

SYSTEMATICS AND ACOUSTIC BEHAVIOR OF  
SCALY CRICKETS (ORTHOPTERA: GRYLLIDAE:  
MOGOPLISTINAE) OF EASTERN UNITED STATES<sup>1</sup>

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INTRODUCTION

Modern techniques have yielded much new information on the biology and taxonomy of the mogoplistine crickets of the eastern United States. Four clearly defined genera of mogoplistines occur in North America: *Cycloptiloides* Sjostedt, *Hoplosphyrum* Rehn and Hebard, *Oligacanthopus* Rehn and Hebard, and *Cycloptilum* Scudder. *Cycloptilum* is retained here contrary to Chopard's 1968 catalog, which splits it among the Old World genera *Ectatoderus* and *Ornebius*. *Hoplosphyrum* does not occur east of the 94th meridian. *Cycloptiloides* and *Oligacanthopus* are represented by single species restricted to southern Florida: *C. americanus* (Saussure) and *O. prograptus* Rehn and Hebard. *Cycloptilum*, with sixteen species in the area covered, nine described as new in this paper, occurs throughout most central Atlantic and southern states. It consists of four species groups based on morphology, song, and habitat: (1) the arboreal, trilling *trigonipalpum* group: *C. trigonipalpum* (Rehn and Hebard), *spectabile* Strohecker, and *albocircum* n. sp.; (2) the arboreal, complex-chirping *slossoni* group: *C. slossoni* Scudder, *C. kelainopum* n. sp. and *C. ainiktos* n. sp.; (3) the terrestrial, chirping *squamosum* group: *C. squamosum* Scudder, *C. zebra* (Rehn and Hebard), *C. comprehendens* Hebard, *C. bidens* Hebard, *C. exsanguis* n. sp., *C.*

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*quatrainum* n. sp., *C. pigrum* n. sp., *C. tardum* n. sp., and *C. velox* n. sp.; and (4) the terrestrial, complex-trilling species, *C. irregularis* n. sp.

North American Mogoplistinae have been revised twice in this century: by Rehn and Hebard in 1912 for species north of Panama, and by Hebard in 1931 for United States species. In this paper we more than double the number of species of mogoplistines known from eastern United States. The new species were discovered by studying calling songs and seasonal life cycles. Such studies have led to similar discoveries in other groups (Walker 1964).

The mogoplistine crickets are small, slender, depressed crickets with well-developed jumping legs and a prognathous head. Perhaps the two most notable features are the minute scales on nearly all exposed surfaces and the prominent clypeus. The latter is bulbous, strongly rounded at mid length, and forms nearly a right angle between the flattened dorsum of the head (the frons and occiput) and the vertical labrum. Its anatomical homology has been confirmed in the genus *Hoplosphyrum* by dissection and tracing of the large internal muscles to the dorsum of the cibarium. The function of this powerful "pump" is unknown; however, since many live in climatically or physiologically arid environments, this and the spirally grooved extensible hypopharynx may be important in obtaining dew as a source of fresh water.

Blatchley (1920) used the common name "Wingless Bush Crickets," but only the females are totally wingless: the males of nearly all species bear small, oval tegmina functional as sound producing organs. Furthermore, most species do not inhabit bushes. We here adopt the name "Scaly Crickets" as more apropos.

The scaly crickets are pan-tropical and pan-subtropical and extend well into the major temperate regions of the world. Each major land mass seems to have endemic genera. Other genera show broader distributions, eg. *Cycloptilum*, as here defined (pan-American), *Mogoplistes* and *Ectatoderus* (Afro-Eurasian), and *Ornebius* (Afro-Eurasian and Indo-Australian). The major genus-groups largely share the worldwide distribution of the family.

#### METHODS

That the mogoplistines are poorly represented in collections

should not be taken as an indication of rarity in natural situations within the range of the group, nor the lack of challenging problems. Most are active, yet small, secretive, cryptic, and nocturnal. Most live in habitats that are personally uncomfortable, physically impenetrable, or visually confusing to the collector. Series of more than a few specimens are seldom obtained by any of the usual collecting methods.

The collecting methods we have used with most consistent success depend on the male's singing behavior. Population densities and distribution, species identification and individual location can be assayed by listening, the latter especially when two collectors can triangulate on a singing individual. Even females and juveniles are most often found by searching with headlamp or flashlight in the vicinity of a male — the females especially when courtship songs are recognizable.

Taxonomic methods were similar to those described for studies of oecanthine crickets and *Orocharis* (Walker 1962a, 1969). The following major collections were studied, each listed with abbreviations used in the text: Academy of Natural Sciences of Philadelphia (ANSP), Florida State Collection of Arthropods (FSCA), University of Michigan Museum of Zoology (UMMZ). Other abbreviations used are JDS (J.D. Spooner), HFS (H.F. Strohecker), REL (R.E. Love), TJW (T.J. Walker), UFT (University of Florida, Department of Entomology, Tape), and MCZ (Museum of Comparative Zoology, Harvard University). The abbreviations ch/sec. (chirps per second), and p/sec. (pulses per second) are used in describing songs.

Holotypes and allotypes of species described herein are deposited in ANSP.

Due to limitations in time and travel, most fieldwork was in the eastern half of the United States. In accord with this, only those species in the subfamily which occur in the generalized limits of the eastern deciduous forest, or roughly, east of the 94th meridian, are included.

In addition to characteristics of song and biology, several morphological characters previously unused or of limited application are important in distinguishing species or groups while others previously thought useful have been discarded or used more nar-

rowly. While many are self explanatory, several need more detailed discussion.

*Dorsal width of clypeus and scape.* — Expressed as the ratio of the length of the epistomal suture exposed between antennal sclerites to the width of the dorsal aspect of the scape measured perpendicular to the inside margin, these measurements indicate the relative breadth of the clypeus, useful in distinguishing some genera and species groups.

*Exposure of wings.* — Rehn and Hebard (1912) used the single character of wings "concealed by pronotum" to define the genus *Cryptoptilum*, and others, including Chopard (1968) have continued to use this character at the generic level. Concealed wings occur in several divergent groups and probably evolved independently several times. In some instances they may prove ancestral but paraphyletically distributed. The alternative, "wings exposed," may be separated into two independent states: pronotum truncate with wings nearly completely exposed; and pronotum extended covering 1/3 to 3/4 of wings. The first is characteristic of one monophyletic group, the genus *Hoplosphyrum*. The second is characteristic of a second group, the terrestrial scaly crickets, most closely related to one part of Rehn and Hebard's (1912) *Cryptoptilum* but much less related to the remainder. This redefinition agrees with a number of other characters including song and habitat distinctions.

*Number of teeth on stridulatory file.* — File teeth may be seen by examining the underside of the stridulatory vein under a microscope. Counts include all recognizable transverse lamellae. These counts usually reflect differences in pulse rates in related species. As all species have songs of approximately the same frequency (Hz) and frequency presumably equals toothstrike rate (Michelsen and Nocke 1974), faster pulse rates (wingstrokes) are correlated with fewer teeth. This correlation holds for all species except the pair *Cycloptilum spectabile* and *C. albocircum*. In the large *Cycloptilum squamosum* group, pulse rates are nearly identical for most species and file-tooth number is generally not a useful character. Exceptions occur in *C. exsanguis*, a very large species with slow pulse rate and many teeth, and *C. zebra*, a very small species with fast pulse rate and few teeth.

*Male titillators.* — Below the epiproct and often obscured by the subgenital plate and cerci, males of *Cycloptilum*, *Oligacanthopus* and *Cycloptiloides* have a pair of appendages arching upward from the paraprocts probably aiding in copulation. Their shape differs among major groups and species. The term "titillator" has been commonly used for abdominal terminalia among many orders of insects, including other Orthoptera. We do not intend to imply homology with titillators of these other groups; the term is simply less cumbersome and more descriptive than "paraproctal processes."

*Male genitalia.* — Genitalia may be dissected out of fresh, alcoholic, or well-relaxed specimens and lightly "squashed" on a microscope slide. The shape and amount of sclerotized tissue are taxonomically important. This procedure yields more comparable information than directly dried or preserved mounts as the soft tissue is expanded; however, many features may be seen in dry, three-dimensional mounts.

*Female subgenital plate.* — The shape and armament of the subgenital plate is useful for species and group identification. Descriptive terms include: a) tapered sides — sides, not including projections, arching moderately and evenly toward apex (when removed and flattened, appears rounded triangular) (Figs. 22-24); b) quadrate shape — sides viewed in profile, not including projections, nearly parallel to ventral margin, lateral angles sharply rounded, apex truncate (when removed and flattened, appears trapezoidal) (Figs. 20, 21); c) armed with teeth — a pair of non-pigmented denticles near apex (Figs. 22-24); d) with finger-like projections — a pair of spatulate, pigmented projections extending posteriorly from disto-lateral angles (Fig. 25); e) with median spike — a narrowly triangular median projection (Fig. 24); f) median cleft — a sharp median indentation (Fig. 19); g) emarginate — apex with a slight rounded indentation, appearing slightly recurved in profile (Figs. 22, 23).

*Coloration.* — As specimens often lose part or most of their scales, the coloration and patterning of both the scale vestiture and cuticle are described for each species. Oily specimens are darker and show less pattern, and alcohol-preserved specimens are usually lighter and have nearly transparent scales.

*Measurements.* — Body length was measured along the midline from the front of the pronotum to the rear margin of the epiproct. This measurement is of some value for comparing overall size, but the length of the flexible abdomen may change greatly during drying. The head was not included as specimens commonly have heads deflexed, twisted or sunk into the thorax. The length of the pronotum was measured along the midline. It is the best size reference for closely related species, and some idea of intraspecific variation is indicated by the ranges of this measurement given for paratypes or other specimens. The length of the hind femur was measured as the maximum from base to apex. The length of the tibia was measured along the dorsal (serrated) margin from the basal notch to the distal end between the terminal spurs. Ovipositor length was measured from the basal angle of the dorsal margin to the apex.

*Songs.* — Songs are described as they are at 25 C. Use of a standard temperature is necessary because temperature has a profound effect on most features of the songs. Characteristics of songs at other temperatures can be estimated from rate vs. temperature graphs (Figs. 26, 27, 29-34) or by applying generalizations derived from studies of other subfamilies (Walker 1962b).

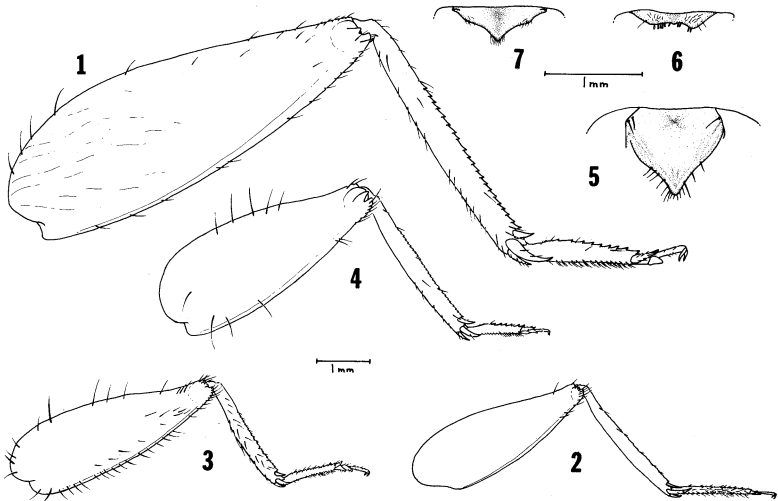
#### KEY TO GENERA

- 1 Last three segments of maxillary palpi each longer than greatest diameter of eye; facial angle weakly obtuse, clypeus evenly rounded throughout length (Figs. 8, 9); ovipositor with blade narrower than shaft, weakly differentiated, with tip slightly down-curved (Figs. 15, 16) . . . . . 2
- 1' Last three segments of maxillary palpi each shorter than greatest diameter of eye; facial angle weakly acute, clypeus sharply rounded at mid-length, flattened below and behind (Figs. 10-14); ovipositor with blade wider than shaft at junction, well differentiated, with tip sharp and up-curved (Figs. 17-19) . . . . . 3
- 2(1) Body longer than 8mm; hind basitarsus less than 1/2 as long as hind femur, about 5 times longer than greatest width, strongly narrowing distally (Fig. 1); rear margin of pronotum truncate in both sexes, covering less than 1/4 wing surface in males (Fig. 8); blade of ovipositor compressed, tip with broad point, shaft of even width throughout (Fig. 15); epiproct a rigid equilateral triangle (Fig. 5); titillators absent . . . . *Hoplosphyrum*
- 2' Body shorter than 6mm; hind basitarsus more than 1/2 as long as hind femur, about 10 times longer than wide, of even width throughout (Fig. 2); rear margin of pronotum in males greatly extended, rounded behind,

- entirely covering wings (Fig. 9); blade of ovipositor acute conical, tip sharply rounded, shaft narrowing distally (Fig. 16); epiproct emarginate, flexible (Fig. 6); titillators present. . . . . *Cycloptiloides*
- 3(1') Fore tibia lacking tympana; hind tibia 1/2 as long as hind femur (Fig. 3); adult males wingless, rear margin of pronotum truncate (Fig. 10) . . . . .  
 . . . . . *Oligacanthopus*
- 3' Fore tibia of adults with tympanum on front face; hind tibia about 3/4 as long as hind femur (Fig. 4); adult males with tegmina, pronotum strongly extended caudally with rounded margin, covering more than 1/3 the area of the wings (Figs. 11-14) . . . . . *Cycloptilum*

DESCRIPTION AND DISCUSSION OF GENERA AND SPECIES

Four genera of mogoplistines are known from North America, three of them occurring within the area covered by this paper. The fourth, *Hoplosphyrum*, is included to complete the discussion of genera, but no species will be considered. Hebard (1931) and Rehn and Hebard (1912) give detailed synonymies; only the major changes in nomenclature are listed below.



FIGURES 1-4. — Rear legs of scaly crickets. 1. *Hoplosphyrum boreale*. 2. *Cycloptiloides americanus*. 3. *Oligacanthopus prograptus*. 4. *Cycloptilum slossoni*.

FIGURES 5-7. — Male epiprocts of scaly crickets. 5. *Hoplosphyrum boreale*. 6. *Cycloptiloides americanus*. 7. *Cycloptilum velox*.

## Genus HOPLOSPHYRUM

*Hoplosphyrum* Rehn and Hebard, 1912:122. Type species, *Mogoplistes occidentalis* Scudder, 1868, by original designation.

The members of *Hoplosphyrum* are larger than nearly all other North American mogoplistines. The long, narrowing shape of the hind basitarsus (Fig. 1), quadrate pronotum with wings present in males, wide, broadly rounded clypeus (Fig. 8), very small scape, lack of male titillators, compressed, broadly tipped ovipositor (Fig. 15), and rigid triangular epiproct (Fig. 5) serve to distinguish the members of this genus from all others in North America. We have recorded the songs of two species, and both produce long trains of chirps with 3-7 pulses per chirp at about 60 p/sec. The chirp rate approximates 2.5 for one and 5.0 for the other.

## Genus CYCLOPTILOIDES

*Cycloptiloides* Sjöstedt, 1909:109. Type species, *Cycloptiloides meruensis* Sjöstedt, 1909, by monotypy.

*Glaphyropus* Rehn and Hebard, 1912:189. Type species, *Cycloptilum americanum* Saussure, 1870, by original designation. Synonymy by Hebard, 1922.

The original description of this genus, based on African material, agrees on all counts with North American specimens of *C. americanus* (Saussure). Common characters include the very long, thin maxillary palpi, the extended rounded prothorax in males (Fig. 9), very long, thin hind basitarsus bearing delicate pale chaetaform spines (Fig. 2), and the very deep, large bowl-like male subgenital plate.

A single species has been described from the Western Hemisphere, and it may have been introduced from Africa.

***Cycloptiloides americanus* (Saussure)**

Saussure's Scaly Cricket (Figs. 2, 6, 9, 16)

*Cycloptilum americanum* Saussure, 1874:426, pl 8, figs. 41, 42, (plate designation, *Cycloptilum poeyi*.) Type locality, Cuba. Two syntypes, 1 ♂, 1 ♀, in the Saussure Collection.

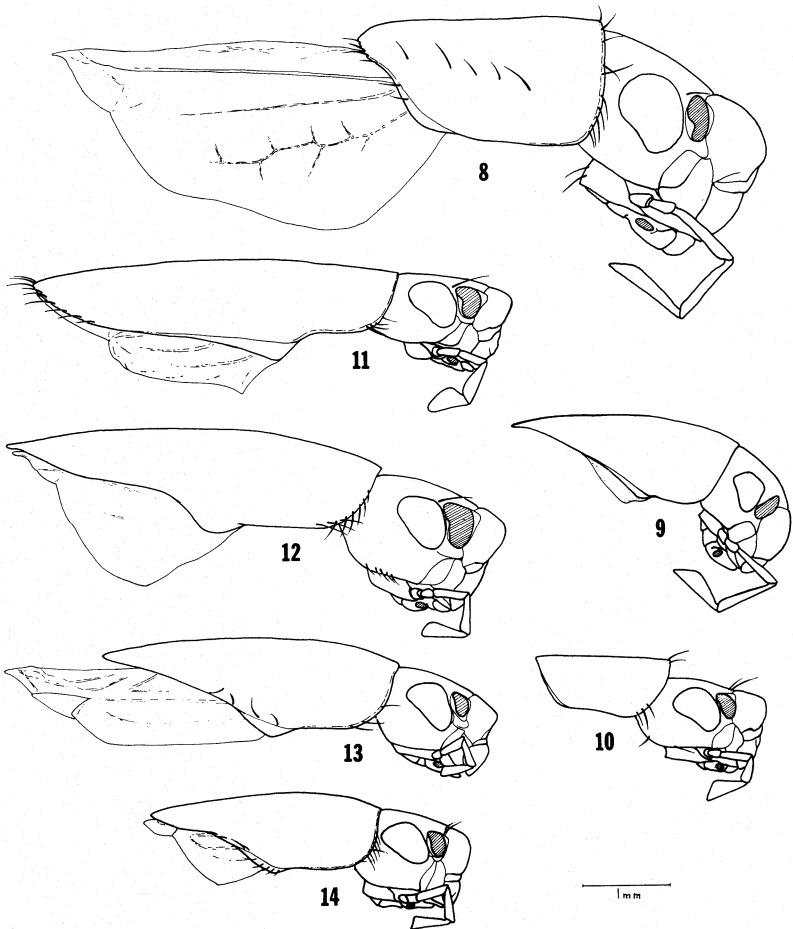
*Glaphyropus americanus* (Saussure). Rehn and Hebard, 1912:190.

*Cycloptiloides americanus* (Saussure). Hebard, 1922:352.

