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CALLING SONGS OF *ORCHELIMUM* MEADOW KATYDIDS (TETTIGONIIDAE) I. MECHANISM, TERMINOLOGY, AND GEOGRAPHIC DISTRIBUTION¹

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Abstract

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A terminology useful in describing conocephaline amplitude modulation patterns is presented in this first part of a three-part study of calling songs in *Orchelimum* meadow katydids. Geographical distributions are mapped for the 18 species which occur in North America north of Mexico and several substantial range extensions reported. Comparison of stridulatory files indicates two types within the genus, one characterized by more widely spaced teeth near the basal end of the file. Teeth are asymmetrical in accordance with the generation of the loudest song components on wing closure.

Introduction and Literature Survey

The present paper is the first of a three-part comparative study of calling song structure in 18 species of *Orchelimum* meadow katydids. Subsequent papers will deal with amplitude modulation patterns and carrier frequencies. Two members of the genus are omitted: *O. fraternum* Rehn and Hebard, and *O. unispina* (Saussure and Pictet); these two forms occur in Mexico and nothing is known of their sound signals. *Orchelimum* is apparently restricted to North America and the greatest diversity of species occurs in northern Florida and along the coastal plain of the eastern seaboard. A new species, *O. carinatum* Walker, was discovered in Florida only a few years ago (T. J. Walker 1971).

Most *Orchelimum* occur in moist freshwater habitats among sedges or reeds, along roadside ditches or the margins of ponds and streams; but one form, *O. vulgare* (Harris), frequents dry weedy fields, two species, *O. minor* Bruner and *O. sylvaticum* McNeill, are arboreal, and one species, *O. fidicinium* Rehn and Hebard, is confined to salt marshes. Colour shades of green and brown are common, matching the vegetation on which these katydids live; but in some species, such as *O. erythrocephalum* Davis, *O. pulchellum* Davis, and *O. nigripes* Scudder, red, blue-green, and black are prominent. All *Orchelimum* have a conspicuous brown stripe in the dorsal midline of the pronotum.

Rehn and Hebard (1915) carried out the only comprehensive taxonomic treatment of the genus; their synopsis and Blatchley's 'Orthoptera of northeastern America' (1920) remain the most useful aids to morphological identification. Taxonomic confusion surrounding the '*concinnum* group' was resolved by Thomas and Alexander (1962). Recently Vickery and Johnstone (1974) examined some "lost types" of Burmeister which indicate that *O. glaberrimum* Burmeister is a senior synonym of *O. vulgare* (Harris). To avoid the loss of a well established name an application has been made to the International Commission on Zoological Nomenclature to suppress *O. glaberrimum* (Vickery 1974). We support this recommendation and have employed here the name changes which this proposal entails.

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The calling songs of *Orchelimum* are produced only by the males; they stridulate with modified forewings (tegmina). Singing occurs both day and night but not when the temperature falls below 17°C; singers are usually more active and in greater numbers during the day. When disturbed a male falls silent and adopts a characteristic hiding posture which places the perch substrate between him and the source of the disturbance (Allard 1910; Morris 1972). This behaviour contrasts with that of many Acrididae, which leap away at the approach of a human, and is a reflection of the territorial habit of male meadow katydids.

Song occurs in the contexts of pair formation (evocation of female phonotaxis) and male aggression. The role of the calling song in the former instance has been demonstrated by experiment in *O. gladiator* Bruner (Morris *et al.* 1975b): females developed responsiveness to the speaker playback of conspecific male song 5 or 6 days after their moult to adult; this response was rapidly extinguished following successful mating.

Males of *O. gladiator* and *O. vulgare* have been observed to interact aggressively in the field, approaching and fighting with neighbouring conspecific singers (Morris 1971). *O. concinnum* Scudder exhibits the same behaviour (Morris unpub.). Male approaches have been elicited to speaker playback of calling song (Morris 1972). The males apparently maintain an exclusive broadcast area in their immediate vicinity and interact aggressively with conspecifics that display acoustically within this area. As a result of this male aggression, singers are regularly spaced within the habitat. Regularity has been shown quantitatively for *O. gladiator* by mapping a population of singers and applying techniques of nearest-neighbour analysis (Morris 1967).

Distinctive rivalry songs are not known in *Orchelimum*. In *O. gladiator*, calling song is produced up to the moment of overt aggression (physical contact) by the approached male of an aggressively interacting pair and is renewed by the dominant male immediately after grappling. Changes do occur in the calling song during this aggression (e.g. altered tick and song rates) but these are not sufficiently distinctive, discontinuous, or stereotyped to justify designation as an 'aggressive call'.

Courtship songs, although they occur in some Decticinae (Morris *et al.* 1975a), have never been observed in *Orchelimum*. A number of *O. gladiator* matings have been monitored (Morris unpub.) and no distinctive sounds were detected; the male simply ceased his calling song when in copula. It is possible, as suggested by Thomas and Alexander (1962), that the visual modality replaces the acoustic in close-range signalling of conocephalines.

Female sound signals are also absent (apparently) from *Orchelimum*, although tooth-like tegminal spines (Fig. 1A, B) are present on the dorsal surface of the female tegmen (Fulton 1933). These spines differ in shape but occur in the same wing region as spines used by certain phaneropterine females (Fig. 1C) to make answering sounds during pair formation (Spooner 1964). Fulton reported that every *Orchelimum* in his collection (13 species) possessed such spines; we can augment his list to include the 18 species treated here. It is possible that these structures are devices for latching the tegmina together and have no acoustic role.

In some cases *Orchelimum* calling song changes with the time of day. Cantrall (1943) distinguishes day and night songs in *O. gladiator*; *O. erythrocephalum* makes the smack but not the buzz portion of its day song during night singing (T. J. Walker unpub.). Variation in song structure also results from the close proximity of a human observer; under such circumstances *O. gladiator* increases the number of ticks in the tick phase of its calling song (Cantrall 1943).

The ticks of *Orchelimum* can be imitated by forming a pocket between tongue, palate, and upper front teeth, then suddenly drawing saliva away from the teeth by depressing the tongue. Done in close proximity to a silent male of the appropriate

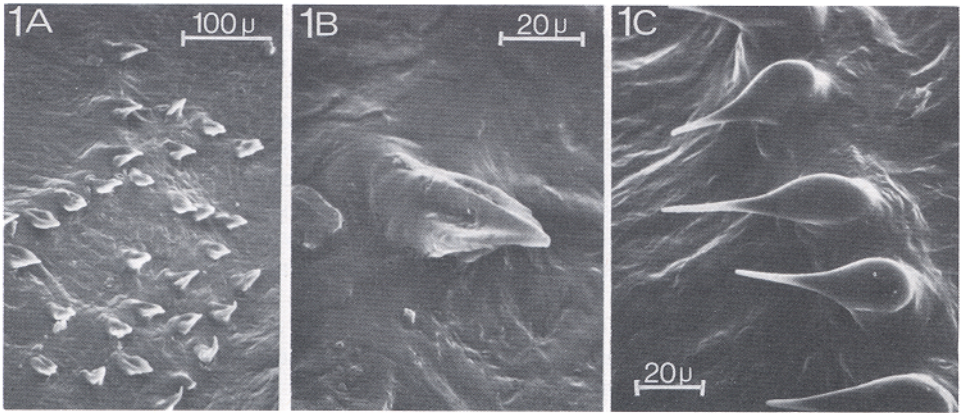


FIG. 1. Scanning electron micrographs of tegminal spines from *O. fidicinium* (A, B) and *Scudderia texensis* Saussure and Pictet (C).

species (e.g. *O. gladiator*), this 'mouth noise' will often release stridulation. A wary singer may be induced in this way to reveal his location. The behaviour evoked is referred to as a phonoresponse: the production of sound upon hearing a sound (Alexander 1967). Phonoresponses exchanged by conspecifics are the basis of chorusing behaviour in singing Orthoptera.

