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**SYSTEMATIC AND BEHAVIORAL STUDIES ON THE
MEADOW GRASSHOPPERS OF THE
ORCHELIMUM CONCINNUM GROUP
(ORTHOPTERA: TETTIGONIIDAE)**

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VARIOUS species have been included in the *Orchelimum concinnum* group, seven by Blatchley (1920) and two by Rehn and Hebard (1915). In this paper we discuss three species which form the core of the group, however it is constituted, but which have been treated in different ways by earlier investigators—usually as subspecies or other categories within a single variable species.

Orchelimum concinnum was described by Scudder (1862) from Cape Cod, Massachusetts. In 1891, Bruner described *O. delicatum* (as *gracile*, a homonym; see Bruner, 1892) from Nebraska, from “about the margins of ponds and along the edges of streams where it frequents rank growing grasses and sedges” (p. 71). Blatchley (1893) described *O. campestre* and *O. indianense* from northern Indiana.

Rehn and Hebard (1915) treated *campestre*, *indianense*, and *delicatum* as synonyms of *concinnum*, though, as Blatchley pointed out in 1920, they were forced to bring *concinnum* out at two different points in their key owing to the difference in relative lengths of the ovipositor and hind femora of western (*delicatum*) and eastern (*concinnum*) specimens. They considered the dark red stripe down the middle of the face of some specimens useless as a taxonomic character, stating that immature individuals kept under observation did not develop the red stripe until after they had molted to adulthood and had become thoroughly hardened. This conclusion apparently was based on an

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observation by Hebard, who stated in 1934 (p. 214) that a single, large immature from Ventnor, New Jersey, had an immaculate face until after its molt to adulthood when "a heavy red-brown vertical stripe gradually appeared on its face."

Concerning what they called *concinnum*, Rehn and Hebard (1915) stated (p. 60): "The present species is probably the most variable, as it is the most widely distributed, form in the genus The present authors have given more time and consideration to it than to any other member of the genus, and after the most critical examination of the specimens in hand and a careful testing of the evidence on which the numerous synonyms were erected, we are thoroughly convinced that *concinnum* is a very variable form, showing decided geographic size variation, probable environmental adaptations in ovipositor characters in the female and certainly great individual variation in certain structural and several color features."

In 1920, Blatchley retained both *delicatum* and *campestre* as "varieties" of *concinnum*, stating (p. 555) that *concinnum* "is quite common among the rank grasses and sedges growing about the margins of tamarack swamps and lakes" in northern Indiana, and occurs "in small numbers about a large marsh in Marion County." He wrote (p. 557) that *delicatum* was found in Marshall and Starke counties, Indiana, "in lowland meadows near large lakes," and (p. 556) that *campestre* inhabits "for the most part upland bluegrass pastures and the tall grasses of the dryer prairies . . . being seldom, if ever found about the lakes and marshes in company with typical *concinnum*." Hebard (1934) remained convinced that *campestre* was a synonym of *concinnum*, though he treated *delicatum* as a trinomial of *concinnum*, stating that the males of these two forms were still inseparable.

As early as 1931, field work by Thomas in Ohio had indicated that three distinct entities were involved in this group, separable on the basis of coloration, ecological relationships, and characters of the ovipositors and the male cerci. Thomas also recognized the distinctiveness of the song of *campestre*, but did not distinguish the songs of *concinnum* and *delicatum*. Reproductive isolation of the three species was indicated by the fact that *concinnum* and *campestre* were found together in two different marshes, and that in a third location all three species were individually intermixed with no indication of intergradation.

Thomas (1951) accordingly treated *concinnum*, *delicatum*, and *campestre* as distinct species and postulated that they had diverged as a result of isolation during the Pleistocene Epoch. He suggested that

concinnum, an abundant species of the Atlantic Coast, had invaded the Great Lakes region in early post-Wisconsin times, perhaps by way of the Hudson-Mohawk glacial outlet, and existed now as a relict in marl bogs and other alkaline situations within the boundary of the Wisconsin glaciation. He believed that *delicatum*, known to have a wide range west of the Mississippi, occurred eastward in the Prairie Peninsula as a relict of the Xerothermic Period; and that *campestre*, the dominant form in the Midwest, had existed in this general region during Wisconsin time, perhaps not far south of the glacial front.

Since 1951, we have accumulated additional information on the relationships of these three species. The distribution of each species has been found to be more extensive than was previously supposed, and the three species have been found to be macro-geographically, and perhaps micro-geographically, sympatric in localities at the northern and southern ends of their ranges. Audiospectrographic analyses have clarified the song differences and shown that songs vary less than most morphological characters do across the ranges of the three species. The newly revealed distributional relationships of these species provide an almost optimal model for the study of the influence of sympatry and allopatry upon the genetic structure of closely related species and disjunct populations within species. The fact that each of the three species is relict in only a portion of its range is associated with interesting geographic variations in the ability to produce functional migrants. This group should provide an important link in the reconstruction of species evolution and the distributional history of faunas affected by glaciation in eastern North America.

SYNONYMY

We have examined the types of all of the nominal species mentioned above: *campestre* Blatchley, based on a male lectotype (Blatchley, 1930) located in the Blatchley collection at Purdue University, Lafayette, Indiana; *concinnum* Scudder, based on a female holotype located in the Museum of Comparative Zoology at Harvard University, Cambridge, Massachusetts; and *delicatum* Bruner, based on a male lectotype selected by Rehn and Hebard (1912) and located in the Philadelphia Academy of Sciences. Of the four paralectotypes of *delicatum* Bruner from West Point, Nebraska, located in the Philadelphia Academy of Sciences, two males and one female are *campestre* Blatchley; the remaining female is *delicatum* Bruner.

O. indianense Blatchley, based on a male located in the Purdue Collection, and *O. longipennis* Scudder (Texas), based on a female located in the Museum of Comparative Zoology at Harvard University, are both synonyms of *concinnum* Scudder.

Redtenbacher's (1891) name, *inerme*, was to all indications proposed as a replacement for Scudder's (1862) name, *longipennis*, made necessary by Redtenbacher's placement of *longipennis* in the genus *Xiphidium* Serville, which already contained *X. longipenne* de Haan, 1841. Redtenbacher cited Scudder's "*longipenne*" (sic) as a synonym of *inerme*; he listed Scudder's material along with (and in precisely the same way as) the specimens that he had seen in the Brunner collection and in the Geneva and Vienna museums; he designated no type, though he gave measurements for both males and females. He gave the same locality for the Brunner, Geneva, and Vienna material as Scudder gave for his material ("Texas"), and because Scudder's and Brunner's collections were listed together for several species in Redtenbacher's paper, with "Texas" and "Dallas, Texas" given as the localities, it is very likely that Brunner's material and Scudder's *longipennis* type were part of a single series taken by the same collector. On the basis of this evidence and our interpretation of paragraphs 72b and 72d of the International Code of Zoological Nomenclature (1961), we are designating Scudder's type of *longipennis* as the lectotype of Redtenbacher's *inerme*, thereby placing the latter as a synonym of *concinnum* Scudder.

MORPHOLOGICAL CONSIDERATIONS

In the present study, 1262 specimens were examined, representing most parts of the range of each species: 402 of *concinnum*, 260 of *delicatum*, and 600 of *campestre*.

As with other groups of sibling species in the Orthoptera, such as *Gryllus* (Alexander, 1957b, 1962) and *Nemobius* (Alexander and Thomas, 1959), we have found that morphological characters in the *Orchelimum concinnum* group vary, both geographically and within local populations, tending to obscure significant differences, and that song features are the most reliable characteristics for separating the species. Surprisingly enough, *campestre*, which Hebard considered to be a synonym of *concinnum*, is the most distinctive of the three, in both song and morphological characters.

The study of preserved material in this group presents certain problems. Specimens quickly become putrescent after death and color

characters are often destroyed; this may happen within a few hours under conditions of high temperature and humidity. At the Ohio State Museum the practice has been to eviscerate material as soon as possible after killing it; at The University of Michigan Museum of Zoology, collected material is dried in a wooden cabinet heated by an electric light bulb. Both methods produce excellent results. The cerci of most male specimens in collections are pulled together, concealing significant characters on their inner faces; this makes it necessary to relax the specimens and spread the cerci for study. Finally, characters of ovipositor and cerci vary, perhaps no more than in most *Orchelimum*, but because three such similar species are involved, differences are often obscured.