We have examined a single pair of specimens from the eastern United States, taken in Miami, Florida, by H.F. Strohecker. We



failed to find this species in spite of a number of trips to the Miami area though Strohecker (1952) listed them as common at his house giving collection dates "extending from March 1949 to October 1950," and noting "a feeble song." Perhaps this was a temporary



FIGURES 8-14. — Side views of head, pronotum and wings of male scaly crickets. Antennae and labial palpi omitted. 8. *Hoplosphyrum boreale*. 9. *Cycloptiloides americanus*. 10. *Oligacanthopus prograptus*. 11. *Cycloptilum trigonipalpus*. 12. *Cycloptilum slossoni*. 13. *Cycloptilum tardum*. 14. *Cycloptilum irregularis*.

adventive population transported from Cuba or some other more tropical area. *C. americanus* has been reported from Vera Cruz and San Jose del Cabo (Baja California), Mexico, and Venezuela (Rehn and Hebard, 1912), and Hawaii (Hebard, 1922). Such a distribution suggests a well traveled adventive. Perhaps *C. americanus* came to the New World in the same slave ships that brought the "American" cockroach (Rehn 1945).

However, the systematics of this "species" are without doubt far more complex than presently known. Mr. Dave Weissman has recently collected two morphologically similar *Cycloptiloides* in the Cape region of Baja California, Mexico. Both sing short trills of single pulses, one at ca. 18 p/sec, the second at ca. 115 p/sec (personal communication to REL). Whether either of these is conspecific with Florida *Cycloptiloides* is not known.

This is the smallest mogoplistine in the United States. It may be easily recognized by the generic characters listed above and in the key, and its very thin limbs and general aspect with a rounded profile from labrum to rear of pronotum.

#### Genus OLIGACANTHOPUS

*Oligacanthopus* Rehn and Hebard, 1912:218. Type species, *Oligacanthopus prograptus* Rehn and Hebard, 1912, by original designation.

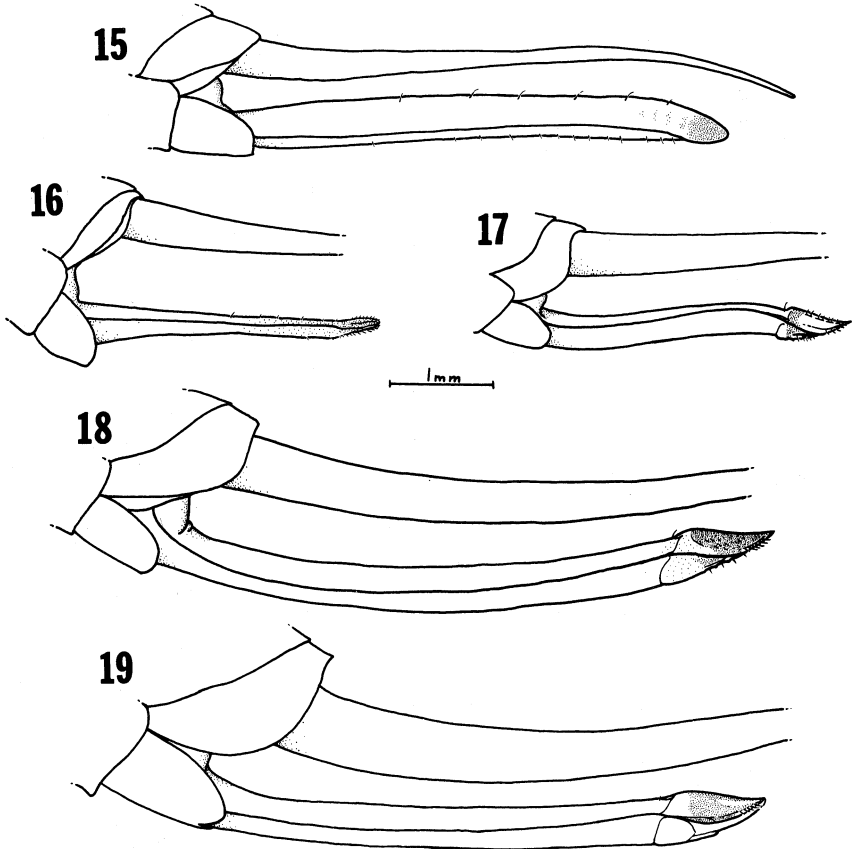
As this genus remains monotypic, characteristics are discussed under the species below.

#### ***Oligacanthopus prograptus* Rehn and Hebard** Silent Scaly Cricket (Figs. 3, 10, 17, 52)

*Oligacanthopus prograptus* Rehn and Hebard, 1912:219, figs. 21-23. Type locality, Miami, Florida. Holotype, ♀, 6 Feb 1904, ANSP.

In general appearance and in most characters this species is well within the range of variation found in the genus *Cycloptilum*. The differences seem related to two focal characteristics: *O. prograptus* is songless, and frequents narrow cracks and crevices in and under tree bark, while all known *Cycloptilum* have a calling song produced by adult males and seem to inhabit foliage, twigs or litter and ground cover, though they may on occasion utilize crevices. The following distinguishing characters are associated with songlessness: wings always absent, male pronotum not extended, similar

to that of female (Fig. 10), tympanum always absent. In probable relation to living in crevices, the hind tibia is very short, half the length of the hind femur, and the terminal spurs on the hind basitarsus are very short and robust with sharply hooked tips (Fig. 3). The last two characteristics probably reduce the dangers of entrapment in confined spaces while allowing firm purchase for jumping.



FIGURES 15-19. — Ovipositors of scaly crickets. 15. *Hoplosphyrum boreale*. 16. *Cycloptiloides americanus*. 17. *Oligacanthopus prograptus*. 18. *Cycloptilum trigonipalpum*. 19. *Cycloptilum slossoni*.

Rehn and Hebard (1912) and Hebard (1931) consider this a very rare species, collecting only a few at a time by stripping bark into a net and capturing escaping crickets. We also met with low success by this method; however, on two occasions REL took large series by searching the boles of palm trees at night when the crickets are active on the surface or teasing them out of retreats with a grass blade, capturing individuals in small jars. With this method, 23 were collected in less than 30 minutes in 1966, and another series was taken on the same trunks in 1970.

Adults have been taken April through November (FSCA) and February (ANSP) in south Florida; juveniles at several times from June to November (FSCA).

*O. prograptus* is known only from southern Florida (Fig. 52). Peripheral records are Charlotte Harbor, Charlotte Co. (FSCA), Miami, Dade Co. (ANSP, FSCA), and Middle Torch Key, Monroe Co. (FSCA). Habitats include subtropical hammock, white mangrove (*Languncularia racemosa* L.) and palm boles in coastal live oak forest. Specimens have not been reported on the ground.

#### Genus CYCLOPTILUM

*Cycloptilum* Scudder, 1868:142. Type species, *Cycloptilum squamosum* Scudder, 1868, by monotypy.

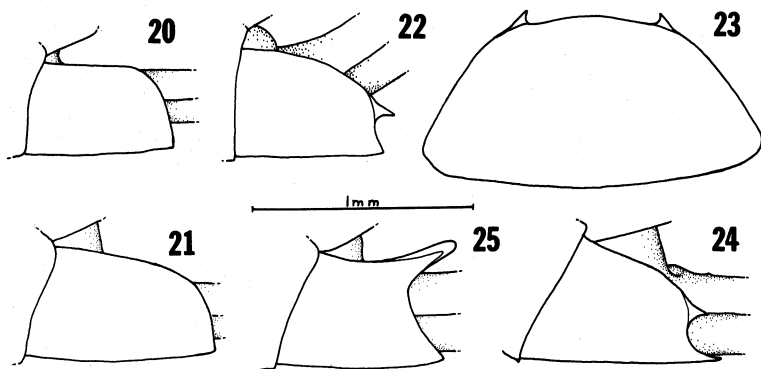
*Cryptoptilum* Rehn and Hebard, 1912:192. Type species *Ectatoderus antillarum* Redtenbacher, 1892, by original designation. Synonymy by Blatchley, 1920.

A number of generic names have been used for various North American species now included in this genus, including *Mogoplistes* Serville, 1839, *Mogisoplistus* Saussure, 1877 (an unjustified emendation), several subsequent misspellings (*Mogosi-plitus*, *Mogosiplictus*, *Mogisoplistes*, etc.), *Ornebius* Guerin, 1844, *Ectatoderus* Guerin, 1849, and *Liphoplus* Saussure, 1877. These seem to be misapplications of Old World genera except for *Liphoplus*, described from Tahiti and of presently unknown affinities, though probably the closest relative of *Cycloptilum*. Rehn and Hebard (1912) based *Cryptoptilum* on a single character, and Blatchley (1920) justly synonymized it. In this study, we show that the species placed by Rehn and Hebard in *Cryptoptilum* have their closest affinities to different species groups within *Cycloptilum*. Unfortunately Chopard (1968) returned to Rehn and Hebard's

(1912) division, making *Cycloptilum* a synonym of *Ornebius* Guerin and *Cryptoptilum* a synonym of *Ectatoderus* Guerin. This combines two divergent species groups in the latter genus and places a third species group phyletically closely related to one of them in *Ornebius*. We feel that arguments discussed in the last section of this paper preclude this, and that understanding is for the moment best served by retaining *Cycloptilum* as separate from the Old World genera.

This genus is characterized by the extended pronotum in adult males, rounded behind, covering  $1/3$  or more of the wings, the presence of tympana, the production of a calling song, the nearly rectangular basitarsus shorter than  $1/2$  the tibia (Fig. 4), scapes wider than  $1/3$  the exposed length of the epistomal suture, post clypeus divided, strongly produced to form an acute facial profile (Figs. 11-14), ovipositor compressed with lanceolate tip wider than shaft, sharply acute and weakly upturned (Figs. 18, 19), and male titillators present. The male epiproct is intermediate between *Cycloptiloides* and *Hoplosphyrum*: obtusely triangular with sinuate margins and slightly flexible (Fig. 7).

The genus *Cycloptilum* is divided into three distinct groups of species, the *trigonipalpum* group, the *slossoni* group, and the *squamosum* group. One species does not fit into any of these, and is treated separately.



FIGURES 20-25. — Female subgenital plates of *Cycloptilum*. Side views except Fig. 23 ventral view, flattened. 20. *zebra*. 21. *squamosum*. 22. *bidens*. 23. *bidens*. 24. *tardum*. 25. *comprehendens*.

## KEY TO THE GROUPS AND SPECIES OF CYCLOPTILUM

- 1 Terminal segment of maxillary palpi strongly expanded distally, end strongly oblique, length of short side half long side, equal to or shorter than largest diameter of end (Fig. 11); width of exposed epistomal suture less than 1.25 dorsal width of scape; length of male pronotum more than 2.5 head width; titillators conical in profile; song a train of simple pulses . . . . . *trigonipalpum* group . . . . . 2
- 1' Terminal segment of maxillary palpi weakly expanded distally, end slightly oblique, short side ca. equal to long side and much longer than greatest diameter (Figs. 12-14); width of exposed epistomal suture more than 1.25 dorsal width of scape; length of male pronotum less than 2.5 head width; titillators tubular; song a train of pairs of pulses . . . . . 4
- 2(1) Dorsal scale covering grey-brown, never cinnamon or orange, abdomen not banded by whitish fringes on tergites; ovipositor length ca. equal to or longer than hind femur; male pronotum under 4mm long; under 100 teeth on stridulatory file; song a fast buzzy trill, pulse rate over 50 p/sec. . . . . *trigonipalpum*
- 2' Dorsal scale covering of thorax cinnamon or orange-brown, abdomen with distinct whitish fringes on tergites; ovipositor shorter than hind femur; male pronotum over 4mm long; over 100 teeth on stridulatory file; song a slower trill, pulses distinct, pulse rate under 35 p/sec . . . . 3
- 3(2') Largest *Cycloptilum*, male pronotum over 4.5mm long; cuticle of legs and sides of prothorax distinctly tinged with red; over 165 teeth on stridulatory file; pulse rate over 20 p/sec. . . . . *spectabile*
- 3' Generally smaller, male pronotum under 5mm long; cuticle of legs and pronotum not reddish; under 165 teeth on stridulatory file; pulse rate under 10 p/sec . . . . . *albocircum*
- 4(1') Sides of clypeus viewed from front converging toward top; female subgenital plate tapered with margins curving into a deep acute apical cleft; ovipositor with a step-like notch on ventral margin ca. one blade-width from tip (Fig. 19); male pronotum longer than 3mm and covering wings entirely (Fig. 12); song a rapid series of pulse-pairs under 1/2 second duration, pair interval under 3 times pulse interval; arboreal. . . . . *slossoni* group . . . . . 5
- 4' Sides of clypeus viewed from front nearly parallel; female subgenital plate variously shaped but not acutely cleft (Figs. 20-25); ovipositor smooth or weakly scalloped ventrally; male pronotum not covering wings (Fig. 13) or shorter than 3mm if wings covered (Fig. 14); song a slower series of pulse-pairs usually over 1 second duration, pair interval over 7 times pulse interval; usually terrestrial . . . . . 7
- 5(4) Dorsal scale color dark brown, slightly lighter brown on sides of head and pronotum and on venter; cuticle of legs distinctly purple tinged; song a series of complete pulse-pairs, pulse rate under 100 p/sec., pair rate under 30 p/sec . . . . . *ainiktos*

- 5' Dorsal scale covering light tan or waxy-white, ventral scale color waxy-white; cuticle of legs pale tan or yellowish, without purple tinge; song a series of pulse-pairs but beginning with an unpaired pulse, pulse rate over 100 p/sec., pair rate over 35 pr/sec. . . . . 6
- 6( 5') Scales on dorsum greyish-tan, on lateral pronotum and head and on venter waxy white, distinctly differing from dorsum; clypeus light brown to dark brown; under 78 teeth on stridulatory file (Fig. 28); song with pair rate over 41 pr/sec. . . . . *slossoni*
- 6 Dorsal, lateral and ventral scales uniform waxy-white; clypeus piceous; over 78 teeth on stridulatory file (Fig. 28); song with pair rate under 41 pr/sec. . . . . *kelainopum*
- 7( 4') Ovipositor less than 0.75 length of hind femur, less than 1.6 length of pronotum; male pronotum shorter than hind tibia, shorter than twice head width and covering more than 3/4 wing surface (Fig. 14); titillators tubular, not expanded distally; song a beady trill of pairs of non-identical pulses produced in short bursts ca. 1 sec. in duration, pair rate rapid, over 10 pr/sec., pulse rate very rapid, over 120 p/sec. . . . . *irregularis*
- 7' Ovipositor more than 0.75 length of hind femur, more than 1.6 length of pronotum; male pronotum longer than hind tibia, longer than twice head width and covering less than 3/4 wing surface (Fig. 13); titillators expanded distally, drying spoon-shaped; song of pairs of identical pulses usually produced in long series, pairs sounding like chirps, chirp rate under 9 ch/sec., pulse rate under 80 p/sec. . . . . *squamosum* group 8
- 8( 7') Small size, male pronotum under 3.0mm long, female under 2.0mm long; scale coloration grey with dark stripes on the body and annuli on the legs; abdominal cuticle piceous, remainder very pale tan; wings exposed for ca. 1/2 length, with three distinct black spots on caudal border; song with pulse rate very rapid, over 68 p/sec.; under 100 teeth on stridulatory file; beaches and saltmarsh margins, coastal peninsular Florida to southeast Georgia . . . . . *zebra*
- 8' Without the above combination of characters . . . . . 9
- 9( 8') Song very slow, chirp rate under 2 ch/sec<sup>4</sup> . . . . . *pigrum*
- 9' Song faster, chirp rate over 2 ch/sec., or song unknown . . . . . 10
- 10( 9') Female subgenital plate tapered, with two subapical teeth (Figs. 22-24); with dark spots or solid dark caudal wing borders, wings exposed less than 1/3 length; east of Mississippi River . . . . *bidens complex* . . . . 11

<sup>4</sup>Song is the only known character distinguishing *C. pigrum* from several other species in the *squamosum* group. We expect females to key within the *bidens* complex. However, males without song data, based on variations in color, pattern and geography exhibited by paratypes, may key elsewhere in the *squamosum* group. No means has been discovered to identify these without song.

- 10' Female subgenital plate quadrate, projections absent (Fig. 21) or when present spatulate and arising from near midpoint of lateral angles (Fig. 25); male lacking dark wing margins . . . . . 13
- 11(10) Female subgenital plate without median spike between subapical teeth (Figs. 22, 23); song with a chirp rate between 3.3 and 4.3 ch/sec.; 2 generations per year . . . . . *bidens*
- 11' Female subgenital plate with median spike between subapical teeth (Fig. 24); song with chirp rate under 3.1 ch/sec. or over 4.4 ch/sec.; single generation per year . . . . . 12
- 12(11') Chirp rate over 4.4 ch/sec.; hardwood woodland habitats . . . . . *velox*
- 12' Chirp rate under 3.1 ch/sec.; pine flatwood habitats . . . . . *tardum*
- 13(10') Scale coloration uniformly pale, lacking dark markings; clypeus ivory with reddish or brownish mottling; over 145 teeth on stridulatory file; song with pulse rate under 45 p/sec . . . . . *exsanguis*
- 13' Scale coloration brown to tan with numerous dark scales and patches of scales, dark lines above white lateral bands on head and pronotum; clypeus uniform brown or with darker markings; under 140 teeth on stridulatory file; song with pulse rate over 45 p/sec . . . . . 14
- 14(13') Scale coloration pale greyish-tan with darker patterning; song usually short, irregular bursts of four chirps, chirp rate over 7 ch/sec.; coastal habitats, Gulf of Mexico . . . . . *quatrainum*
- 14' Scale coloration brown to tan with darker patterning; song usually long trains of regular chirps or paired chirps at chirp rates under 7 ch/sec.; interior habitats west of Mississippi River . . . . . 15
- 15(14') Female subgenital plate quadrate, unarmed (Fig. 21); song a long series of evenly spaced chirps at ca. 2.8 ch/sec . . . . . *squamosum*
- 15' Female subgenital plate with long finger-like projections at lateral angles (Fig. 25); song a long series of pairs of chirps at ca. 6 ch/sec. and 1.6 pairs/sec . . . . . *comprehendens*

#### Trilling Scaly Crickets, the *trigonipalpus* Group

The trilling scaly crickets have a number of characteristics separating them from the other *Cycloptilum*. They are relatively longer and narrower than other species, the pronotum being 2.5 or more times as long as the head width; the terminal segment of the maxillary palpi is broadly triangular, the ends strongly oblique (Fig. 11); the male titillators are narrowly isosceles triangular, attached at the side of the base; the male genitalia are broad and fleshy with a small, dorsal oval of weakly sclerotized cuticle; and the song is a trill of evenly spaced pulses (Figs. 35-37). Three species occur in the eastern United States, and several more farther south in this hemisphere.



**Cycloptilum trigonipalpus** (Rehn and Hebard)  
Forest Scaly Cricket (Figs. 11, 18, 26, 35, 55)

*Cycloptilum trigonipalpus* Rehn and Hebard, 1912:204, Figs. 11, 12, 15, 16.

Type locality: Isle of Hope, Chatham Co., Georgia. Holotype: ♂, 3 Sept 1911, ANSP.

*Cycloptilum trigonipalpus* (Rehn and Hebard). Blatchley, 1920:668.

*Ectatoderus trigonipalpus* (Rehn and Hebard). Chopard, 1968:234.

A few standard comments and new information are given below. For a more complete description, see Rehn and Hebard, 1912, and Hebard, 1931.

