# The Taxonomy and Calling Songs of United States Tree Crickets (Orthoptera: Gryllidae: Oecanthinae). II. The *nigricornis* Group of the Genus *Oecanthus*[1]

THOMAS J. WALKER[2]

ABSTRACT

Two species of the *nigricornis* group occur in coniferous trees—*pini* Beutenmuller (pine and fir) and **laricis** n. sp. (tamarack and hemlock). The remaining members of this group are primarily herb inhabiting and have often been placed in a single species; however, at least four species are involved—*nigricornis* F. Walker, **celerinictus,** n. sp., *argentinus* Saussure, and *quadripunctatus* Beutenmuller. These four species differ in geographical distribution, habitat, seasonal life histories, calling songs, morphological characteristics, and courtship interactions. No significant interspecific hybridization is known even though the geographical and ecological distributions of the four broadly overlap. Calling songs of all species except *laricis* were tape-recorded repeatedly under controlled laboratory conditions as well as in the field, and the effects of temperature upon frequency and pulse rate are described in detail. In central Ohio *nigricornis* has two distinctive "song forms" which differ significantly in pulse rate and in the characteristics of the stridulatory file. The two occur in the same fields at the same time without intermediates. They probably represent distinct species.

This paper is the concluding portion of a two-part revision of the Oecanthinae of the United States. The methods of study are described in the first part (Walker 1962a).

Of all the species of Nearctic Oecanthinae, those most frequently collected and the most difficult to analyze in their relationships and differentiating characters are the herb-inhabiting members of the *nigricornis* group. The group also includes two species that are restricted to certain coniferous trees and are rarely collected because they can seldom be reached from the ground.

The tree crickets that live not in trees but in herbaceous plants have long represented a taxonomic enigma. Three species—*nigricornis, quadripunctatus,* and *argentinus*—have been recognized by some authors. Others have considered them merely three varieties of a single species. B. B. Fulton, the first to make an intensive study of the group, found (1926a) that in some parts of the United States two or even three of the forms were easily distinguished; however, in other places the morphological distinctions seemed to break down. He concluded that "until better characters are discovered for separating the three tree crickets of this group, it seems advisable to consider them as subspecies." And such they have generally been considered ever since.

Studies described in this paper indicate that the three herb-inhabiting forms recognized by all previous workers are distinct species and that at least one additional species is involved. The previously unused characters that justify this conclusion include the nature of the calling song, the structure of the stridulatory file, and the seasonal life history.

Although there has been no controversy over the taxonomic status of the conifer-inhabiting members of the *nigricornis* group, the species here described as *laricis* has not previously been considered distinct from *pini.*

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[2] Department of Entomology, University of Florida, Gainesville.

The following abbreviations are used to substantiate certain records: ANSP, Academy of Natural Sciences of Philadelphia, Pennsylvania; BBF, B. B. Fulton collection, North Carolina State College, Raleigh; CAS, California Academy of Sciences, San Francisco; CIS, California Insect Survey, University of California, Berkeley; DR, David Rentz collection, California Academy of Sciences, San Francisco; MC, Macdonald College collection, Quebec, Canada; OSM, Ohio State Museum, Columbus; TJW, author's collection; UA, Department of Entomology, University of Arizona, Tucson; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, U. S. National Museum, Washington, D. C.

The reader is encouraged to refer to papers by B. B. Fulton (1915, 1926a, 1926b) for much additional information on the life history and biology of species of the *nigricornis* group.

## *Oecanthus nigricornis* GROUP

Members of the *nigricornis* group have no swelling on the inner edge of the first antennal segment, and the vertex and basal segments of the antennae are never colored with red or pink. The males have narrow tegmina and closely spaced file teeth; the females have a narrowly notched subgenital plate. The calling song is a continuous trill and is often produced both day and night. At least six species occur in the United States.

### *Oecanthus nigricornis* F. Walker

The Black-Horned Tree Cricket,
Figs. 1, 2, 11, 12, 15, 16, 17, 18

*Oecanthus nigricornis* F. Walker, 1869, p. 93 (type locality, Illinois; type, a female in the British Museum, London, England).

*Oecanthus fasciatus:* Fitch, 1856 (*not* De Geer, 1773) p. 414.

*Oecanthus niveus:* Scudder, 1862 (*not* De Geer, 1773), p. 432.

*Oecanthus forbesi* Titus, 1903, p. 260 (type locality, Urbana, Illinois; type, a male, 6 September 1891, C. A. Hart, Illinois Natural History Survey, Urbana, Illinois).

David Ragge, of the British Museum, wrote (personal communication) that the holotype of *nigri-*

*cornis* "is in reasonable condition and is labeled as type."

The name *fasciatus* was used for this species as a result of Fitch's misidentification of De Geer's *Gryllus fasciatus* (now placed in *Nemobius*). The name *niveus* was applied to this species by some of the early writers because they thought there was but a single species of North American *Oecanthus*. The use of *niveus* was continued well into this century by writers who mistakenly ascribed the characteristic oviposition scars of *nigricornis* to the snowy tree cricket, then known as *niveus*.

The type of *forbesi* belongs to the *nigricornis* group, but it has a peculiar combination of features which makes for difficulty in placing it to species. Its tegmina are usually narrow (3.5 mm.). Its pale coloration is evidently what led Blatchley (1920, p. 778) to regard *forbesi* as a synonym of *quadripunctatus*. However, the broad inner mark of the first antennal segment and the characteristics of the stridulatory file (34 teeth, 0.98 mm.) cause me to place *forbesi* as a synonym of *nigricornis*. Actually the type's pigmentation is not much lighter than normal for western *nigricornis* (see discussion under Morphological Characters).

### ***Oecanthus celerinictus,*** new species

The Fast-Calling Tree Cricket, Figs. 1, 3, 7, 13, 17, 18

*Oecanthus quadripunctatus:* Allard, 1910 (in part) (*not* Beutenmuller, 1894b), p. 36.

*Oecanthus nigricornis quadripunctatus:* Fulton, 1926a (in part) (*not* Beutenmuller, 1894b), p. 53.

This species has been confused with *quadripunctatus* but is distinct from that species in having a faster calling song, fewer file teeth, and more extensive dark markings on the antennae and legs. The structure of the egg of *celerinictus* differs from that of *quadripunctatus* where the ranges of the two species overlap. H. A. Allard (1911) seems to have been the first to notice the contrast between the songs of *celerinictus* and *quadripunctatus*. The name *celerinictus* refers to the fast song (Latin *celer* fast; *nictus* calling).

*Holotype:* Male; Gainesville, Alachua County, Florida, 5 July 1960, T. J. Walker, collector. Type No. 63590, U. S. National Museum. Background color like that of *quadripunctatus*, but with distal portions of legs and entire flagellum of antenna somewhat darker. Ventral face of basal segment of antenna with an inner longitudinal black mark and a distal transverse black mark; second segment with two longitudinal black marks (Fig. 18, F). Apex of caudal femur with one transverse dark mark and two pairs of lateral dark marks. Two transverse dorsal dark marks near the proximal end of each tibia, the marks on the mesothoracic tibiae being especially conspicuous. Except for dark tips of tibial spines, remainder of cricket without prominent markings.

*Allotypic Female:* Same data and disposition as holotype. Color and markings as in holotype.

*Measurements of Holotype and Allotype* (in millimeters): Length of body ♂, 11.8, ♀, 10.9; length of pronotum ♂, 2.0, ♀, 2.0; caudal width of pronotal disk, ♂, 1.8, ♀, 1.7; length of tegmen, ♂, 9.9, ♀, 9.7; greatest tegminal width, ♂, 3.9, ♀, 2.6; length of hind femur ♂, 7.6, ♀, 7.1; length of ovipositor, 4.4.

*Paratypes:* None is listed since the type-series includes more than 1,000 specimens from more than 100 localities (Fig. 1); however, paratypes were labeled as such.

### ***Oecanthus argentinus*** Saussure

Prairie Tree Cricket, Figs. 1, 2, 4, 8, 17, 18

*Oecanthus argentinus* Saussure, 1874, p. 460 (type locality, uncertain; type, a female in the Muséum d'Histoire Naturelle, Geneva, Switzerland).

*Oecanthus nigricornis argentinus* Saussure. Fulton, 1926a, p. 13.

*Oecanthus rehnii* Baker, 1905, p. 82 (type locality, Stanford University, Santa Clara County, California; type, a male in the Pomona College Collection, Clarmont, California, on loan to the U. S. National Museum).

In his original description of *argentinus*, Saussure stated that the type was from La Plata, Argentina. However, in 1897, Saussure reported *argentinus* from Texas and Mexico and stated, "This species was described upon two specimens [only one is mentioned in the original description and only one is preserved at Geneva] labelled as from Argentina; but the locality requires confirmation, to judge from the fact that numerous specimens have been found in the central parts of America." The type locality is still in question since there have been no new records of *argentinus* from South America. Examination of the type of *argentinus* revealed nothing to set it apart from U. S. specimens of the species.

*O. confluens* Hart and Hood is a nomen nudum which has appeared in the literature several times (e.g., Folsom 1909, p. 145) and probably refers to *argentinus*.

### ***Oecanthus quadripunctatus*** Beutenmuller

Four-Spotted Tree Cricket, Figs. 1, 2, 5, 9, 14, 17, 18

*Oecanthus quadripunctatus* Beutenmuller 1894b, p. 250 (I have examined three male syntypes, two from Ellenville, New York, and one from Woodstock, Connecticut; lectotype, here designated, a male labeled, "Ellenville, N. Y." and "A.M.N.H. 240," and cataloged as Type No. 65924, U. S. National Museum).

*Oecanthus nigricornis* var. *quadripunctatus* Beutenmuller. Houghton 1909, p. 114.

*Oecanthus nigricornis quadripunctatus* Beutenmuller, E. M. Walker 1910, p. 356.

### ***Oecanthus laricis*** new species

Tamarack Tree Cricket, Fig.1

*Oecanthus pini:* Cantrall, 1943 (*not* Beutenmuller, 1894a), p. 171.

Cantrall (1943) reported a species of *Oecanthus* as occurring on tamarack (*Larix*) in two localities in southern Michigan. B. B. Fulton had identified specimens of this species as *pini*, evidently on the basis of their coniferous host and their brown and green coloration.

In letters to me, E. S. Thomas and R. D. Alexander have indicated that when they first saw the

species from tamarack (Thomas in 1933 and Alexander in 1958), they thought it was an undescribed species rather than *pini*. Specimens and a tape recording supplied by Alexander have convinced me that the species is distinct from *pini*, and it is here described as *laricis* in reference to its usual host.

*O. laricis* differs from *pini* strikingly in both size and coloration, *laricis* being much smaller and darker than *pini*. The teeth of the stridulatory file are more closely spaced, and the pulse rate of the song is slower than in *pini*.

