The Great Lakes Entomologist

Volume 3 Number 3 -- Fall 1970 Number 3 -- Fall 1970

Article 2

July 2017

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Cantrall, Irving J. 2017. "Appalachian Orthopteron Relicts in Michigan," *The Great Lakes Entomologist*, vol 3 (3) DOI: https://doi.org/10.22543/0090-0222.1124 Available at: https://scholar.valpo.edu/tgle/vol3/iss3/2

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APPALACHIAN ORTHOPTERON RELICTS

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I have recently plotted the known Michigan distribution of the various species of Orthoptera which occur in the state (Cantrall, 1968). When this distribution of any single form is compared with its range, it is usually quite clear by what path the insect reached Michigan.

There are species which are so wide-ranging that Michigan lies within the boundaries of their overall distribution. Also, some taxa, ranging to the north, reach a southern limit in Michigan. *Melanoplus huroni* Blatchley is a good example of a species with the latter type of distribution. Other species, such as *Metaleptea brevicornis brevicornis* (Johannson), with ranges to the south, reach a northern limit in the state. In each of these cases, and probably with most other species with similar distribution, demes close to the limits of distribution tend to be under ecological stress, and, as a result, the species may occupy marginal or less than optimal habitats, or may occur as relict populations.

There are orthopterous species, such as *Schistocerca emarginata* (Scudder), *Phoetaliotes nebrascensis* (Thomas), and *Ageneotettix deorum deorum* (Scudder), which have less obvious origins. Several of these reached Michigan from the west during the Xerothermic Period of the Pleistocene. Others moved from the east by way of the Mohawk - Hudson Valley during the recession of the Wisconsin Glaciers. These last two modes of invasion have been commented upon by Hubbell (1960; 57-61).

The evidence is strong that many species now confined to the southeastern United States, or to the Appalachian area in general, at one time enjoyed a much wider distribution to the west and to the north. Changing climates resulted in extirpation or withdrawal, leaving relict populations. Hubbell (1960; 60-61) pointed out that following the recession of the Pleistocene ice, several species such as *Odontoxiphidium apterum* Morse, *Conocephalus allardi* (Caudell), and *Tettigidea prorsa* Scudder, with present - day southern and southeastern distributions, were able to move northwardly as far as Allardt, Tennessee, where relict populations of these species exist today.

The northward extension and retraction of the ranges of animals following the recession of the glaciers could have been more extensive than Hubbell has indicated. If this is true, several present-day disjunct orthopteron distributional patterns extending far north of Tennessee may be explained in this manner. For instance, I have taken *Melanoplus decoratus* Morse in southern Indiana. This grasshopper ranges through the Appalachians from Georgia and Alabama to Virginia. It is known from Cocke and Fentress Counties in Tennessee, and has been taken by E.S. Thomas at several localities in southeastern and central Ohio. My specimens, taken in Orange and Monroe Counties, Indiana, probably represent disjunct and relict demes.

There are several species of Orthoptera with disjunct populations in Michigan, or which are closely related to taxa with all, or part of their ranges centered in the Appalachians. I believe that their relationships can be explained in terms of post-glacial range extensions and contractions.

SOME ORTHOPTERON RELICTS IN MICHIGAN

Appalachia arcana Hubbell and Cantrall is known only from the sand plains area of the northern part of the Lower Peninsula of Michigan (Fig. 1). As indicated by Hubbell and Cantrall (1938), arcana is closely related to Appalachia hebardi Rehn and Rehn. A. hebardi occurs in the mountains of east-central Pennsylvania, east-central West Virginia, and west-central Virginia.

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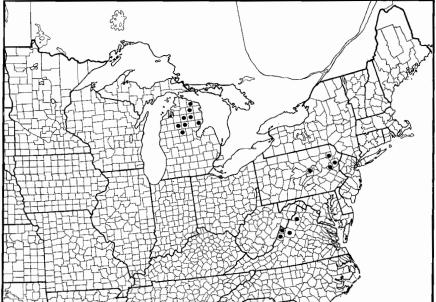


Fig. 1. Distribution of the genus Appalachia. Based upon the literature and UMMZ specimens. In northern Lower Michigan, arcana; in the Appalachians, hebardi.