Although identification by color and structure can usually be made with ease within any given region, it is sometimes necessary to resort to combinations of characters if one wishes to separate preserved specimens throughout the ranges of the three species. Next to song, face color is probably the most helpful single character in distinguishing species. The ground color of the face of *delicatum* is a clear pea-green. Under low magnification, minute, red dots are apparent, scattered over the upper portions of the face and occasionally more concentrated along the upper mid-facial line (Fig. 1). Most Ohio material shows a bright yellow mid-facial stripe, but a series of specimens taken in Huron County, Michigan, along Wildfowl Bay at the mouth of Mud Creek, shows completely green faces with only the mouthparts yellow, and with varying amounts of the usual red speckling on the upper part of the face. This red speckling on the face of *delicatum* may be the basis for the sketches presented by Urquhart (1941) as an indication of intergradation between *concinnum* and *delicatum*; discoloration might also be involved. But differences in song and ovipositor, in the material from Huron County, Michigan, show that light speckling is not an indication of hybridization. Although we have seen no specimens of *delicatum* with other kinds of red or brown facial markings, in his field notes, T. H. Hubbell states that two of eleven specimens taken at Devil's Lake, North Dakota, exhibited a brown stripe on the face, and a third specimen had a faint indication of such a condition. This feature is not evident in the material preserved from Hubbell's collections at Devil's Lake. However, a series of specimens collected by H. B. Baker at Colorado Springs, Colorado, in 1915-1916, provides possible confirmation of Hubbell's observation. Many of Baker's specimens are excellently preserved, and several of them have a pale brownish mid-facial stripe that does not seem to be attrib-

utable to discoloration. Two specimens also show pale brown areas on the lateral facial margins. These specimens are characteristic of *delicatum* in all other regards, and the facial stripe differs in color, distinctness, and conformation from that on the face of *concinnum*.

The groundcolor of the face of *campestre* is nearly always a translucent dull amber (rarely green or greenish-yellow), more or less suffused with red. Under magnification, the red markings appear as a network of red lines (Fig. 1). The red coloration is concentrated along the lateral margins of the face, though in intensively colored individ-

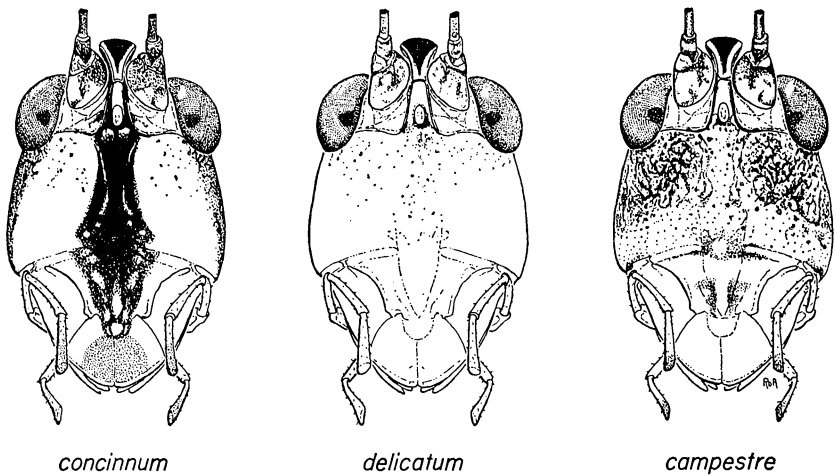


FIG. 1. Typical facial markings of the *Orchelimum concinnum* group, drawn from living individuals: *concinnum* and *delicatum*, Huron Co. Mich.; *campestre*, Washtenaw Co. Mich. Black facial areas are red-brown; stippled areas are pale reddish or brownish except on tips of palpi where they are pink; ground color varies from green in *delicatum* to yellowish in *campestre* and putty-colored in *concinnum* (see text).

uals the entire face may exhibit a reddish suffusion. Face color, though somewhat variable, is usually a reliable character for distinguishing *campestre* throughout its range. An exceptional case of variation in coloration in a given locality is provided in a series of 15 specimens collected by Alexander in a marsh east of Ann Arbor, Washtenaw County, Michigan, on 22 August 1962. These vary from a female with an almost completely green face, having only the faintest of red markings, to a male with an amber face, heavily suffused with red and with a conspicuous red mid-facial stripe of much the same shape and conformation as in *concinnum*. This latter individual had a typi-

cal *campestre* song (cf. Pl I). As with the stripe-faced *delicatum* mentioned above, no other species of the *concinnum* group is known to occur in or near this particular marsh.

Sexual dimorphism is indicated in this series; the faces are pale in the four females and intensively marked in all of the eleven males. The series is too small for generalization, but it tends to support the suggestion made below that facial markings may be related to close-range visual interactions.

The face in *concinnum* varies from translucent amber to a putty color, and there is nearly always a conspicuous, reddish, mid-facial stripe (Fig. 1). Usually there are also reddish lateral markings, which are especially intense in some midwestern material. Individuals with plain faces have been reported from the Atlantic and Gulf coasts, but none has been found in the Midwest. Some preserved specimens from the Atlantic Coast have greenish faces.

As already noted, Hebard (1934) reported a nymph with a plain face, kept in captivity, which developed a facial stripe upon reaching maturity. We have both collected nymphs of several instars in Ohio, and all of these had typical facial stripes. It is possible that the stripe is not evident until a teneral individual has hardened; also its development may differ along the Atlantic Coast where occasional pale-faced specimens have been reported.

Obvious similarities in the shape and conformation of the mid-facial stripe when it occurs in the different species, and even similar markings in individuals without facial stripes (compare *concinnum* and *campestre*, Fig. 1), suggest that the mid-facial stripe may have occurred in some individuals of the common ancestor of the members of the *concinnum* group. This may be the explanation for its occasional appearance in *campestre* and *delicatum* where these species do not interact with *concinnum*.

The green coloration of the body parts of fresh specimens from Ohio differs slightly among the three species. The body color of *delicatum* is invariably a clear, pale pea-green; that of *campestre* is a darker, more neutral shade; and *concinnum* has a blue-green cast. This character does not hold across the ranges of the three species, and it is difficult to describe in terms that would make it useful in a key or in the identification of individuals when only one or two of the three species are available. It is one of many subtle differences that are quickly visible to the local collector when he has living individuals of all three species to compare, or after he has already made tentative identification on the basis of song or some other character.

Two instances of dimorphism in body color have been noticed in the *concinnum* group. Three of 14 individuals of *concinnum* collected in Huron County, Michigan, by T. H. Hubbell, I. J. Cantrall, and the present authors, are erythristic, with the extreme example, a female, being suffused with purple-red across much of the body, including wings and ovipositor. Concerning dimorphism in *delicatum*, T. H. Hubbell wrote in his field notes from Devil's Lake, North Dakota, that: "The brown color form seems to be about equal to the green in numbers, since six out of the eleven are of this coloration." This note may refer only to wing color, which appears to vary between green and brownish hues.

The color of the male terminalia of *delicatum* is often distinctive, the 8th and 9th tergites, the supra-anal plate, and the cerci usually being a bright, butter yellow, with little or no brown shading. However, fresh material from Huron County, Michigan, showed considerable variation in this respect, ranging from the above condition to intensively colored individuals with distinctly brown-stained cerci and a definite, red-brown middorsal stripe involving the supra-anal plate. Characteristically, *campestre* and *concinnum* have brown-stained cerci and a well-developed brown middorsal stripe completely involving the supra-anal plate. This generalization will not hold, however, for specimens of *campestre* from the extreme southwestern portions of the range (e.g. Mississippi, Oklahoma) or for *concinnum* from Mississippi, Louisiana, and Texas. Material of both species from those areas shows bright yellow terminalia with a minimum of brown shading.

In general, variations in the shades of green, blue, and brown on the wings, legs, and bodies of meadow grasshoppers are related to the color of the vegetation where the species lives. Along with the characteristic "flattening" and "hiding" behavior of startled meadow grasshoppers, this coloration probably has a selective advantage in escape from predators. But variations in the sometimes gaudy facial markings of the *concinnum* group (and in localized bright markings on legs and other body parts in other meadow grasshoppers) seem more likely to be related to behavioral interactions among the individuals of each species. There are several reasons for this suggestion. First, meadow grasshoppers are active during the day, and they are characteristically more "visual" insects than most other Tettigoniidae and Gryllidae, showing obvious visual reactions to many kinds of motion and to one another at close range. Second, the face of a

meadow grasshopper is directed somewhat ventrally, in a position where it would be obvious to another insect, such as a meadow grasshopper, in a head-on position. For example, this position has been observed by Alexander in *Orchelimum gladiator* Bruner during the preliminaries to mating behavior as the male was starting to pass by the female on a grass stem and assume the typical end-to-end copulatory position of the Conocephalinae. Finally, in the material that we have studied, variations of the sort that would seem to represent intergradation or convergence among the usual facial markings of the three species can scarcely be so interpreted since they occur only in single species populations, usually existing far from the other two species.