Chorusing usually takes the form of alternation or synchronization of songs between neighbouring males and it occurs in *Orchelimum*. Fulton (1934) observed alternation in *O. bradleyi* Rehn and Hebard: the buzzes of one male were sounded "between those of a neighbouring singer". Alternation is also evident when a male of *O. gladiator* is exposed to speaker playback; the insect initiates its buzz coincident with the end of the recorded buzz (Morris unpub.). Alexander (1960) observed synchronized chorusing in a population of *O. vulgare*. In a recent paper (1975) he presents an interpretation of phonoresponses as the outcome of competitive interactions between males forced into singing aggregations by the processes of sexual selection.

Information on *Orchelimum* song structure originates with the classic 'Insects Injurious to Vegetation' of T. W. Harris (1841). In describing *O. vulgare* as a new species, Harris mentions the "sharp clicking noise" of the males. At least eight other authors have had something to say about *O. vulgare* song, making it the most frequently described song in the genus. For all of the 18 species considered here some sort of song description, often grossly inadequate, exists in the literature. In most cases these are prose descriptions confined to song features discernible with the unaided human ear.

McNeill (1891), Scudder (1892), E. M. Walker (1905), and Allard (1910) produced useful 'human ear descriptions' of *Orchelimum* song. These early workers used onomatopoeia (xr, jip, tsip, zip, ze, kr, zr, and ts); Scudder even rendered the song of *O. vulgare* in musical notation. In view of the diagnostic value of the calling songs, apparent to any amateur field naturalist, Rehn and Hebard's 1915 synopsis is remarkable in avoiding song description almost completely.

Fulton (1932) constructed a key to the singing Orthoptera of North Carolina which includes eight *Orchelimum* species. His terminology reflects the two-part structure of many meadow katydid songs: a repetition of "short notes" (designated as ticks in the present work) alternating with a "long phase" or "long note" (here a buzz). Songs are distinguished by differences in sound level, stereotyped volume changes, the presence or absence of silent pauses between song elements, quality differences ("fluttering"), and the rate of delivery of the "notes". A more recent key concerns itself with the

singing insects of Michigan (Alexander *et al.* 1972), employing human ear song descriptions in the identification of seven *Orchelimum* meadow katydids.

In 1948 the physicist G. W. Pierce published the results of a "pleasant diversion" into insect sounds. His work marks the first extensive use of microphone and recorder in insect song analysis. Stridulation mechanisms and physical parameters, especially carrier frequencies, were examined in more than 30 Orthoptera, among which were three species of *Orchelimum*. Pierce's chart recorder revealed that the apparently homogenous long notes consisted of a serial repetition of 'pulses' (major pulse trains of the present paper). He gives the principal carrier frequency of both *O. vulgare* and *O. gladiator* as 16 khz; for *O. concinnum* Scudder a dominant frequency of 20.3 khz was obtained.

Pierce also made a movie of *O. vulgare* stridulation, an unfortunate choice of research material, since at any temperature this species has the highest buzz wingstroke rate of any member of the genus. The wingstroke rate at 30°C is about 90/s (Walker 1975). Pierce had available a film speed of only 64 frames/s and was unable to correlate the 'pulses' of his chart recorder with the direction of wing movement. A measure of song intensity in this species was obtained by Pielemeier (1946): using a sound level meter, he located a carrier frequency peak at 14.2 khz with an intensity of 70 db 1 ft from the singer.

The development of the portable magnetic tape recorder made it practical to carry songs home from the field and American workers began at the same time to use audiospectrographs in the analysis of animal sounds. Such techniques made possible Alexander's extensive (1956) survey of singing Orthoptera and Cicadidae. His study includes song descriptions for 12 *Orchelimum* species. Patterns resolvable with the human ear are given in greater detail and precision than previously, and information is provided on "pulse" (wingstroke) rates. The wingstroke rate of *O. vulgare* is plotted as a function of temperature, and temperature data are given routinely as a necessary adjunct of "pulse" rate.

Alexander describes the characteristic slowing of wingstroke rate which occurs at the end of the buzz of *Orchelimum volantum* McNeill. He detected the "double-pulse" nature (minor as well as major pulse train in our terminology) of the ticks of *Orchelimum agile* (De Geer), *O. delicatum* Bruner, and *O. vulgare*. The resolution of his audiospectrograms did not reveal the "double-pulse" structure of the buzz "pulses". The audiospectrograph, though very effective in portraying changes in carrier frequency, is inferior to the oscilloscope in the display of amplitude modulation.

Thomas and Alexander (1962) were able to separate *O. concinnum*, *O. delicatum*, and *O. campestre* on the basis of differences in calling song structure. The buzz wingstroke rate of *O. concinnum* is slower than that of *O. delicatum* at any given temperature and *O. campestre* produces buzz wingstroke cycles in pairs. These authors note the absence of a minor pulse train in the ticks of *O. gladiator* ("single-pulse ticks").

Previously published calling song descriptions fail to convey the stereotypy and complexity of amplitude modulation in this genus. The simplest sound element in these acoustic displays is a pulse lasting a fraction of a millisecond. Such elements, separated usually by intervals of silence, are grouped into highly stereotyped patterns in time and delivered at rates of several hundred pulses/s. Whereas such patterning is lost on the human ear, it is now clear that it survives transduction into the katydid nervous system (Lewis *et al.* 1971).

Where such stereotypy occurs and is furthermore not filtered peripherally, we may reasonably suspect signal function. The richness of the katydid repertoire has not been appreciated. The present trio of papers documents these intricate patterns as a first step to experimental analysis of their behavioural significance. We present the view that the

calling song is a composite signal, combining information for different recipients (male and female) in a single behavioural unit.

Geographic Distribution

Distributions are mapped for the 18 species (Figs. 2, 3). One record of *O. unispina* is included, its only known occurrence north of Mexico. Relict populations of *O. delicatum* were discovered in the Owens Valley of California; specimens were taken in 1972 (23.VII) along U.S. 395 near Lone Pine. In 1974 (30.VIII) *O. nigripes* were detected in abundance on the Potomac R., Marsden Tract, near Cabin John, Md., a substantial eastward range extension. Thanks to Dr. D. C. Rentz we recently became aware of Virginia localities for *O. carinatum*, but these are not shown on the distribution map of Fig. 3.