*Measurements* (mm). — Holotype ♂, selected ♀ (Alachua Co., Fla., 6 Sept 1961, JDS): body length, ♂ 8.6<sup>5</sup>, ♀ 7.5; greatest head width, ♂ 1.52, ♀ 1.60; length of pronotum, ♂ 3.84<sup>5</sup>, ♀ 2.08; length of hind femur, ♂ 4.50<sup>5</sup>, ♀ 4.98; length of hind tibia, ♂ 3.20, ♀ 3.44; length of ovipositor, 5.06.

Range in length of pronotum, 15 ♂, 15 ♀, from Florida, Georgia and Tennessee, ♂ 3.4-4.05, ♀ 1.62-2.10.

*Coloration*. — ♂, Scales: dorsal covering grey-brown, slightly lighter on ventral surfaces, with patches of a few dark scales near sides of abdomen; side of head behind and below eyes and lateral fields of pronotum silvery-white, bordered above by dark scales. Cuticle: abdomen dark brown to black; other body parts orange-brown to yellow-brown, head and clypeus often slightly darker; legs yellow-brown, darker on dorsum and apex of hind femur. Wings: dorsal fields transparent, hind margin often distinctly reddish, hidden completely or very nearly so by pronotum; lateral fields pale, reddish, or dark brown. ♀ similar, slightly darker.

*Geographical distribution*. — *C. trigonipalpus* is found throughout the south and central portions of the eastern deciduous forest, and subtropical forests of southern Florida (Fig. 55). Peripheral records include the following: TEXAS, Victoria Co. (UMMZ), Jasper Co. (FSCA); LOUISIANA, Natchitoches Par. (UMMZ), Richland Par. (ANSP); TENNESSEE, Lake Co. (FSCA); ILLINOIS, Alexander Co. (UMMZ); OHIO, Hocking Co. (FSCA); VIRGINIA, Arlington Co. (U.S. Nat. Mus.); MARYLAND, Worcester Co. (FSCA); FLORIDA, Monroe Co., West Summerland Key (FSCA).

**Cycloptilum spectabile** Strohecker  
Spectacular Scaly Cricket (Figs. 26, 36, 53)

*Cycloptilum spectabile* Strohecker, 1939:174. Type locality: Miami, Florida. Holotype: ♀, 3 July 1937, ANSP.

This is the largest species of *Cycloptilum* described from the United States, and is easily the most colorful and has the loudest and most melodious song.

*Measurements* (mm). — Selected ♂ (Dade Co., Fla., 3 July 1965, UFT 449-11) and holotype ♀: body length, ♂ 12.1, ♀ 12.9; greatest head width, ♂ 2.06, ♀ 1.90; length of pronotum, ♂ 5.06, ♀ 2.52; length of hind femur, ♂ 6.47, ♀ 6.00;

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<sup>5</sup>These measurements, made directly from the holotype, are at variance with those published in the original description.

length of hind tibia, ♂ 4.44, ♀ 4.05; length of ovipositor, 4.80.

Range in length of pronotum, 12 ♂, 8 ♀, from Dade Co., Florida, ♂ 4.52 — 4.95, ♀ 2.45 — 2.85.

*Coloration.* — ♂, Scales: body of abdominal nota greyish-brown with waxy-white caudal fringes; entire venter waxy-white; remainder of body pale cinnamon. Cuticle: abdomen piceous; remainder of body pale yellow-tan, tinged with red on ventral sides of legs and lateral fields of pronotum. Wings: dorsal fields transparent tinged with red on caudal border, covered by pronotum; lateral fields tinged with red, veins accented. ♀, similar to that of male.

*Geographical distribution.* — *C. spectabile* is restricted to coastal mangroves in southern FLORIDA (Fig. 53). Peripheral records are Manatee Co. (FSCA), Miami, Dade Co., (FSCA, ANSP), and Key West, Monroe Co. (FSCA).

### ***Cycloptilum albocircum*, n. sp.**

#### **Banded Scaly Cricket (Figs. 26, 37, 54)**

This species is intermediate between *C. trigonipalpus* and *C. spectabile* in size and coloration, and commonly occurs in habitats spacially between those of the latter two. The song, however, has the slowest pulse rate, less than half that of *C. spectabile*, 1/5 that of *C. trigonipalpus*. Another species, *C. contectum* (Rehn and Hebard, 1912) from Haiti, appears very similar, but has a keel on the subgenital plate (lacking in *C. albocircum*), is larger, and has a shorter ovipositor.

*Holotype.* — ♂, subtropical hammock, Matheson Hammock County Park, Dade Co., Florida, 20 June 1964, TJW and REL collectors, UFT 446-4. ANSP. Scales: abdomen greyish-brown, the posterior margin of each notum bearing a fringe of waxy-white scales giving a ringed appearance; remainder of body and legs pale cinnamon-tan. Cuticle: abdomen piceous, cerci pale ivory; remainder of body and legs pale yellow-tan, lacking any reddish tinge. Wings: dorsal fields clear, caudal border tinged with red, nearly entirely covered by pronotum; lateral fields tinged with red.

*Allotype.* — ♀, hardwood tree near red mangroves (*Rhizophora mangle* L.), Matheson Hammock County Park, Dade Co., Florida, 3 July 1965, REL collector. Coloration similar to that of male.

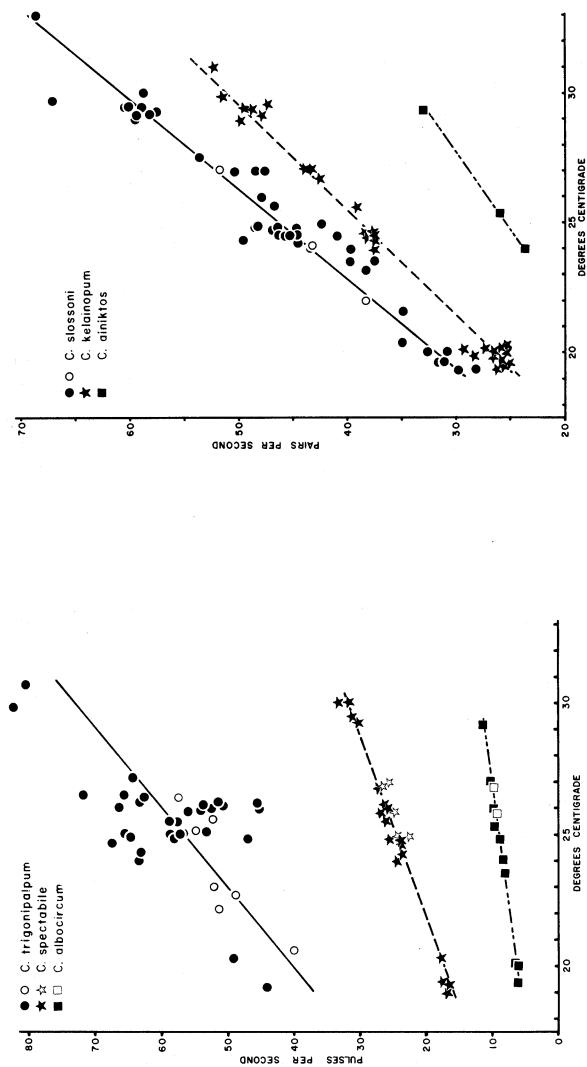
*Measurements* (mm). — Holotype ♂, allotype ♀: body length, ♂ 8.1, ♀ 8.4; greatest width of head, ♂ 1.57, ♀ 1.62; length of pronotum, ♂ 4.22, ♀ 2.00; length of hind femur, ♂ 4.40, ♀ 4.98; length of hind tibia, ♂ 3.00, ♀ 3.15; ovipositor, 3.97.

*Paratypes.* — 7 ♂ (4 taped), 1 ♀. All records FLORIDA. Dade Co., 2 ♂, 27 Nov 1961 (UFT 446-1,2), 1 ♂, 1 ♀, 20 June 1964 (UFT 446-5); Monroe Co., Key Largo, 2 ♂, 22 June 1964 (incl. UFT 446-8); Manatee Co., 1 ♂, 16 May 1965 (All FSCA), 1 ♂, 4 Jan 1925 (UMMZ).

Range in length of pronotum, 7 ♂ paratypes, 4.00-4.50.

Coloration in the paratypes agrees well with the holotype.

*Geographical distribution.* — Like *C. spectabile*, *C. albocircum* is restricted to coastal areas, but it occurs slightly more inland and is not restricted to mangroves. The holotype, allotype, and paratypes include all records except UFT 446-9, Saddle Bunch Keys, Monroe Co., 24 June 1964 (Fig. 54).



FIGURES 26-27. — 26. Pulse rate as influenced by temperature in trilling *Cycloptilum: trigonipalpus* (36 individuals from 13 counties in 6 states), *spectabile* (9 indiv., 2 counties), *albocircum* (16 indiv. from 3 counties). Solid symbols — laboratory tapes; open symbols — field tapes. 27. Pulse-pair rate as influenced by temperature in complex-chirping *Cycloptilum: slossoni* (52 individuals from 17 counties in 6 states), *kelainopus* (17 indiv. from 5 counties in 2 states), *ainiktos* (2 indiv., 2 counties). Solid symbols — laboratory tapes; open symbols — field tapes.

### Discussion and Comparison of the Trilling Scaly Crickets

In most characteristics, the three U.S. species of the *trigonipalpus* group form the series *trigonipalpus*, *albocircum*, *spectabile*. This is true for increasing size and robustness, coloration change from brown to cinnamon, increasing number of teeth on stridulatory file, and general spacial relations of the habitat from higher inland forest to tidal mangrove swamps.

The songs, however, do not fit this sequence (Fig. 26). *C. albocircum* has the slowest pulse rate of any *Cycloptilum* we have recorded, with trills frequently lasting 2 seconds; the song is a melodious "tinkle" in which the pulses are distinct, easily recognized in the field. *C. spectabile*, with an intermediate pulse rate, usually trills for ca. 1.5 seconds. This is also very melodious, but the pulses are not individually distinguishable, sounding like a slow, beady trill. *C. trigonipalpus*, with the fastest pulse rate, has a short, buzzy trill lasting 0.25 to 1 second. All three species sing irregular groups of 3-5 trills produced in decreasing frequency from dusk to dawn, a song pattern common to other groups of crickets (e.g. *Orocharis*, Walker, 1969) as well as several other *Cycloptilum*.

With practice, each of these species may be recognized in the field by its song. Perhaps the most confusing are *C. albocircum* and two species of *Orocharis* occurring in similar habitats, but the latter normally sing much longer sequences. *C. trigonipalpus* may be confused with *Cycloptilum slossoni* (see below), but the latter song is shorter and even more buzzy due to the internal pairing of pulses (Figs. 35, 39).

All three species are arboreal, though they may land on the ground when disturbed. *C. trigonipalpus* is predisposed to broad leaved, predominantly deciduous forests where the frequent branches, vines and dead leaves are preferred. However, they may occasionally be found in other habitats where deciduous plants occur, e.g. in a pine forest in Louisiana, individuals were singing exclusively from wild grape vines in the understory near a road clearing (REL), and in a partially cleared pine flatwoods in Charlotte Co., Florida, a large population was restricted to a dead hardwood sapling where they took refuge in the curled leaves (REL). Both *C. albocircum* and *C. spectabile* are confined to coastal habitats within the range of subtropical influences, the

former occurring farther inland in subtropical hammocks, the latter farther seaward in mangrove swamps. As with *C. trigonipalpus*, they are commonly found on branches and leaves, though *C. spectabile* in sparse mangroves may descend the trunks (most often turning back) and cross to other trees.

*Cycloptilum barbicorne* Strohecker (Bahamas) and *C. contectum* (Rehn and Hebard) (Haiti) probably belong to this group.

#### Chirping Scaly Crickets

The remainder of the species of *Cycloptilum* covered in this paper do not produce uniform series of pulses, but group them in pairs produced at species-characteristic pair rates. Such species may be divided into the *slossoni* and *squamosum* groups on the basis of the pattern of pulse-pair production and constellations of correlated morphological characters. One additional pair-producing species is described separately as its morphology and song do not fit either of these groups.

The word "chirp" indicates a short, crisp sound irrespective of internal patterns. Hence, in a very slow series of pulse-pairs, each pair constitutes a chirp and a song of pairs of these becomes a sequence of chirp-pairs, while a rapid, short series of pairs sounding as a unit is a single "complex chirp." This usage facilitates verbal description of the song and discussion of the distinguishing characteristics in the field. However, in each case the pulse-pairs appear to be basic homologous units of song structure, rarely incomplete in any one song (except for two species that start each song with an unpaired pulse, Figs. 39, 40). The pair series, whether complex chirp, chirp sequence or chirp-pair sequence is the song. Evidence for the biological importance of the pair series lies in the uniform rate of pair and chirp-pair production within a species and the dissimilarity of these rates between species, while complex chirps and chirp series (and trills of the preceding group) are often irregular in length and frequency of repetition, and as with pulse rates, commonly overlapping in these parameters between sympatric species.

Complex-chirping Scaly Crickets,  
the *slossoni* Group

The members of this group are distinguished from the *trigonipalpus* group by weakly-flared maxillary palpi, the scape narrower than 80 percent the length of the exposed epistomal suture, and the pronotum shorter than 2.5 times the head width in males; and from other *Cycloptilum* by the subgenital plate having a deep, acute cleft and the ovipositor notched ventrally near the tip in females, and male titillators tubular, pointed and slightly recurved. All others except *C. irregularis* have wings exposed for 1/4 or more of their length, and lack the complex-chirp form of song (see below).

***Cycloptilum slossoni* (Scudder)**

Slosson's Scaly Cricket (Figs. 4, 12, 19, 27, 28, 38, 39, 59)

*Mogosiplotus slossoni* Scudder, 1897:55. Type locality: Biscayne Bay, Dade Co., Florida. Holotype: ♀, collected by Annie Slosson, ANSP.

This species has been the most difficult to deal with in terms of nomenclature, principally due to incomplete knowledge of the biogeography and songs of the named populations involved and evidence of a number of undescribed and highly cryptic species in this group. *Ectatoderus antillarum* Redtenbacher 1892:218 was described from St. Vincent Island, West Indies, and until the present has been considered senior synonym for most of the other names applied to this group, including *Liphoplus krugii* Saussure (1897) (Cuba), *Mogoplistes slossoni* Scudder (Miami, Florida), and *Mogisoplistus barbouri* Morse (1905) (Nassau, Bahama Ids.). TJW has collected and taped in several of the islands in the Antilles Group. He did not find the U.S. species on Grand Cayman, Jamaica, Hispaniola, Puerto Rico, St. Croix or Trinidad, and only on the last of these did he find any other species (3) in the same group, one of which may be *antillarum*. This indicates that *E. antillarum* is almost certainly not present in the northern Antilles and that the U.S. species is not *antillarum*. Other species occur in Mexico but have not been taped. The relationship of *L. krugii* Saussure is unknown beyond that it is a member of the same group and at least very close to the U.S. species; *M. barbouri* Morse, also

untaped, is morphologically indistinguishable from U.S. specimens. Because of the lack of data, we have used the name *Mogosiplistus slossoni* Scudder 1897 as the only certainly applicable name for the U.S. species in the literature, described from a specimen collected in Miami, Florida. *M. barbouri* Morse is provisionally placed in synonymy until further field work clarifies the situation. *L. krugii* Saussure is not listed as a synonym, but it may prove to be one. If it does, it is senior to *M. slossoni* by one month. The present treatment gives the advantage of relative certainty of identity with a type specimen while not adding significant confusion to the literature should *L. krugii* prove conspecific.

*Measurements.* — Selected ♂ (Dade Co., Florida, 20 June 1964, UFT 441-14), holotype ♀: body length, ♂ 8.3, ♀ 7.9; greatest head width, ♂ 1.80, ♀ 1.81; length of pronotum, ♂ 4.00, ♀ 2.15; length of hind femur, ♂ 5.10, ♀ 5.22; length of hind tibia, ♂ 3.80, ♀ 3.85; length of ovipositor, 4.72.

Range in length of pronotum, 15 ♂, 15 ♀, from Florida and North Carolina, ♂ 4.0-4.4, ♀ 2.1-2.5.

*Coloration.* — ♂, Scales: dorsal covering of body, head and distal parts of legs grey-brown, distinctly darker than venter; entire venter, bases of legs and sides of head behind and below eyes waxy-white, the latter bordered above with a dark brown line; dark blotches on hind tibia and inside margin of hind femur. Cuticle: abdomen dark brown to black; pronotum yellow-brown with a reddish cast; legs pale translucent ivory with tibia and dorsum of apex of femora light brown; clypeus yellow-brown to dark brown, never piceous. Wings; dorsal fields transparent, hind margins light brown to dark brown, hidden completely or nearly so by pronotum; lateral fields light brown to dark brown. ♀ similar.

*Geographical distribution.* — *C. slossoni* is found throughout the southeastern coastal plain from North Carolina to Texas (Fig. 59). Peripheral records include the following: TEXAS, Grimes and Calhoun Cos. (FSCA); LOUISIANA, Natchitoches Par. (UMMZ); MISSISSIPPI, Hancock Co. (FSCA); FLORIDA, Escambia, Leon and Nassau Cos. to Dry Tortugas, Monroe Co. (FSCA); GEORGIA, Chatham Co. (FSCA, ANSP); SOUTH CAROLINA, Horry Co. (UMMZ); NORTH CAROLINA, New Hanover Co. (ANSP).

### ***Cycloptilum kelainopum*, n. sp.**

Black-faced Scaly Cricket (Figs. 27, 28, 40, 58)

This species is very similar to *C. slossoni*, and has a contiguous distribution along the southern coastal margins of the U.S. where it is restricted to mangroves in Florida and to "windblown, cedar-like trees just back of the Gulf of Mexico beach," in Texas. The song is very similar but slightly shorter and slower, while its coloration is distinctive.

*Holotype*. — ♂, dense black mangrove (*Laguncularia racemosa* (L.)), Cedar Key, Levy Co., Florida, 14 Sept 1961, TJW and JDS collectors; UFT 456-3. ANSP. Scales: entire covering waxy-white, undifferentiated on sides or venter. Cuticle: abdomen piceous; head and thorax orange-brown, turning yellowish on sides; clypeus, labrum, and genae piceous, strikingly distinct; femora yellow-ivory at bases, turning reddish-brown at apices; tibia tan with a slight violet cast; tarsi pale tan. Wings: dorsal fields clear with black hind border, completely concealed by pronotum; lateral fields very dark brown shading to black.

*Allotype*. — ♀, same data as holotype. Coloration similar, but genae and labrum brown.

*Measurements*. — Holotype ♂, allotype ♀: body length, ♂ 9.8, ♀ 10.7; greatest head width, ♂ 1.92, ♀ 2.10; length of pronotum, ♂ 4.40, ♀ 2.50; length of hind femur, ♂ 5.50, ♀ 6.00; length of hind tibia, ♂ 4.10, ♀ 4.50; length of ovipositor, 5.10.

*Paratypes*. — 20 ♂ (10 taped), 20 ♀. FLORIDA: Levy Co., 8 ♂, 10 ♀, 14 Sept 1961 (incl. UFT 456-4,5), 3 ♂, 28 July 1964 (incl. UFT 456-6), 3 ♂, 2 ♀, 10 July 1965 (incl. UFT 456-16), Charlotte Co., 1 ♂, 2 ♀, 27 Aug 1964 (UFT 456-13), 2 ♀, 15 May 1965. Monroe Co., 3 ♂, 3 ♀, 22 June 1964 (UFT 456-7, 10,11), 1 ♀, 4 July 1965, 1 ♂, 22 Aug 1958 (UFT 456-1). TEXAS: Jefferson Co., 1 ♂, 19 Aug 1965 (UFT 456-17) (all FSCA).