*Holotype:* Male; K-25 (see Map 2, Cantrall 1943), E. S. George Reserve, Livingston County, Michigan, 7 Aug. 1939, I. J. Cantrall, collector; University of Michigan Museum of Zoology. Tegmina and lighter portions of body a dusky green as in dark *nigricornis* but with a slight olive hue. Head and thorax dark brown with two ill-defined pale longitudinal stripes extending from behind the eyes to the caudal margin of the pronotum. Abdomen dark brown below and paler above. Antennae and legs dark brown except for slightly paler caudal femora. Basal segments of antennae with ventral black marks similar to those of *celerinictus* (Fig. 18, F) but the lateral marks less heavily pigmented and with less distinct edges than the mesal marks.

*Allotypic Female:* Same data and disposition as holotype. Color and markings as in holotype.

*Measurements of Holotype and Allotype* (in millimeters): Length of body, ♂, 10.7, ♀, 10.0; length of pronotum, ♂, 2.1, ♀, 2.2; caudal width of pronotal disk, ♂, 2.1, ♀, 2.0; length of tegmen ♂, 10.4, ♀, 10.4; greatest tegminal width, ♂, 3.8, ♀, 3.2; length of hind femur, ♂, 7.4, ♀, 7.6; length of stridulatory file, 1.27 (46 teeth); length of ovipositor, 5.4.

*Paratypes:* 7 ♂♂, 12 ♀♀, 3 juveniles, as follows: University of Michigan Museum of Zoology (20)—MICHIGAN: Livingston Co., E. S. George Reserve, 24 July 1939 (2 juv.), 7 Aug. 1939 (2 ♀♀), 24 Aug. 1936 (1 ♂, 1 ♀), I. J. Cantrall; 14 Aug. 1937 (1 juv.), J. S. Rogers; Aug. 1959 (1 ♂), Aug. 1961 (1 ♂), R. D. Alexander. Oakland Co., Milford, 4 Sept. 1921 (1 ♀), 13 Aug. 1933 (2 ♂♂, 4 ♀♀), 17 Aug. 1933 (1 ♂, 2 ♀♀), T. H. Hubbell; 17 Aug. 1933 (1 ♀), I. J. Cantrall.

Ohio State Museum (2)—OHIO: Lake Co., Perry, 18 Aug. 1935 (1 ♂), 19 Aug. 1935 (1 ♀), E. S. Thomas.

### ***Oecanthus pini*** Beutenmuller

Pine Tree Cricket, Figs. 1, 6, 10, 17

*Oecanthus pini* Beutenmuller 1894a, p. 56 (six male and four female syntypes from Windham County, Connecticut; lectotype, here designated, a male labeled, "Woodstock, Ct. Sept. 1893" and "A.M.N.H. 244," and cataloged as Type No. 65925, U. S. National Museum).

#### DISTRIBUTIONAL RELATIONSHIPS

Figure 1 shows the geographical distribution of the six species of the *nigricornis* group.

Only *quadripunctatus* occurs throughout the United States. I have seen specimens also from British Columbia, Ontario, and Quebec, Canada, but none from Mexico. Peripheral records for the United States are FLORIDA, Cape Sable, Monroe Co. (TJW); TEXAS, Brownsville (USNM); ARIZONA, Huachuca Mts. (UMMZ), Yuma (USNM); OREGON, Wheeler Co. (TJW); NORTH DAKOTA, Ramsey Co. (UMMZ); MICHIGAN, Mackinac Co. (UMMZ); MAINE, Somerset Co. (Morse 1920).

*O. argentinus* occurs throughout Western United States and ranges eastward into Ohio and Alabama. Its occurrence in Eastern United States seems to involve two phenomena: First, the eastward extension is largely correlated with the occurrence of pre-Columbian prairies. For instance, the occurrence of *argentinus* in parts of Ohio, Kentucky, and Indiana may be a manifestation of the "Prairie Peninsula" discussed by Transeau (1935). Second, there is evidence that *argentinus* is presently extending its range eastward in response to prairielike habitats produced by agriculture. Nearly all the easternmost records are from specimens collected in the past decade. In fact, all the Tennessee records, all but one of the Kentucky records, and all but four of the Ohio records are since 1954.

The most convincing evidence of the recent spread of *argentinus* eastward is found in the collection of the Ohio State Museum. Of the more than 300 specimens of herb-inhabiting tree crickets collected in Ohio in the 1930's by E. S. Thomas, only 3 are *argentinus*, and the same collecting techniques are successful with all the herb-inhabiting species. When I collected in Ohio in 1955-57, *argentinus* was as abundant as the other herb-inhabiting species in many of the same areas where Thomas had collected 25 years before.

The southeastern limits of *argentinus* are poorly delineated because of inadequate material from Mississippi and Alabama. The "Black Belt" prairie area of Alabama and Mississippi could form part of the pre-Columbian range of *argentinus*. Two specimens of *argentinus* I have examined may be chance introductions—one is labeled Port Jervis, New York (UMMZ), and the other "Ft.M." (Fort Myers?) Florida (CAS). Outside of the United States, *argentinus* is known from Mexico (Sonora and Sinaloa—DR, UMMZ) and probably extends into the prairie areas of Canada. Peripheral U. S. records of *argentinus* are: ALABAMA, Auburn (Auburn University Collection); MISSISSIPPI, Wilkinson County (UMMZ); TEXAS, Brownsville (USNM), Presido Co. (JA); ARIZONA, Santa Cruz Co. (UA); CALIFORNIA, San Diego (USNM); OREGON, Washington Co. (BBF); WASHINGTON, Colfax (UMMZ); MONTANA, Lewistown (Hebard 1928); NORTH DAKOTA, Devils Lake (UMMZ); MINNESOTA, Ottertail Co. (ANSP); OHIO, Knox Co. (TJW), Gallia Co. (OSM).

*O. nigricornis* is a Northeastern species that extends westward along the major river systems to the Continental Divide. It extends southward along the Appalachian Mountains into North Carolina and

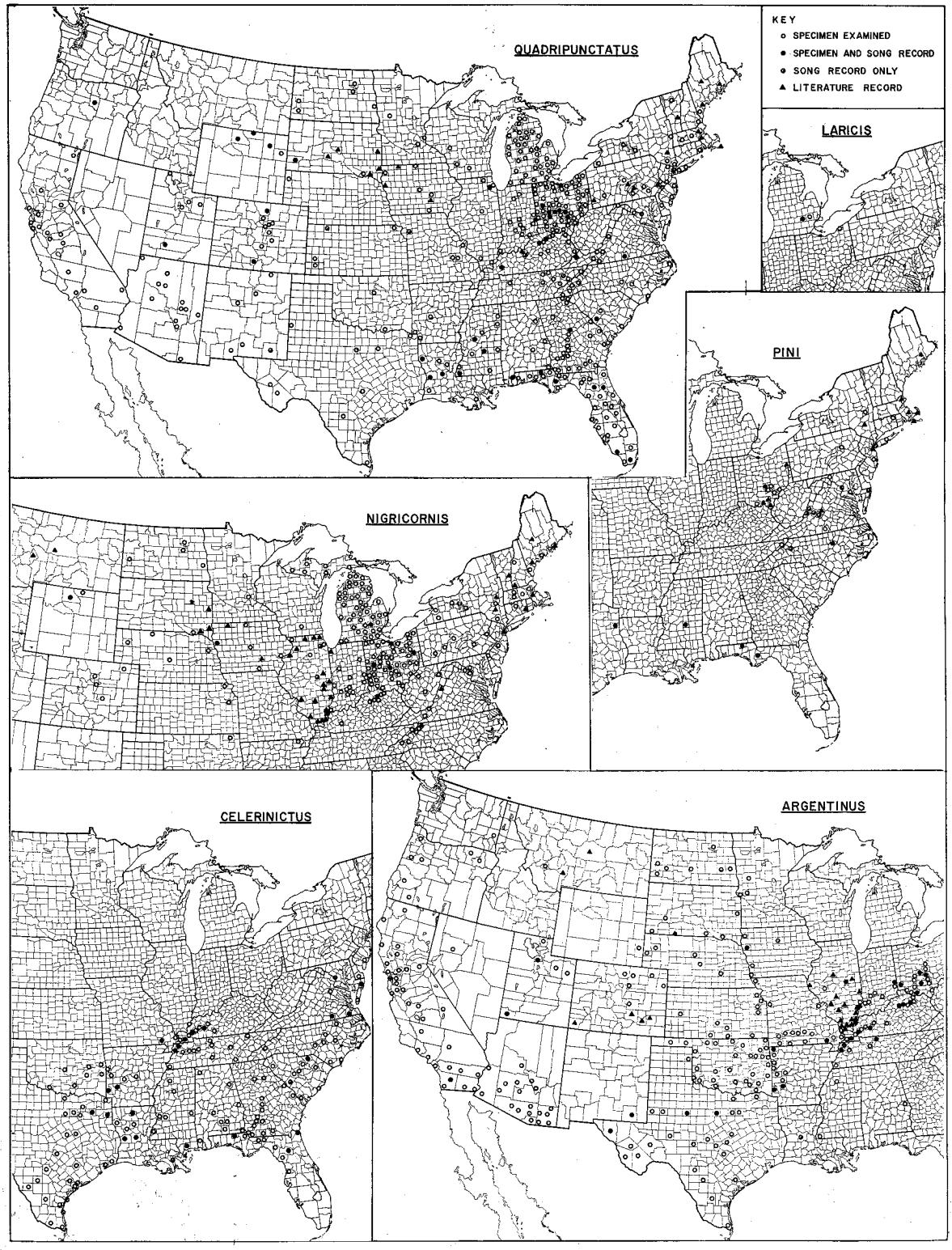



FIG. 1.—Geographical distribution of the species of the *Oecanthus nigricornis* group. Records from the United States only are included.

Tennessee. It occurs in Quebec (MC), Ontario (MC), Manitoba (Fulton 1926a), and probably elsewhere in southeastern Canada. Peripheral U. S. records are: DELAWARE, Newark (USNM); VIRGINIA, Arlington (USNM); NORTH CAROLINA, Waynesville (BBF); KENTUCKY, Muhlenberg Co. (TJW); ARKANSAS, Clay Co. (UMMZ); OKLAHOMA, Craig Co. (UMMZ); COLORADO, El Paso, Jefferson, and Boulder Counties (UMMZ); WYOMING, Big Horn Co. (TJW); MONTANA, Broadwater Co. and Lewistown (Hebard 1928); NORTH DAKOTA, Devils Lake (UMMZ); MAINE, Hoxie (Morse 1920).