Peripheral records are substantiated below, using the following abbreviations: FSCA (specimen in Florida State Collection of Arthropods, Fla. Dept. Agr., Div. Plant Industry, Gainesville); GKM (G. K. Morris); ROM (specimen in Royal Ontario Museum); TJW (T. J. Walker); UFT (University of Florida Tape, in tape library of Dept. Entomology); UMMZ (specimen in University of Michigan Museum of Zoology, examined by TJW); ANSP (specimen in Acad. Nat. Sci. Philad., examined by TJW); UMMZ-RDA (specimen in Univ. Mich. Mus. Zool., record supplied by R. D. Alexander).

O. agile: TEXAS, Harris Co. (Hebard 1934: 213); TENN., Giles Co. (UMMZ-RDA), Rutherford Co. (*ibid*), Knox Co. (Powders and Goodwin 1969: 82); VA., Alleghany Co., Clifton Forge (UMMZ-RDA); PENNA., Bucks Co. (Hebard 1938: 36); FLA., Dade Co., Princeton (FSCA, UFT 252-22, 23).

O. bradleyi: LA., Vernon Par. (specimen from Dr. M. E. Dakin, Univ. Southwestern La., Lafayette); GA., Lee Co., Leesburg (UMMZ-RDA); N. CAR., New Hanover Co. (Rehn and Hebard 1916: 264); FLA., Dade Co., Everglades Nat. Pk. (UFT 252-2, 3).

O. bullatum: TEXAS, Cameron Co. (Rehn and Hebard 1915: 53), Hidalgo Co. (*ibid*), Comanche Co. (*ibid*), Wichita Co. (*ibid*), Potter Co., Amarilla (ANSP); LA., St. Tammany Par., U.S. 90 e. of junc. U.S. 190 (FSCA, UFT 264-3, 4), Orleans Par. (Rehn and Hebard 1915: 53); IND., Tippecanoe Co., Lafayette (UMMZ); MO., Buchanan Co., St. Joseph (ANSP).

O. campestre: OKLA., Marshall Co., Texoma St. Pk. (FSCA, UFT 266-1); NEBR., Cuming Co. (Thomas and Alexander 1962: 15); IOWA, Winnebago Co. (*ibid*); MICH., Newaygo Co. (*ibid*); ONT., Norfolk Co., Long Point (ROM, GKM); W. VA., Hancock Co. (Thomas and Alexander 1962: 15); TENN., Knox Co. (Powders and Goodwin 1969: 81); LA., Lafourche Par. (Thomas and Alexander 1962: 15).

O. carinatum: LA., St. Mary Par., Amelia (ROM, GKM); TENN., Obion Co. (Walker 1971: 277); FLA., Franklin Co. (*ibid*); VA., New Kent Co. (ANSP), Norfolk Co. (*ibid*), Charles City Co. (*ibid*), King William Co. (*ibid*).

O. concinnum: TEXAS, Nueces Co. (Thomas and Alexander 1962: 15); FLA., Alachua Co. (*ibid*), Dade Co., Everglades Nat. Pk., sawgrass (FSCA, UFT 253-11); MASS., Essex Co. (Thomas and Alexander 1962: 15); IND., Vigo Co. (*ibid*); ILL., Lake Co. (*ibid*); MICH., Huron Co. (*ibid*); OHIO, Ross Co. (*ibid*).

O. delicatum: CALIF., Inyo Co., Lone Pine (ROM, GKM); COL., Larimer Co., Loveland (ROM, GKM); ARIZ., Santa Cruz Co. (Thomas and Alexander 1962: 15); N. MEX., Sandoval Co., nr. Corrales (FSCA, UFT 250-1, 2, 3, 4); MONT., Stillwater Co. (Thomas and Alexander 1962: 15); N. DAK., Ramsey Co. (*ibid*); MICH., Huron Co. (*ibid*); N.Y., Erie Co. (*ibid*); OHIO, Wyandot Co. (*ibid*); OKLA., Mayes Co. (*ibid*); TEXAS, Dallas Co. (*ibid*), Brewster Co. (Tinkham 1948: 628); LA., Jefferson Par. (Thomas and Alexander 1962: 15).

O. erythrocephalum: LA., Calcasieu Par., West Lake (UMMZ); MISS., Jefferson Co. (GKM, ROM and by song); TENN., Shelby Co., Memphis (TJW by song), Hardin Co., 5 mi s. Savannah (*ibid*); N. CAR., Cherokee Co. (UMMZ-RDA), Catawba Co. (TJW, by song and specimens); VA., Amelia Co. (UMMZ-RDA); N.J., Morris Co., Morristown (ANSP); FLA., Dade Co., Fla. 94 (GKM, by song and specimens).

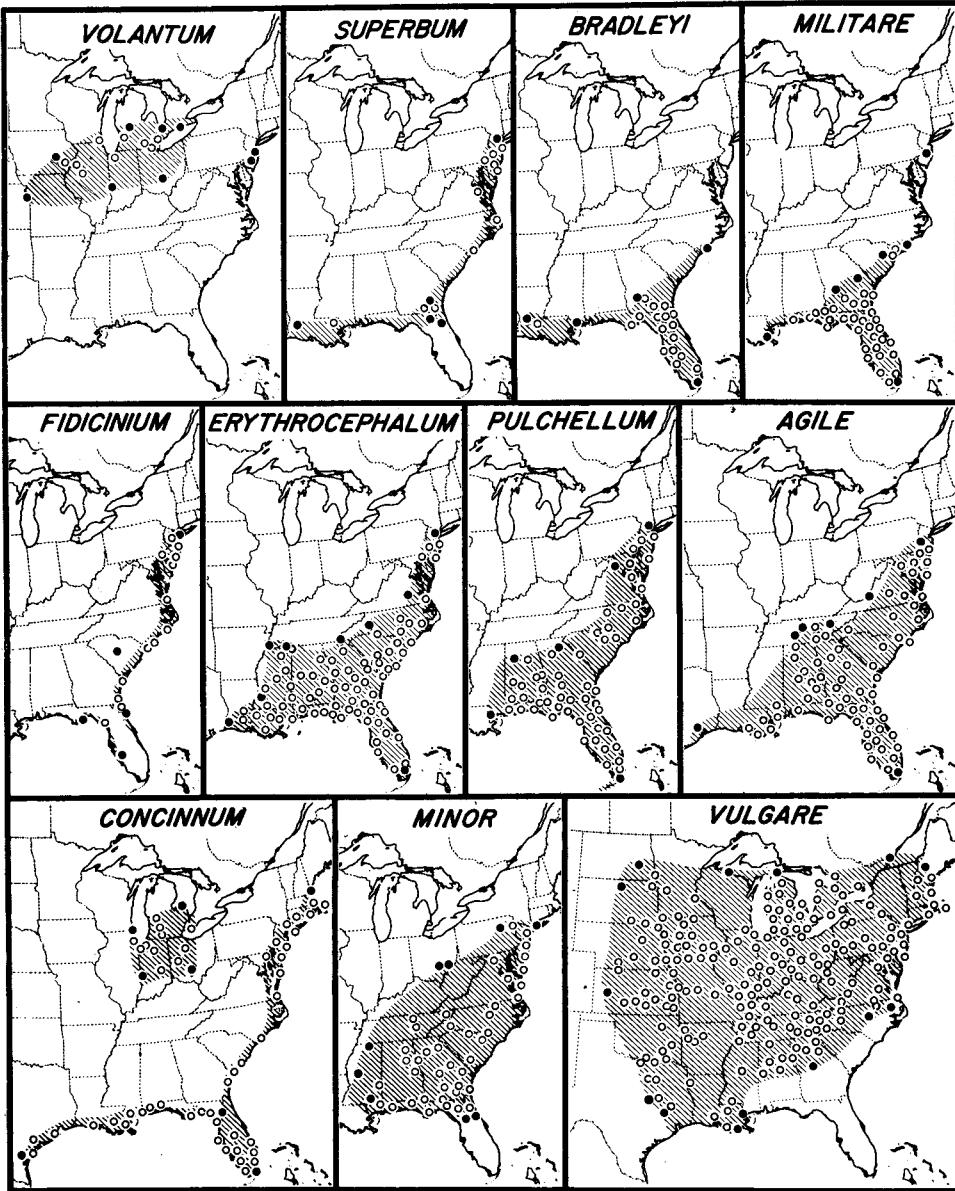
O. fidicinium: FLA., Wakulla Co., Panacea (UFT 259-22), Charlotte Co., Port Charlotte (FSCA), St. Johns Co., nr. Marineland (FSCA, UFT 259-20, 21); S. CAR., Lexington Co. (Rehn and Hebard 1915: 70); N.Y., Queens Co. (Rehn and Hebard 1915: 70).