Range in length of pronotum, 14 ♂, 12 ♀ paratypes, ♂ 3.9-4.4, ♀ 2.1-2.5, from Levy Co., Fla.

Coloration of the paratypes agrees closely with the holotype except some lack black on the labrum and genae.

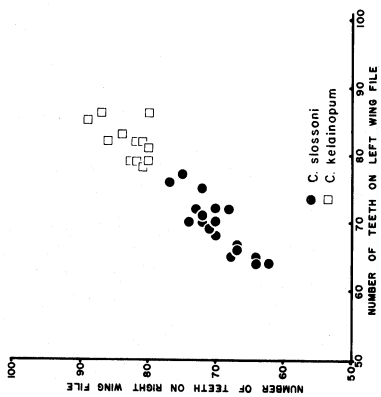
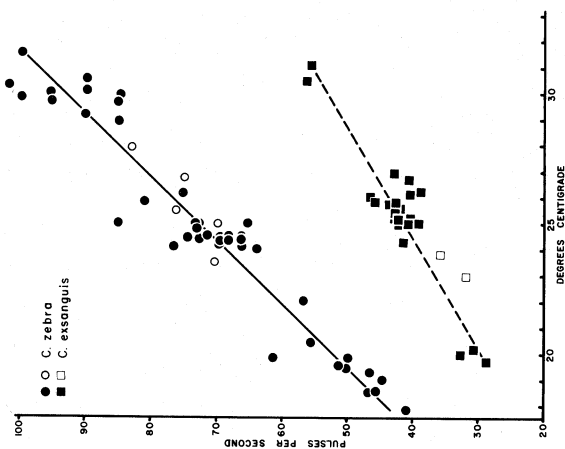
*Geographical distribution*. — The presently known distribution includes two widely disjunct restricted populations in Texas and South Florida (Fig. 58). We feel sure there is no connection in the U.S., but expect collections in Mexico or the Caribbean to yield further records, perhaps supporting a double northward invasion.

### ***Cycloptilum ainiktos*, n. sp.**

Obscure Scaly Cricket (Figs. 27, 41, 57)

The name of this cricket stems from the Greek word meaning obscure or baffling, well suited for this species of which only two specimens are known. One of these was collected as a nymph on a bare sea-wall at Key West, Florida, and reared to adult. It was recognized as different from the other known species immediately, and this was borne out when the cricket sang its unique song (Fig. 41). The other specimen, also male, and also collected as a nymph, went unrecognized until it matured and sang in the laboratory. The second was selected as holotype as the first was partly destroyed by ants shortly after it was taped. Females remain unknown.





FIGURES 28-29. — 28. Number of stridulatory file teeth in *Cycloptilium slossoni* (9 counties in 3 states) and *C. kelainopum* (5 counties, 2 states). 29. Pulse rate as influenced by temperature in *Cycloptilium zebra* (31 individuals from 6 counties in 2 states) and *C. exsanguis* (19 indiv., 5 counties, 3 states). Solid symbols — lab tapes; open symbols — field tapes.

*Holotype*. — ♂, mangrove swamp near Punta Gorda Isles, Charlotte Co., Florida, 15 May 1965 (reared from late instar nymph) REL collector; UFT 438-2. ANSP. Scales: dark brown, slightly lighter on sides of head and prothorax, caudal fringes of abdominal nota and venter. On the abdomen, the fringe scales are similar in size to those of others in the *slossoni* group, but the body scales are much smaller and more oval, giving a pebbled texture to the segments. Cuticle: abdomen dark brown; head and thorax orange-brown; antennae tan with black annulae ca. every fourth segment, more widely separated near the base; legs distinctly purple except tarsi pale tan. Wings: dorsal fields clear with a black caudal margin, entirely covered by pronotum; lateral fields black.

*Measurements*. — Holotype: body length 8.3; greatest head width, 1.60; length of pronotum, 3.60; length of hind femur, 4.20; length of hind tibia, 2.75.

*Paratype*. — 1 ♂ (pronotum, tegmina, and hind legs only) Key West, Monroe Co., FLORIDA, 24 June 1964 (reared from late instar nymph) (UFT 438-1, FSCA). Map Fig. 57.

### Discussion and Comparison of the Complex-chirping Scaly Crickets

The first two species discussed in this group are very similar in nearly all ways, but do show consistent differences that make identification possible. Some *slossoni* have a very dark clypeus, especially if oily, but the contrast with the rest of the head is never so striking as in *C. kelainopum*. The number of teeth on the stridulatory file is greater in *C. kelainopum* (Fig. 28). The habitats of these two are also different and while they may be adjacent, do not overlap. *C. slossoni* occurs in shrubs and low in trees in woodland and scrub situations over most of the coastal plain. Ornamentals commonly support populations in urban situations. *C. kelainopum*, on the other hand, has not been collected in other than coastal mangroves, either *Rhizophora mangle* L. or *Avicenna nitida* Jacq. in southern Florida, or the single western collection from beachside trees. While the latter sample is too small to generalize from, it does agree with a coastal affinity.

There is a greater difference between *C. ainiktos* and the other species: it is darker and relatively narrower with other differences mentioned in the above description, but it seems safe at this time to assume habitat relations similar to *C. kelainopum* in Florida.

The songs of the first two species are difficult to distinguish in the field except by habitat, but good separating characters are evident upon analysis (Figs. 27, 39, 40), *C. kelainopum* singing slower

and shorter chirps (ca. 38.5 pr/sec at 25 C and 5-15 pulses per chirp vs. ca. 46 pr/sec and 15-25 pulses for *C. slossoni*). For both species, the complex chirps show internal pairing of pulses but uniformly have an odd number, the first pulse unpaired (if it is assumed the closer pulses are homologous with the chirps of other *Cycloptilum*. This is supported by comparison with *C. ainiktos*, which sings complete pairs at a much slower pair-rate, but a pulse rate only slightly slower than *C. kelainopum*).

The songs of *Cycloptilum trigonipalpum*, *C. kelainopum* and *C. antillarum* sound very similar in the field but, as with the latter pair, the former pair may be separated by habitat differences. With practice *C. trigonipalpum* may be distinguished from *C. slossoni* by its slightly longer and less buzzy trill.

The complex chirp of *C. ainiktos* (Figs. 27,41) sounds more musical and beady than the above, and though we have never recorded it in the field, should be easily recognized. The most similar songs are made by the trigonidiine *Cyrtoxipha confusa* Walker, but these are long trills of paired pulses.

Other species belonging to this group are *C. hesperum* (Rehn and Hebard) and *C. tubulatum* (Rehn and Hebard) (Mexico), *C. medium* (Rehn and Hebard) (Panama) and several South American species.

#### Terrestrial Scaly Crickets, the *squamosum* Group

Like the preceding groups, the members of the *squamosum* group share a number of morphological and song characteristics which differentiate them from other *Cycloptilum*. Unlike the preceding, members of this group have wings exposed for more than 25% of their length; they are relatively small and robust; and they sing trains of paired pulses (chirps, and in one, paired chirps also) at chirp rates slow enough to be readily distinguished by ear. Male titillators are dilated toward the tip, drying spoon-shaped, and female subgenital plates lack a median acute cleft but may be otherwise variable. Some species in this group may frequent dense herbaceous ground cover or even dense lower portions of shrubs and trees which reach the ground but the tendency is to be terrestrial, not arboreal as in the first two groups discussed.

Within this group are several species not apparently forming sub-

groups and two species complexes, one with remarkably similar morphology and song characteristics, the other with a unique syn-copated song but with only one species occurring in the east.

***Cycloptilum zebra* (Rehn and Hebard)**

**Zebra Scaly Cricket (Figs. 20, 29, 30, 42, 62)**

*Liphoplus zebra* Rehn and Hebard, 1905:49, pl 1, fig. 12. Type locality: Miami, Dade Co., Florida. Holotype: ♂, 6 Feb 1904, ANSP.

*Cycloptilum zebra* (Rehn and Hebard) Rehn and Hebard, 1912:214.

*Cycloptilum squamosum zebra* (Rehn and Hebard) Blatchley, 1920:666.

*Ornebius zebra* (Rehn and Hebard) Chopard 1968:226.

Due to characters uniform in *C. zebra* but overlapping in one or more populations of what was then considered *C. squamosum*, Blatchley (1920) was of the opinion that *C. zebra* was inseparable at the species level, yet he retained the name in a subspecies rank. Information now available has aided in finding unambiguous differences dividing the populations among several species as set forth in the key and final discussion of the group.

*Measurements.* — Holotype ♂, selected ♀ (4 July 1965, Monroe Co., Fla., REL): body length, ♂ 5.4, ♀ 6.3; greatest head width, ♂ 1.25, ♀ 1.38; length of pronotum, ♂ 2.85, ♀ 1.54; length of hind femur, ♂ 3.15, ♀ 3.40; length of hind tibia, ♂ 2.33, ♀ 2.36; length of ovipositor, 2.64.

Range in length of pronotum, 10 ♂, 10 ♀, all Florida, ♂ 2.40-2.90, ♀ 1.50-1.90.

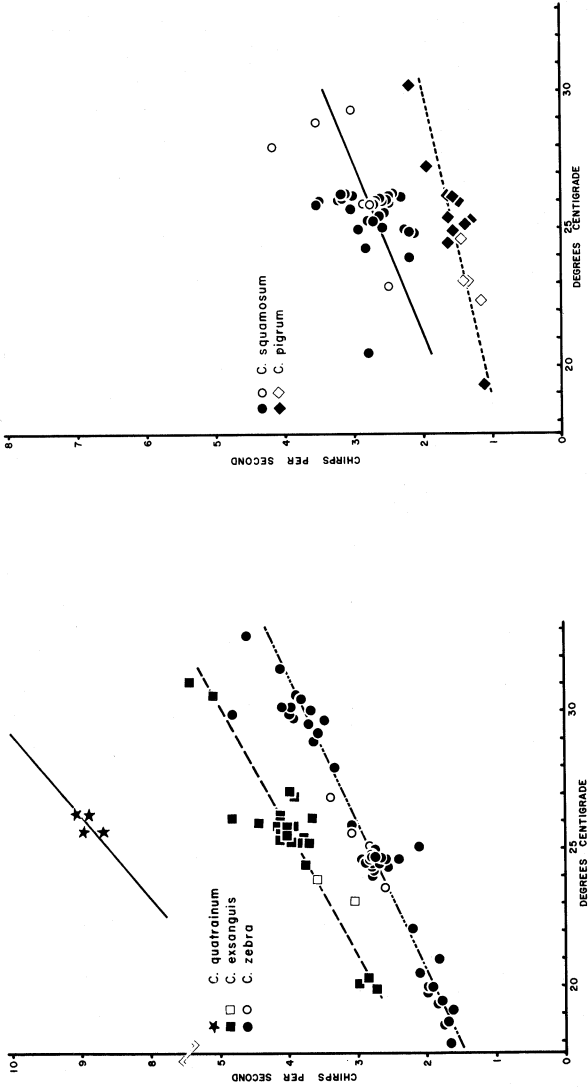
*Coloration.* — ♂ Scales: dorsum greyish-tan, pronotum with two indistinct median longitudinal dark lines becoming stronger toward caudal border, abdomen flecked with brown; venter lighter tan; sides of head behind eyes and lateral fields of pronotum silvery-white, sharply bordered above with dark brown; legs banded and spotted irregularly with dark brown and grey-white, less on hind femur. Cuticle: abdomen dark brown, lighter at midline; pronotum pale yellow-brown, darker toward head; head olive-brown to light tan, dark bars from labrum to eyes and center of labrum and clypeus; legs pale translucent cream. Wings: dorsal field transparent, caudal border with three black spots, extending for ca. half their length beyond pronotum; lateral fields pale to smoky. ♀ similar, tending slightly darker.

*Geographical distribution.* — This species extends along the coast from Sea Island, Glynn Co., GEORGIA, and Cedar Key, Levy Co., FLORIDA, south through the Florida Keys to Stock Island, Monroe Co., and Bush Key, Dry Tortugas (all FSCA). Searches made just north of Cedar Key yielded *C. exsanguis*, a new species with a contiguous range, but no *C. zebra*. Figure 62 gives the known distribution.

***Cycloptilum exsanguis*, n. sp.**

**Pale Scaly Cricket (Figs. 29, 30, 43, 60)**

This is the species responsible for records of *C. squamosum* at Cedar Key, Levy Co., Florida (Hebard, 1931:145). However, the information available now easily



FIGURES 30-31. — 30. Chirp rate as influenced by temperature in *Cycloptilium quatrainum* (4 individuals), *C. exsanguis* (19 indiv., from 5 counties in 3 states), and *C. zebra* (31 indiv., 6 counties, 2 states). Solid symbols — lab tapes; open symbols — field tapes. 31. Chirp rate as influenced by temperature in *Cycloptilium squamosum* (33 individuals from 10 counties in 2 states) and *C. pigrum* (13 indiv., 5 counties, 4 states). Solid symbols — lab tapes; open symbols — field tapes.

separates it from the type of *C. squamosum* and specimens presently identified with it. *C. exsanguis* is the palest *Cycloptilum* in coloration, and the largest member of the *squamosum* group.

*Holotype*. — ♂, *Juncus* salt marsh, Shell Mound, Levy Co., Florida, 10 July 1965, REL collector; UFT 447-8. ANSP. Scales: entire covering almost uniform, very pale yellow-tan, slightly more whitish on sides of head, prothorax, and on the venter of the abdomen. The scales on the head and thorax are smaller and more rounded than those on the remainder of the body. Cuticle: abdomen black dorsally, yellow-brown ventrally; remainder of the integument pale yellow-tan. Wings: uniform cloudy yellowish tan, extending for ca. 1/4 their length beyond the pronotum.

*Allotype*. — ♀, same collection data. Coloration nearly identical but slightly darker tan.

*Measurements*. — Holotype ♂, allotype ♀: body length, ♂ 8.5, ♀ 9.5; greatest head width, ♂ 1.55, ♀ 1.78; length of pronotum, ♂ 3.60, ♀ 2.40; length of hind femur, ♂ 4.40, ♀ 4.60; length of hind tibia, ♂ 2.92, ♀ 3.20; length of ovipositor, 4.20.

*Paratypes*. — 21 ♂ (14 taped), 11 ♀. FLORIDA: Levy Co., 1 ♂, 14 Sept 1961 (UFT 447-1), 1 ♂, 28 July 1964 (UFT 447-2), 12 ♂, 3 ♀, 10 July 1965 (incl. UFT 447-5, 7, 9-14), 3 ♀, 18 Oct 1924 (UMMZ); Santa Rosa Co., 1 ♂, 17 July 1965 (UFT 447-19); MISSISSIPPI: Hancock Co., 6 ♂, 5 ♀, 17 Aug 1965 (incl. UFT 447-16-18). All records FSCA unless otherwise indicated.

Range in length of pronotum, 8 ♂, 6 ♀ paratypes, ♂ 3.35-3.60, ♀ 1.70-2.70, from Florida and Mississippi.

Coloration of the paratypes agrees closely with the holotype.

*Geographical distribution*. — The distribution of *C. exsanguis* is given in Fig. 60, the localities include Lewis Airport, Cedar Key, Levy Co., Florida, a few miles south of the type locality, and near Waveland, Hancock Co., Mississippi. Excluded from Fig. 60 are two song records from Savannah Beach, Chatham Co., Georgia (UFT 447-3,4). No specimens were collected, and no other evidence suggests the occurrence of *C. exsanguis* on the Atlantic coast.

### ***Cycloptilum quatrainum*, n. sp.**

#### **Four-pair Scaly Cricket (Figs. 30, 44, 63)**

There is great variation in the regularity of chirp-trains and number of chirps per train, both between and within species of the *squamosum* group. *C. quatrainum*, however, has both the shortest and most uniform song, nearly always singing sequences of just four pairs of pulses.

*Holotype*. — ♂, *Spartina* flats above tide, near Waveland, Hancock Co., Mississippi, 17 Aug 1965, REL collector; UFT 450-9. ANSP. Scales: mostly greyish tan, sides of head and pronotum white; hind femora tan, suffused with dark brown; fore and middle legs mottled tan and dark brown. Cuticle: dorsum of abdomen dark brown, lighter to sides; remainder of head and body yellow-tan; legs pale yellowish, slightly darker at the apex of the hind femora, the outer face of which is longitudinally striated due to slight ridges in the integument appearing

darker than the background. Wings: dorsal fields transparent, caudal margins lightly marked in light brown with veins accented and a dark spot at the juncture of the lateral field, extending ca. 1/3 their length beyond the pronotum; lateral fields slightly darker with accented veins.

*Allotype*. — ♀, same collection data. Coloration similar to holotype but slightly darker, the hind femora with a distinct patch of dark scales on the dorsal margin.

*Measurements*. — Holotype ♂, allotype ♀: body length, ♂ 7.5, ♀ 7.7; greatest head width, ♂ 1.42, ♀ 1.52; length of pronotum, ♂ 3.48, ♀ 1.95; length of hind femur, ♂ 3.80, ♀ 4.20; length of hind tibia, ♂ 3.12, ♀ 3.20; length of ovipositor, 3.66.

*Paratypes*. — 13 ♂ (7 taped), 4 ♀. MISSISSIPPI: Hancock Co., 9 ♂, 4 ♀, 17 Aug 1965 (incl. UFT 450-7, 8, 10) (all FSCA).

Range in length of pronotum, 8 ♂, 4 ♀ paratypes, ♂ 2.95-3.48, ♀ 1.80-2.00.

Coloration in the paratypes agrees closely with the holotype.

We have one record of this species other than the type locality (Fig. 63). R.D. Alexander (personal communication) taped and collected a male, 4 June 1958, La Fourche Parish, Louisiana, in a marshy area that may have been brackish. The song agreed with our measurements except that some groups had only three chirps. TJJW taped and collected specimens resembling *C. quatrimum* in Hildalgo Co., Texas, 18 Aug 1964. The chief differences were in habitat (xeric woodland in Rio Grande Valley) and number of chirps per group (highly variable, often more than 10).

### **Cycloptilum squamosum** Scudder Scudder's Scaly Cricket (Figs. 21, 31, 45, 61)

*Cycloptilum squamosum* Scudder, 1868:142. Type locality: Texas. Holotype: ♂, ANSP.

*Cycloptilus squamosus* Scudder. Saussure, 1877:477. Unjustified emmendation.

*Cycloptilus borealis* Bruner, 1891:37. Type locality: near Niobrara River at Valentine, Nebraska. Holotype: ♀, ANSP. Synonymy by Rehn and Hebard, 1912:209.

*Ornebius squamosus* (Scudder). Chopard, 1968:226.

This was the first mogoplistine described in the Western Hemisphere, and is the type of the genus. It is unfortunate that the locality data is so inexact, as topotypic song and habitat records are therefore unobtainable. However, the geographic range of only one potentially conspecific taxon discussed here could include the Texas record.