Atlanticus davisi Rehn and Hebard is disjunct in Michigan where its distribution is limited to the northern part of the Lower Peninsula (Fig. 2). It is a common species in the Appalachians. Westwardly, it is locally distributed through central and southern Ohio, has been taken at several localities in southern Indiana, and has been recorded from Keokuk in extreme southeastern Iowa. It has not yet been reported from Illinois.

Although having different ecological requirements, *Melanoplus viridipes eurycercus* Hebard (Fig. 3) is sympatric with *Appalachia arcana* and *Atlanticus davisi* in Michigan. This subspecies of *viridipes* also occurs in the Appalachians from northwestern Vermont to extreme northwestern North Carolina, thence westwardly through eastern and southern Ohio. *M. viridipes viridipes* Scudder is found in the western portions of the Upper Peninsula of Michigan, and in Wisconsin, Illinois, Minnesota, and Iowa. Intermediate stocks are known to occur through much of Indiana and into southwestern and southern Michigan. E.M. Walker and Urquhart (1940; 18) reported specimens of *viridipes* from Leamington, Ontario. They indicated that E.S. Thomas considered this material to be intermediate between the nominate form and *eurycercus*. Vickery and Kevan (1967;46) repeat this record, and report *viridipes* without subspecific indication from Maynooth, Ontario. Maynooth is almost due north of Rochester, New York, and over 300 air miles northeast of Leamington.

Melanoplus punctulatus (Scudder) (Fig 4) is represented in the southern half of the Lower Peninsula of Michigan by the subspecies griseus (Thomas). Although the nominate form occurs far to the east, demes of *punctulatus* in the northern half of the Lower Peninsula are made up of intermediates between *punctulatus* and griseus.

The Tamarack Tree Cricket, *Oecanthus laricis* T.J. Walker, occurs in Livingston and Oakland Counties, Michigan, and, again, in Lake County in extreme northeastern Ohio. The closely related Pine Tree Cricket, *O. pini* Beutenmuller, is known to occur from Maine southwardly to Mt. Cheaha, in Alabama (T.J. Walker, 1963). Outlying populations have been noted in east Texas, in Mississippi, and in western Florida. T.J. Walker also plots several localities for *pini* in southeastern Ohio. He writes (T.J. Walker; 776) that "There are

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no Canadian records for *pini*," although Urquhart (1942;97) states that he found this species at Turkey Point, Ontario where it was taken on white, red, and jack pines. O. laricis has been taken on tamarack and hemlock; *pini* seems to be limited to species of pine and to balsam fir.

DISCUSSION

There is little doubt that the present distributions of the Orthoptera discussed above are owing to the effects and influences of the Pleistocene Glaciers. The eastern and western subspecies of *Melanoplus punctulatus* and of *M. viridipes* were more than likely produced by an advancing glacial front. Ancestral populations of these species probably occupied much of the northeastern United States. Advancing ice sheets, probably the Wisconsin, isolated the eastern and western populations long enough for them to differentiate into the subspecies recognized today. Other species, such as *Melanoplus decoratus, Appalachia hebardi, Atlanticus davisi,* and *Oecanthus pini,* occurred in the Appalachians during pre-Wisconsin times. As the last glacial advance of the Wisconsin began to melt back, plants and animals followed the retreating ice as new and suitable environments became available. Subsequently, climatic changes produced shifts in distribution as plants and animals responded to changing ecological conditions.