*O. celerinictus* occurs throughout Southeastern United States except for south peninsular Florida. Its northern limits correspond approximately to the southern limits of *nigricornis,* but there is some overlap. It extends southward into Mexico (Neuvo Leon and Tamaulipas—UMMZ, CAS). Westward it stops where deciduous forest gives way to prairie. Peripheral U. S. records are: TEXAS, Dimmit Co. (USNM); OKLAHOMA, Cotton and Cleveland Counties (UMMZ); MISSOURI, Butler Co. (TJW); ILLINOIS, Hardin Co. (UMMZ); KENTUCKY, Ohio Co. (TJW); TENNESSEE, Campbell Co. (OSM); NORTH CAROLINA, Haywood Co. (UMMZ); DISTRICT OF COLUMBIA (DR); NEW JERSEY, Atlantic Co. (UMMZ); FLORIDA, Hernando Co. (UMMZ).

The distribution of *laricis* and *pini* is poorly known because these species are rarely collected even in areas where they are abundant. The known distribution of *laricis* is detailed in the list of paratypes. Careful collecting on tamarack and hemlock probably will reveal a much more extensive range.

It seems likely that *pini* occurs in most areas where pines of the appropriate species are numerous. So far the only apparent exception to this generalization is that *pini* does not extend into peninsular Florida even though one of its hosts, loblolly pine, does. Whether *pini* extends northward on balsam fir into areas where there are no pines is not known. There are no Canadian records for *pini.* The peripheral records for *pini* are: FLORIDA, Liberty and Jackson Counties (TJW); MISSISSIPPI, Scott Co. (TJW); TEXAS, Harrison Co. (TJW); TENNESSEE, Carter Co. (UMMZ); OHIO, Adams and Fairfield Counties (OSM), Columbiana Co. (E. S. Thomas, personal communication); PENNSYLVANIA, Columbia (BBF); NEW YORK, Ulster Co. (TJW); MAINE, Hancock Co. (Procter 1946).

## HABITAT RELATIONSHIPS

*O. pini* and *laricis* are the only species of the *nigricornis* group that occupy habitats that are largely nonoverlapping with those of other species. In areas where the ranges of any of the four remaining species overlap, individuals of different species may be found intermingled upon the same herbaceous plants. With single sweeps of a beating net I have taken three different combinations of three species. Nevertheless, between some of the four herb-inhabiting species in some situations a considerable degree of differentiation in habitat may be observed.

*O. pini* is known almost exclusively from pine, but Fred Hough of Accord, New York, has found it in the crowns of balsam fir (*Abies balsamea*) on Slide Mountain, Ulster County, New York. I examined a specimen collected from fir by Mr. Hough and found no differences between it and specimens from pine. The species of pine that *pini* is known to inhabit are pitch, scrub, shortleaf (TJW, Florida), loblolly (TJW, Florida), and white (Fred Hough, New York)—*Pinus rigida, virginiana, echinata, taeda,* and *strobus,* respectively. Since *pini* characteristically occupies the crown of its hosts, it is usually difficult to collect. Most specimens come from small trees or low branches. Occasionally, a specimen can be obtained by sweeping the undergrowth beneath host trees.

*O. laricis* is known from tamarack (*Larix laricina*) in southeastern Michigan and from hemlock (*Tsuga canadensis*) in northeastern Ohio. Cantrall (1943, pp. 54, 172) has summarized what is known of the habitat of *laricis* in Michigan. He states that it has been found only in tamarack and seems to prefer the upper portions of vigorous, young trees 20 to 40 feet in height. He did not find it in dense stands of tamarack but on the younger trees in more open areas. E. S. Thomas collected the only two specimens of *laricis* known from hemlock. He writes (personal communication) that he collected one specimen at night by its song and on the following day swept the hemlocks at the same place and collected the second specimen.

*O. nigricornis* is most frequently encountered on coarse weeds and brambles such as occur in the more fertile old-field situations and along waterways. It is occasionally found on fine-stemmed weeds and is sometimes locally abundant on small trees such as sumac and willow. It is not commonly found in dry, sparsely vegetated fields nor is it known from the crowns of tall trees. Goldenrod, great ragweed (*Ambrosia*), blackberry, and horse-weed (*Erigeron*) are plants with which *nigricornis* is commonly associated. (Common names of plants are from Fernald 1950.)

*O. celerinictus, argentinus,* and *quadripunctatus* are most commonly found on herbaceous plants that are not so coarse as the ones upon which *nigricornis* is usually found. However, they are occasionally numerous on coarse weeds and brambles, and males often sing from the lower branches of small trees in open situations. Females of these three species restrict their egg laying to finer and less woody stems than do females of *nigricornis.* For instance, while both *nigricornis* and *quadripunctatus* may oviposit in the same blackberry plant, *nigricornis* punctures the coarse canes while *quadripunctatus* is restricted to the finer, more tender parts. Only slight differences in habitat have been observed among *celerinictus, argentinus,* and *quadripunctatus. O. celerinictus* is less frequently taken in dry or sparsely

vegetated habitats than are *quadripunctatus* and *argentinus* and resembles *nigricornis* in this respect. While both *argentinus* and *quadripunctatus* occur in prairie and desert areas, *argentinus* is much the more frequent of the two in such situations.

To give a better idea of the type of habitat in which *celerinictus, argentinus,* and *quadripunctatus* occur, listed below are 20 plants from which I have collected series of one or more species (*c, a,* and *q* refer to the 3 species in question): Common ragweed (*c, a, q*), wild carrot (*c, a, q*), daisy fleabane (*c, a, q*), goldenrod (*c, a, q*), small oaks (*c, a, q*), blackberry (*c, q*), broom-sedge (*c, q*), Johnson grass (*c, a*), cotton (*c, a*), sweet clover (*a, q*), Joe-Pye-weed (*a, q*), sunflower (*a, q*), corn (*c*), soybeans (*c*), sassafras (*c*), alfalfa (*a*), timothy (*a*), mullein (*a*), willow (*q*), buffalo-currant (*q*).

## SEASONAL LIFE HISTORIES

Significant differences occur in the seasonal life histories of the species in the *nigricornis* group. *O. nigricornis, laricis,* and *pini* have but one generation a year, while *celerinictus* always has two generations a year. *O. quadripunctatus* is known to have one generation a year in the north and two or more generations each year farther south. The same is probably true of *argentinus,* but in this species the bivoltine populations extend farther north than in *quadripunctatus.*

Figure 2 shows the seasonal life histories of *nigricornis, argentinus,* and *quadripunctatus* in central Ohio. It is derived from frequent observations and weekly sampling of two weedy vacant lots near Columbus in 1956. The first generation of *argentinus* dies out as the single generations of *nigricornis* and *quadripunctatus* mature and the second generation of *argentinus* matures about 7 weeks later. Adults of all three species are then present until frost.

Throughout the range of *nigricornis* its seasonal life history seems to be similar to that pictured in Fig. 2. July 5 is the earliest record for an adult (Indianapolis, Indiana—UMMZ), and late July is the earliest time of appearance recorded for most states.

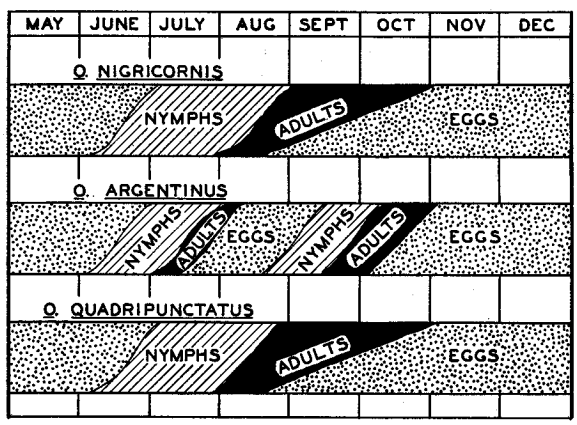


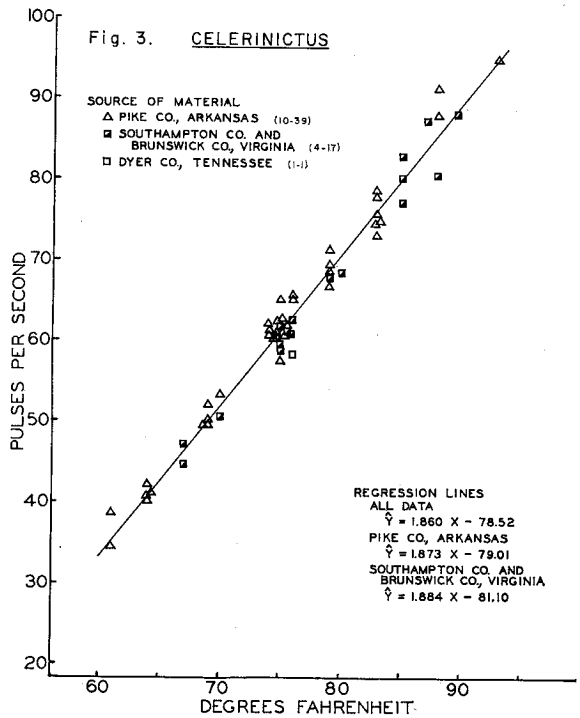

FIG. 2.—Seasonal life histories of the herb-inhabiting species of the *nigricornis* group, Columbus, Ohio, 1956.

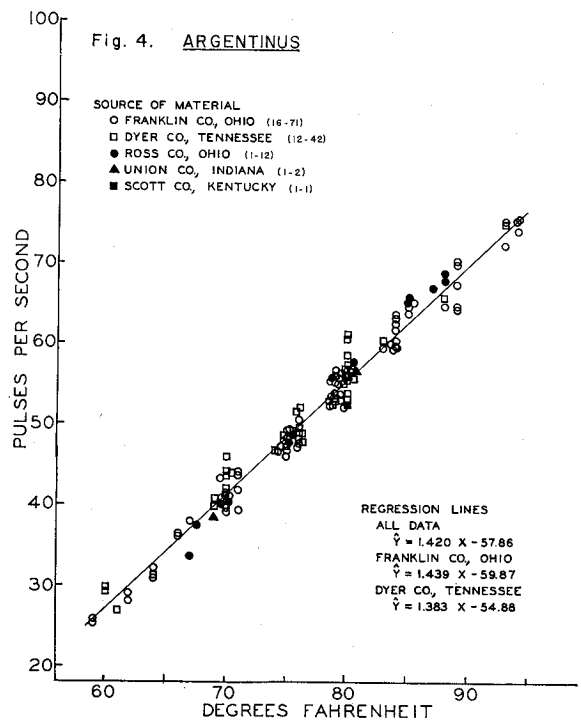
In contrast to *nigricornis, celerinictus* evidently has two generations a year throughout its range. At Gainesville, Florida, the first generation matures in mid-May and dies out by about the first of August. The second generation begins to mature by the middle of August and large numbers of adults are present by the end of August. Unless frost intervenes, adults may then be found until at least as late as mid-November. The appearance of the first adults is delayed until early or mid-June in the northern part of the range of *celerinictus,* but the remainder of the life cycle is evidently similar to that in Florida. Fulton (1951) indicates that the break between generations occurs about the first of August at Raleigh, North Carolina (*celerinictus* is included in Fulton's *quadripunctatus*).