*Measurements*. — Holotype ♂, selected ♀ (Holotype of *C. borealis* Bruner): body length, ♂ 7.2, ♀ 7.0; greatest head width, ♂ 1.21, ♀ 1.50; length of pronotum, ♂ 3.30, ♀ 1.80; length of hind femur, ♂ 3.50, ♀ 3.95; length of hind tibia, ♂ 2.90, ♀ 3.20; length of ovipositor, 3.30.

Range in length of pronotum, 2 ♂, from Kerr and Tyler Cos., 1 ♀ from Jefferson Co., Texas, ♂ 3.42, 3.46; ♀ 2.03.

*Coloration*. — ♂, scales: largely missing on the holotype, but showing pale tan on most of the body, whitish indicated on sides of head and thorax. Other males show variations to darker tan, with some darker lines indicated on the pronotum,

and dark flecks on the legs, and dark dorsal margins on the white lateral stripes on the head and thorax. Cuticle: holotype abdomen dark brown dorsally; thorax and head pale yellow-brown, lighter on sides; legs yellow-tan. Wings: pale yellow-tan, caudal border without markings, extending beyond pronotum ca. 1/3 their length; lateral fields cloudy pale tan. ♀ similar, but usually darker, often with longitudinal rows of dark spots on the dorsum of the abdomen.

*Geographical distribution.* — As presently understood, all records for the *squamosum* group west of the Mississippi River except those specifically attributable to *C. pigrum*, *C. quatrainum* or *C. comprehendens* are included in the species *C. squamosum* (Fig. 61). Peripheral records include TEXAS, Uvalde Co. (FSCA), OKLAHOMA, Cimmaron and Tulsa Cos. (ANSP), ARKANSAS, Baxter Co. (UMMZ), NEBRASKA, Cherry Co. (ANSP), and LOUISIANA, St. Landry Par. (ANSP). Hebard's (1934) records of "*squamosum*" from Massac and Shelby Counties, Illinois, are either *squamosum* or a species of the following complex.

### The *bidens* Complex

Within the *squamosum* group (indeed, among all eastern mogoplistines) the *bidens* complex, a subgroup of at least four species, has proved to be the most challenging and least understood group. Extensive collection of specimens and songs indicate the probability of many populations with slight differences in morphology, habitat, song, and life history, but these are difficult to correlate geographically. In addition to *C. bidens*, three new species are described here, *C. pigrum*, *C. tardum* and *C. velox*, based primarily on such differences in sympatric populations, especially those of Alachua Co., Florida. An attempt is made to correlate these over the combined range of the four species, but local studies are needed to clarify many ambiguous applications.

### *Cycloptilum pigrum*, n. sp.

#### Reluctant Scaly Cricket (Figs. 31, 48, 68)

This species, as presently circumscribed, contains a considerable amount of variation, particularly in coloration, and is known only from males of three widely disjunct populations. Females may have been collected but remain unrecognized, probably confused with *C. bidens* or other very similar species. Within the *bidens* complex, this species is easily distinguished only by song.

*Holotype.* — ♂, litter under trees back of beach, 11 mi. east of High Island, Jefferson Co., Texas, 19 Aug 1965, REL collector; UFT 448-17. ANSP. Scales: generally pale tan; head and thorax with white lateral band bordered above with a thin black line; legs and venter lighter except hind femora with tan dorsal margin and a small dark spot on outer face near the ventral margin. Cuticle: dorsum of abdomen dark brown; legs ivory, darker to apex of hind femur; remainder pale tan. Wings: dorsal field cream-colored, lacking dark markings, extending beyond pronotum ca. half their length; lateral fields similar.

*Measurements.* — holotype ♂, body length, 5.8; greatest head width, 1.40; length of pronotum, 3.22; length of hind femur, 3.40; length of hind tibia, 2.75.

*Paratypes.* — 7 ♂ (all taped). TEXAS, Jefferson Co., 3 ♂, 19 Aug 1965 (UFT



448-13, 18, 19); GEORGIA, Glynn Co., 1 ♂, 8 Aug 1965 (UFT 448-4), 1 ♂, 26 Aug 1965 (UFT 448-15); MARYLAND, Worchester Co., 2 ♂, 25 Aug 1965 (UFT 448-32, 34) (all FSCA).

Range in length of pronotum, 2 ♂, 3.40 (Texas), 3.30 (Georgia).

Coloration in western males agrees closely with the holotype; specimens from Georgia, however, are much darker brown in general coloration, patterned as above but with wings clear with a slight reddish tinge on the hind border.

*Geographical distribution.* — Three known localities for *C. pigrum* are given with the paratype series. Additional song records are from Nassau Co. (UFT 448-1) and Palm Beach Co. (UFT 448-36, 37), Florida, and Chatham Co., Georgia (UFT 448-5, 6) (Fig. 68). All records come from coastal habitats.

### **Cycloptilum bidens** Hebard

#### **Two-toothed Scaly Cricket (Figs. 22, 23, 32, 50, 66, 69)**

*Cycloptilum bidens* Hebard, 1931:147, figs. 7-11. Type locality: St. Simon's Island, Glynn Co., Georgia. Holotype: ♀, 30 Aug 1911, ANSP.

*Ornebius bidens* (Hebard). Chopard, 1968:227.

When Hebard described *C. bidens* he selected as holotype a female with a narrow "U" shaped notch between two short teeth at the apex of the subgenital plate. He describes (p. 147) the apical portion as "shallowly emarginate, concave on each side but convex mesad." By varying the angle of view or flattening the subgenital plate this description is justified but when viewing dried specimens from the rear and side the notch appears simply planar "U" shaped. TJW has found such females associated with males producing a particular calling song (approx. 3.8 ch/sec) in Alachua Co., Florida, but rarely with males producing two other similar songs (approx. 2.7 and 5.1 ch/sec). Females associated with the latter males have a long median spike between the apical teeth, forming a rounded "W" shaped outline of the apex. For the present, females similar to the type and males with songs approximating 3.8 ch/sec are considered *C. bidens*, but there is considerable geographical variation in songs and as yet no known morphological distinctions among males. A taped male, rather than the allotype of *C. bidens*, was measured because the song of Hebard's allotype is unknown and females of both morphs are present in the type series.

*Measurements.* — Selected taped ♂ (Alachua Co., Fla., UFT 453-22) and holotype ♀: body length, ♂ 4.5, ♀ 6.4; greatest head width, ♂ 1.21, ♀ 1.38; length of pronotum, ♂ 2.71, ♀ 1.64; length of hind femur, ♂ 3.22, ♀ 3.75; length of hind tibia, ♂ 2.49, ♀ 2.80; length of ovipositor, 3.05.

Range in length of pronotum, 6 ♂, 6 ♀, from Alachua Co., Fla., ♂ 2.5-3.1, ♀ 1.5-1.8.

*Coloration.* — holotype ♀, scales: dorsum dark brown flecked with grey, white on sides of head and pronotum bordered above with dark brown; venter lighter tan; legs brown, inner surface light. Cuticle: abdomen very dark brown, other parts light tan. Male selected above, scales: dorsal covering light grey-tan mixed with light brown, slightly darker on abdomen, two converging rows of three patches of dark scales between humeral angles and center of pronotum, four dark patches of

scales on caudal margin of pronotum, four rows of dark scales, one per tergum per row on abdomen; sides of head and prothorax pale tan-white, bordered above by thin black line; venter pale tan; apex of front and middle femora with light grey patches on darker background, bases and venter light grey-tan, hind femora mottled brown and tan, lighter at base and darker on dorsal edge, tibia annulate brown and tan, hind basitarsus with pale median band. Cuticle: pale orange-brown, abdomen darker; venter pale yellow-tan, abdomen dark brown; legs pale yellow-tan. Wings: dorsal fields transparent, hind margin with three dark spots, extending for ca. 1/3 their length beyond pronotum; lateral fields dark tan, pale above.

*Geographical distribution.* — Peripheral records of taped males are SOUTH CAROLINA, Dillon Co., GEORGIA, Cobb Co., MISSISSIPPI, Pike Co., and FLORIDA, Monroe Co. (Big Pine Key) (Fig. 66) (All taped records FSCA).

### ***Cycloptilum tardum*, n. sp.**

#### **Slow-chirp Scaly Cricket (Figs. 13, 24, 32, 49, 65, 69)**

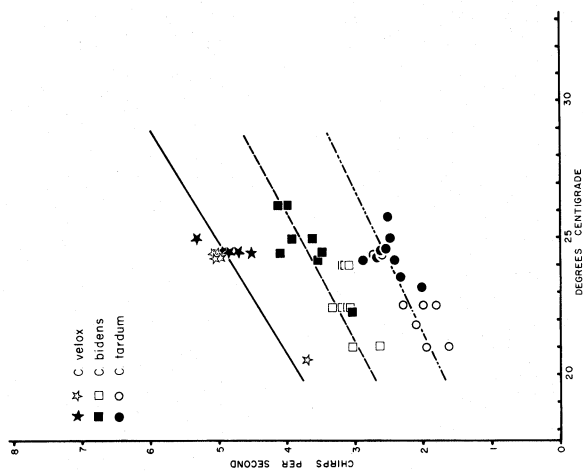
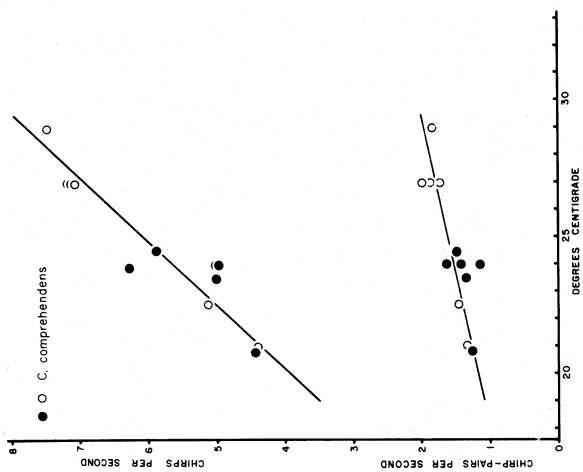
This and the following species are separable from *C. bidens* by the chirp rate in males and the shape of the female subgenital plate; however, only one character is known at present which separates this pair: the slow chirp rate of *C. tardum* and the very fast chirp rate of *C. velox*. Local populations appear to maintain habitat distinctions (see discussion of the *squamosum* group) so females may be identified by association with known males.

*Holotype.* — ♂, pine flatwoods, Pinetop, NW 1/4, Sec. 31, T9S, R19E, Alachua Co., Florida, 5 Oct 1975, TJW, J.J. Whitesell and D.A. Nickle collectors; UFT 454-13. ANSP. Scales: dorsal covering grey-brown to tan with a darker brown stripe behind eye and at humeral angles of pronotum, four dark spots at hind margin of pronotum, and four longitudinal rows of spots on abdomen, one of each row on each notum; venter pale tan; sides of head below and behind eye and sides of pronotum silvery white; femora mottled pale tan and dark brown, darker dorsally, single dark spot on outer face of hind femur distal to and below middle; tibia annulate dark brown and tan, hind basitarsus dark brown with central tan band. Cuticle: yellow-brown, lighter on sides of pronotum, darker on dorsum of abdomen; venter pale yellow-brown; legs pale tan. Wings: dorsal fields transparent, hind margins with three dark spots, the lateral pair connected on the inside by a thin line, marginal clear areas with pinkish tinge, extending for ca. 1/3 their length beyond pronotum; lateral fields brown below, pale above.

*Allotype.* — ♀, same data as holotype. Coloration similar, but scales of head darker, with five weak longitudinal stripes on occiput; venter of abdomen pale tan; cuticle orange-brown, distal half of abdomen dark brown, venter and legs pale tan.

*Measurements.* — Holotype ♂, allotype ♀: body length, ♂ 5.4, ♀ 5.1; greatest head width, ♂ 1.36, ♀ 1.51; length of pronotum, ♂ 3.00, ♀ 1.83; length of hind femur, ♂ 3.74, ♀ 4.01; length of hind tibia, ♂ 2.90, ♀ 3.07; length of ovipositor, 3.61 (slightly downcurved).

*Paratypes.* — 7 ♂ (6 taped), 9 ♀. All Alachua Co., FLORIDA: 3 ♂, 4 Oct 1971 (UFT 454-14, 18, 19), 5 ♀, 5 Oct 1971, 4 ♂, 4 ♀, 7 Oct 1971 (incl. UFT 454-15, 16, 20) (all FSCA).



FIGURES 32-33. — 32. Chirp rate as influenced by temperature in *Cycloptilium velox* (9 individuals), *C. bidens* (16 indiv.) and *C. tardum* (17 indiv.), Alachua Co., Florida. Solid symbols — lab tapes; open symbols — field tapes. 33. Chirp and chirp-pair rate as influenced by temperature in *Cycloptilium comprehendens* (12 individuals from 7 counties in 4 states). Solid symbols — lab tapes; open symbols — field tapes.

Range in length of pronotum of paratypes, ♂ 2.9-3.2, ♀ 1.6-2.0.

Coloration of the paratypes agrees closely with holotype but some females are generally darker with more dark cuticle on the abdomen.

*Geographical distribution.* — The type series is restricted to the area studied in Alachua Co., Florida. Recorded specimens with similar songs occur north to NORTH CAROLINA, Moore Co., west to ALABAMA, Baldwin Co., and south to FLORIDA, Charlotte Co., with field tapes from VIRGINIA, Northampton Co., and MARYLAND, Worchester Co. (Fig. 65) (All taped records FSCA).

### ***Cycloptilum velox*, n. sp.**

#### **Fast-chirp Scaly Cricket (Figs. 7, 32, 51, 67, 69)**

The last species in the *bidens* complex to be discussed here, though certainly not the last to be discovered in the eastern U.S., *C. velox* remains inseparable from *C. tardum* except on the basis of song and habitat differences. Much field work remains to clarify the range of this species and the relationships of its many isolated populations.

*Holotype.* — ♂, hammock, Pinetop, NW 1/4, Sec. 31, T9S, R19E, Alachua Co., Florida, 5 Oct 1971, TJW, J.J. Whitesell and D.A. Nickle Collectors; UFT 452-28. ANSP. Scales: dorsum light brown, darker stripe behind eye and at humeral angles of pronotum, four dark spots on hind margin of pronotum, and four longitudinal rows of small dark spots on dorsum of abdomen, one of each row per tergite; venter pale tan; legs mottled dark brown and tan, darker dorsally, dark spot on outer face of hind femur distal to and below center, tibia annulate dark brown and pale tan. Cuticle: Orange-brown, abdomen darker, legs pale tan. Wings: transparent, with three dark spots on distal margin connected on inner portion with thin dark line, extending for ca. 1/3 their length beyond pronotum; lateral fields pale above, dark below.

*Allotype.* — ♀, same data as holotype. Coloration similar, abdominal cuticle dark for posterior 4/5.

*Measurements.* — Holotype ♂, allotype ♀: body length, ♂ 5.2, ♀ 5.0; greatest head width, ♂ 1.40, ♀ 1.50; length of pronotum, ♂ 3.05, ♀ 1.76; length of hind femur, ♂ 3.82, ♀ 4.06; length of hind tibia, ♂ 2.90, ♀ 3.00; length of ovipositor, 3.45.

*Paratypes.* — 4 ♂ (all taped), 1 ♀. All same data as holotype (UFT 452-29-32) (all FSCA).

Range in length of pronotum of paratypes, ♂ 3.0-3.2, ♀ 1.8.

Coloration of the paratypes agrees closely with that of the holotype.

*Geographical distribution.* — The type series has been restricted to the population studied in Alachua Co., Florida. However, similar songs have been recorded from collected males north to GEORGIA, Glynn Co., west to MISSISSIPPI, Hancock Co., and south to FLORIDA, Pinellas Co., with additional field tapes from Brevard and Dade Cos. (Fig. 67) (All taped records FSCA).

**Cycloptilum comprehendens** Hebard  
Plains Syncopated Scaly Cricket (Figs. 25, 33, 46, 64)

*Cycloptilum comprehendens* Hebard, 1929:421, pl. 11, figs. 3-5. Type locality: Baculite Mesa, Pueblo Co., Colorado, 5000 to 6000 ft. Holotype: ♀, 13 Sept 1921, ANSP.

*Cycloptilum comprehendens comprehendens* Hebard. Hebard, 1931.

*Ornebius comprehendens* (Hebard). Chopard, 1968:227.

*C. comprehendens* is more similar to *C. squamosum* than any other of the western complex sharing the syncopated song, but the song and the development of the projections on the female subgenital plate differ markedly. The ratio of the distance the clypeus projects in front of the epistomal suture to the distance the antennal sockets extend behind it is also generally useful, 1.8:1 or greater in *C. comprehendens* and 1.7:1 or less in *C. squamosum*. However, there is occasional overlap, and the measurements are difficult to reproduce. The best results occur by measuring parallel to the head surface at the midpoint of the epistomal suture. Any rotation will change the ratio of the measurements.

For distinguishing the described taxa of syncopated crickets, see Hebard (1931), who described two western populations as subspecies. Records for these are not included in our distribution map as they are well outside the scope of this paper, and unpublished data suggest they are full species.

*Measurements.* — Selected ♂ (Pike Co., Arkansas, 23 Aug 1964, UFT 437-3) and holotype female: body length, ♂ 5.7, ♀ 9.2; greatest head width, ♂ 1.43, ♀ 1.75; length of pronotum, ♂ 3.23, ♀ 2.13; length of hind femur, ♂ 3.95, ♀ 5.20; length of hind tibia, ♂ 3.12, ♀ 4.20; length of ovipositor, 4.50.

Range in length of pronotum, 10 ♂, 8 ♀, from Texas, New Mexico and Arkansas, ♂ 3.10-3.75, ♀ 2.00-2.40.

*Coloration.* — ♂, scales: dorsal covering pale tan, white on sides of head and thorax and reduced on abdomen, weakly bordered above with brown; venter white with brown speckling; legs light tan, indistinctly annulate, darker on the dorsum of the femora and on the crests of weak, short, sinuous longitudinal carinae on the outer surface of the hind femora, the latter easily abraded as to expose the darker cuticle, base of hind femora white between sinuous carinae, dark brown spot on outer face distal to and below center. Cuticle: abdomen black, other parts pale orange-tan; humeral calli dark brown, transverse, teardrop shaped; legs pale yellow-tan with sinuous carinae on hind femur darker. Wings: dorsal fields cloudy-tan with slightly darker margins with veins accented, slightly reddish to brown, about 2/3 covered by pronotum; lateral fields darker below, pale above, with accented veins. ♀ similar, with four distinct rows of dark scale clusters on dorsum of abdomen, one of each row near the rear margin of each tergite. The holotype female is darker than most specimens and has lost nearly all of its scale covering.

*Geographical distribution.* — The holotype represents the northernmost record of this species (Fig. 64). Other peripheral records include the following: NEW MEXICO, Hidalgo Co. (ANSP), Quay Co. (FSCA); TEXAS, Gray, Brewster and Star Cos. (ANSP); OKLAHOMA, Marshall Co. (FSCA); ARKANSAS, Pike Co.

(FSCA); LOUISIANA, Evangeline Par. (FSCA). Hebard (1931) records Stevens Co., KANSAS which is probably correct, and the species certainly extends some distance into Mexico.