The male cerci of *campestre* are distinctive, having a deep, oval or subquadrate depression on the inner face of the base (Fig. 2). The dorsal and ventral carinae are weakly developed. In *concinnum* and *delicatum*, the carinae are conspicuously developed and tend to join midway between the tooth and the base of the cercus, forming a small, shallow, subtriangular depression at the base of the tooth. We have been unable to find a character to separate the cerci of *concinnum* and *delicatum*.

The ovipositors of the three species, while exhibiting a certain amount of individual and geographic variation, still show characteristic forms and dimensions (Fig. 3). The ovipositor of *campestre* is definitely upcurved from about the middle, while in *concinnum* and *delicatum* the upper margin of the ovipositor is relatively straight for the distal two-thirds of its length. The ovipositor of *delicatum* is always more than half as long as the caudal femur, that of *concinnum* is usually less than half, and that of *campestre* averages still shorter. While there is overlap in the ovipositor-femur ratio when all parts of the species' ranges are considered, the ratio in material measured has proved different for each species in a given region (Fig. 4).

Urquhart (1941, p. 19) listed only "*concinnum concinnum*" from Essex County, Ontario, noting that "in so far as the amount of curvature and size of the ovipositor are concerned, individuals in the material from Essex County may apply to both forms [*concinnum* and *delicatum*]." However, Thomas has examined Urquhart's excellent series of specimens and had no difficulty in distinguishing the three species. Of the ovipositors illustrated in Urquhart's Figure 3, "e" and "f" are clearly *delicatum*, "h" and "j" clearly *campestre*, and "g" and "i" almost certainly *concinnum*.

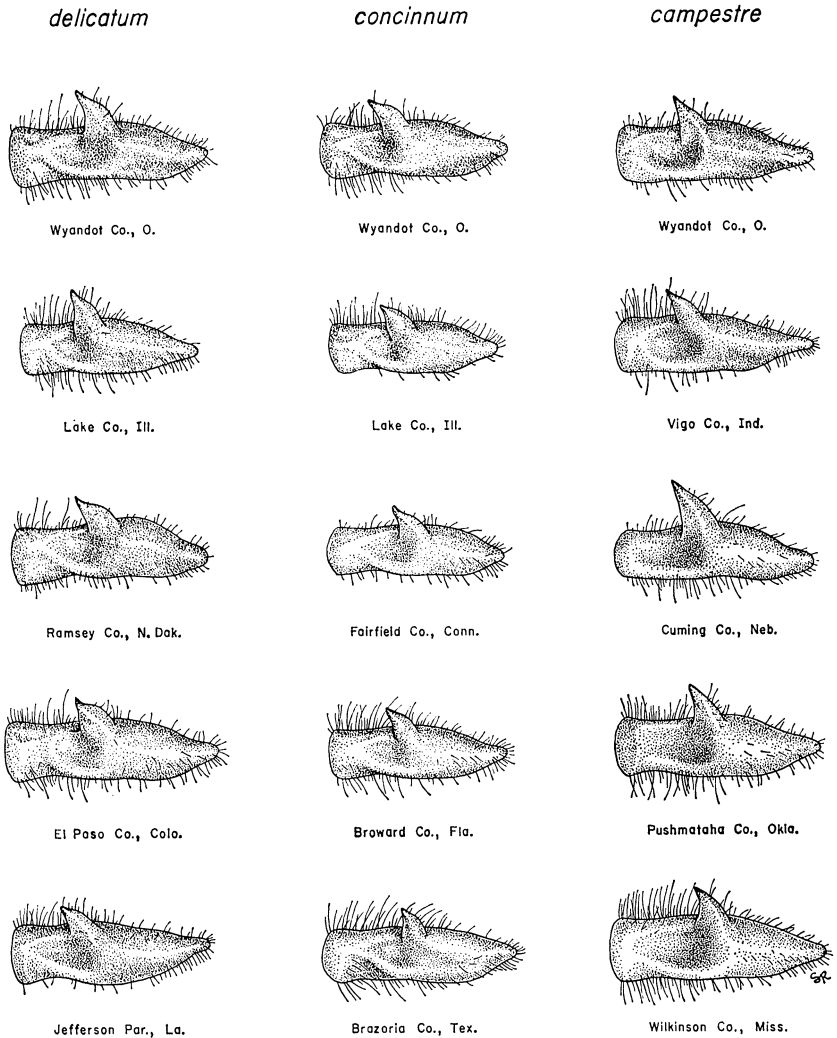


FIG. 2. Dorsomedial views of the right cerci of males of the *Orchelimum concinnum* group, representing most parts of the range of each of the three species. In this view, drawn to show the shape, size, and depth of the depression at the base of the cercal tooth, the tooth itself is somewhat foreshortened. The drawing of Indiana *campestre* is from Blatchley's lectotype; that of Nebraska *campestre* is from one of the paralectotypes of *delicatum*.

DISTRIBUTIONAL AND ECOLOGICAL RELATIONSHIPS

The geographic distribution of the three species is shown in Figure 5; it largely corresponds to that given by Thomas (1951)¹, except that the known range of each species has been considerably extended. We do not know how accurately the disjunctness of the midwestern populations of *concinnum* and *delicatum* is depicted by the known distributions. The Louisiana population of *delicatum* may also be disjunct, for it is not only several hundred miles from other known populations, but also east of the old mouth of the Mississippi River. The southern populations of *campestre* are probably not disjunct, but only appear so owing to inadequate field work.

The three species are known to be sympatric in only two areas—the coastal regions of Louisiana and the Lower Great Lakes region. In Louisiana, Alexander has found *concinnum* and *delicatum* together in the marshy areas along the canals lining State Route 1 below Raceland and in swales behind the dunes on Grand Isle. In both Mississippi and Louisiana, *campestre* is abundant in marshy areas along the highways, and it is the only one of the three species found inland.

In Ohio, all three species have been studied extensively in the field by Thomas. In this region and in Michigan, *campestre* is the common species, occurring widely in various types of marshes, usually in vegetation over standing water. It is often plentiful in Rice Cut-grass, *Leersia oryzoides*,² one of the most abundant marsh grasses in the region. The other two species, in contrast, are quite restricted in distribution. *O. concinnum* is characteristic of a few northern relict marl bogs and other alkaline situations. *O. delicatum* is largely restricted to swales adjacent to sand dunes or sand beaches, where it is often associated with Blue-joint Grass, *Calamagrostis canadensis*.

Except for the Louisiana populations, on only four occasions have we found two or more of the three species in the same marsh. In three of the four instances, definite evidence of ecological segregation was noticed. In Champaign County, Ohio, at Cedar Swamp (a northern relict bog), *campestre* was found around the margins of the bog in ordinary marshland, such as occurs throughout most of the state. In contrast, *concinnum* was found only in a wet marl flat dominated by the sedge, *Eleocharis rostellata*, in association with the beak-rushes,

¹ Thomas' three *concinnum* records along Lake Erie in Ohio resulted from an error in construction of the maps, and properly apply to *delicatum*.

² Technical names of plants have been taken from Fernald, M. L. 1950. Gray's Manual of Botany, 8th ed.

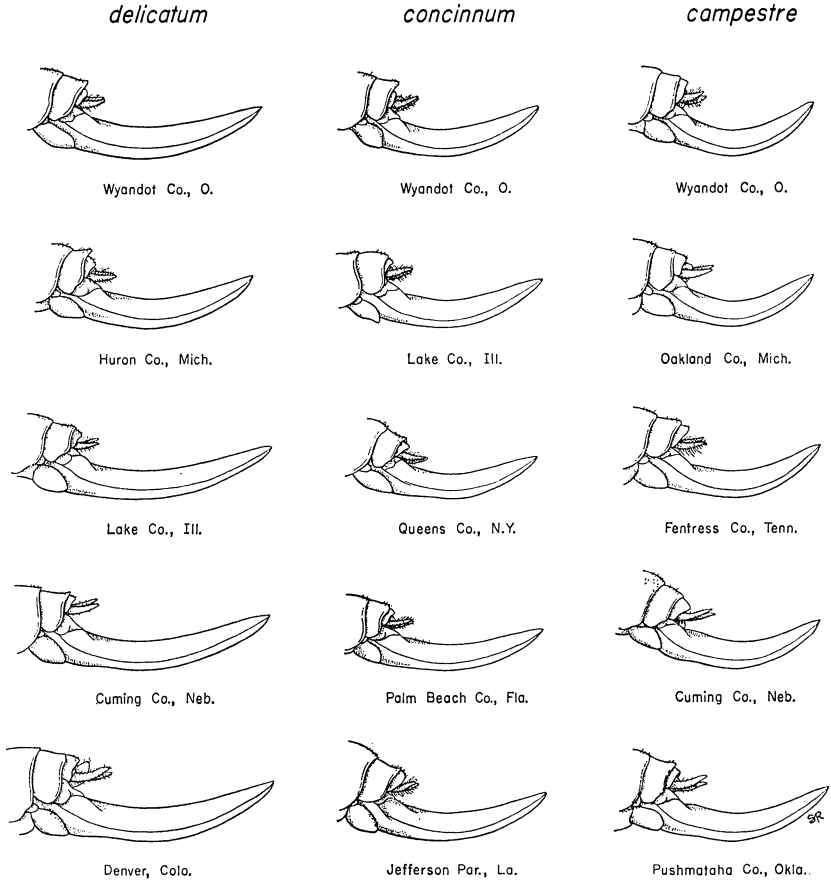


FIG. 3. Side views of the ovipositors of females of the *Orchelimum concinnum* group, representing most parts of the range of each of the three species. The drawings of Nebraska *delicatum* and *campestre* are from the paralectotypic series of *delicatum*.