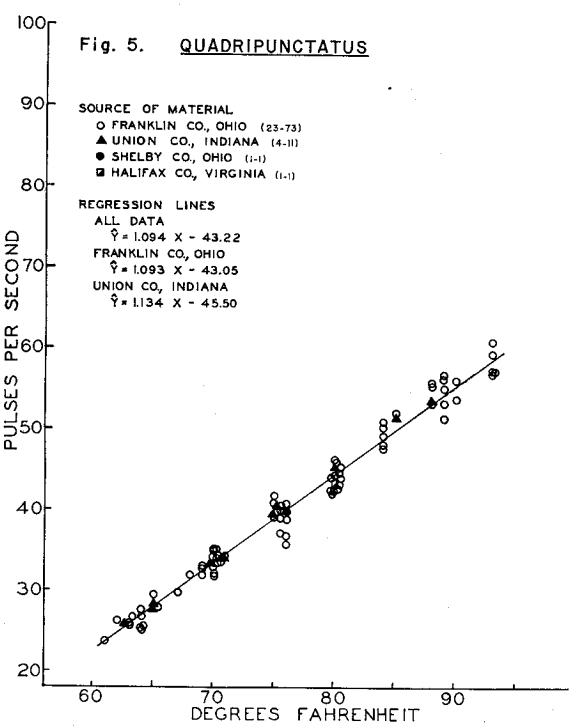
*O. argentinus* has proved to be bivoltine in the three places it has been carefully studied—Ohio (Fig. 2); Lawrence, Kansas (Beach 1938); and western Tennessee (TJW). However, consideration of the brevity of the frost-free period in the northern portion of the range of *argentinus* (as much as one-third shorter than in central Ohio) suggests a single generation there. This supposition is supported by a lack of records of adults before 28 July in Oregon, Washington, Montana, Wyoming, North Dakota, South Dakota, and Minnesota. In the southernmost portion of the range of *argentinus,* more than two generations may occur. Adult specimens have been collected in Pima County, Arizona, as early as 4 February and as late as 12 December.

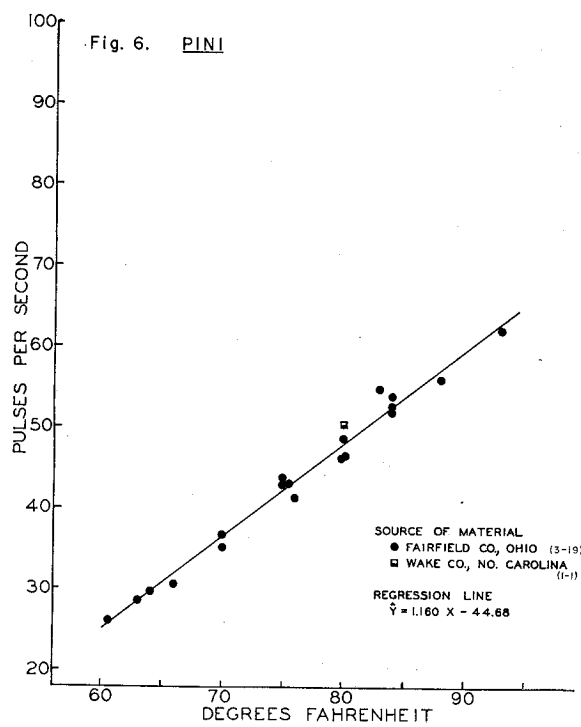
*O. quadripunctatus* is univoltine in the north and bivoltine or multivoltine in the south. The geographical limits of the various life-history types are poorly known, but the univoltine populations probably extend about as far south as those of *nigricornis* (Fig. 1). At Gainesville, Florida, the seasonal life history of *quadripunctatus* is similar to that of *celerinictus* (see above). Observations in 1960 suggested that the second generation of *quadripunctatus* begins maturing slightly before that of *celerinictus.* Adults have been collected as early as June in the following States and two generations probably occur: Alabama, Arizona, Arkansas, California, Georgia, Kentucky, Louisiana, Mississippi, New Mexico, North Carolina, Oklahoma, and Texas. Only from Florida and south Texas (Brownsville, 1 May—USNM) have I seen adults collected as early as May. In south Florida adults have been collected during every month, and more than two generations are probably produced during a year. It is not known whether nymphs survive during the brief winter.

All evidence suggests that both *laricis* and *pini* are always univoltine. Adults of *laricis* in Michigan appear about the first of August and have been heard as late as 14 September (Cantrall 1943). Adults of *pini* have been collected in southeastern Ohio as early as 24 July and as late as 28 October. The corresponding dates in Wake County, North Carolina, are




FIGS. 3–6.—Effect of temperature on pulse rate in *Oecanthus celerinictus, argentinus, quadripunctatus,* and *pini,* laboratory recordings. Numbers in parentheses after each locality indicate the number of individuals and the number of tape recordings from that locality. The regression line drawn in each figure is the one for all data for the species.

10 July and 22 September. In north Florida adults of *pini* have been collected as early as 13 June, and they were still numerous as late as 7 August.

## CALLING SONG

The special significance of calling songs in cricket taxonomy and the nature of intraspecific variation in calling songs have recently been discussed by Alexander (1962) and Walker (1962a, 1962b).

Study of the calling songs in the *nigricornis* group led to the initial recognition of *celerinictus* as distinct from *quadripunctatus*. The fact that calling songs have proved less variable geographically than the morphological features which have been used traditionally to separate members of the *nigricornis* group has helped confirm the identification of several populations of doubtful affinity.

The calling songs of all species in the *nigricornis* group are long-continued trills. The herb-inhabiting forms commonly sing both day and night, while the tree-inhabiting forms ordinarily sing only at night.

The pulse rate, which corresponds to the wing-stroke rate, is a particularly significant feature in the calling songs of the *nigricornis* group (Walker 1957). Females of species that are reproductively active at the same time and in the same place have been demonstrated to discriminate the calling songs of their own species from those of others by the characteristic pulse rates. The particular pulse rates to which a female responds change with temperature in the same fashion as do the pulse rates produced by the males of her species.

Figures 3 to 6 show the temperature-pulse rate relations in *celerinictus, argentinus, quadripunctatus,* and *pini.* The data are from laboratory recordings under controlled temperatures. It is apparent in each species that individuals from widely separated localities have closely similar temperature-pulse rate relations. Any geographical variation is minor as compared to the consistent differences between the species. The lack of major geographical variation in pulse rate in these four species is further substantiated by extensive field recordings (Figs. 7 to 10). In interpreting Figs. 7 to 10 one should keep in mind that for individuals from a single locality the points for field recordings should have a greater average deviation from the regression line than those for laboratory recordings because of the difficulties in accurately measuring temperatures in the field and because of less precise tape speed control in spring-driven tape recorders.

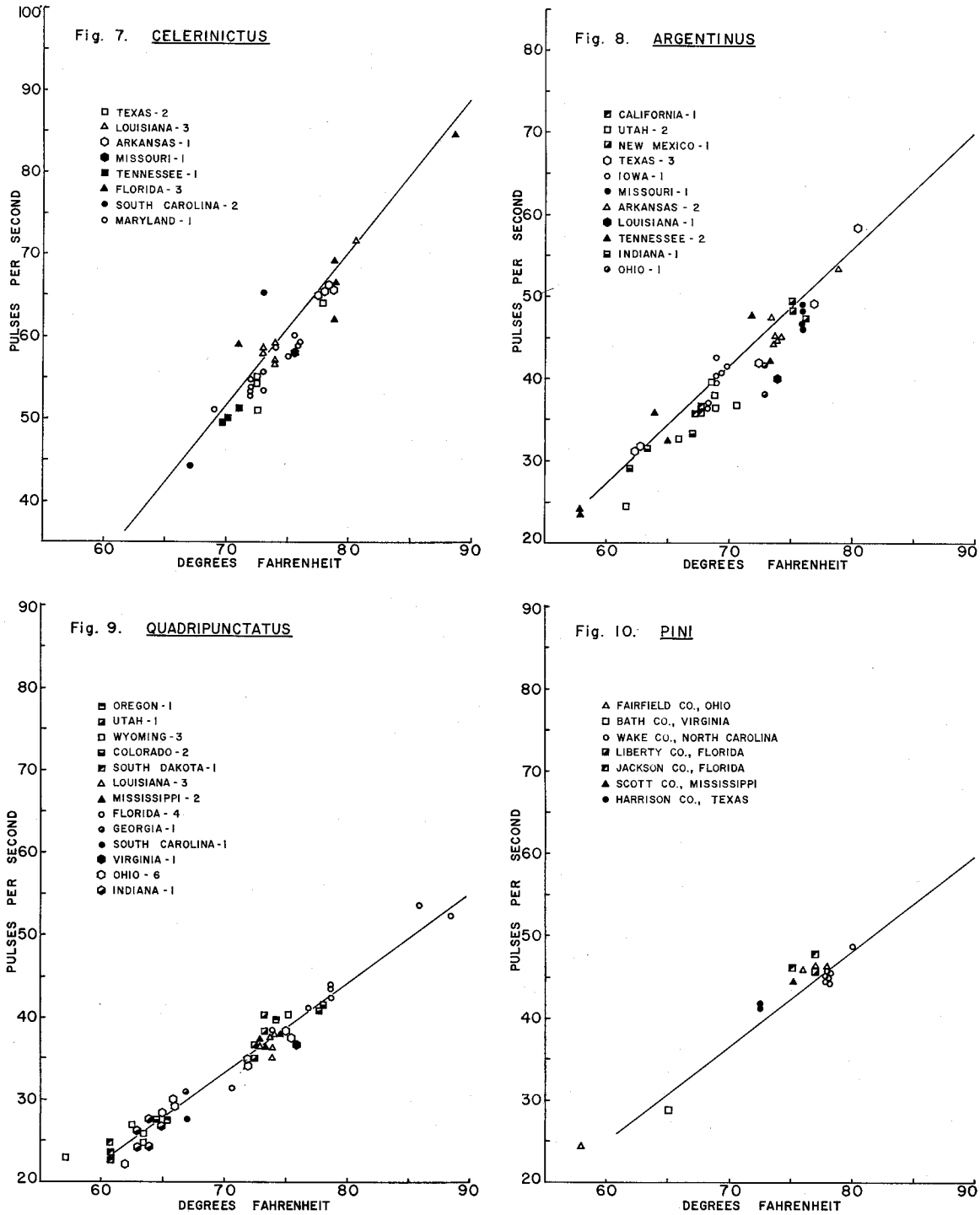
The data in Figs. 7 to 10 are too scattered to reveal minor geographical variation in temperature–pulse rate relations, but there is evidence of such variation in the song of *quadripunctatus* from another source. Laboratory recordings of Alachua County, Florida, specimens were made in 1961 under carefully controlled conditions of temperature and humidity. At temperatures near 81° F., 42 recordings of 12 individuals averaged 3.6 pulses per second higher than that predicted by the regression line in Fig. 5, and no recording was at a pulse rate as low as that predicted by the regression line in Fig. 5.

