made at Bartlett Cove, Alaska, some 50 kilometers south of Muir Inlet, but there no icebergs were present in the water.



FIGURE 2. Tidal flat showing dense growth of *Puccinellia nutkaënsis* (Presl) Fern & Weath. with icebergs left by a receding tide.

Although lack of time prevented complete observations of the life cycle of this insect, the eggs are apparently laid upon the grass. The nymphs appear to hatch and remain in this periodically submerged habitat during their period of growth and development, and the resultant adults do not attempt to leave this habitat, although their wings are fully developed and functional.

An interesting observation made during the limited time available for study was that there was a relationship between leafhopper population size and the degree of tidal submergence. As mentioned above, the tidal flat was gradually sloping and at least one hundred meters long, and the percentage of grass submerged varied from day to day. The largest populations of leafhoppers were observed at the middle of the tidal flat, where the grass was submerged by each high tide, usually for a minimum of an hour, depending upon the day of the tidal periodic cycle. The areas of greatest submergence and those of least submergence, including the grass often not submerged, supported the smaller populations.

Genitalically the leafhopper specimens agree with the species now designated

No. 2

as *Macrosteles fascifrons* (Stal). However it is difficult to believe that this is exactly like the species (fascifrons) which is the vector of aster yellows virus, or the tropical form described as M. scriptus (DeLong) and now placed in fascifrons, especially since M. scriptus living in a subtropical habitat, instead of ice water, is only 2.5 mm long (in contrast to the 5.1 mm length of this Alaskan form).

The *Macrosteles fascifrons* complex as now recognized by taxonomists (Beirne, 1952) is geographically distributed from Mexico and Puerto Rico to Alaska As thus interpreted, *fascifrons* is composed of a great variety of genetic mutants which vary in size and coloration, cannot be separated morphologically, but which differ biologically, physiologically, and ecologically.

Beirne (1952, p. 224), after a detailed study of all of the material in the genus *Macrosteles*, states, "It is possible that some of the forms may be physiological species that are poorly defined morphologically. The wide range of the complex as a whole and the apparent habitat differences between different forms indicate this." He further states, "It is possible that some of the forms may represent populations that are or were isolated ecologically from other populations and that developed independently during their isolation, though not to the species level. It may be significant that the largest number of local forms are in ecologically diverse regions, as in the mountains of the west. Moreover, the habits appear to be relatively sedentary, which would favour isolation: Linn (1940) found that the common form of [M. fascifrons in] the eastern United States did not spread in perceptible numbers more than 200 feet in four weeks."

Severin (1940) was unable to interbreed a short-winged form from the Montera Mountains, California, with a long-winged eastern United States form and, in correspondence, urged that it be described. The best characteristics for separating closely related species are those which the insects use themselves, one of which is mating response. If two populations will not interbreed, they must be considered to be distinct biological forms, and genetic species, regardless of morphological similarities.

The Alaskan ice-water, *Puccinellia* form is certainly severely selected and specifically adapted to live in an unusual leafhopper environment. It has become ecologically isolated and, like the short-winged biological form, deserves a subspecies name.

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