Rhynchospora alba and *R. capillacea*; the rush, *Juncus brachycephalus*; White Camass, *Zigadenus elegans*; Kalm's Lobelia, *Lobelia kalmii*; and other plants. All of the plants mentioned are northern relict species, and all except White Camass occur in similar situations along the north Atlantic Coast. At Silver Lake, Miami County, Ohio, *concinnum* was found in a habitat almost identical with that at Cedar Swamp, with *Eleocharis rostellata* again the predominant plant.

In the marsh at Wild Fowl Bay, Huron County, Michigan, *concinnum* and *delicatum* were found in direct association in some places.

However, *concinnum* was restricted to a sparsely vegetated flat dominated by Chair-maker's Rush, *Scirpus americanus*, while *delicatum* was most plentiful in dense stands of Blue-joint Grass where *concinnum* was absent.

The only place in which either of us has found all three species together was in a prairie swale in Pitt Township, Wyandot County, Ohio (4-5 September 1938, E. S. Thomas). Here the three were mingled together, with no observed ecological segregation. At that season the water level in the swale was greatly lowered, possibly forcing the insects into the central portion which still retained water. It is possible that the three species had occupied separate habitats earlier in the season.

In all of the places where two or more of the species have been found in association, there is no evidence whatever of hybridization or intergradation. On the contrary, color and structural differences have actually seemed more pronounced than usual.

Although the three species all inhabit marshy areas of one sort or another, their specificities in this regard and their abilities to invade newly available habitats obviously vary considerably, both among the species and from one part of the range to another for each species. Of the three, *campestre* appears to be least specific in this regard, inhabiting a variety of different marshy and swamp situations. In the Midwest this species seems to be holding its own, and is probably still invading new marshes on the rare occasions when these appear. This is in striking contrast to the precarious midwestern existence of *concinnum*, which must hinge on the persistence of those few unusual habitats in which the species is found today. In most portions of the Midwest, *concinnum* is actually much more restricted in distribution than the maps in Figure 5 suggest, occurring only in small colonies within the marsh it inhabits; at Cedar Swamp, for example, *concinnum* is found in a colony a few yards in diameter near the center of the bog, while *campestre* occurs throughout an area several times as large in a part of the swamp which, with regard to its vegetational aspects, is more "modern" for central Ohio.

Along the Atlantic and Gulf coasts, and inland in Florida, *concinnum* exists abundantly in a wide variety of marshy areas, including brackish locations, and it is surely invading new areas regularly there and holding its own very well under present conditions. This thriving and almost continuously distributed coastal population is probably completely isolated from the entire midwestern population, and every midwestern colony is probably totally isolated from every other one.

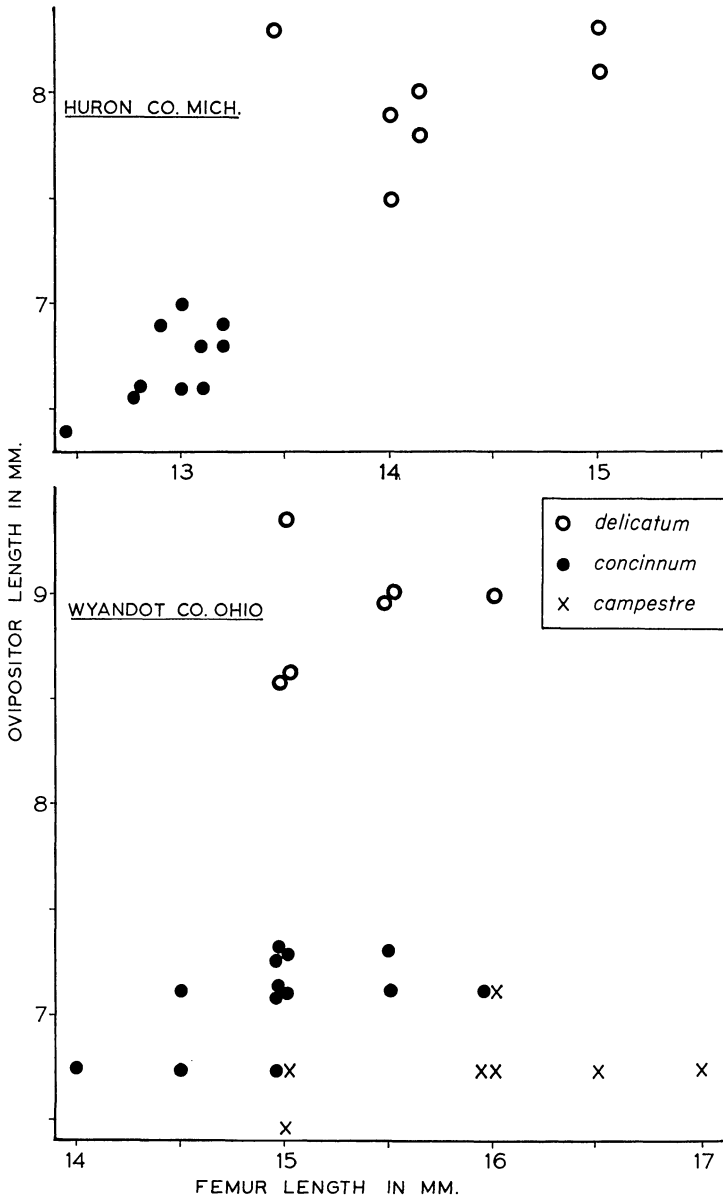


FIG. 4. Relative lengths of ovipositor and hind femur in females of three species of the *Orchelimum concinnum* group, collected more or less intermingled in the same habitat, and showing that geographic variation can obscure differences that are consistent within any given area. Top: from large marsh along Lake Huron at the mouth of Mud Creek in Wildfowl Bay, Huron County, Michigan. Bottom: from Pitt Township, Wyandot County, Ohio.

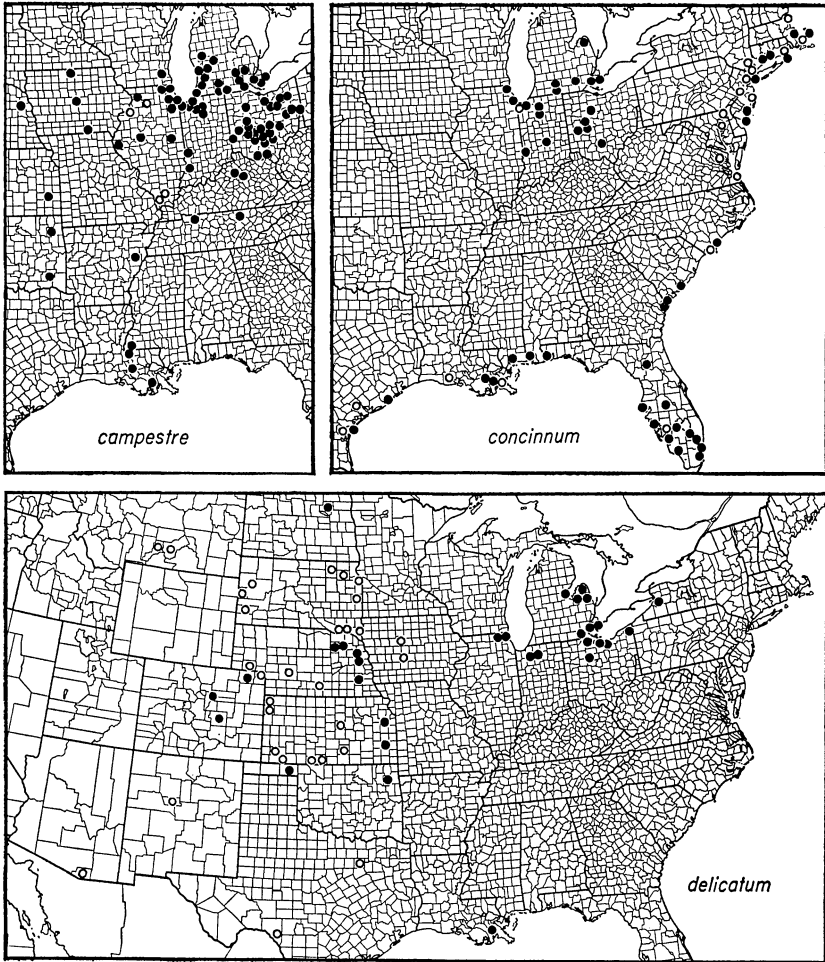


FIG. 5. Geographic distribution of the *Orchelimum concinnum* group. Solid circles indicate specimens examined; open circles are unverified literature records.