The details of the song of *laricis* are known to me only from a single tape recording made at 80° F. by R. D. Alexander. The pulse rate of this recording is 39 pulses per second and the frequency is 3.5 kilocycles per second. These measurements do not serve to distinguish the song from that of *quadripunctatus.* Cantrall (1943, p. 172) says of the song of *laricis,* "Very similar to those of both *nigricornis* and *quadripunctatus,* it can be distinguished by its lower pitch as well as by its source in a tamarack . . . ."

Study of the calling song of *nigricornis* in Ohio revealed a dichotomy in the temperature-pulse rate relations. In 1956, the songs of 32 individuals of *nigricornis* were recorded in the laboratory under controlled temperatures. Fifteen of these were of a pale form collected on willow. Analysis of the recordings of these individuals gave the data depicted in Fig. 11. The other 17 individuals were the darkly pigmented, robust form which typically occurs in weedy fields in Ohio. Of these, 14 produced a fast-trilling song closely similar to that of the willow-inhabiting form, but three individuals produced an appreciably slower song (Fig. 12). Two of the slow-trilling individuals had been collected from the same weedy fields as some of the fast-trilling forms. The other had been collected from *willow* by R. D. Alexander in Carroll County, Ohio. It was included with the individuals collected from weed fields because its morphology was typical of herb-inhabiting *nigricornis* and not at all like that of the form labeled here as "willow-inhabiting" *nigricornis.* Obviously further study was needed.

In the summer of 1957 (the end of my stay in Ohio), I collected specimens of *nigricornis* from two weedy fields in Upper Arlington, a suburb of Columbus, Ohio, and succeeded in recording the songs of 24 individuals at temperatures between 75° and 76½° F. Thirteen individuals produced slow trills, ranging from 49¾ to 53¾ pulses per second. Eleven individuals produced fast trills, ranging from 62¼ to 67¼ pulses per second. No songs of intermediate pulse rates were recorded. The 13 slow-trilling individuals and 5 of the fast-trilling individuals came from one field. The six recorded individuals from the other field were all fast trillers. The two fields were similar in vegetation and topography and less than a half-mile apart.

There are, then, two types of song produced by herb-inhabiting *nigricornis* in central Ohio. Any given individual produces one type of song but not the other. Individuals of both song types may occur in the same weedy field at the same time. Individuals of the two song types cannot as yet be easily distinguished except on the basis of song, and even here tape recording and careful analysis is required. A partial differentiation of the two types on the basis of the stridulatory files is described in the section on morphological characters. The taxonomic significance of the situation will be discussed later.




FIGS. 7–10.—Effect of temperature on pulse rate in field recordings of *Oecanthus celerinictus, argentinus, quadripunctatus,* and *pini.* In Figs. 7–9, the number following the name of each State indicates the number of counties represented in the data. Usually the names of the counties can be deduced by referring to Fig. 1; however, song records by other persons and those made in sunlight are omitted here but are included in Fig. 1. The counties (or parishes) represented in Figs. 7–9, not deducible from Fig. 1, are as follows: Fig. 7, La.—Lincoln, Rapides, Vernon; Ark.—Pike; Tenn.—Dyer. Fig. 8, Ark.—Benton, Pike; Tenn.—Dyer, Robertson; Ohio—Fairfield. Fig. 9, Miss.—Holmes, Scott; Fla.—Alachua, Holmes, Liberty, Putnam; Va.—Dickenson; Ohio.—Clarke, Franklin, Greene, Hocking, Madison, Shelby. The lines are the regression lines for laboratory recordings (see Figs. 3–6).

Outside of Ohio the songs of *nigricornis* have not been carefully studied. The few recordings available from other States were, with one exception, made in the field and often in sunlight. Temperature measurements in such situations are frequently inaccurate, so the following conclusions are tentative.

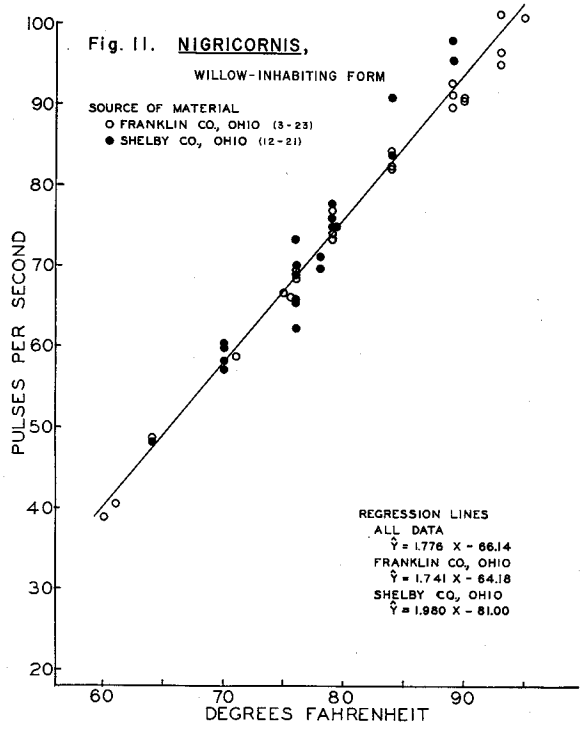
The slow-trilling form occurs at least as far west as Sioux City, Iowa. Evidence for this consists of recordings made at night of the songs of three individuals in Sioux City (41, 39½, and 43½ pulses per second at 68° F.) and one individual in Du Page County, Illinois (43¾ p/s at 72° F., recording by R. D. Alexander). The slow-trilling form probably extends even farther west, since one individual recorded near Greybull, Wyoming, in sunlight produced 63½ p/s at 84° F., and another produced 63¼ p/s at 83° F. However, a third individual from the same locality produced an intermediate pulse rate (night; 57½ p/s at 75° F).

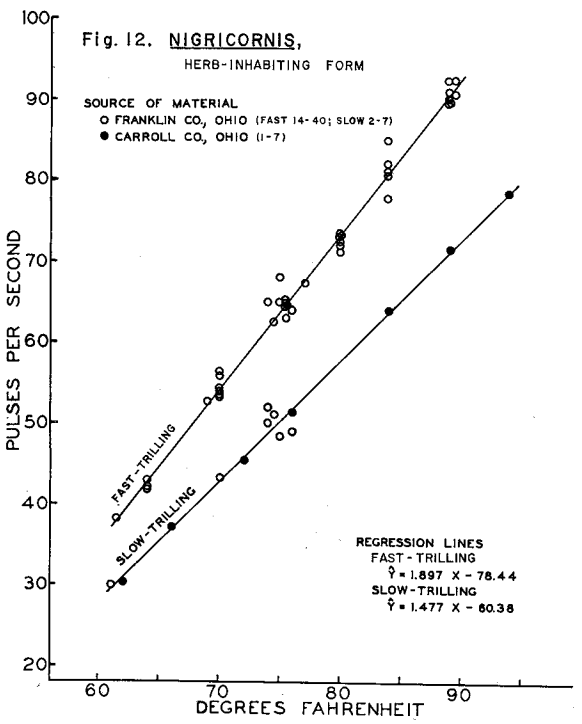
Outside of Ohio the fast-trilling form is known only from Du Page County, Illinois (66¼ p/s at 78° F., recording by R. D. Alexander). Songs with pulse rates apparently intermediate between fast-trilling and slow-trilling *nigricornis* have been recorded from Kentucky (Harrison County; sunlight; 75½ p/s at 86° F.), Illinois (Du Page County; 62 p/s at 78° F.; R. D. Alexander), and Michigan (Livingston County; laboratory; 67¾ p/s at 82° F.; R. D. Alexander).

No recordings of *nigricornis* east of Ohio have been made. Obviously further recordings under carefully controlled conditions are needed before reliable statements can be made as to the nature and extent of the variation in calling song in what is here called *nigricornis*.

The frequency (subjectively interpreted as *pitch*) of the songs of the *nigricornis* group varies from 2.5 to 5.2 kilocycles per second. In each species the frequency increases with increasing temperature and pulse rate (Figs. 13 to 17). At most *temperatures* the frequencies of the songs of *nigricornis, celerinictus, argentinus,* and *quadripunctatus* are closely similar, and the frequency of the song of *pini* is somewhat lower. For instance, at 75° F., the first four species produce songs of approximately 3.7 to 3.9 kilocycles per second while the song of *pini* is about 3.4 kilocycles per second. Since at any given temperature the various species produce different characteristic pulse rates, it follows that the relation between pulse rate and frequency is of taxonomic value (see Fig. 17).

Unfortunately there is considerable intraspecific variation in frequency-pulse rate relations, and species often cannot be reliably separated on this basis. In general, species with markedly different temperature-pulse rate relations will also have markedly different pulse rate-frequency relations. For example, *quadripunctatus* and *celerinictus* are easily



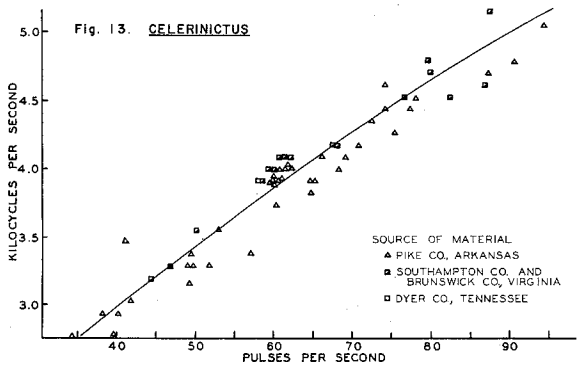



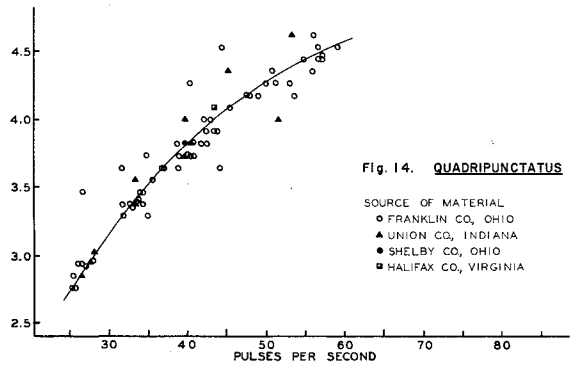

FIGS. 11 and 12.—Effect of temperature on pulse rate in *Oecanthus nigricornis,* laboratory recordings. Numbers in parentheses indicate the number of individuals and the number of recordings for each locality.