The brief hypothetical history of the changes in distributions of the several Orthoptera discussed below conforms rather well with distributional changes in the ranges of some vertebrate populations as postulated by Smith (1957). It was probably during the Climatic Optimum Period following recession of the Wisconsin Glaciers that the Orthoptera which now exist as isolates in Michigan inhabited the hiatus so evident today. The development of the Climatic Optimum Period was characterized by the northward movement of vegetation into areas previously occupied by ice. Tundra was succeeded by spruce and fir forest, and this, in turn, was replaced by oak, beech, hemlock, and elm. The climate gradually changed from cool and humid to hot and dry as the Climatic Optimum Period gave way to the

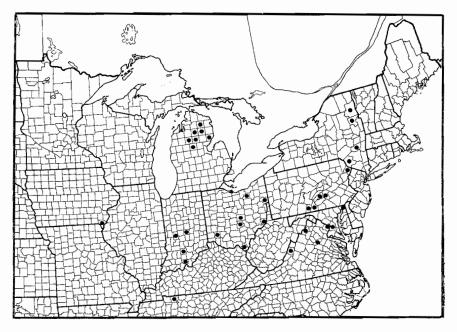


Fig. 2. Distribution of Atlanticus davisi. Based upon the literature and UMMZ specimens.

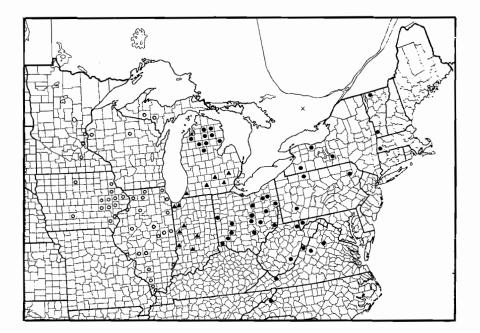


Fig. 3. Distribution of Melanoplus viridipes. Based upon the literature and UMMZ specimens. Symbols: solid dots, viridipes eurycercus; circles, viridipes viridipes; triangles, intermediates between viridipes viridipes and viridipes eurycercus; x, Canadian records.

Xerothermic Period. Orthoptera which were able to extend their ranges under ecological conditions produced by a cool and humid climate were subsequently extirpated in the portions of their ranges where a hotter and drier environment was created during the Xerothermic Period.

Of the species discussed above, Melanoplus punctulatus and Melanoplus viridipes now range as far north as Minnesota and Maine. Oecanthus pini, although more eastern, also ranges as far north as Maine. Since northern demes of these species are now adapted to colder conditions, and at least two of them, punctulatus and pini, are associated with conifers, it is reasonable to assume that these species rather closely followed the retreating ice sheets. Migrants from the eastern populations of punctulatus, eurycercus, and pini moved northwardly and westwardly until they reached the northern part of the Lower Peninsula of Michigan. Some probably moved from southern Michigan eastwardly between the upper and lower bays of Glacial Lake Lundy, and on into Ontario. Taylor (in Leverett and Taylor, 1915:399) states that "... the waters of the Lake Huron and Erie Basins were connected by a shallow strait, which varied greatly in width and at one or two constricted points was so narrow and shallow that it may have had a slowly flowing current, though not one sufficient to constitute a river in the ordinary sense . . . " He mapped (Leverett and Taylor, 1915; Plate XXXI) a large number of post-glacial distributaries associated with what is now the Detroit River Channel. These are located in southeastern Wayne County, Michigan, and could have provided the route by which punctulatus, eurycercus, and pini reached Canada. In early post-Wisconsin times access to Ontario from the east for these species would have been blocked, first by ice, then by the Mohawk-Hudson Glacial Drainage, and finally by the Champlain Sea; each of these serving as barriers as the ice receded. Farther to the east these three species were able to push north into New England, and to the west the Western components of punctulatus (Fig. 4) and of viridipes (Fig. 3) spread to the north as far as Minnesota, and to the east into Illinois where the drainage from

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Glacial Lake Chicago may have slowed, if not temporarily stopped, eastward movement.

As the Climatic Optimum Period developed, Melanoplus decoratus, Appalachia hebardi, and Atlanticus davisi were able to extend their ranges. A. davisi reached as far as Iowa, and, with A. hebardi, as far as the northern part of the Lower Peninsula of Michigan where the Straits of Mackinac probably eventually served as a barrier. How far M. decoratus got is problematical, but this species must have moved considerably farther than its present range would indicate. Appalachia hebardi and Atlanticus davisi were not able to reach Ontario because by the time these species were able to extend their ranges, the drainage of melt waters had shifted from the North Bay Channel to the present Great Lakes Drainage by way of the St. Lawrence River.