O. delicatum is not abundant in any of the eastern locations where we have studied it, and it does not give the impression of being a highly successful species in this region. This is probably not the case in the western parts of its range, where we have not worked.

Figures 6 and 7 contain information that is relevant to the question of the locations of relict populations within the three species. A glance at any large collection of pinned specimens of this group reveals that there is considerable variation in the length of the hind

wings, which nearly always project beyond the forewings. A few individuals stand out as obviously macropterous, and some of these are labelled "taken at light." The nature of the intergradation between shorter-winged individuals and these occasional strongly macropterous individuals was not clear until we plotted wing length against pronotal length, an easily measurable and reliable indicator of general body size (Figs. 6, 7). The two characteristics vary together in a more or less linear fashion in most of the individuals plotted, but a small group of individuals in each species is displaced on the graph by vir-

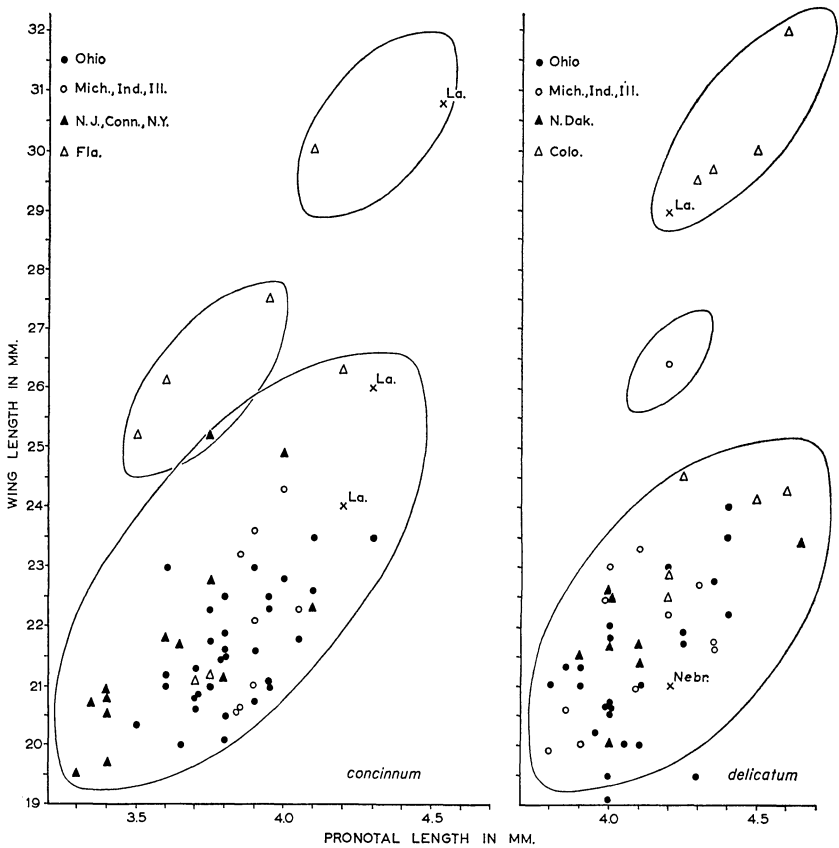


FIG. 6. Relative lengths of hind wing and pronotum in females of *Orchelimum concinnum* and *O. delicatum* from all parts of the range of each species. Ovals enclosing symbols were drawn arbitrarily to emphasize the probable dimorphism or trimorphism suggested by comparing scatter diagrams of all three species. Note geographic restriction of macropterous individuals in each species.

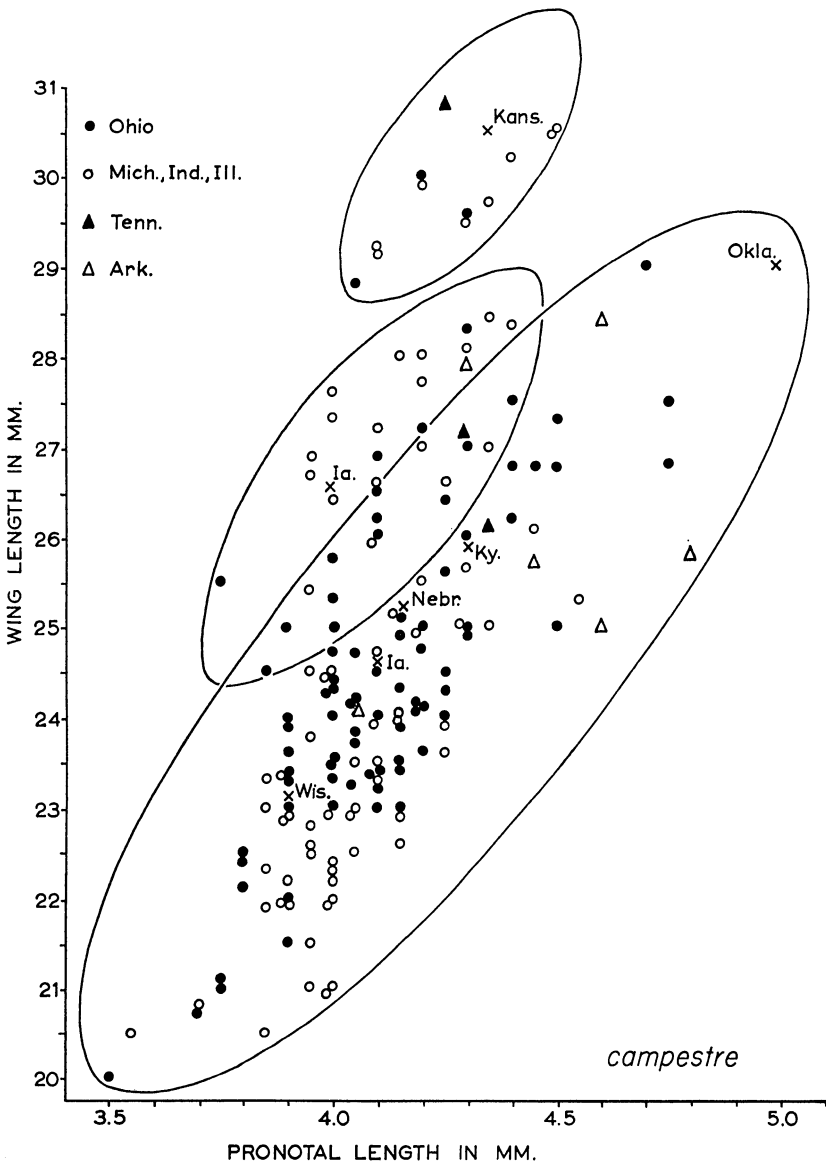


FIG. 7. Relative lengths of hind wing and pronotum in females of *Orchelimum campestre* from all parts of the range of the species. Ovals enclosing symbols were drawn arbitrarily to emphasize the probable dimorphism or trimorphism suggested by comparing scatter diagrams of all three species.

tue of having unusually long wings. These long-winged individuals in turn seem to break up into two groups, as indicated by the ovals drawn so as to roughly enclose the symbols in Figures 6 and 7. Some of the less macropterous individuals are also labelled "at light," suggesting that migrants are probably included in this group as well as in the strongly macropterous group.

Each of the three species is apparently geographically restricted with regard to the production of migrant individuals; migrants are rare in the regions that we have presumed contain relict populations. Thus, *concinnum* produces migratory individuals only in its coastal population, *delicatum* only in the western part of its range; *campestre* apparently produces macropterous individuals over most of its range. The two exceptions to these rules are a long-winged *delicatum* female and a long-winged *concinnum* male taken in Lake Huron coastal marshes. The presence of these individuals suggests that the Great Lakes coastal populations of *concinnum* and *delicatum* may still produce occasional successful migrants.

The precise functional locomotory differences among the individuals plotted in Figures 6 and 7 are still unknown. Individuals of all three species spread and flutter their hind wings when they leap after being disturbed, and this apparently lengthens the distance traveled, even when the underwings are short. Fairly long flights must occur in macropterous individuals, for Thomas took a macropterous *campestre* at light on a ridgetop in Ashland County, Ohio, at a considerable distance from any known suitable habitat. There is no apparent explanation for the trimorphism suggested in the figures. This trimorphism is only presumed, and it is all but obscured in *campestre*, where, if it is present at all, it is represented only by a sideways displacement of the distribution of individuals at about the same level where, in *delicatum* and *concinnum*, a few individuals seem to fall well apart from the main micropterous population.