### Discussion and Comparison of the Terrestrial Scaly Crickets

The songs of all the species in the previous groups have been unique, with little intraspecific variation and no overlap for at least some parameters of interspecific differences. Pulse rates differ among the trillers and pulse and pair rates and length of chirp differ among the complex chirpers. Within the terrestrial scaly crickets, pulse rates do not appear to be important isolating mechanisms in most cases. *C. zebra* with a relatively fast pulse rate of 68-79 p/sec at 25 C and *C. exsanguis* with a relatively slow rate of 36-46 p/sec may be exceptions (Fig. 29) for this is the only song parameter separating them from some members of the *bidens* complex and *C. squamosum* which overlap broadly in the intermediate rates between 43 and 60 p/sec. Even so there is slight overlap in the case of *C. exsanguis* and the slowest singer in the *bidens* complex, *C. pigrum*.

Chirp rate appears the most reliable parameter for identifying the species within the *bidens* complex, *C. quatrainum* and *C. comprehendens* (Figs. 30-33). However, two groups have species overlapping in this parameter: *C. squamosum*, *C. tardum* and *C. zebra* (Figs. 30-32); and *C. bidens* and *C. exsanguis* (Figs. 30, 32). No sympatric populations where chirp rates overlap have yet been closely studied.

An additional differentiation lies in further patterning, specifically, the pairing of chirps in *C. comprehendens* (Fig. 46) and quartets of chirps in *C. quatrainum* (Fig. 44). Both of these are to some extent variable: *C. comprehendens* occasionally sings evenly spaced chirps at intervals identical to those between the first chirps of a normal chirp-pair series but deleting the second chirp of each pair, often lapsing into the normal song; *C. quatrainum* occasionally sings longer series of chirps. The other species vary from a few to more than 80 chirps per train (see Figs. 42-51 for sonograms).

By combining the above differences, all species but *C. squamosum* and *C. tardum* may be distinguished; geography and

morphology must be considered for these. The geographical ranges of *squamosum* group species largely overlap. However, two species in which females differ but males have identical songs and are otherwise inseparable appear to have exclusive ranges: *C. squamosum* occurring west of the Mississippi River, *C. tardum* east of it. (But see discussion of *bidens* complex below.)

Several species appear to have strong affinities for coastal habitats, especially salt marshes: *C. exsanguis*, *C. zebra* and *C. pigrum* have been collected only in such habitats. *C. zebra* is most commonly associated with *Salicornia* mats at edges and around high spots in salt marshes, but also occurs in beach wrack deposited at the high tide level along the coast. *C. exsanguis* has been collected in *Juncus* and *Spartina* marshes. Our collections are from *Juncus* except for one where they were feeding on grass seed heads adjacent to *Juncus* in Taylor Co., Fla.

The spacial relationships of *C. zebra* and *C. exsanguis* are intriguing. Their distributions are contiguous, *C. exsanguis* the more northern (Figs. 60, 62). General habitats are very similar, but microhabitats appear distinct if occasionally forming mosaics, *C. exsanguis* well up on marsh vegetation consistent with the periodic flooding common in *Juncus* habitats, *zebra* on the ground, litter or mat vegetation just above the tide zone. Their chirp rates are very close, which may be a factor influencing their unusually widely divergent pulse rates; morphologically they are quite different including considerable disparity in size. The contact zone is apparently limited to a few hundred yards at Cedar Key, Levy Co., Fla., as several searches to either side yielded only the species consistent with this, and a similar situation may occur between Glynn Co. (*C. zebra*) and Chatham Co. (*C. exsanguis*), Georgia.

*Cycloptilum pigrum* also occurs in coastal habitats, but very little is known about this species. The holotype came from litter beneath needle-bearing trees (conifer or casuarina) on high beach in Texas, others from *Spartina* marsh in Maryland and marshy edge of a coastal waterway in Georgia; field tapes from Nassau and Palm Beach Co., Florida and Chatham Co., Georgia are also coastal.

The other species in this group occur in woodland, scrub and grassland habitats generally inland from strictly coastal com-

munities. *C. squamosum*, and some of the remaining members of the *bidens* complex have been collected near the margins of saltmarshes or on islands in them but not in the adjacent marshes.

In Alachua Co., Florida, TJW found habitat differences among the three inland members of the *bidens* complex. Each species had its greatest abundance in habitats different from the others, yet they coexisted in all possible pairings. *C. bidens* was abundant on well-drained, sandy sites that burn frequently. Some of these sites were treeless old fields while others were dominated by longleaf pines (*Pinus palustris*) and xerophytic oaks (*Quercus laevis*, *Q. cinerea*, *Q. virginiana*). *C. tardum* was most frequent on poorly drained sites that burn frequently or occasionally. Some of these sites had typical "flatwoods" vegetation — splash (*P. elliotii*) and longleaf pines and a dense scrubby understory. Others were more disturbed; one had been clear cut and replanted with slash pine. *C. velox* occurred in a greater variety of habitats than the other two species and was the only species to achieve significant populations in mesic broadleaved forests — where the litter is thick and fire does not occur.

The ranges of these three appear broadly overlapping on the central and southern coastal plain. Songs like *C. velox* have been recorded as far north as southern Georgia, *C. bidens* to South Carolina and *C. tardum* to Maryland. All three occur throughout most of Florida and west to Mississippi or Alabama. Collections of specimens in the complex but not identified to species extend as far north as Long Island, New York, and into the southern Appalachians to Tishomingo Co., Mississippi, and Walker Co., Georgia. The distribution maps (Fig. 65-67) indicate the combined range of the complex (except for *pigrum*) and song records for each species. Localities known to have more than one species are numbered; and song records that are intermediate between species are indicated by letters (see legend).

The present situation in the systematics of the *bidens* complex serves to point out several difficulties with these and probably other mogoplistines, especially other cryptic species in the *squamosum* group. These crickets are small and secretive, and often sing from microhabitats which may have temperatures differing from ambient measurements usually taken at the parabola when field tap-



ing: as little as one degree C difference may change our identification of songs. They are flightless, and so probably do not disperse readily over long distances and, in Florida at least, there are many habitats which seem not to support populations of one or any species. It is probable that numerous isolated populations of each exist within the general range. Considering how great this range is and the complexity of habitats within, it is highly possible that the Alachua Co. species are not the same as those of Maryland, Mississippi or even other areas in Florida, and that complex clines exist between even neighboring areas. This complexity is further indicated by a Jasper Co., Texas population with a song inseparable from *C. squamosum* or *C. tardum* but females that have *bidens*-like subgenital plates. Males of this and a similar Pike Co., Arkansas, population have solid black rear margins on their wings, unlike the pale margins characteristic of *C. squamosum*. It is evident that much more field work is needed in this complex.

*Cycloptilum comprehendens* is the easternmost species of a large and varied complex of syncopated crickets in the western U.S. and Mexico (of which only two others have been described — as subspecies of *C. comprehendens*). It ranges through much of the xeric woodland and grassland of Texas and neighboring states where the most common habitat is relatively open grassland, including ruderal and savanna associations. However, near Austin, Texas, a large population sang from grasses and up to about five feet high in shrubs and even large live oaks which had dense branches drooping to the ground, but not from neighboring trees with canopies not touching the ground. As they commonly ascend stems in thick grass clumps, such dense cover and ground contact probably afford adequate conditions lacking in high-crowned trees perhaps relating to daily vertical migrations. Other species in the *squamosum* group commonly sing from low, dense vegetation; the only strictly arboreal record for the group is of a male in the *bidens* complex singing from high in a palm immediately after a ground fire in a pine flatwoods in Charlotte Co., Florida.

Very little is known about the remaining species, *C. quatrainum*. The two records are from coastal marshes.

### The Complex-trilling Scaly Cricket

The following species does not fit into any of the preceding groups, but has some unique characters and some shared with each of them. Its song has paired pulses, but the pulses in each pair are dissimilar, unlike all other *Cycloptilum* which have identical pulses throughout the calling song. Its general shape is similar to *C. trigonipalpus* and its wings are covered by the pronotum as in both the *trigonipalpus* and *slossoni* groups yet the pronotum is relatively shorter than any other *Cycloptilum*, measuring only about as long as in the much smaller *C. zebra*. It is terrestrial in habit, sings the pairs slowly enough to be distinguished by ear at least at moderate temperatures yet with an extremely rapid pulse rate, has a quadrate female subgenital plate, and male genitalia similar to members of the *squamosum* and *slossoni* groups. It probably has its closest relatives in the West Indies.

#### *Cycloptilum irregularis*, n. sp.

#### Keys Scaly Cricket (Figs. 14, 34, 47, 56)

*Holotype*. — ♂, subtropical hammock, north Plantation Key, Monroe Co., Florida, 4 July 1965, REL collector; UFT 440-8. ANSP. Scales: dark brown over most of the body, venter slightly lighter; pronotum and head with lateral white stripe sharply bordered above and below with dark scales; abdomen with four dorsal longitudinal rows of darker clusters of scales; legs mottled dark and lighter brown, hind femora with several rows of light spots. Cuticle: abdomen dark brown; head and thorax orange-brown, darker at lateral angles and lighter on sides, dark median stripe on labrum dividing to three on clypeus; legs pale whitish. Wings: dorsal fields with piceous hind border, entirely covered by pronotum; lateral fields dark brown.

*Allotype*. — ♀, same data as holotype. Coloration similar to male but scale color more uniform dark brown with light side stripe continued on first three segments of abdomen.

*Measurements*. — Holotype ♂, allotype ♀: body length, ♂ 5.8, ♀ 8.7; greatest head width, ♂ 1.45, ♀ 1.60; length of pronotum, ♂ 2.60, ♀ 2.01; length of hind femur, ♂ 3.80, ♀ 4.39, length of hind tibia, ♂ 2.80, ♀ 2.90; length of ovipositor, 3.10.

*Paratypes*. — 13 ♂ (8 taped), 5 ♀. All records FLORIDA. Monroe Co., 8 ♂, 2 ♀, Sugarloaf Key, 24 June 1964 (incl. UFT 440-3, 4, 5, 6, 7), 5 ♂, 3 ♀, Plantation Key, 4 July 1965 (incl. UFT 440-10, 13, 14) (all FSCA).

Range in length of pronotum, 12 ♂, 5 ♀ paratypes, ♂ 2.40-2.85, ♀ 1.55-2.00.

Coloration in the paratypes agrees closely with the holotype and allotype.

*Geographical distribution*. — The paratypes are from two localities (Fig. 56). In addition TJW has song records from Big Pine Key, Monroe Co., Florida.

The song of *C. irregularis* (Figs. 34, 47) is easily distinguished in the field as slower than the complex chirping and trilling scaly crickets (except for *C. albocircum*) and much more melodious than the former, and by coming from ground litter; it is shorter and much faster than the song of other terrestrial scaly crickets that oc-

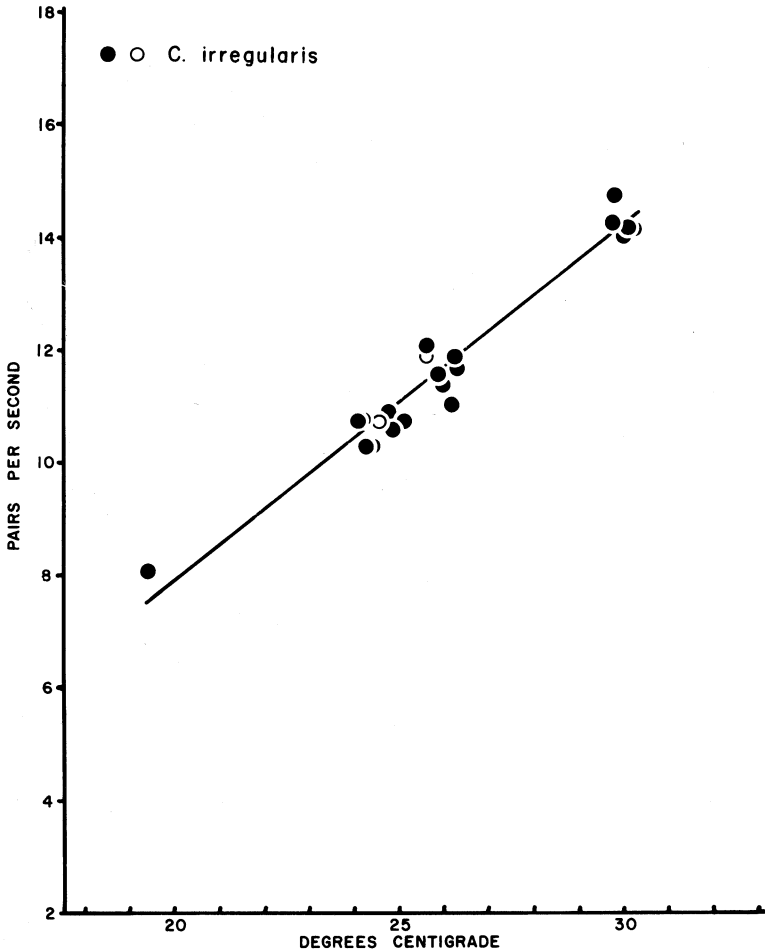


FIGURE 34. — Pulse-pair or complex-pulse rate as influenced by temperature in *irregularis* (14 individuals). Solid symbols — lab tapes; open symbols — field tapes.

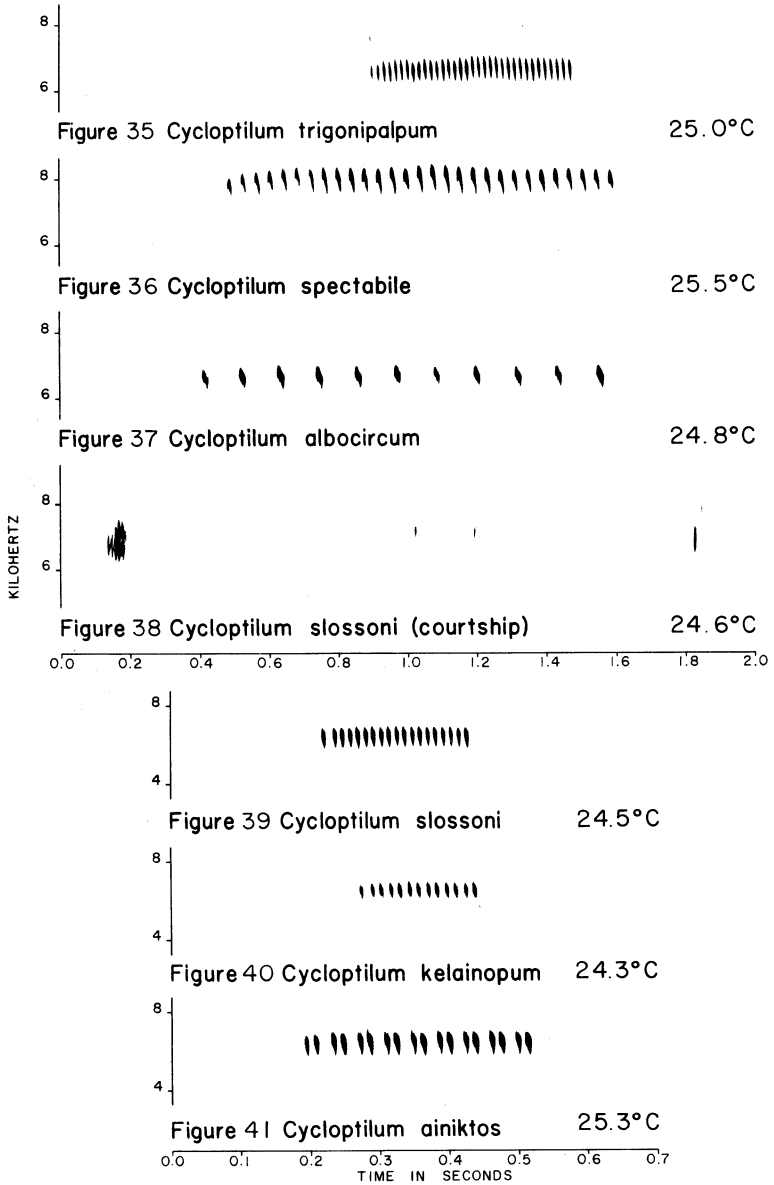
cur in the same area. It is also unique in that the chirp rate decreases by ca. 10% toward the end of each phrase, giving the illusion of a decrease in pitch; the sound is a very melodious, rapid, lilting tinkle. The similarity in song to *C. albocircum* (which also decreases in rate, in this case pulse rate, but only by about 6%) emphasizes the uncertainty of relationship of this species. It is as yet uncertain whether *C. irregularis* is derived from one of the trilling group, from the ancestor of both trillers and chirpers, or from an intermediate between them; some of the similarities to each group have already been mentioned. However, the unique form of pairing is evidence against the latter for the first pulse of each pair is different from the second, probably made on the opening phase of the wing cycle but perhaps the first part of a two part wing-closure. In the chirping *Cycloptilum*, all pulses are identical, probably derived from doubling or grouping pulses in a uniform train. The pulse rate of *C. irregularis* is faster than any other known *Cycloptilum*, nearly double that of the *squamosum* group species. These data are not contrary to other data and indicate independent origins of this species and the chirping *Cycloptilum*.

*Cycloptilum irregularis* has been found only in the Florida Keys. Habitats include litter in and near subtropical hammocks, wiregrass clumps, and a single individual from under black mangrove. It is terrestrial, primarily in the inland, drier parts of the keys where its neutral color and small size make it extremely difficult to collect in spite of its noticeable song.

#### Seasonal Distribution in *Cycloptilum*

Relatively little is known about seasonal distribution in this genus but collection data indicate that in most of the U.S. adults occur in mid and late summer. This suggests one generation a year

FIGURES 35-41. — Audiospectrograms of the calling songs of trilling and complex-chirping *Cycloptilum* and courtship of *C. slossoni*. 35. *trigonipalpus* (UFT 442-5, Dillon Co., S. Car.). 36. *spectabile* (UFT 449-10, Dade Co., Fla.). 37. *albocircum* (UFT 446-8-a, Monroe Co., Fla.). 38. *slossoni* — mixed courtship (UFT 441-50, Alachua Co., Fla.) 39. *slossoni* (UFT 441-15-a, Dade Co., Fla.). 40. *kelainopus* (UFT 456-9-a, Monroe Co., Fla.). 41. *ainiktos* (UFT 438-2-b, Charlotte Co., Fla.).