O. gladiator: CALIF., Siskiyou, Sisson (= Mt. Shasta) (Rehn and Hebard 1915: 46); WASH., Kittitas Co. (*ibid*); ALTA., Millicent (ROM, GKM); SASK., Belle Plaine (ROM, GKM); MAN., Ashdown (Blatchley 1920: 546); ONT., Chelmsford, nr. Sudbury (GKM by song); QUE., Berthier Co., Berthierville (Vickery *et al.* 1974: 65), Papineau Co., Notre Dame du Laus (*ibid*); MAINE, Oxford Co. (Rehn and Hebard

1915: 45); DEL., New Castle Co. (Hebard 1938: 36); PENNA., Allegheny Co. (*ibid*); OHIO, Washington Co. (FSCA); TENN., "Tennessee, 1 ♀" (Rehn and Hebard 1915: 46); ILL., Champaign Co. (Hebard 1934: 213); KANS., Douglas Co. (Rehn and Hebard 1915: 45); UTAH, Cache (Barnum 1952: 191).

O. militare: LA., Plaquemines Par. (Rehn and Hebard 1915: 72); GA., Sumter Co. (UMMZ-RDA), Emanuel Co. (*ibid*); S.C., Florence Co. (Rehn and Hebard 1916: 264); N.C., New Hanover Co. (*ibid*); N.J., Burlington Co. (Hebard 1938: 158); FLA., Dade Co., Everglades Nat. Pk. (FSCA, UFT 257-1).

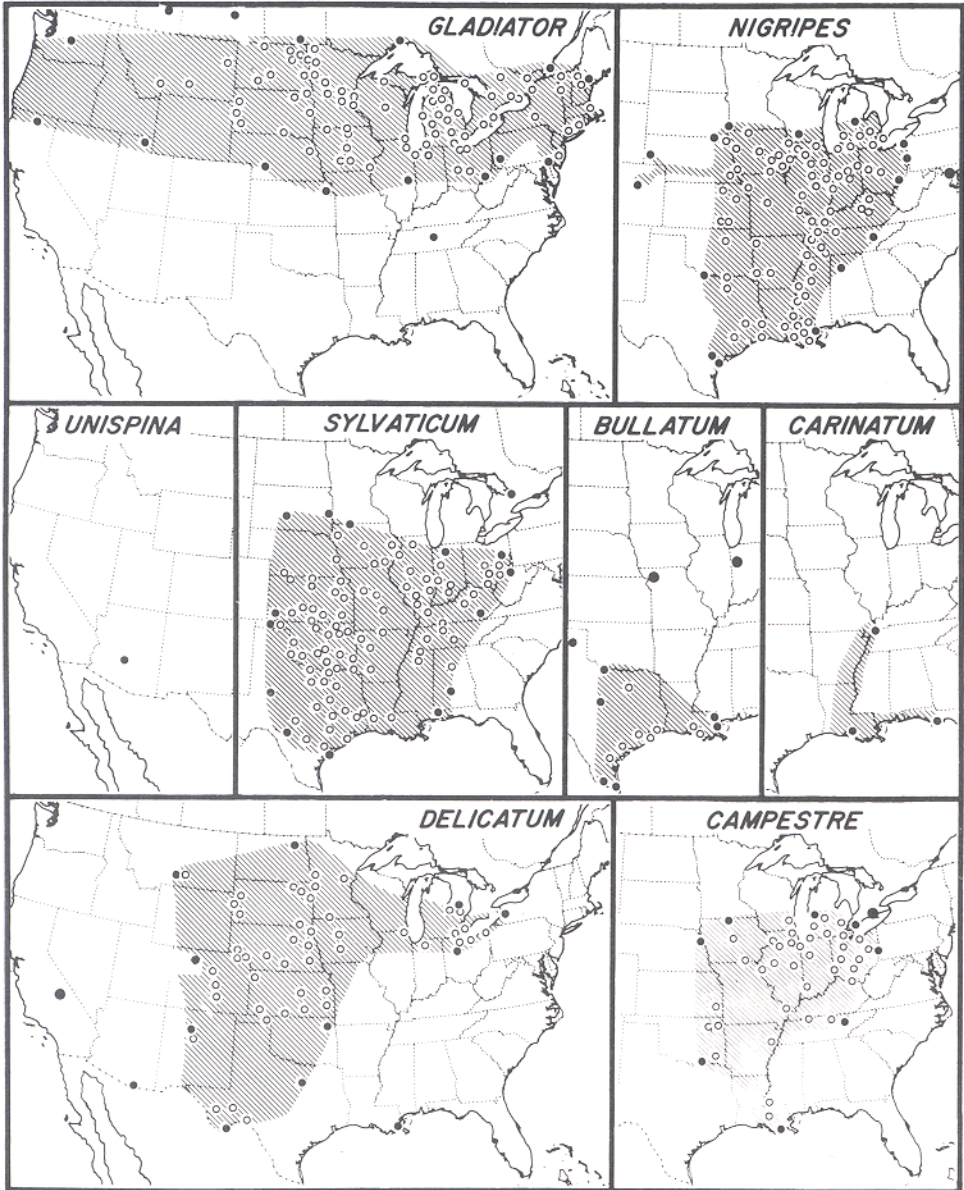
O. minor: MISS., Forrest Co., Shelby St. Pk. (TJW by song), Attala Co. (*ibid*), Lafayette Co., Abbeville (ROM, GKM, by song and specimen); OHIO, Hocking Co., Good Hope Twp. (UMMZ-RDA), Washington Co., Marietta (TJW by song); PENNA., Union Co. (Hebard 1938: 37); N.Y., Suffolk Co. (*ibid*); FLA., Volusia Co. (UMMZ-RDA), Marion Co. (TJW by song).



FIGS 2-3. Distribution of *Orchelimum* in the United States and Canada. For each species the predicted general distribution is shaded. The open circles indicate specific records by county. The solid circles are peripheral records, substantiated in the text.