Male specimens were not plotted in Figures 6 and 7, to avoid any confusing effects of sexual dimorphism. However, we have examined the collection for obviously long-winged males, and find a few for each of the three species. All are from the same regions represented by macropterous females in Figures 6 and 7, with the exception given above.

DISTRIBUTIONAL HISTORY

Thomas (1951) suggested that *campestre* survived glaciation "not far" from the ice front, that *concinnum* penetrated the Great Lakes

region in early post-Wisconsin times, and that *delicatum* spread eastward as a result of the postglacial Xerothermic Period. The information presented here supports these conclusions, with the addition that *campestre* probably survived glaciation farther south than previous evidence indicated, either in addition to or instead of survival in refugia north of its presently known southern limits.

In the Midwest today, *concinnum* occurs only inside the limits of Wisconsin glaciation; in at least one location (Colerain Township, Ross County, Ohio) it occurs in a marl bog at the very foot of the terminal moraine. It is worthy of note that in the lower Great Lakes area *concinnum* is sometimes associated with two other species of Orthoptera otherwise known only from the Atlantic Coast—*Neoconocephalus lyristes* Rehn and Hebard (Tettigoniidae) (Thomas, 1933) and *Paroxya atlantica* Scudder (Acrididae). These species occupy habitats very similar to those of *concinnum* and show essentially the same distribution; they probably invaded the Midwest at the same time as *concinnum*. The only exception to this generalization is that *N. lyristes* has been taken in a large bog in Wayne County, West Virginia, by T. H. Hubbell, where neither *P. atlantica* nor *concinnum* has been found.

The western distribution of *delicatum*, with an eastward extension to Buffalo, New York, presents the familiar distributional pattern shown by a large number of western prairie plants and animals which occur as disjuncts eastward along the Prairie Peninsula and are believed to be relicts of the Xerothermic Period (Sears, 1942; Conant, Thomas, and Rausch, 1945; Smith, 1957). The known stations for *delicatum* are disjunct, and with few exceptions they are in swales and marshes adjacent to sand dunes or sand beaches along the shores of the southern portions of the Great Lakes. One of the exceptions is the station in Wyandot County, Ohio, which is a swale in one of the largest relict prairie areas in that state. It may not be pure coincidence that this area is also the easternmost recorded locality for the Plains Garter Snake, *Thamnophis radix* Baird and Gerard, which has a distribution remarkably similar to that of *delicatum* (Conant, 1958, p. 328).

SONG RELATIONSHIPS

Song differences among these three species have, as in other Orthoptera, proved to be more diagnostic than any other set of characteristics and to exhibit little, if any, geographic variation. Like other Conocephalinae, the three species sing both day and night. However,

all three species greatly increase their chorusing activity at dusk, and do most of their singing at night. Generally, only a few individuals in a colony can be heard singing in the daytime. Only one sound, the calling song, has been heard for each species. There was no evidence in the field of any special elaboration of chorusing activity, such as synchronization or alternation of song phrases by neighboring individuals. In the laboratory, however, synchronization was often apparent in individuals caged in close proximity. Some such interaction seems to appear more or less incidentally in all species with rhythmical songs, perhaps in association with reinforcing auditory feedback. It has been elaborated in only a few cases (Alexander, 1960).

The songs of all three species are high-pitched and not loud to the human ear. Singing males are most often found perched on vertical stems from one to five feet above the ground.

The calling songs have been recorded as follows: nine individuals of *concinnum* (two from Cedar Swamp, Champaign County, Ohio; one from the Cape Fear Peninsula, New Hanover County, North Carolina; one from Glades County, Florida; one from Jefferson Parish, Louisiana; two from Brazoria County, Texas—one each from Freeport and Surfside; and two from Wildfowl Bay at the mouth of Mud Creek in Huron County, Michigan); nine individuals of *delicatum* (four from the marsh at the mouth of Mud Creek in Wildfowl Bay, Huron County, Michigan; four from a Lake Erie marsh in Erie County, Ohio; and one from Jefferson Parish, Louisiana—same marsh as for *concinnum* above); thirteen individuals of *campestre* (six from Cedar Swamp in Champaign County, Ohio; one from Franklin County, Kentucky; one from DuPage County, Illinois; one from Wilkinson County, Mississippi; one from Jefferson Parish, Louisiana; two from Iberville Parish, Louisiana; and one from Washtenaw County, Michigan). These recordings represent totals of about 15 minutes of song each for *concinnum* and *delicatum*, and 35 minutes for *campestre*.

Figures 8–9 and Plate I show a comparison of the songs of the three species. Plate I shows diagrams of the typical singing rhythms of the three species and audiospectrographs of songs recorded in the laboratory. These “noise-like” sounds (having a broad frequency spectrum) are probably the most difficult insect sounds to portray clearly on audiospectrographs, forming rather nondescript pictures in which the individual elements of rhythm are apparent only upon careful examination, and in which the gross rhythm involves such long time periods that it can only be portrayed satisfactorily through diagrams. In tettigoniid sounds the wings continue to vibrate between tooth-

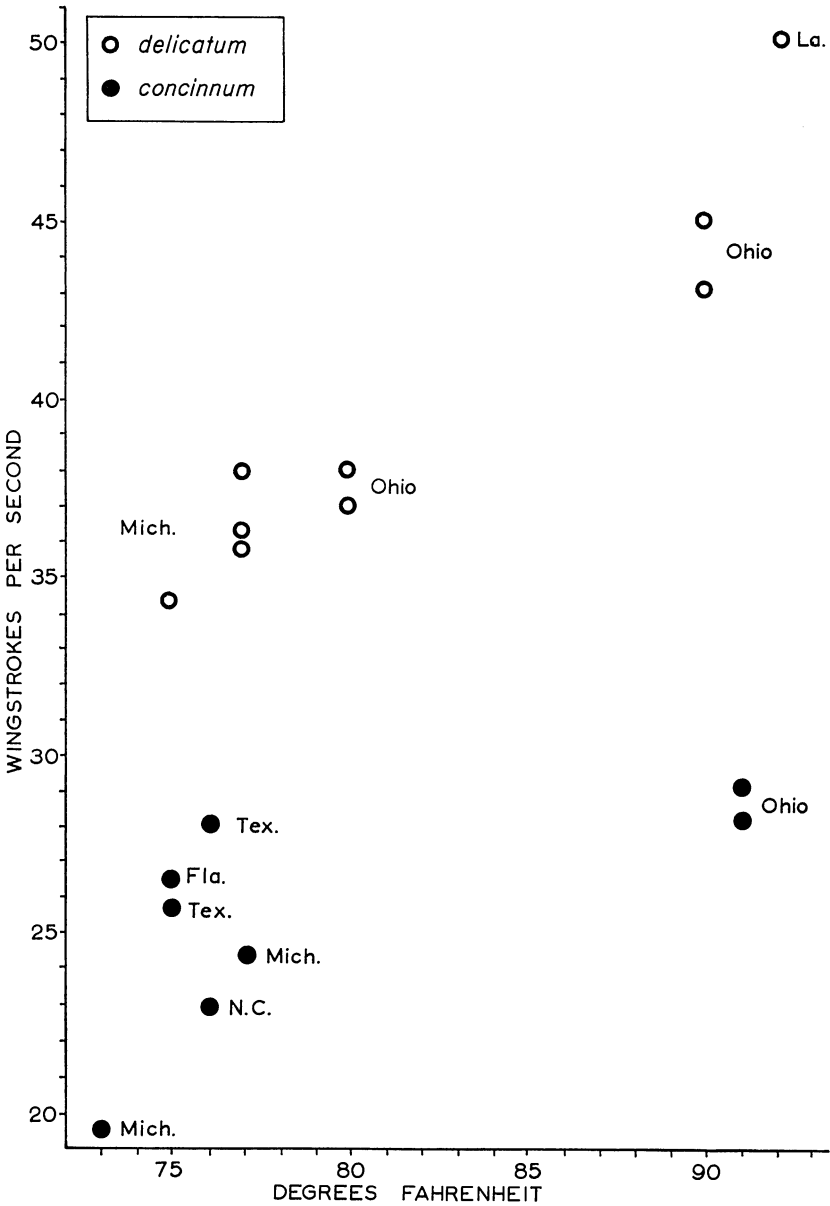


FIG. 8. A comparison of wingstroke rates in the buzzing part of the calling songs of different individuals of *Orchelimum concinnum* and *O. delicatum* recorded at different places and at different temperatures.

strikes, and the individual toothstrikes and pulse terminations are not as clear-cut as in cricket sounds. Nevertheless, individual toothstrikes can be discerned in many places on the audiospectrographs in Plate I, and they can be counted in the first pulse of the buzz of *concinnum*. Differences in pulse rates and rhythms among the three species are obvious.