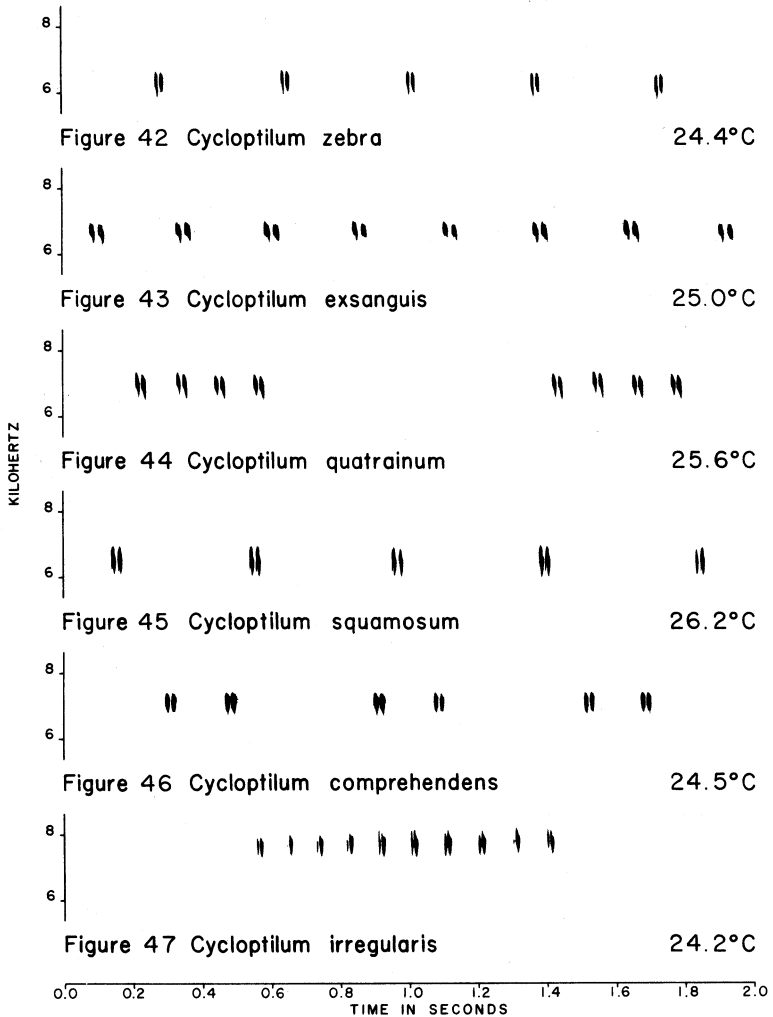
with overwintering in the egg stage. The most complete data are listening records in north central Florida, where TJW (1979) surveyed local populations of *C. tardum*, *C. bidens*, *C. velox*, *C. trigonipalpus* and *C. slossoni*. Fig. 69 shows that at this latitude only *bidens* has two generations, an additional indication that it is distinct from *C. tardum* and *C. velox*. Whether this species has two generations farther north is not known.

The species occurring in southern Florida probably have at least two generations a year and in many cases probably breed continuously except during the most severe cold periods. Song surveys on Big Pine Key, Monroe Co., Florida, taken by TJW and J.J. Whitesell, revealed males of *C. irregularis* every month but December, when the temperature on the sample date was very cold, and September, when the negative observation is in some doubt. However, greater numbers were heard from March to October (average, 11 for seven samples excluding Sept., highest, 21 in May), least from November to February (average, 1.4 for five samples). Juveniles of *C. slossoni* have been collected in all months but February, adults March through December in southern Florida; in northern Florida collections for either are absent from October to May.

#### Mating and Oviposition in *Cycloptilum*

Little is known of mating and oviposition in *Cycloptilum*. Alexander and Otte (1967) gave brief notes on pairing in two unidentified Florida species and referred to REL's unpublished observations on copulation in *C. slossoni*.

In 1965 REL placed a male and a virgin female *C. slossoni* in a 6-inch circular plastic container with a screen top and made notes on a tape recorder. The male soon touched the female with his antennae and began courting. She moved away repeatedly at first and the male excitedly searched for her each time until contact was reestablished. Antennal flagellation by the male seemed to quiet the female and she paused for increasing amounts of time between moves until mating occurred. The male showed several stereotyped patterns of behavior. During contact, he antennated her and repeatedly sang a "mixed courtship" song consisting of abbreviated chirps interspersed with short pauses and series of click-



FIGURES 42-47. — Audiospectrograms of the calling songs of chirping *Cycloptilum* and *C. irregularis*. 42. *zebra* (UFT 443-18, Glynn Co., Ga.). 43. *exsanguis* (UFT 447-10, Levy Co., Fla.). 44. *quatrainum* (UFT 450-7, Hancock Co., Miss.). 45. *squamosum* (UFT 451-33, Tyler Co., Tex.). 46. *comprehendens* (UFT 437-9-b, Marshall Co., Okla.). 47. *irregularis* (UFT 440-3-a, Monroe Co., Fla.).

like pulses usually paired but sung at a very slow rate of 5-7 pairs per sec and 20-50 p/sec at 24.6 C and with a much wider than normal range in frequency (Hz) (Fig. 38). In addition, he interspersed bouts of rapid jerking and an audible tapping of his foretibia on the substrate. (The latter was originally thought to be made by the vibrating of the maxillary palpi against the substrate [Alexander and Otte, 1967], a movement which occurs almost continuously, but observations on other *C. slossoni* as well as several other species of arboreal crickets have convinced REL that it is the tibia which make the faint buzzing sound.) Both the tapping and jerking would probably be perceived by a female on the same leaf or twig. When contact was broken the male sang more nearly normal chirps, usually in groups of two or three but still abbreviated and repeated more often than in the calling song.

After about 15 minutes the female quieted and responded by elevating her body. After she repeated this several times the male backed under her from the front and passed a spermatophore, then moved back out and faced her. Male postcopulatory behavior consisted of antennating the female. When she moved, he shook vigorously, tapped his fore-tibia and antennated her vigorously until she quieted. The bout ended when she failed to respond to repeated quieting behavior by the male, moved out of contact, kicked away the spermatophore which adhered to the plastic, backed over it and ate it.

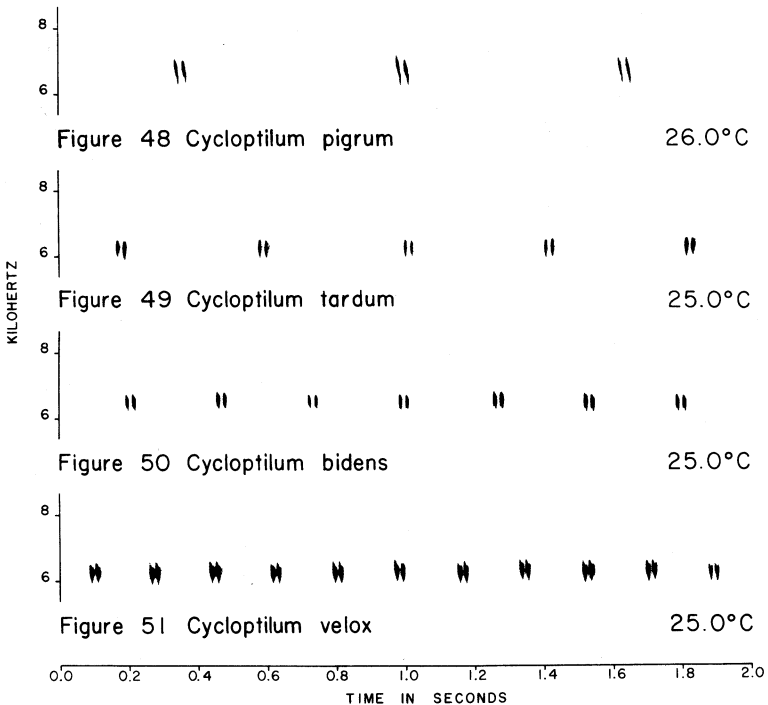
REL observed part of a *C. spectabile* courtship in the field. A male on a small mangrove branch sang what sounded like a calling trill slightly shorter than normal repeated at one or two second intervals, and rapidly explored the branchlets. A female on one of the branchlets nearer the trunk moved slowly and stopped and rapidly shook the twig she was on after each male trill. The male quickly located the appropriate twig and established antennal contact. Unfortunately the sequence was accidentally interrupted at this point and both fled.

Another pair placed together in a plastic container failed to mate. The male followed the female, singing a song similar to the above and antennating her, but the female continued to move away. She reacted several times by placing her mandibles on the floor of the container and jerking rapidly backwards 3-5 times

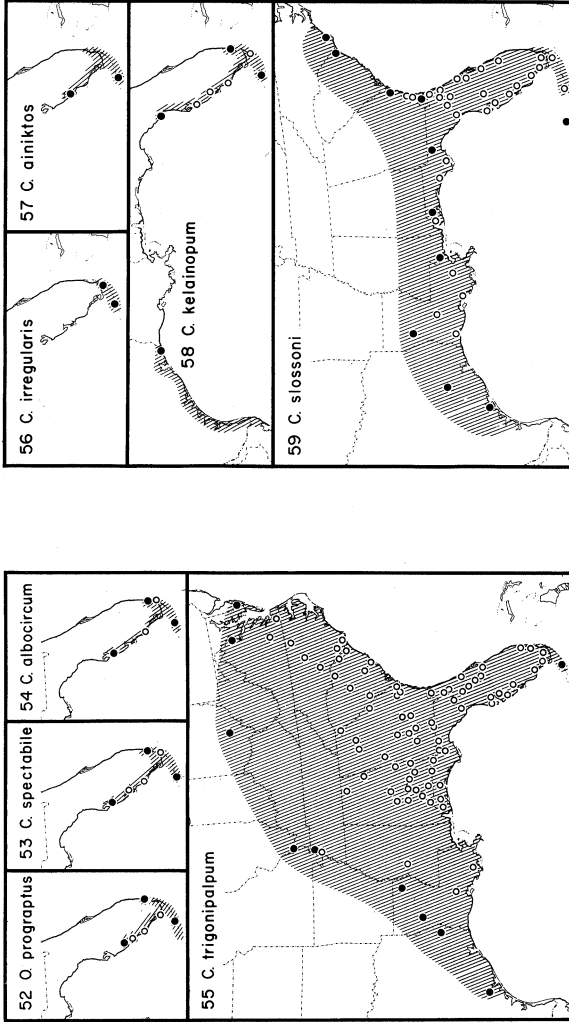


making a loud scraping sound, and turning away in apparent refusal. However, the male was persistent and after an hour the female appeared to become more receptive, raising her abdomen when he approached. His response seemed unusual in that he moved forward under her from her front, and palpated her subgenital plate from beneath. After each such occurrence the female would dismount and move away, and the observation was terminated after another hour.

Occasionally members of the *bidens* complex have been heard in the field singing long series of short groups of chirps separated by short pauses equivalent to one or two skipped chirps but otherwise

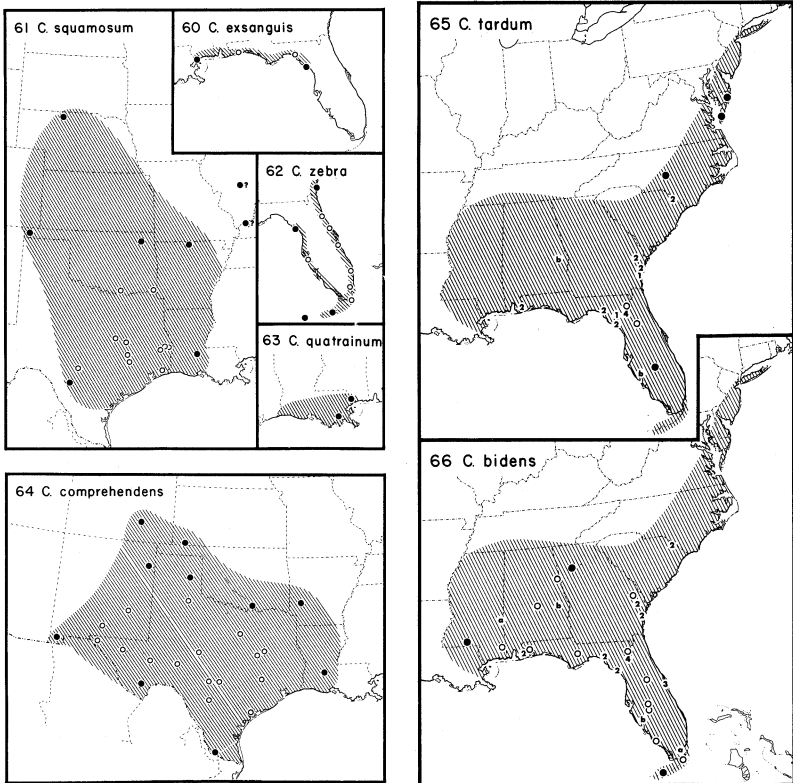


FIGURES 48-51. — Audiospectrograms of the calling songs of the *Cycloptilum bidens* complex. 48. *pigrum* (UFT 448-13, Jefferson Co., Tex.). 49. *tardum* (UFT 454-16, Alachua Co., Fla.). 50. *bidens* (UFT 453-21, Alachua Co., Fla.). 51. *velox* (UFT 452-32, Alachua Co., Fla.).

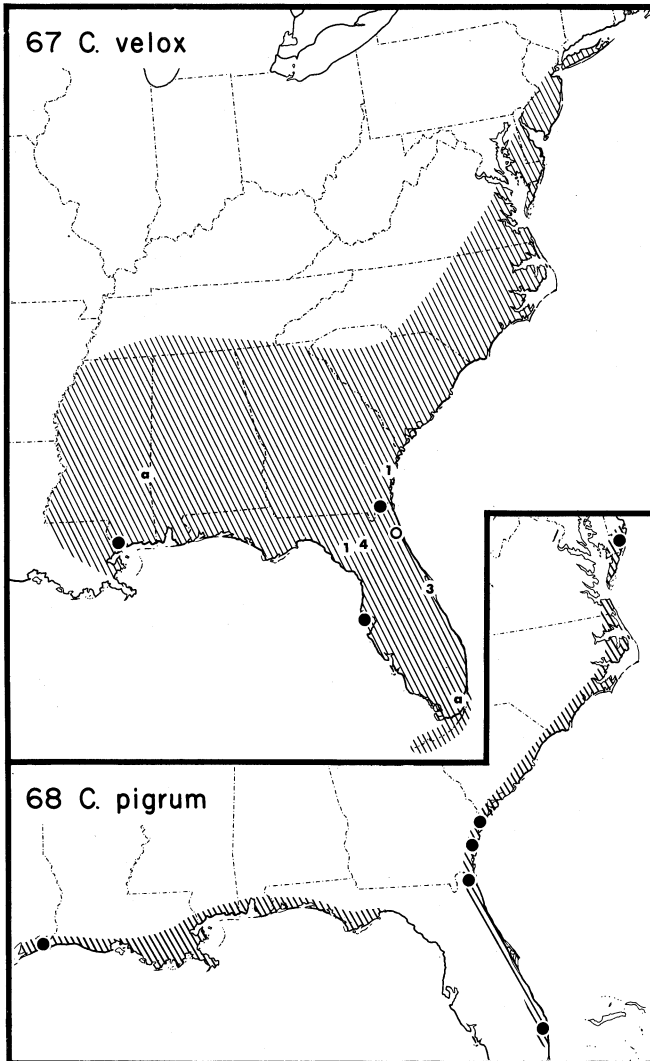


FIGURES 52-59. — Distribution maps of *Oligacanthopus* and *Cycloptilum*. 52. *O. prographus*. 53. *C. spectabile*. 54. *C. albocircum*. 55. *C. trigonipalpus*. 56. *irregularis*. 57. *ainiktos*. 58. *kelainopum*. 59. *slossoni*. Circles show country records except upper and lower Florida Keys and Dry Tortugas each indicated separately. Solid circles are peripheral records substantiated in the text; shading indicates predicted general distribution.

indistinguishable from the calling song. In every case where these have been seen a female has been in contact with or close to the singing male. Similar songs have been heard in cages housing pairs. While no matings have been seen, this is probably part of the courtship pattern and, as in one field observation the female had a spermatophore, may also function as a postcopulatory song.



FIGURES 60-66. — Distribution maps of *Cycloptilum*. 60. *exsanguis*. 61. *squamosum*. 62. *zebra*. 63. *quatrainum*. 64. *comprehendens*. 65. *tardum*. 66. *bidens*. Numbers indicate song sympatry: 1. *tardum* and *velox*, 2. *tardum* and *bidens*, 3. *bidens* and *velox*, 4. *tardum*, *bidens* and *velox*. Letters indicate songs intermediate between named populations: *a*. between *velox* and *bidens*. *b*. between *bidens* and *tardum*. Shading in 65-66 indicates the predicted general distribution for the *bidens* complex because many records were assignable to the complex but not to a particular species.



FIGURES 67-68. — Distribution maps of *Cycloptilum*. 67. *velox*. 68. *pigrum*. Numbers indicate song sympatry: 1. *tardum* and *velox*. 3. *bidens* and *velox*. 4. *tardum*, *bidens* and *velox*. Letter *a* indicates songs intermediate between *velox* and *bidens*. Shading in 67 indicates predicted range of the *bidens* complex because many records were assignable to the complex but not to a particular species; shading in 68 is the predicted range for *pigrum* only.

In October, 1972, REL observed and photographed a female *Cycloptilum hesperum* (Rehn and Hebard) ovipositing in a dead twig near La Paz, Baja California, Mexico. *C. hesperum* is apparently closely related to *C. slossoni*; since nothing else is known of oviposition in *Cycloptilum*, the female's behavior, as she deposited several eggs in the stem, is described below. For each egg, she chewed a small notch in the barkless surface, then curved her ovipositor under her elevated body and guided it initially with her mouthparts. Once the ovipositor was inserted, her head lifted and she rocked her body slightly forward until the ovipositor was nearly perpendicular to the stem. She took about 15 minutes to work the blade about half way into the relatively soft wood, then her movements altered and an egg slid down the blade and into the twig. Egg transfer took about seven minutes; withdrawing the ovipositor required about five minutes. Then a new site was prepared. The end of one sequence, two complete ovipositions, and the beginning of a fourth were observed. The twig had several additional egg sites. No hatching occurred.

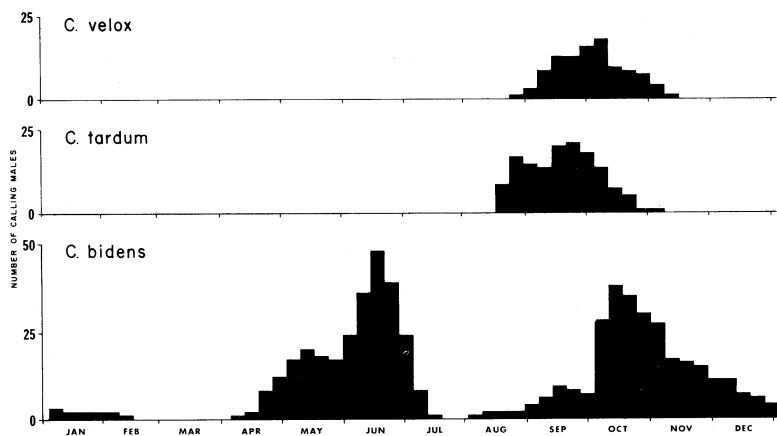


FIGURE 69. — Seasonal occurrence of calling males of three species in the *Cycloptilum bidens* complex in Alachua Co., Fla. Top, *velox*. Center, *tardum*. Bottom, *bidens*. Based on weekly or biweekly censuses at 12 sites. Data tabulated for weekly intervals (Walker, 1979).

## PHYLOGENY OF THE MOGOPLISTINAE

There are enough comparative data to allow a preliminary construction of evolutionary relationships among eastern North American mogoplistines. This is presented as a stimulus to further studies, especially a critical examination of similar Old World genera which have often been based on single characters without regard to probable phylogenetic significance. As new information is gathered and more species added to the cladogram presented here the relationship will presumably be refined and corrected and eventually supported quantitatively.