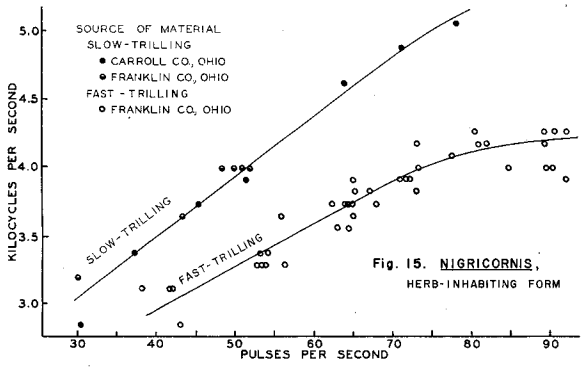
separable on the basis of pulse rate-frequency relations.

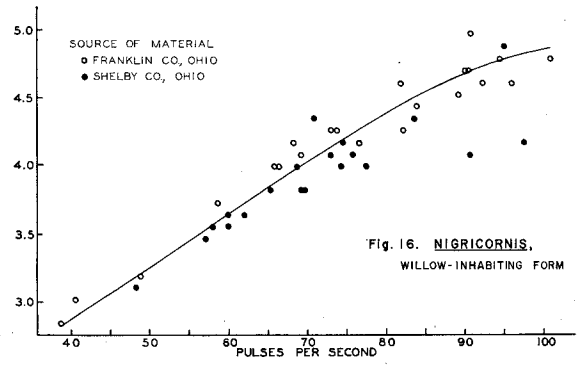
## MORPHOLOGICAL CHARACTERS

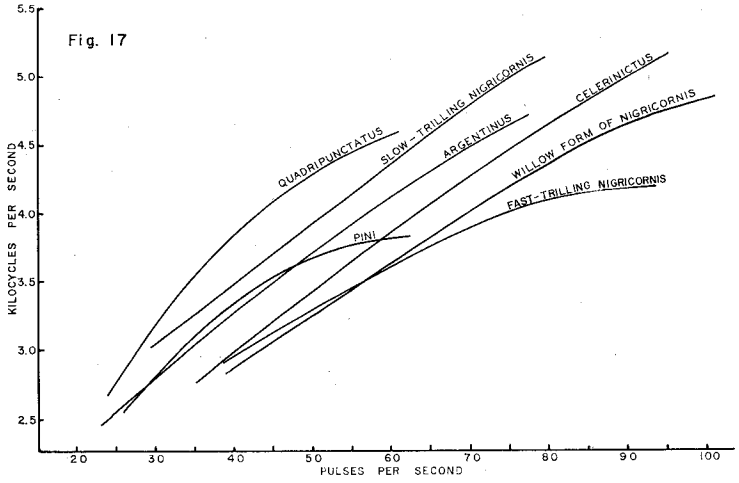
Most specimens belonging to the *nigricornis* group can be identified easily to species on the basis of conspicuous external morphological characters. Some specimens, however, are difficult to identify with certainty. This difficulty is especially true of teneral specimens and, in some cases, of specimens that have been preserved for longer than a year or so. Identification is much more difficult in some geographical




FIGS. 13–17.—Relationship between pulse rate and frequency in the *Oecanthus nigricornis* group. Figs. 13–16.—Detailed data for *Oecanthus celerinictus, quadripunctatus,* and *nigricornis,* laboratory recordings. All curves fitted by eye. Detailed data for *argentinus* and *pini* are given in Walker 1962b, Figs. 11 and 12. Fig. 17.—Composite graph showing curves for all species.

areas than in others, not only because there may be a different assemblage of species but also because some of the species show geographical variation in their identifying characteristics. Morphological characters and their variation are discussed below, and their use is summarized in the key that follows.

The general pigmentation of a specimen is sometimes enough to place it to species. *O. nigricornis* is the only species that ever has black legs and large areas of black on the head and pronotum. Unfortunately, specimens of *nigricornis,* especially from the western portion of its range, frequently lack the distinctive black pigmentation, and other characteristics must be used. Only *pini* and *laricis* have conspicuous brown pigment. In both species the head, pronotum, and legs are brown and the tegmina green. In fresh specimens of *pini,* the brown is light to medium in intensity and somewhat reddish, and the light green of the tegmina is distinctively clear and brilliant. In *laricis* both the browns and the greens are darker than in *pini,* and in a few specimens the browns appear nearly as dark as the blacks of *nigricornis.* The different shades of brown and green in *laricis* and *pini* correspond to different colors of the trees they inhabit, and each species is extraordinarily difficult to detect when at rest among the needles of its usual host. The browns and blacks of tree crickets do not fade; but as preserved specimens age, the greens fade to a light brown. Therefore, in both *pini* and *laricis* the contrast between the color of the tegmina and that of the head and pronotum gradually diminishes in preserved specimens.

The specimens not identifiable on the basis of general pigmentation can usually be identified by the dark markings on the ventral surface of the first two segments of the antennae. *O. argentinus* is perhaps the easiest to identify on this basis (Fig. 18, I-L). The markings are broad and any general infuscation is usually restricted to the immediate vicinity of the marks. The two marks on the second segment are confluent, contiguous, or narrowly separated. The marks on the first segment may be similarly close, or more rarely they are separated by a space nearly as wide as the longitudinal mark (Fig. 18, L). *O. nigricornis* frequently has a general infuscation obscuring or clouding the outlines of the antennal markings (Fig. 18, A and B). In the paler specimens of *nigricornis* this infuscation is lacking (Fig. 18, C and D), and the markings are characterized by the widespaced marks on the second segment, the broad longitudinal mark on the first segment, and the blackness of the outer marks. However, some specimens of *nigricornis* cannot be distinguished from *celerinictus* on the basis of the antennal markings. The markings in *celerinictus* are shown in Fig. 18, E-H. The longitudinal mark of the first segment is usually narrower than in *nigricornis.* The outer mark of the first segment is never round, indistinct, or lacking as is typical of *quadripunctatus.* In *quadripunctatus* the outer marks offer the best identifying features. They are usually less heavily pigmented than the inner marks (Fig 18, N and O) or may be lacking (Fig. 18, P). When present, the outer mark of the first segment is usually round; occasionally a paler extension (Fig. 18, N) makes it similar in shape to the mark of *celerinictus.* In both *pini* and *laricis* the antennal markings are partially obscured by brown pigment. The markings of *pini* are similar to those of *quadripunctatus.* The markings of *laricis* are like those of *celerinictus,* but the outer markings are often less heavily pigmented than the inner ones (as in *pini* and *quadripunctatus*).

Dark markings on the tibiae and hind femur were noted in the description of *celerinictus.* These markings, especially the ones on the middle and hind tibiae, are usually conspicuous in *celerinictus;* how-

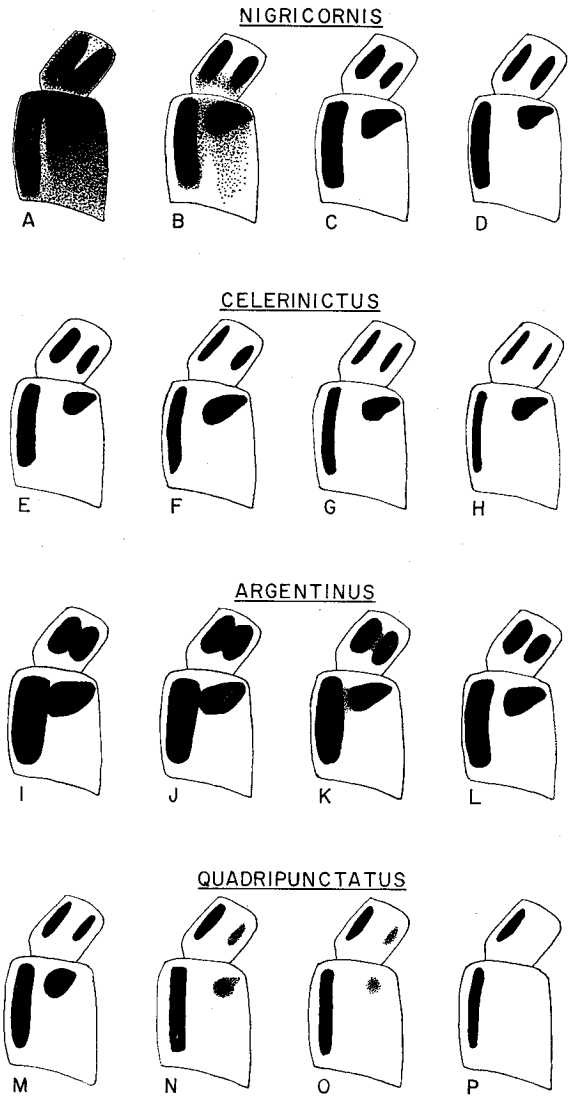



FIG. 18.—Markings on the ventral surface of the first two segments of the left antenna in *Oecanthus nigricornis, celerinictus, argentinus,* and *quadripunctatus.* For each species the middle two drawings represent the usual antennal markings. F. Holotype.

ever, they are lacking in a few specimens from the western part of its range. In *quadripunctatus* the marks are usually absent or very weakly developed; however, one population from California (discussed below) has the marks strongly developed. The marks are absent or weakly developed in *pini* and *laricis* but strongly developed in *nigricornis* (unless obscured by a general infuscation). *O. argentinus* is highly variable in respect to the markings, but most frequently they are absent or weakly developed.

Since the species of the *nigricornis* group have distinctive calling songs, the characteristics of the sound-producing apparatus might be expected to be of taxonomic value also. Examination of Table 1 will reveal that the characteristics of the stridulatory file are useful in separating some species. For instance, *quadripunctatus* can nearly always be distinguished from *nigricornis* and *celerinictus* by the number of teeth in the file; and since *pini* has more widely spaced teeth than any other species, the identification of faded or damaged male specimens can usually be confirmed on the basis of this characteristic. However, it is abundantly clear from Table 1 that many species which show no overlap in the characteristics of their calling songs show considerable overlap in the characteristics of their stridulatory files.

The size of the adults of the herb-inhabiting species of the *nigricornis* group is too highly variable to be of much taxonomic value. Nevertheless the *average* size of individuals in Eastern United States certainly ranks like this: *nigricornis*>*quadripunctatus*>*argentinus*≅*celerinictus*. In many localities in the deciduous forest region, *nigricornis* is consistently larger than the other species. In *pini* and *laricis* the observed intraspecific variation in size is small, and there is a consistent difference between the species. The smallest specimen of *pini* observed had a tegminal length of 12.2 mm., whereas the largest *laricis* had tegmina measuring 11.1 mm.

The cephalic end of a tree cricket egg is a white, caplike structure with regular rows of minute projections. Fulton (1926a) examined eggs of *quadripunctatus* from New York, Ohio, Iowa, and Florida and found that they had longer projections and more conical caps than the eggs of *argentinus* and *nigricornis;* however, he found that eggs of *quadripunctatus* from Colorado and Idaho lacked these distinctive features. I have found the eggs of *celerinictus* to be like those of *nigricornis* and *argentinus* and have confirmed Fulton's results with *quadripunctatus*. Eggs of *quadripunctatus* from Ohio, Indiana, Kentucky, Tennessee, Louisiana, and eastern Texas had the distinctive features while those from Wyoming did not. The eggs of *quadripunctatus* vary considerably from place to place in Eastern United States but apparently remain distinct from those of *nigricornis, celerinictus,* and *argentinus*. The western limits of identifiable *quadripunctatus* eggs have not been established.