The songs of all three species are typical of meadow grasshoppers, consisting of an alternation of individual wingstrokes (ticks) with prolonged, rapid wing vibration (buzzes). They are noise-like sounds with a wide frequency spectrum, some of the principal frequencies concentrated between seven and 16 kilocycles per second. In the songs of *concinnum* and *delicatum*, the rhythm of delivery of ticks and buzzes is very similar, and the songs are nearly indistinguishable to the ear. However, audiospectrographic analysis reveals that the pulse rate in the buzz of *concinnum* is only about two-thirds as fast as that of *delicatum* at any particular temperature (Fig. 8). This difference has been confirmed by alternately tape-recording both Ohio and Michigan individuals of the two species caged adjacent to one another in the laboratory. Under such conditions the songs of the two species can easily be separated by ear.

The stridulating mechanisms of *concinnum* and *delicatum* appear to be identical. For each species, the file length in a single Ohio individual was 1.9 mm., and each file had about 60 teeth. *O. delicatum* had 35 teeth in the central 1.33 mm. of its file while *concinnum* had 36 teeth in the same portion of its file. Using audiospectrographs with the time scale greatly expanded, the pulse length in the song of a single individual was found to be 0.009–0.012 sec. for *delicatum* and 0.020–0.025 sec. for *concinnum*. The pulse interval in each species was about 0.075 sec. *O. delicatum* used 16–21 teeth per wingstroke (sound pulse) and *concinnum* used 22–31 teeth per wingstroke. This suggests toothstrike rates of 1100–1250 per second for *delicatum* and 1700–1800 per second for *concinnum*. Thus, the song differences in these two species result entirely from differences in rhythm, one species vibrating its wings more rapidly and with shorter strokes (using fewer file teeth) than the other. Apparently, pulse rate is the only possibility for behaviorally significant differences between the two songs. The only other difference noted was that the ticks of *delicatum* are strongly and usually audibly double (wingstroke acoustically effective in both directions). The ticks of *concinnum* (and *campestre*) are usually single, and when they are double, the sound produced by the opening of the tegmina is much softer than that produced by the closing stroke

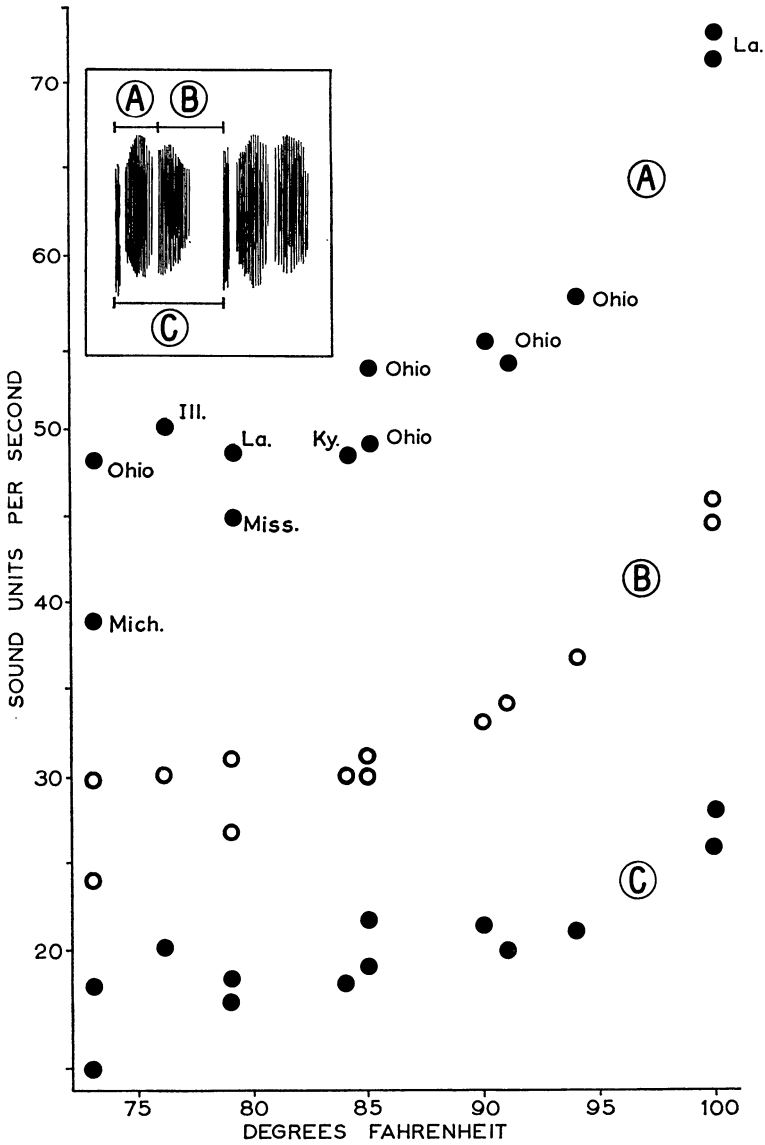


FIG. 9. The rates of delivery of three different rhythm elements in the buzzing part of the calling songs of different individuals of *Orchelimum campestre* recorded at different places and at different temperatures. (A) and (B) are based on extrapolation from the length of the pulse and the pulse interval, showing the rate of motion of the tegmina at particular times within the buzz, and (C) is the rate of delivery of pairs of pulses in the buzz.

(Pl. I). In the songs of both *concinnum* and *delicatum*, there are from one to five ticks delivered at two to four per second, and the buzzes last from one to two seconds (at 70–90° F.). As in other meadow grasshoppers, the number of ticks increases when the singer is slightly disturbed, and when two males are caged in close proximity. Rarely, two or three buzzes are produced in these species without intervening ticks.

There appears to be little variation between the songs of coastal and midwestern *concinnum* or between the songs of Louisiana and midwestern *delicatum*. The variation shown in Figure 8 between individuals of *concinnum* from Texas, Florida, and Louisiana and those from other parts of the range could represent geographic variation, but because of the small sample and the difficulty in obtaining accurate temperature readings for singing individuals, it would be premature to draw this conclusion.

Fulton (1932) stated that males of *concinnum* from Raleigh, North Carolina, produced 1–5 ticks at a rate of 2–3 per sec., with each buzz lasting $\frac{1}{2}$ –1 sec. at ordinary temperatures. For Connecticut specimens, Pierce (1948) recorded 6–9 ticks delivered at 3 per sec. between buzzes lasting 2–3 sec. each. He obtained a pulse rate of 26 per sec. and a principal frequency of 20.3 kilocycles per sec. He did not mention temperature. He found the duration of pulses within buzzes to be about 0.02 sec., but noted only five toothstrikes per pulse. Since he obtained the toothstrike rate by dividing the number of “serrations” (apparently toothstrikes) per pulse by the length of the pulse, he got a figure of 250 toothstrikes per sec., which differs considerably from those obtained here. All of Pierce’s other figures, including the pulse length, correspond closely with those obtained here, and it seems possible that he erred in estimating the number of toothstrikes per pulse. It would be quite unusual for an insect with 60 teeth in its stridulatory file to use only five of them during each wingstroke. It is possible that Pierce was measuring the minor pulse, or backstroke, of the wings, which contains only four to eight toothstrikes in each of the three species discussed here. An evaluation of the differences between the principal frequencies obtained by Pierce and those reported in the present study is difficult because our equipment is probably unreliable above 15–20 kilocycles per second; further, Pierce obtained frequencies which in many cases differed considerably from those obtained in the same species with the equipment used here and with that used by other investigators. When high-pitched sounds with broad frequency spectra are recorded and analyzed with instru-

ments designed to handle human-produced and human-appreciated sounds, as in the present study, the intensity spectrum which results may principally reflect characteristics of the microphone or some other "weak link" in the recording-analyzing apparatus. Fortunately, the precise nature of the frequency spectrum does not seem to be critical in most systematic and behavioral work, and so the proper procedure is to use the equipment that is available and practical and not to place much reliance upon the precise frequency characteristics obtained. All insects so far demonstrated to have ultrasonic or supersonic elements in their songs have broad frequency spectra with strong components within the sonic range, and all evidence indicates that so long as the rhythm remains unaltered, the high frequencies change only the carrying power of the sound for the insect.

The stridulating mechanism of *campestre* differs somewhat from those of *concinnum* and *delicatum*. The file of a single specimen examined was about 1.67 mm. long, and contained about 66 teeth. The central 1.33 mm. of the file contained 48 teeth. As expected from these figures, the toothstrike rate in the song of this species was somewhat higher than in the other species, 1850–1900 per second. From 15 to 20 teeth were used in the major pulses, and 5–7 in the minor pulse.