O. nigripes: TEXAS, Calhoun Co., Indianola (TJW by song), Victoria Co. (Hebard 1931: 199), Wichita Co. (*ibid*); COL., Denver Co. (Rehn and Hebard 1915: 58); NEBR., Scotts Bluff Co. (*ibid*); S. DAK., Bon Homme Co. (Hebard 1925: 131), Lincoln Co. (*ibid*); WISC., Iowa Co. (Rehn and Hebard 1915: 58); MICH., Isabella Co. (Cantrall 1968: 334); OHIO, Ashtabula Co. (Hebard 1938: 37), Columbiana Co. (FSCA), Washington Co. (FSCA); TENN., Knox Co. (Powders and Goodwin 1969: 81); MD., Potomac R., Cabin John (ROM, GKM, by song); ALA., Walker Co. (Dakin and Hays 1970: 75); LA., Orleans Par. (Rehn and Hebard 1915: 57).

O. pulchellum: MISS., Hancock Co. (ROM, GKM, by song and specimen); ALA., Walker Co. (Dakin and Hays 1970: 75); GA., Jackson Co. (Rehn and Hebard 1916: 264); MD., Montgomery Co. (*ibid*); N.J., Middlesex Co. (Hebard 1938: 37); FLA., Monroe Co., Key Largo (FSCA), Escambia Co. (*ibid*).



★ Virginia carinatum see text

FIG. 3.

O. superbum: LA., St. Tammany Par., 3.1 mi e. jct. La. 1090 on U.S. 190 (FSCA); FLA., Columbia Co. (*ibid*), Putnam Co., Welaka (UMMZ-RDA); GA., Charlton Co., Okefenokee Swamp (FSCA, UFT 260-6); N.J., Morris Co. (Blatchley 1920: 558).

O. sylvaticum: TEXAS, Calhoun Co. (UMMZ-RDA), Uvalda Co., Garner St. Pk. (UFT 261-6), Howard Co., Big Spring (TJW by song); OKLA., Texas Co. (UMMZ-RDA); KANS., Grant Co. (Hebard 1931: 198); S. DAK., Jones Co. (Hebard 1931: 199), Brookings Co. (UMMZ-RDA); IOWA, Dickinson Co. (Froeschner 1954: 288); IND., Marshall Co. (Hebard 1934: 213); ONT., Muskoka Dist., 5-7 mi s. Rosseau (UMMZ); OHIO, Tuscarawas Co. (Hebard 1938: 37), Monroe Co. (*ibid*); KY., Laurel, U.S. 25 (TJW by song); ALA., Dallas Co. (Dakin and Hays 1970: 75), Mobile Co. (*ibid*).

O. volantum: KANS., Douglas Co. (Blatchley 1920: 560); IOWA, Iowa Co. (Froeschner 1954: 290); MICH., Kent Co. (Cantrall 1968: 334); ONT., Lambton Co. (Vickery and Kevan 1967: 35), Norfolk Co. (*ibid*); OHIO, Pickaway Co. (R. D. Alexander, pers. comm.); IND., Vigo Co. (Rehn and Hebard 1915: 72); N.J., Gloucester Co. (Hebard 1938: 38), Burlington Co. (*ibid*).

O. vulgare: TEXAS, Grimes Co. (TJW by song), McLennan Co. (UMMZ); KANS., Scott Co. (Hebard 1931: 198); S. DAK., Walworth Co. (Hebard 1925: 129); N. DAK., Barnes Co. (Hebard 1936: 52); MICH., Gogebic Co. (Cantrall 1968: 334), Mackinac Co. (*ibid*); QUE., Laval Co. (Rehn and Hebard 1915: 40); MAINE, Oxford Co. (Rehn and Hebard 1915: 41); N. CAR., Chowan (Rehn and Hebard 1916: 263), Wake Co. (*ibid*); GA., Bibb Co. (Blatchley 1920: 543); LA., St. Tammany Par. (UMMZ-RDA), Terrebonne Par. (FSCA).

O. unispina: ARIZ., Maricopa Co., Phoenix (UMMZ); MEX., Jalisco, Guadalajara (Rehn and Hebard 1915: 81).

Mechanism and Terminology

The songs of *Orchelimum* males are produced by the contact of modified forewings (tegmina), opened and closed while kept flexed over the insect's abdomen. The upturned rim of a scraper (plectrum) on the edge of the right tegmen engages with a row of teeth (file or pars stridens) on the ventral surface of the left tegmen. Usually both opening and closing forewing movements produce sounds. The shock of each tooth-scraper interaction is transmitted to the veins and to the thin membranes of enlarged forewing cells. The vibration of these surfaces generates a wave disturbance in the surrounding air.

Both tegmina bear a file on their ventral surface, but only the more robust file on the left wing functions in stridulation. The teeth run in a nearly straight row (the body of the file) which turns forward near the wing base in a basal arm (Fig. 4). The end most distal to the wing base, i.e. the end with the most closely spaced teeth, is the tail of the file. Wing closure draws the scraper from the tail along the file body toward the turn.

Functional files of several pinned specimens of each of the 18 species were studied with a light microscope. For each species at least one file was examined with a scanning electron microscope. File structure is species characteristic (though not species diagnostic) and two file types can be distinguished within the genus.

Type I files occur in *O. carinatum*, *O. volantum*, *O. bradleyi*, and *O. superbum*. Files of the latter two species are shown in Figs. 4B and 4C respectively. Such files exhibit widely spaced teeth in the basal half of the body of the file, elevated on a greatly swollen vein; the teeth are separated by a distance nearly equivalent to tooth width. All remaining species, excepting *O. minor* and *O. fidicinium*, possess type II files. *O. agile* (Fig. 4E) and *O. concinnum* (Fig. 4F) are examples. The teeth of the basal half of the file body are much closer together (separated by a distance substantially less than the tooth width) and the vein is less developed. Files of the second type show a gradual change in tooth width from the turn to the tail, while type I files exhibit a more sudden change, the teeth decreasing rapidly in width at slightly over half the distance along the file body from the turn. Files of *O. minor* and *O. fidicinium* appear most closely allied to type I but the increase in vein width and inter-tooth distances is not so marked as in the four 'typical' species.

Three genera comprise the North American Conocephalinae: *Orchelimum*, *Conocephalus*, and *Odontoxiphidium*. The latter is a monotypic genus represented by *Odontoxiphidium apterum* Morse. This species is found only in southeastern United

States (Rehn and Hebard 1916). The file of *O. apterum* (Fig. 4A) is similar to the type I files of *Orchelimum*. *Conocephalus* files (Pipher and Morris 1974, Fig. 4D) resemble type II *Orchelimum* files, but have fewer teeth, and in proportion to their smaller size, a more pronounced tooth separation.

The significance of these morphological differences is not clear. For certain song components (modes) there is apparently a relationship between increased spatial separation of file teeth and increased temporal separation of sound pulses within pulse trains. Temporal separation is particularly evident in the major pulse trains of *O. carinatum* zips and *O. bradleyi* smacks. *Odontoxiphidium* likewise generates major pulse trains with pulses well separated by silence.