In the preceding paragraphs I have summarized the morphological distinctions among what are here recognized as *nigricornis, celerinictus, argentinus, quadripunctatus, pini,* and *laricis*. Some examples of intraspecific variation have been noted, and now it is appropriate to describe in some detail three cases in which the nature of the "intraspecific" variation suggests that unrecognized species may exist.

The first case involves a dwarf variety of *quadripunctatus* in the San Francisco Bay area of California. The 30 specimens I have examined from this area were collected by David Rentz (CAS) and Kenneth Frick (CIS) from 10 localities in 5 counties (Marin, Contra Costa, San Mateo, Santa Cruz, Santa Clara). These specimens are *quadripunctatus* on the basis of the antennal markings (about like Fig. 18, 0) and the number of teeth in the stridulatory file (Table 1); however, they differ in several respects from *quadripunctatus* found in other States. The most striking difference is in size. Fifty specimens of *quadripunctatus* from Eastern United States had an average tegminal length of 11.1 mm. (range: 9.5-12.8) while the 30 specimens from the Bay area averaged 8.0 mm. in tegminal length (range: 6.5-10.5). I have seen no other series of U.S. tree crickets which averaged so small, and the only

Table 1.—Characteristics of the stridulatory file in the *Oecanthus nigricornis* group.

| Species | Localities | Sample size | No. of teeth | | Length (mm.) | | Teeth per mm. | |
|---|---|---|---|---|---|---|---|---|
| | | | Mean ± S.D. | Range | Mean ± S.D. | Range | Mean ± S.D. | Range |
| *nigricornis* | | | | | | | | |
| "willow form" | Ohio, Shelby Co. | 17 | 36.6±2.8 | 32–43 | 1.00±.07 | 0.87–1.16 | 36.8±1.6 | 34.2–39.8 |
| fast-trilling | Ohio, Franklin Co. | 23 | 38.6±2.4 | 35–45 | 1.16±.07 | 1.03–1.35 | 33.2±1.5 | 29.4–35.5 |
| slow-trilling | Ohio, Franklin Co. | 20 | 45.8±3.7 | 37–51 | 1.28±.09 | 1.06–1.39 | 35.9±2.2 | 32.8–39.8 |
| unclassified | 11 other States | 38 | 41.5±3.6 | 36–50 | 1.18±.08 | 0.99–1.39 | 35.3±2.3 | 31.1–39.5 |
| *celerinictus* | 16 States | 103 | 41.1±2.6 | 35–49 | 1.07±.07 | 0.90–1.30 | 38.5±2.0 | 32.5–43.5 |
| *argentinus* | 15 States | 122 | 47.6±2.5 | 42–53 | 1.26±.07 | 1.09–1.45 | 37.9±2.0 | 32.8–43.7 |
| *quadripunctatus* | | | | | | | | |
| dwarf | Calif., Bay area | 10 | 54.9±3.8 | 49–62 | 1.22±.13 | 1.07–1.50 | 45.1±2.5 | 41.3–49.1 |
| non-dwarf | Calif., 5 counties | 7 | 52.1±3.1 | 48–57 | 1.43±.08 | 1.34–1.55 | 36.5±1.5 | 34.3–38.1 |
| typical | 22 other States | 93 | 56.7±3.2 | 50–67 | 1.47±.09 | 1.16–1.78 | 38.7±2.2 | 34.8–44.8 |
| *laricis* | Michigan; Ohio | 5 | 46.4±2.2 | 43–49 | 1.27±.05 | 1.19–1.33 | 36.4±0.9 | 35.3–37.6 |
| *pini* | 8 States | 19 | 49.4±2.6 | 45–56 | 1.59±.07 | 1.48–1.74 | 31.1±1.7 | 28.2–34.8 |

species of *Oecanthus* in which such small size is believed typical is *minutus* of Brazil. Other peculiarities in the Bay area series are the close spacing of the file teeth (Table 1) and the pigmentation of the appendages. The appendages of *quadripunctatus* are usually uniformly pale, and the tibia and hind femora lack the markings typical of *celerinictus* and *nigricornis*. In the Bay area *quadripunctatus,* these markings are quite distinct; furthermore, the legs and antenna are dusky as a result of dark pigment sometimes diffuse and sometimes in the form of many dark dots. The few specimens of *quadripunctatus* that I have seen from other areas of California seem to fall into three categories: three specimens from three counties in southern California do not differ from *quadripunctatus* from other States; nine specimens from six localities in the Great Interior Valley are peculiar in having the outside mark of the first antennal segment very dark and heavy and close to the longitudinal mark (Fig. 18, M); and six specimens from three localities in the Sierra Nevada are similar to the Bay area series but do not average so small or so dark.

The second case of especially noteworthy intraspecific variation pertains to pale and dark forms of *nigricornis*. Within any population of *nigricornis* there is considerable variation in the amount and distribution of dark pigment. For example, the pronotum may be totally black, or there may be three dark longitudinal stripes, or the median one may be in evidence and the lateral ones missing, or the lateral ones may be present and the median one missing, or in some cases individuals may occur which have no dark areas on the pronotum at all. The same type of variation exists in the coloration of the legs, antennae, and abdomen. Superimposed on this intrapopulation variability is a definite westward increase in the proportion of paler forms. In Eastern United States nearly every specimen of *nigricornis* is heavily marked with black, and the pale extremes do not occur (if teneral specimens are excluded). In Wyoming and South Dakota many specimens are scarcely darker than *argentinus* or *celerinictus* and the dark extremes are unknown. It would seem that there is clinal variation in the degree of pigmentation in *nigricornis,* a situation fairly common in insects with extensive ranges. However, careful study of *nigricornis* in Ohio has revealed the situation, at least in that State, to be more complicated.

Soon after I started studying tree crickets in Ohio, E. S. Thomas told me of a variety of *nigricornis* occurring in willow along the edges of some lakes and streams. This variety is much paler and somewhat less robust than the *nigricornis* which occurs in Ohio weedy fields, brambles, and similar situations. Thomas had series of the pale *nigricornis* that he had collected from willow at Sardinia, Brown County, and Lake Loramie, Shelby County, Ohio (OSM). I succeeded in collecting a few specimens from sandbar willow (*Salix interior*) along the Olentangy and Scioto Rivers in Franklin and Delaware Counties, and large numbers from sandbar willow and dogwood (*Cornus drummondi*) at Lake Loramie.

The willow-inhabiting *nigricornis* in Ohio usually has a single faint dark line on the pronotum whereas the herb-inhabiting form usually has three dark lines. The antennal markings are like Fig. 18, C and D, rather than like Fig. 18, A and B. The venter, legs, and antennae of the willow-inhabiting form average much lighter than those of the herb-inhabiting form. Difference in size is substantiated by measurements of 21 males of the willow form and 25 males of the herb form. Tegminal length averaged 10.5 mm. (range: 9.2-11.6) in the former and 12.1 mm. (11.1-13.5) in the latter, while the length of the hind femur averaged 7.8 (7.0-9.0) and 8.7 (7.7-9.5) respectively.

In Ohio, then, both pale and dark populations of *nigricornis* occur in the same areas but occupy different habitats. Farther east in the United States, populations of pale *nigricornis* are not known unless represented by the "decidedly atypic condition" of *nigricornis* found in abundance by Hebard (1938) in high weeds in the marshes along the Delaware River in southeastern Pennsylvania. Westward from Ohio greater and greater proportions of pale forms appear in collections, and no one has reported ecologically distinct populations of pale and dark forms occurring in the same areas.

The third case of intraspecific variation concerns the fast-trilling and slow-trilling forms of *nigricornis*. These forms were first recognized on the basis of the calling song, and no reliable morphological distinction has been found. However, study of the stridulatory files of Franklin County, Ohio, specimens revealed significant differences in the *average* number of file teeth and length of file (Table 1). The two populations show a wide overlap in the characteristics of the file, and identification on this basis is unreliable. For instance if 42½ file teeth is used as the dividing point between fast- and slow-trilling *nigricornis,* 5 of the 43 Franklin County specimens known as to song would be misidentified. The file characteristics might be useful in determining from preserved specimens whether both fast- and slow-trilling forms occur in a given area, since a distinct bimodality in file-tooth number would be evidence of two forms.

## KEY TO SPECIES

The following key is a summary of the characters most useful in identifying both living and preserved specimens of the *nigricornis* group. Walker (1962a) gives a key to the groups of United States *Oecanthus* and to the species of other groups.

1. Pronotum black or with one, two, or three black or dusky longitudinal stripes; venter and distal portions of legs and antennae black ..... ***nigricornis*** (in part)

1'. Pronotum never black, never with black or dusky stripes (except that *laricis* may have brown stripes with the lateral ones somewhat dusky); venter and distal portions of

legs and antennae sometimes dusky or brown but never black ..... 2

2(1'). Head, pronotum, and legs largely brown; tegmina a contrasting green or dusky green in fresh specimens; found only in or (rarely) beneath conifers ..... 3

2'. Head, pronotum, and legs without brown pigment and not contrasting in color with the tegmina; seldom found in conifers ..... 4

3(2). Length of tegmina greater than 12 mm.; brown areas light and slightly reddish; in pines and balsam fir ..... *pini*

3'. Length to tegmina less than 12 mm.; brown areas dark, sometimes dusky; in tamarack and hemlock ..... *laricis*

4(2'). Black marks on second antennal segment confluent, contiguous, or separated by no more than one-third the width of the inside mark (Fig. 18, I-L) ..... *argentinus*

4'. Black marks on second antennal segment separated by more than one-third the width of the inside mark ..... 5

5(4'). Outside marks on first and second antennal segments usually less heavily pigmented than inside marks (sometimes they are missing, and rarely they are as heavily pigmented as the inside marks); outside mark on first segment often round; tibiae and apex of hind femur usually without conspicuous dark markings; more than 47 teeth in stridulatory file ..... *quadripunctatus*

5'. Outside marks on first and second antennal segments as heavily pigmented as inside ones; outside mark on first segment never round; tibiae and apex of hind femur with conspicuous dark markings; less than 47 teeth in stridulatory file ..... 6

6(5'). Width of inside dark mark on first antennal segment less than distance between inside and outside marks (Fig. 18, E-H); no dusky areas on pronotum; Southeastern United States (Fig. 1) ..... *ce'erinictus*

6'. Width of inside dark mark on first antennal segment often greater than distance between inside and outside marks (Fig. 18, B and C); pronotum usually with anteriomedian and or lateral dusky areas; North Central and Northeastern United States (Fig. 1) ..... *nigricornis* (in part)

## CROSSING EXPERIMENTS

Differences in calling songs in tree crickets are without question of great importance in preventing contact between the sexually responsive females of one species and the males of other species in the same locality. The usual initial event leading to the insemination of a female is evidently the moving of the female toward the sound produced by a male of her own species. Nevertheless, differences in calling song cannot be the only mechanism preventing hybridization among the four herb-inhabiting species of tree crickets. Dense populations of two or even three of these species may occur intermingled on the same plants, so that chance encounters between individuals of different species as well as those of the same species must be frequent. Observations of caged individuals reveal that when a female comes in contact with a silent male he often will begin to court her by producing brief trills, shaking his body (and the substrate) violently, and backing toward her with tegmina raised and metanotal glands exposed. Copulation (by transfer of a spermatophore) may ensue without the calling song ever being produced.