The song of *campestre* is variable with respect to the rhythm of delivery of ticks and buzzes, but it is quite distinct from the songs of the other two species. At times it resembles the rhythm of the songs of *delicatum* and *concinnum* rather closely, and at other times as many as 150 ticks have been counted in succession, produced without buzzes by a lone, undisturbed male. Continuous buzzes without intervening ticks have been timed up to three minutes duration. The ticks are frequently omitted between short buzzes. Both single- and double-pulse ticks are produced, and the pulses in the buzzes are grouped peculiarly. They are paired (Pl. I), and the pairs of pulses are delivered at 20–22 per second at 90° F. It was first believed that each of these pairs of pulses represented a single stroke of the forewings, acoustically effective in both directions. However, examination of audiospectrographs of all recorded specimens suggests instead that each pair of pulses represents two complete wingstrokes, sometimes acoustically effective in both directions (producing four pulses per group, two short and two long), and sometimes acoustically effective in only one direction. This suggestion fits with the observation that some ticks are single-pulse and some are double-pulse. Thus, the wings are apparently stroked twice, at a rate of 50–60 per sec. (90° F.), then held for an instant before another pair of strokes is produced. This

hold causes another pulse interval, that between the last pulse of one pair and the first of the next pair; if extrapolated, the pulse rate in this rhythm would be around 35 per second. Unfortunately, these conclusions must be based on indirect evidence, since no high-speed movies of the singing of these species are available, and the wings are moved too rapidly to confirm visually what is happening. High-speed movies (128 frames per sec.) of the ticking of *Orchelimum vulgare* Harris, a species producing double-pulse ticks and an alternation of narrow and broad pulses in its buzz, reveal that the wingstroke in this species is acoustically effective in both directions, the major pulse being produced during the closing and the minor pulse during the opening of the wings. *Orchelimum gladiator* Bruner, a species with a song very similar to that of *O. vulgare*, produces single-pulse ticks; the relationship between the songs of these two species is, therefore, very similar to that existing between the songs of *concinnum* and *delicatum* in this particular respect. A pairing of pulses within groups similar to that in the song of *campestre* has been noted in the song of the snowy tree cricket, *Oecanthus fultoni* Walker (Alexander, 1960), and occurs also in *Phyllopalpus pulchellus* Uhler (Trigonidiinae) and in two or three *Gryllus* species from western North America (Alexander, 1956; in press). Such pairing of pulses within trills represents a possible mode of transition from trilling to chirping songs (and vice versa), additional to that suggested by Alexander (1957a) in which occasional pulses are deleted from a continuous trill, as in *Nemobius maculatus* Blatchley.

Cantrall's (1943) description of the singing rhythm of *campestre* on the George Reserve, Livingston County, Michigan, fits that given here, except that he did not observe as great a range of variation. He counted 2-7 ticks per buzz, and stated that the buzz may last 4-8 seconds. As in the present study, he found that the ticks between buzzes are often omitted.

The difference in pulse rate in the buzzes of *concinnum* and *delicatum* is about what we have come to expect in the songs of sympatric siblings—one song with a pulse rate one and one-half to two times as fast as the other. But the difference between songs of *concinnum* and *delicatum* is as great across the parts of their ranges where the species do not interact as it is where they are sympatric. If the song differences have been exaggerated through interaction, as we would expect, then the interaction must have occurred prior to the time that *concinnum* and *delicatum* became sympatric in the Midwest by invading it from opposite directions following Wisconsin glaciation. It seems unlikely

that song differences sufficiently great to resist exaggeration under the localized conditions of sympatry exhibited today by these species could evolve without interaction. Consequently, it seems probable that speciation between *concinnum* and *delicatum* was not a result of late glacial events. Earlier sympatry could have occurred during interglacials in the Midwest; but it might also have occurred in some other area during a time when the species' distributions were much more restricted than they are today. An extremely long time would surely be necessary to transmit genetic changes affecting song all the way from one end to the other of the present ranges of these species.

SUMMARY

Three species in the *Orchelimum concinnum* group are distinguished through both morphological and song differences. All three have somewhat linear distributions: *O. concinnum* Scudder around the Atlantic and Gulf coasts and inland in the Midwest; *O. delicatum* Bruner in a semicircle west of the Mississippi River and eastward to the western tip of New York; and *O. campestre* Blatchley from the southern portions of the Great Lakes and the Midwest south to the Gulf Coast and Oklahoma. The three species overlap geographically and ecologically at the ends of their ranges in Ohio and Louisiana. *O. concinnum* and *O. delicatum* are relict in the Midwest where, with the exception of Great Lakes coastal marshes, only micropterous individuals of these species have been taken. Both micropterous and macropterous individuals occur elsewhere across the ranges of the three species.

Song varies less than any of the morphological characters examined, and is diagnostic throughout the ranges of the three species. Song differences result from differences in rates and rhythms of wingstroke rather than from structural differences in the stridulatory apparatus. Because the songs of *concinnum* and *delicatum* are as distinct where the species do not interact as they are in the localized regions of sympatry at opposite ends of the species' ranges, it is postulated that song divergence occurred during an earlier sympatry than that now in evidence. It seems likely that *concinnum* invaded the Midwest from the Atlantic Coast in early post-Wisconsin times, *campestre* invaded from refugia somewhere to the south, and *delicatum* penetrated eastward during the postglacial Xerothermic Period. Owing to climatic and vegetational changes, only *campestre* is abundant and ecologically aggressive in the Midwest today.

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DIAGRAMS OF TYPICAL SINGING RHYTHMS

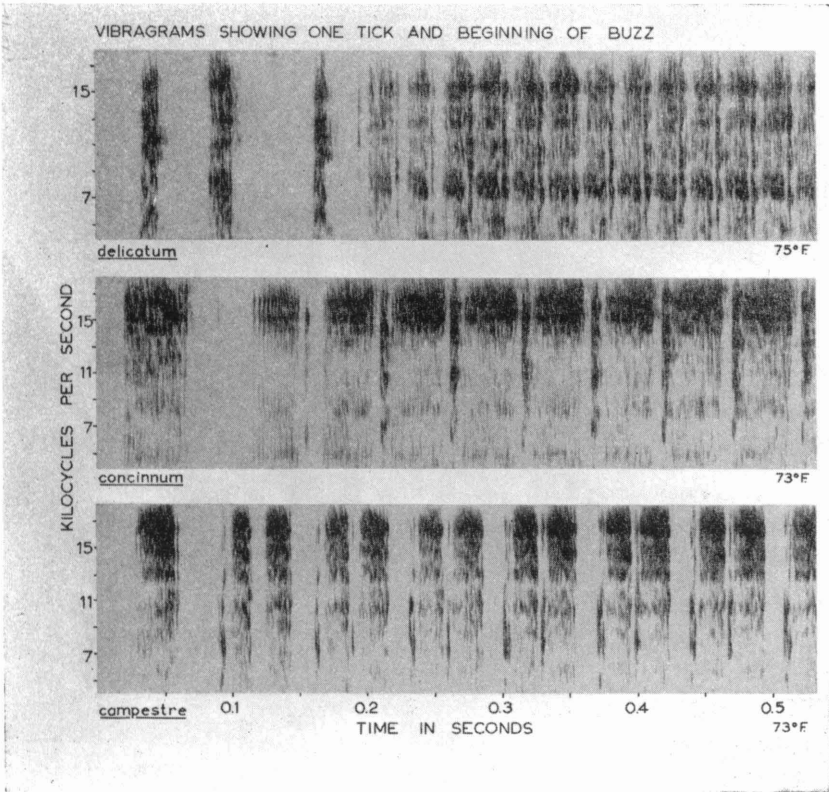
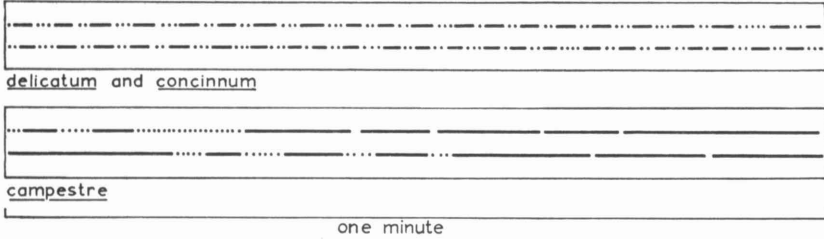


PLATE I

Diagrams and audiospectrographs (Vibragrams) of the calling songs of the *Orchelimum concinnum* group. All recordings were made at tape speeds of 15 inches per second with either a Magnemite Tape Recorder, Model 610-E, or a Magnecord Tape Recorder, Model PT63A2HZ, and using in all cases an American Microphone Company Microphone, Model D-33A. The audiospectrographs were made with a Vibralyzer (Kay Electric Company, Pinebrook, New Jersey).