The design of type I files increases the likelihood of the scraper lodging at a particular file locus (behind a particular tooth). It becomes easier mechanically to generate a single isolated sound pulse bearing a stereotyped temporal relationship to the cycle of wing movement. It is possible that temporal patterning of sound pulses holds particular signal value for those *Orchelimum* having widely spaced file teeth (Fig. 5G, H), while those species with type II files employ critical signal parameters (releasers) at the level of the pulse trains.

Having in mind the identification of (silent) museum material, Moss *et al.* (1970) argued that the file's morphology will reflect the song structure it generates. There is undoubtedly a relationship, as between widely spaced teeth and widely spaced pulses; but in *Orchelimum* and katydids in general, this relationship does not permit inferring from file structure the principal differences between the songs of closely related species. (See Walker and Dew 1972; Walker and Carlyle 1975.)

In all *Orchelimum* the file teeth have an asymmetrical profile (Fig. 5B, C): they are strongly buttressed on their basad aspect. On closure the scraper encounters a steep face, on wing opening a sloped face. When the wings close, this asymmetry enhances the momentary 'trapping' of the scraper ridge in the intertooth space, thereby increasing the energy stored in the bent scraper lobe (see below). Thus tooth structure suggests that *Orchelimum* generates its most intense sounds on wing closure.

Amplitude modulation (AM) is change in amplitude with time. This term was first applied to insect sounds by Pumphrey (1940). A terminology useful in describing AM components of *Orchelimum* songs is illustrated (Fig. 6). A pulse is the simplest 'element of amplitude' which is convenient to recognize and is defined here as a wave train isolated or nearly isolated in time by a substantial amplitude modulation. Frequently this modulation is complete and ends in separating one pulse from the next by an interval of silence. In most cases this definition of pulse agrees with its past usage by those studying cricket sounds.

The wave train of many cricket and some tettigoniid pulses is prolonged and sinusoidal, the wave form approaching that of a pure tone. Furthermore, it is nearly constant in amplitude over several to many waves. Uniform amplitude suggests ongoing energy input and a single prolonged pulse apparently involves many successive tooth-scraper interactions, one interaction per wave. Bailey and Broughton (1970) describe the likely mechanism: each tooth-scraper interaction "evokes one wave, reinforced by the next before any decay can set in". The tegmina are driven, displaced as a unit, with minimal resonance.

In contrast to the pulses of most crickets those of *Orchelimum* are of very short duration. They too may show a sustained amplitude and sinusoidal form, but only over the first two or three waves, following which the train always ends in a few, rapidly-decaying, complex waves. This wave form suggests that as in crickets, more than one tooth of the file is involved in a single pulse.

The mechanism may be similar to that proposed for the generation of the 33 khz prolonged pulses of *Metrioptera sphagnum* (F. Walker) (Morris and Pipher 1972).

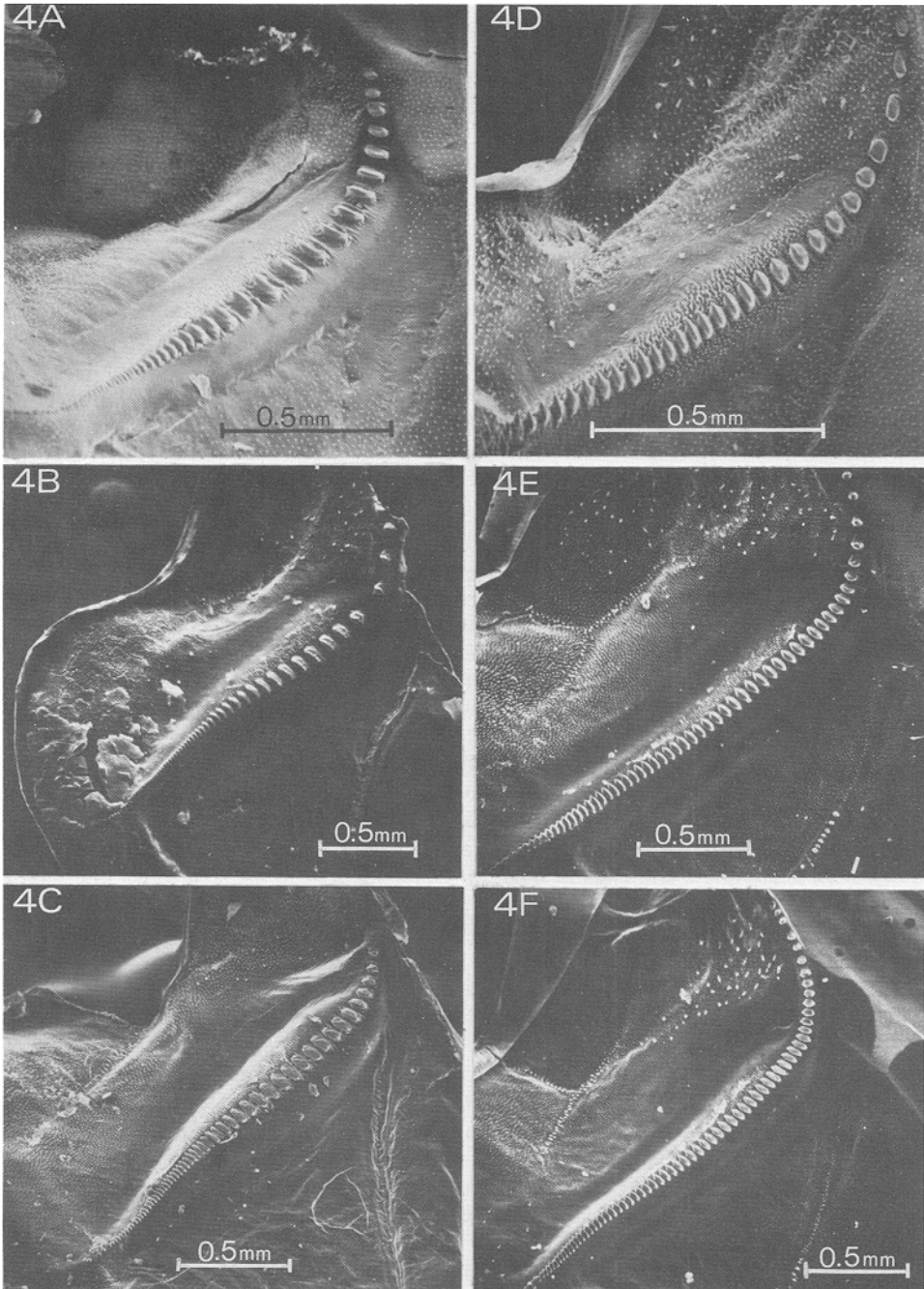


FIG. 4. Ventral view scanning electron micrographs of functional (left tegmen) conocephaline files. *O. apterum* (A), *O. bradleyi* (B), *O. superbum* (C), *Conocephalus brevipennis* (Scudder) (D), *O. agile* (E), and *O. concinnum* (F). B and C are type I files; E and F are type II.