Since differences in calling songs cannot entirely account for the lack of hybridization among herb-inhabiting tree crickets, one or more additional isolating mechanisms must be involved. The possibilities, in order of action, are (1) male will not court a female of another species, (2) female will not respond (by mounting the male and cooperating in the transfer of the spermatophore) to the courtship of a male of another species, (3) the spermatophore cannot be transferred because of morphological or behavioral incompatabilities in the transfer process, (4) the spermatophore is transferred but no viable offspring are produced.

A series of tests were set up to determine which, if any, of these possibilities were realized among various pairs of species. For each pair of species, the following procedure was used. Two males and two females of each species were placed in individual cages (a total of eight cages) and assigned to one of these four crosses: (1) male of first species, female of first species, (2) male of first species, female of second, (3) male of second, female of first, (4) male and female of second species. These sets of four crosses were replicated five or more times if possible. Usually the females were initially virgin, having been reared from late-instar nymphs in isolation from males. In a few instances, field-collected females which had been isolated from males for at least a week were used. Virgin and field-collected females of the same species were never mixed in a single replicate.

After the individuals to be used had been isolated and labeled, each pair was placed together in a 1-gallon battery jar with a semicircle of corrugated cardboard, which served as a walking surface. The behavior of the various pairs was observed for 1 or 2 hours; then the crickets were returned to their individual cages. The longer observation period was discontinued after it was discovered that no new type of behavior was likely to occur after the first hour. However, if a spermatophore was passed during the first hour, a second one was often transferred during the second hour. One hour and ten minutes was the shortest observed interval between the transfer of two spermatophores by a single pair.

As time allowed, the pairs were placed together for additional observation periods on successive days. Observations were discontinued on a replicate (set of four crosses) when any of the individuals died and could not be replaced by an individual of similar experience. Some replicates were abandoned before others, and the number of trials (observation periods) per replicate varied from one to six.

The results of these tests are summarized in Table 2. It can be seen that whenever males of one species were confined with females of another, the males courted the females in a fewer number of trials than did their fellows confined with females of their own

Table 2.—Results of courtship and mating tests.

| Form A | Form B | No. of replicates | Total No. of trials | Trials in which ♂ courted ♀ | | | | Total spermatophores passed | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | AA | A♂B♀ | B♂A♀ | BB | AA | A♂B♀ | B♂A♀ | BB |
| *nigricornis*[a] | *nigricornis*[b] | 5 | 24 | 12 | 16 | 11 | 17 | 5 | 6 | 7 | 11 |
| *nigricornis*[c] | *celerinictus*[d] | 1 | 6 | 6 | 0 | 0 | 2 | 7 | 0 | 0 | 2 |
| *nigricornis*[c] | *argentinus*[c] | 6 | 14 | 7 | 1 | 2 | 8 | 7 | 0 | 0 | 5 |
| *nigricornis*[c] | *quadripunctatus*[c] | 5 | 22 | 18 | 9 | 2 | 15 | 14 | 0 | 0 | 5 |
| *nigricornis*[b] | *quadripunctatus*[c] | 5 | 27 | 23 | 9 | 2 | 12 | 10 | 1 | 0 | 7 |
| *nigricornis*[b] | *pini*[e] | 2 | 8 | 8 | 1 | 0 | 6 | 7 | 0 | 0 | 4 |
| *celerinictus*[d] | *argentinus*[c] | 5 | 27 | 9 | 0 | 1 | 14 | 7 | 0 | 0 | 11 |
| *celerinictus*[d] | *quadripunctatus*[c] | 3 | 7 | 3 | 1 | 0 | 7 | 2 | 0 | 0 | 7 |
| *argentinus*[c] | *quadripunctatus*[c] | 10 | 40 | 33 | 10 | 1 | 16 | 29 | 2 | 0 | 10 |
| *quadripunctatus*[c] | *pini*[e] | 1 | 2 | 2 | 0 | 0 | 2 | 0 | 0 | 0 | 2 |

[a] Franklin County, Ohio, and Union County, Indiana (dark; weeds).
[b] Shelby County, Ohio (pale; willow).
[c] Franklin County, Ohio (weeds).
[d] Pike County, Arkansas.
[e] Fairfield County, Ohio.

species. Furthermore, within a trial in which heterospecific courtship occurred, it was usually less frequent and less intense than conspecific courtship in the same trial. These observations indicate that in a chance encounter between a male and a female, the male is less likely to court the female if she is of another species than if she is of the same species.

When a male of one speices did court a female of another species, the female usually walked away or simply ignored the male. In a few instances she mounted the male and began feeding at the metanotal glands. When this occurred, the spermatophore was usually successfully transferred. The difficulties in transferring the spermatophore between the male and the mounted female appeared no greater in heterospecific pairs than in conspecific pairs. Therefore, the last four columns in Table 2 reflect a usual complete lack or response of the female to heterospecific courtship and not merely a lack of success in completing the transfer of the spermatophore.

These facts establish two mechanisms other than response to calling song as important in maintaining isolation between sympatric species of tree crickets: (1) the response of the male to an encountered female, and (2) the response of the female to a courting male.

It is not known if sterility barriers exist between species. It seems unlikely that interspecific copulation occurs in the field, so the apparent lack of hybrids cannot be cited as evidence of sterility. Failure to develop a suitable technique for getting hatch in laboratory-laid eggs precluded any attempt to get progeny from interspecific matings.

## DISCUSSION

*Number of Herb-Inhabiting Species.*—The populations here called *nigricornis, celerinictus, argentinus,* and *quadripunctatus* have proved to be reproductively isolated from one another wherever they have been carefully studied. Furthermore, examination of series of specimens from many localities scattered throughout the United States has revealed no evidence of significant interspecific hybridization. The distinctness of *celerinictus* and *nigricornis* is questionable if only specimens from the western part of their ranges are compared. However, there is evidently no contact between the species in this area, and the morphological distinctness of the two in the East, where they overlap slightly in their distributions, is striking. Consistent differences in seasonal life histories and evidence of sexual isolation (Table 2) further support the distinctness of these two species.

The evidence seems overwhelming that there are at least four species of herb-inhabiting tree crickets in the United States. Furthermore, within two of these four species there are populations which may prove to be distinct species. In *quadripunctatus,* specimens of the dwarf variety from the San Francisco Bay area are easily recognizable, but their taxonomic status remains uncertain until their relationship to the normal-sized *quadripunctatus* is determined. The relatively cool summer climate of the Bay area may be responsible for the small size and dark pigmentation. The fact that specimens from the Sierra Nevada showed to some degree the peculiarities of the Bay area *quadripunctatus* supports this idea.

In *nigricornis* the relationships of pale and dark populations, willow- and herb-inhabiting populations, and fast- and slow-trilling populations need more study. Only in the case of the fast- and slow-trilling populations is the evidence strongly in favor of two species. The occurrence of these two forms intermingled in the fields of central Ohio is difficult to interpret in any other way. The pulse rates of their songs differ enough to be effective in maintaining sexual isolation. Experiments with natural and artificial sounds (Walker 1957) revealed that females

which responded to the fast song of *nigricornis* would not respond to the slow song. The *nigricornis* females used in these experiments were evidently all of the fast-trilling form, because an examination of the performances of the individual females (the results published only gave the cumulative results for 10 females) revealed that none of the test females responded to pulse rates near those of slow-trilling *nigricornis*. There are several reasons for delay in giving scientific names to what are probably fast- and slow-trilling species within *nigricornis:* no females of the slow-trilling species have been identified; the occurrence of fast- and slow-trilling males in places other than Ohio is poorly understood; the holotype of *nigricornis* is a female and thus cannot be assigned to either the fast- or slow-trilling species at present.

The occurrence of pale, willow-inhabiting populations of *nigricornis* in Ohio in the same geographical areas as dark, herb-inhabiting populations could be a result of different foods and microclimates for the developing nymphs. The lack of sexual isolation (Table 2, line 1) and the similar pulse rates in the calling songs make it unlikely that the willow-inhabiting *nigricornis* in Ohio is specifically distinct from the weed-inhabiting, fast-trilling *nigricornis;* however, further study is needed.

*Dispersal.*—Until recent times the weed-inhabiting tree crickets of Eastern United States occupied a shifting and highly discontinuous habitat, so evidence of long flights during adulthood is not surprising. The rapid colonization of new suitable habitats is one such evidence. Another type of evidence is the occurrence of adults in habitats in which nymphs are never found. For instance males are occasionally heard singing from trees a mile or more from any habitat known to be suitable for nymphs. In central Ohio the dispersal of males of *argentinus* at the beginning of their breeding season (early July) was especially conspicuous because the tree-dwelling tree crickets had not yet begun their choruses.

Widespread disperal of at least some individuals in each generation makes unlikely any speciation within a limited geographic area and reduces the importance of ecological isolation in explanations of reproductive isolation among closely related species. It also accounts for what seems to be a rapid spread of *argentinus* eastward into agricultural areas (see Distributional Relationships).

*Relation Between File Structure and Calling Song.*—In the discussion of morphological characters, it was noted that the structure of the stridulatory file is not always a reliable means of separating species with distinctly different calling songs. Different patterns and speeds of movement can result in the same stridulatory apparatus producing songs with different physical characteristics. This fact is strikingly demonstrated in each of the many species of crickets and katydids known to produce different sounds in different situations.

Nevertheless, there is some correlation between file structure and calling song in the few groups of cricket species which have been studied in both respects. Within a group of closely related species of crickets, species with lower pulse rates (at a given temperature) usually have longer files with more teeth. This tendency is apparent in each of the three groups of *Oecanthus,* in the genus *Gryllus* (Alexander 1957, 1961; Alexander and Walker 1962), and in *melodius* and *carolinus* of the genus *Nemobius* (Thomas and Alexander 1957).

This correlation between differences in pulse rate and file length contrasts with the relative constancy of both spacing of file teeth and frequency of song (cps) in groups of closely related species. In other words, within a species group an increase or decrease in pulse rate is usually associated with a decrease or increase in the distance the wings move rather than with changes in speed of wing motion.

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