Following the maximum range extension to the north made by the orthopteron species here discussed, some factor, or factors caused a reduction of, or shift in the ranges of these taxa. The development of the Xerothermic Period seems to be the most logical reason for these changes. Changes in climate resulted in changed ecological conditions some of which were untenable in varying degrees and in varying locals to the several orthopteron taxa. Demes effected by the conditions of the Xerothermic Period were extirpated and discontinuities were created in the distributions of the species.

Demes of Appalachia hebardi, left behind as relict in the northern part of the Lower Peninsula, as today, were probably small and widely scattered over a limited area. Small populations and limited range probably contributed strongly to rapid evolutionary change, and differentiation to arcana was accomplished. Relict stocks of Oecanthus pini in southeastern Michigan and Northern Ohio underwent change in much the same way and for the same reasons, giving rise to O. laricis. It will be most interesting to see whether or not the specimens from Turkey Point, Ontario reported by Urquhart in 1942 are laricis as described by T.J. Walker in 1963.

Relict populations of Atlanticus davisi and Melanoplus eurycercus were also left behind in

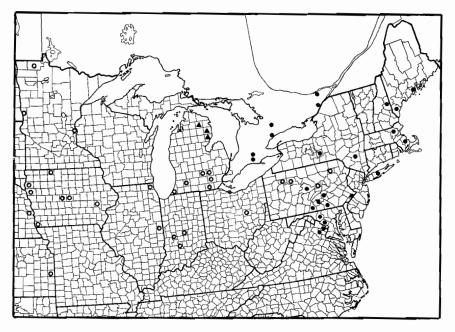


Fig. 4. Distribution of Melanoplus punctulatus in northeastern United States. Based upon Rehn (1946), Vickery and Kevan (1967), and specimens in the UMMZ. Symbols: solid dots, punctulatus punctulatus; circles, punctulatus griseus; triangles, intermediates between punctulatus punctulatus and punctulatus griseus.

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northern Lower Michigan. Subsequently *eurycercus* spread westwardly and *viridipes* eastwardly until they met and interbred in Indiana. Intermediate populations then spread northeastwardly into southwestern and southern Michigan, probably following the Wabash Drainage. Low vagility, or, more likely, ecological barriers prevented the flow of these intermediate stocks as far north as the northern portion of the Lower Peninsula where *eurycercus* lives today. Critical re-examination of specimens from Leamington and Maynooth, Ontario may well show that these demes are made up of *eurycercus*, although there is a possibility that intermediate stocks have been able to move across the Detroit River to nearby Leamington. *Atlanticus davisi* suffered a distributional hiatus as great as that noted for *Appalachia*. Since the relict demes of *Appalachia* were able to speciate in northern Lower Michigan, it is possible that the relict *davisi* stocks no longer represent true *davisi*.

Melanoplus punctulatus is a long-winged species, and hence much more vagil than the previously discussed species. However, the species and its relatives show a predeliction for conifers and this may have a retarding effect upon range expansion.

As in the case of *Melanoplus viridipes, Melanoplus punctulatus* reextended its range, probably following the Xerothermic Period. The western form, griseus, moved eastwardly through Indiana and Ohio until it reached Pennsylvania, Virginia, and Maryland where, according to Rehn (1946; 249-250, 259), some interbreeding with the nominate form must have taken place. In Michigan griseus stocks occupied the southern portion of the Lower Peninsula, and flooded into the northern portion where it encountered and swamped the relict populations of the eastern form, *punctulatus*.

Additional collecting to determine the complete ranges of the several orthopterons discussed in this paper may somewhat alter the hypothesis which I have proposed. This may be particularly true of findings in southern Canada. However, it seems clear that a portion of the Michigan Fauna has distinct affinities with the Appalachian Fauna.

ACKNOWLEDGMENT

I am much indebted to Martha B. Lackey for the preparation of the figures.

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