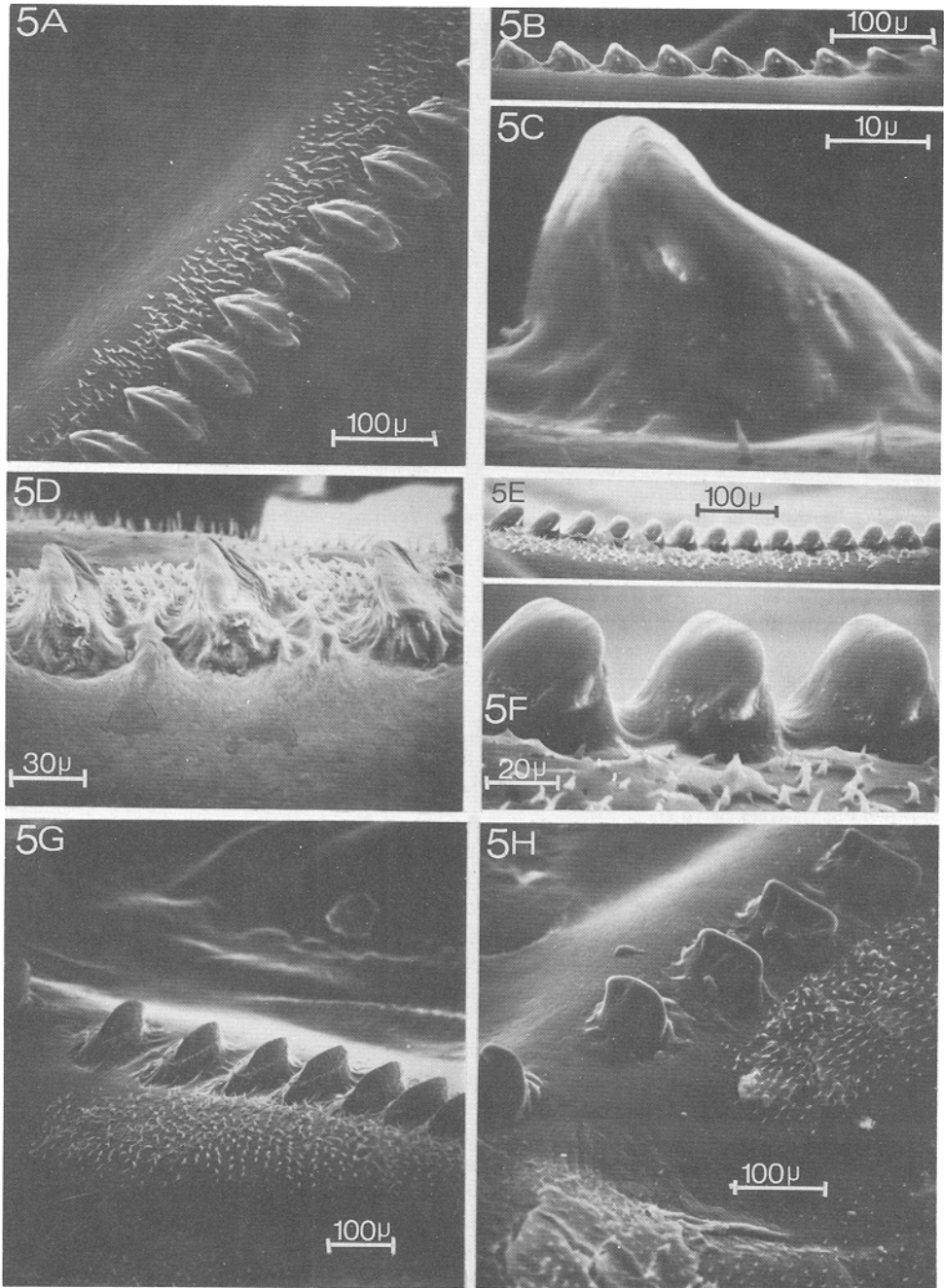


FIG. 5. *O. militare*: several teeth from the file body (A); teeth viewed side-on in the plane of the tegmen (B, C); during closure the scraper moves from left to right, encountering the steepest tooth face first. *O. apterum*: three teeth from the file body viewed nearly side-on (D). *O. concinnum*: teeth from the file body viewed anteriorly (E, F). *O. bradleyi*: widely separated teeth of the file body in the region where it approaches the turn (G, H). In all cases (A, D, E-H) sensillae occur on the anterior surface of the vein buttress and are totally absent from the posterior surface.

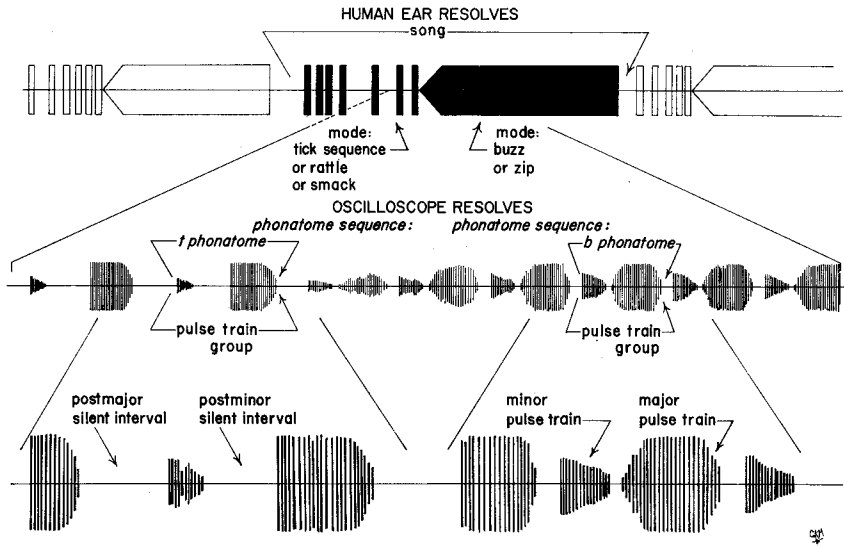


FIG. 6. Diagrammatic representation of *Orchelimum* amplitude modulation patterns illustrating the terminology used here.

According to this model the scraper is trapped briefly behind a file tooth, then slips free and drives over the next two or three teeth, generating the sinusoidal portion of the pulse. During the time interval when the scraper is lodged, energy would be stored in the elasticity of the tegmina. Thus energy is then released in the much shorter time interval of scraper displacement. Thus the power of the driving process would be increased. It appears that the rapidly-decaying complex waves of *Orchelimum* coincide with the vibration of the tegmina in modes inherent to their structure (resonance).

In crickets a complete closing movement of the tegmina with file and scraper engaged results in a single pulse; such a pulse involves the interaction of the scraper with all the teeth along the greater part of the file. In *Orchelimum* travel of the scraper along the file generates a whole *train* of pulses and each pulse involves scraper interaction with one or perhaps a few teeth. The term *pulse train* (PT) can be formally defined as a first order grouping of two or more pulses, preceded and followed by a period of silence substantially greater in duration than any of the time intervals *between* the pulses.

Two or more distinctive pulse trains produced in succession comprise a pulse train group (PTG), a second order grouping of pulses. If such a pulse train group is repeated two or more times, the resulting overall sequence is a train of pulse train groups and is here termed a *mode*. A mode is usually a third order grouping of pulses. All of these terms (pulse, pulse train, pulse train group, and mode) describe nested groupings of pulses in time.

The rate of delivery of the pulses making up a PT or of the PTGs making up a mode is not a criterion for the definition of these terms. For example, in the tick sequence of *O. agile* there are pauses at irregular intervals. Since the PTGs are all more or less the same, such pauses are not taken as the end of a mode. The mode continues until a distinctively different PT is produced or until the pause is atypically long. The same approach can be taken with the regular grouping of the PTGs within the buzz of *Orchelimum militare* Rehn and Hebard. In this species a longer than usual pause occurs after every third PTG; but since each trio consists of similar PTGs the whole sequence is taken as a single mode.

A series of PTs or PTGs that show a gradual (continuous) change in their appearance over time may also cause confusion. Comparisons of early and late PTs or PTGs might suggest that they are sufficiently distinct to be considered different 'types'. But so long as there is not a discontinuous change the entire sequence will be considered one mode. Obviously, PTs and PTGs are never identical, and it is a matter of judgment and common sense as to how different they must be before they are considered distinct.

In *Orchelimum* most PTGs consist of two PTs: major and minor (Fig. 6). A major pulse train (MaPT) is of longer duration and greater intensity than a minor pulse train (MiPT). The silent interval which follows a major pulse train is identified as a postmajor silent interval (PmaSI) while that following a minor pulse train is termed a postminor silent interval (PmiSI). The pulses of MiPTs usually overlap while those comprising MaPTs are discrete and separated by silence. The pulse rate of a MiPT is always markedly higher than the pulse rate of its associated MaPT.

Most katydids and crickets stroke their tegmina to and fro so rapidly that time consuming techniques of photography or tooth removal are necessary to determine that a particular PT coincides with either closure or opening. Thomas and Alexander (1962) found that in *O. vulgare* the MaPT of the ticking coincides with tegminal closure, the MiPT with opening. Using the same procedures as Walker and Dew (1972), we plotted tegminal movements from high speed motion pictures of *O. vulgare* and *O. nigripes* (Fig. 7). The oscillographic record of sound on the film revealed that for both species the major pulse trains in the buzzes and in the ticks were produced on closure.

Morris and Pipher (1972) surveyed the literature for instances where the relationship between PT and wing direction had been experimentally established. A total of 10 species in seven tettigonioid subfamilies have been examined by various workers; without exception "the most intense and prolonged song components are produced on closure". On this basis and in view of the tooth asymmetry described earlier, we consider it likely that for all *Orchelimum* species, MiPTs coincide with tegminal opening while MaPTs are produced on closure.

The term phonatome was employed by Leroy (1966) and can be defined as all of the sound produced during one cycle of wing movement. Walker and Dew (1972) used this term extensively in describing the elaborate song structure of Uhler's katydid, *Amblycorypha uhleri* Stål. A phonatome is a behaviourally defined song component. As such it may be difficult to apply where the behavioural (generator movement) basis of the sounds is not precisely known. But if our assumptions above regarding wing direction and PTs are accurate, phonatome can be usefully applied to the songs of the various *Orchelimum* species. In almost every case an *Orchelimum* phonatome will consist of a minor (opening) and major (closing) PT and will coincide with the term PTG. A *phonatome sequence*, a series of similar or only gradually changing phonatomes, will coincide with the term mode.

Some amplitude components of *Orchelimum* songs can be detected with the unaided human ear. Three such are: *buzz*, *rattle*, and *tick sequence*. The distinctions implied by these terms are essentially phonatome repetition rates. *Buzzes* are the result of high phonatome rates; the individual phonatomes cannot be resolved by our ear and the sound gives no impression of the PTs and PTGs within it. If the phonatome rate is very low, making it possible to distinguish and to count individual phonatomes, the song component is identified as a *tick sequence*. At intermediate rates phonatomes may be detected as a buzz with a tremulous quality or a tick sequence in which the units occur too rapidly to count; in such cases we describe the song component as a *rattle*. One must bear in mind the substantial effects of temperature on phonatome rates; the same song component identified as a rattle at a high temperature may sound as a tick sequence at a lower temperature. Most buzzes, rattles, and tick sequences are also modes.

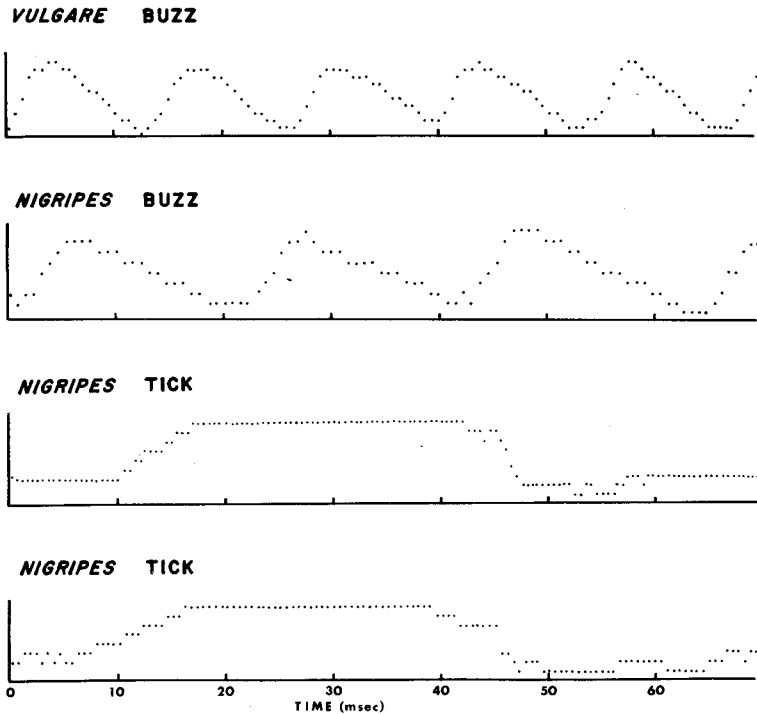


FIG. 7. Stridulatory movements of *O. vulgare* and *O. nigripes* during calling songs, plotted frame-by-frame from high-speed motion picture film. The higher the dots the more the wings are apart and the lower the dots the more nearly closed are the wings.

Two other terms useful at the level of human ear resolution are *zip* and *smack*. A *zip* is a short buzz, less than 1s in duration, which undergoes a noticeable amplitude increase over the first one-third to one-half of its production. A *smack* is a particularly loud 'full-sounding' tick.

Two phonatome types occur in *Orchelimum* calling songs, one (termed here a *b* phonatome) is characteristic of buzz modes, the other (a *t* or *r/t* phonatome) is characteristic of rattle or tick sequences. In the MaPT of *b* phonatomes (Fig. 6) the intensity of successive pulses tends to build gradually over the first portion of the train; but in the MaPT of an *r/t* phonatome, pulses are generated at maximum intensity right from the start. Thus the MaPTs of an *r/t* phonatome present a 'steep face'. In addition the PmiSI of *r/t* phonatomes is *much* longer than the PmiSI of *b* phonatomes. (During this prolonged silent interval *O. nigripes* (Fig. 7) holds its wings maximally open; the event of closing occupies only a few frames of the film and results in the generation of the MaPT.) These several observations suggest that cuticular energy storage is taking place during the lengthened PmiSI of tick and rattle modes. The insect has apparently lodged its scraper behind a tooth and is exerting force without scraper displacement; the accumulated energy is manifest as the steep face of the major pulse train.

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