Methods used to generate the hypothesized cladogram follow Hennig (1966) and allow formulation of a logical and testable theory of relationships based on the characters available. The greatest difficulty arises in determining which character states are ancestral (plesiomorphic) and which therefore may be shared by paraphyletic groups, and which are derived (apomorphic) and indicate a monophyletic group. Such decisions are often made with little more than intuitive judgment to go on, yet Hennig devotes about one third of his book (p. 70 et seq.) to the best methods of determining this. Two methods have been especially useful here: one based on sequential evolution (transformation series), or simply that necessary intermediate steps in the evolution of a complex character are assumed ancestral, and that the complex character is derived from an ancestor possessing such an ancestral character state; and the other based on uniqueness, or that a character shared by several monophyletic groups is considered ancestral within those groups while an alternate unique to one such group is considered derived for that group. Neither of these criteria are absolute and agreement between them is stronger evidence than either alone. Both also are susceptible to misleading possibilities, among them that a complex character state has been evolved independently by two groups or that a complex character has been secondarily lost or otherwise modified or that a derived character is shared by many members of a group while an ancestral state is present in very few and not shared by other less related groups.

## Evolution in Mogoplistine Song

Variation among songs has been used in this paper at nearly all levels of taxonomy. A primary assumption has been made that the ancestral mogoplistine possessed wings, tympana, and made a calling song. The overwhelming presence of singing behavior in the family Gryllidae and the nearly universal similarity of associated morphological and behavioral characteristics dictate this assumption. Furthermore, the ancestral song probably shared the common gryllid characteristics of sequences of simple pulses produced at a uniform rate, either as long trills or grouped into shorter chirps, and in which the pulse rate is the primary species-specific isolating variable. From this base, songs have evolved along several independent lines and exhibit at least three additional grades of complexity characterized by the complete absence of song or the superimposing of additional rate determining mechanisms on previously existing ones. Such changes probably involve concomitant shifting or broadening of the features used by females in recognizing the songs of conspecific males. Figure 70 summarizes the following discussion.

One independent line resulted as uniformly shortened pulse trains (chirps) became rhythmically produced with a probable shift from pulse to chirp rate within a chirp train as the isolating parameter. The genus *Hoplosphyrum* is an example of this, while the *trigonipalpus* group of *Cycloptilum* retains the ancestral characteristics of the subfamily.

A second line resulted in the addition of a second period of sound production in each wing movement cycle, producing paired but unequal sound pulses. There has probably been no shift in the isolating parameter from the basic wing cycle (pulse) rate even though multiple sounds are made; this song form, characterized by the species *C. irregularis*, is considered a modification within the primary grade of complexity.

The majority of species follow a third branching line which shows two changes in grade of complexity and two lines of modification in one of them. The primary change has been to pulse pairs (chirps) forming the basis of the song with an accompanying shift to pair rates as the functional isolating parameter. For most species the song still functions at this level. A secondary

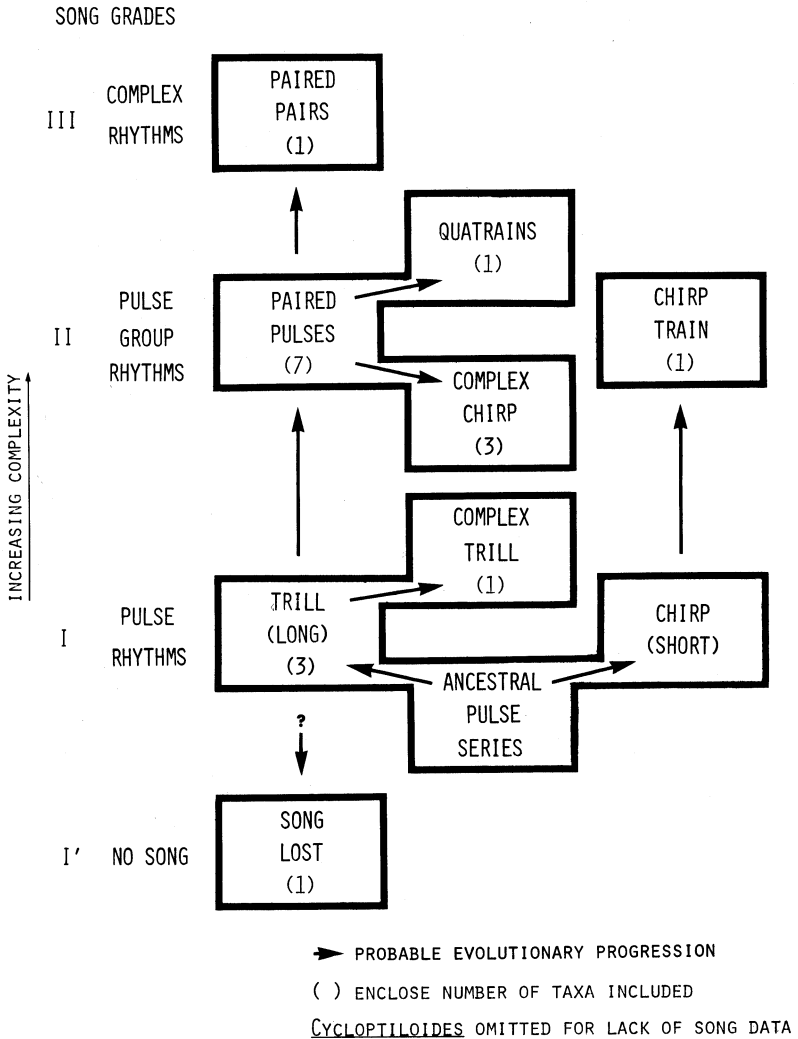


FIGURE 70. — Hypothesized relationships and grades in the evolution of mogoplistine songs. See text for discussion.



line of evolution involves the marked increase in pair-rate production until, in the extreme examples, pairs are difficult to distinguish. At this stage it is not possible to judge whether the cryptic pair-rate, the slightly uneven pulse-rate, or perhaps even the number of pulses in each complex series or all of them function to behaviorally isolate the three species in this, the complex-chirping group.

Another secondary line involves the shortening of the long but variable length of chirp trains to units of four chirps (quatrains). Quatrains, like complex chirps, are not produced at rhythmic intervals, but are sung in irregular series: the chirp rate is unique, so there is no apparent shift in isolating mechanism.

The final branch of this group has superimposed an additional rhythm on the chirp-series, the pairing of chirps. In this case, unlike the above, chirp-pair rates are regular, species specific, and differ among the known species (*C. comprehendens* and several western species) and so are likely involved in species isolation. Whether this is actually the case is not known — both chirp rate and pulse rate also vary among these species. In any case the development of this syncopated song appears dependent upon the prior development of 2-pulse chirps, and so adds to the hierarchy of grades.

The last remaining line involves the loss of song and associated structures. As this is certainly a derived rather than ancestral condition, little can be gained from further discussion here; i.e. this loss cannot a priori be assigned phylogenetic status since there is no indication of what level of complexity in song was lost.

Other song parameters may be useful in defining groups or separating species, but none appear as useful as the above for constructing phylogenies. Some, such as pulse rate in the trillers and chirp rate in others may be arranged in numerical order, but it is doubtful that this ordering reflects relationship. Such rates are the primary isolating mechanisms among species and so must be very sensitive to selective displacement from potentially confusing sympatric species. Considering the number and variety of species, and particularly the complexity in the *bidens* complex, it seems unlikely that such a temporal and spacial mosaic of conflicting pressure would result in a perfectly ordered sequence.

### Phylogenetic Relationships and Discussion of Characters

A proposed phylogeny of Eastern U.S. Mogoplistinae is given in Figure 71, and the characters listed in Table I. At each branching point sets of distinguishing character states are given, one derived set for each branch indicated by a solid symbol and a corresponding ancestral set for each alternate branch indicated by an open symbol. The pairs of complementary derived and ancestral sets constitute the evidence supporting the monophyly of the line bearing the derived character set only, and the adjacent number is used to identify both that derived line and the sets of characters in the following discussion.

The first four character sets are perhaps the most difficult to deal with in terms of the immediacy of division — the three groups indicated by the species studied here all appear circum-equatorial and are almost certainly very old. As a result only a few terminal clades of a complexly branching history may be compared. The assignment of characters is based primarily on comparisons with members of other subfamilies of crickets, those unique to the taxa discussed are considered derived while those widely shared are considered ancestral. Comparative song data as yet missing for *Cycloptiloides americanus* and for other genera may add considerable strength to this or generate alternate proposals.

Somewhat confusing data occurs for species of the genus *Eucycloptilum* Chopard (or at least a very closely related genus) which appear nearly identical to *Cycloptiloides* except in the shorter length of the maxillary palpi and in a presumably ancestral character at the subfamily level of much less extreme development of the clypeus. The combination of reduced clypeus with enlarged pronotum and the presence of titillators would indicate that the latter two characters were very early evolved and that *Hoplosphyrum* is perhaps secondarily lacking them. Studies of considerably greater scope are necessary to resolve this.

TABLE I. — Assessment of phylogenetic character states. See Fig. 71.

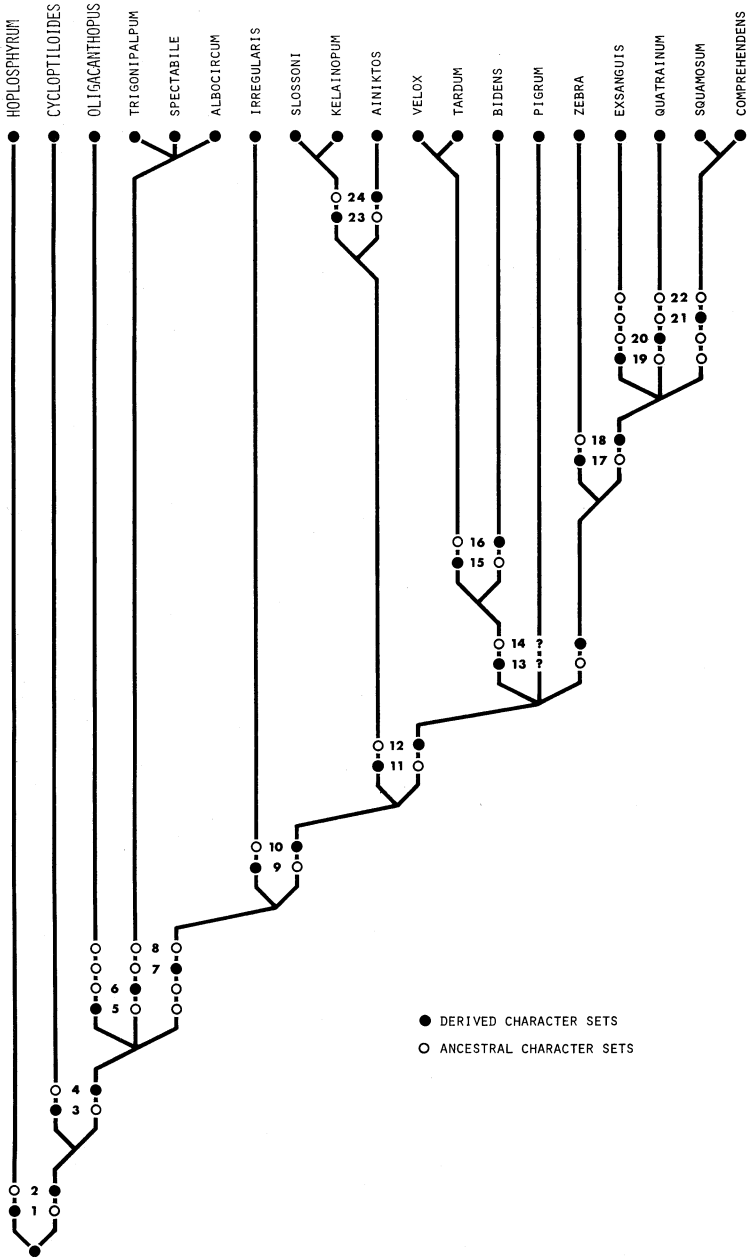
● — Derived character states

○ — Ancestral character states

- 
1. ● Ventral valvulae shorter and narrower than dorsal valvulae; xerophilic.  
○ Valvulae nearly equal in length and width; mesophilic.
  2. ● Males with elongated pronotum, titillators present, and epiproct widely emarginate.  
○ Males with quadrate pronotum, titillators absent, and epiproct rigidly triangular.
  3. ● Basitarsus III elongate, gracile; male subgenital plate broad, bowl-shaped.  
○ Basitarsus III short, robust; male subgenital plate small, trough-like.
  4. ● Clypeus narrow, facial angle acute-angled; arboreal.  
○ Clypeus wide, facial angle obtuse-rounded; terrestrial.
  5. ● Tympanum absent; hind tibia very short; male wingless, pronotum truncated.  
○ Tympanum present; hind tibia normal; male winged, pronotum elongated.
  6. ● Maxillary palpi expanded; scape width ca. equal to epistomal suture length; titillators triangular.  
○ Maxillary palpi narrow; scape width ca. 1/2 epistomal suture length; titillators tubular.
  7. ● Genitalia partly sclerotized, narrow.  
○ Genitalia fleshy, bulbous.
  8. ○ No derived characters known evidencing a closer relationship among 5, 6 and 7.
  9. ● Song of complex pulses; terrestrial.  
○ Song of simple pulses; arboreal.
  10. ● Wing cycle paired; body form robust.  
○ Wing cycles evenly timed; body form narrow.
  11. ● Chirps complex, of several pulses, length determinate; female subgenital plate bilobed, acutely notched.  
○ Chirps simple, 2-pulsed, irregular length trains; female subgenital plate truncate.
  12. ● Male pronotum shortened, exposing wings; terrestrial; dark spot on outer hind femur; titillators expanded distally.  
○ Male pronotum covering wings; arboreal; lacking dark spot on outer hind femur; titillators tubular.

13. ● Female subgenital plate with subapical teeth.  
○ Female subgenital plate without subapical teeth.
14. ● Female subgenital plate quadrate.  
○ Female subgenital plate tapered.
15. ● Female subgenital plate with median spike.  
○ Female subgenital plate truncate.
16. ● Two well defined generations per year.  
○ One generation per year.
17. ● Pulse rate very rapid, over 60 p/sec; size very small.  
○ Pulse rate normal, below 60 p/sec; size moderate to large.
18. ● Wing borders light.  
○ Wing with three black caudal spots and black lateral area.
19. ● Pulse rate very slow, ca. 41 p/sec.  
○ Pulse rate normal, ca. 53 p/sec.
20. ● Song a series of groups of four 2-pulse chirps.  
○ Song a long series of 2-pulse chirps.
21. ● Living in arid continental habitats.  
○ Living in mesic coastal habitats.
22. ○ No derived characters known evidencing a closer relationship among 19, 20 and 21.
23. ● First pulse in each chirp unpaired; pair rate ca. 1/2 pulse rate.  
○ All pulses in pairs; pair rate less than 1/3 pulse rate.
24. ● Ancestral character states not known for characters of line 24.

FIGURE 71. — Proposed phylogenetic relationships of United States Mogoplistinae. Symbols occur in numbered pairs or triplets: solid symbols indicate derived character states, open symbols indicate ancestral character states. Numbers refer to the table of character states (Table 1) and are used to identify the evolutionary line indicated by the solid symbol. See text for discussion.



The absence of definitive derived character states for any pair of lines 5-7 make it impossible to establish closer relationships among them. The discovery of an eighth derived set uniting 6 and 7 would establish the genus *Cycloptilum* as monophyletic with respect to *Oligacanthopus* and justify the present taxonomic treatment. However, no such character set has yet been found, in each case the differences being derived for only one of the three branches while each pair share ancestral character sets. Such a situation most reasonably indicates splitting into three genera or lumping into one, but for the present purposes the taxonomic status quo is retained.

A similar situation exists in the further branching of line 6, but as the three species involved have been treated previously in detail this is not discussed further. As other members of the trilling group are studied these relationships should become more apparent. Strictly species level distinctions have been left to the preceding text as being of relatively little phylogenetic interest.

Ancestral characters of set 5 are shared by *Cycloptiloides* and except for the length of the pronotum by *Hoplosphyrum*, of set 6 except for scape/epistomal suture ratio by *Cycloptiloides*. Genitalia were not studied for these genera, and while the genitalia of lines 5 and 6 are dissimilar, they share the fleshy characteristics absent in line 7. Further studies of the genitalia of other *Cycloptilum* might indicate phylogenetically useful characters.

Sets 9 and 10 follow the discussion of song evolution above. The common ancestor for these lines is presumably a triller of simple pulses with narrow form and arboreal habits similar to members of the *trigonipalpus* group; ancestral song characters are shared with *Hoplosphyrum* and at least Baja California *Cycloptiloides*; habitat and, to some degree, narrow form with *Cycloptiloides*.

Sets 11 and 12 follow the song evolution previously discussed, and ancestral female subgenital plate characteristics are shared by all previous groups. Set 12 indicates that the partial exposure of wings in that line is secondarily derived. *Cycloptiloides* as well as previous groups of *Cycloptilum* all share the covered condition more primitive for this group. The terrestrial scaly crickets, as the name implies, have also returned to primarily ground-dwelling habits, presumably at the same time as the invasion of less humid-tropical and densely vegetated and more arid northern and con-

tinental habitats. To consider alternate paths requires a considerably increased amount of convergence and secondary loss among character sets 5 through 12, so this arrangement appears optimally parsimonious.

The character sets of both 13 and 14 depend upon knowledge of the female which is absent for *C. pigrum*. It is expected that this species will join one of the alternate lines when the females are identified — in fact no females considered potentially *pigrum* have been found which lack the teeth of set 13. The single character of set 14 is difficult to apply with certainty but there does seem to be a real difference (see earlier discussion under Methods). Viewed from the side the dorsal profile of the tapered state appears evenly rounded from base to apex except for the presence of the subapical teeth. In the alternate quadrate state the dorsal profile is more sharply angled, the base nearly straight and parallel to the ventral surface, the apical margin flatter and nearly perpendicular to the ventral surface. The lateral angles may curl inwards on some specimens making them appear more rounded, and in members of the *comprehendens* group these angles bear projections.

Branch 13 splits again with the addition of a terminal spine on the female subgenital plate of branch 15 while 16 is the only species of *Cycloptilum* known to have two well defined generations in northern Florida. Many problems remain in this group, the *bidens* complex, among them the probable inclusion of *C. pigrum* and the strong probability of additional species within the group.

Set 17, separating the single species *C. zebra*, has in addition to those given the entire series of characters unique to this species. Only characters that both have alternate states shared by the complementary branch and are considered ancestral are given. Set 18 consists of a single color character, the loss of pigment on the wing borders, uniting a seemingly amorphous group; the ancestral state is present in all other species in the branch beginning at set 7 as a solidly pigmented caudal border or as 3 black spots except on *C. pigrum*. However, in addition, all line 18 have probably reached their present distributions via a western (Mexican) invasion route while *C. zebra* and all others in the genus except possibly western *C. kelainopum* have invaded through Florida from a more southern origin. It is presently unknown but probable that these

invasions occurred independently for most of these species, rather than by only a few common ancestors (except probably for the *bidens* complex) and so they do not constitute single derived or ancestral characters. However, it is likely that ancestors of these branches inhabited different geographical areas: in fact a *C. zebra*-like species has been found on Jamaica (TJW) while the *comprehendens* group and probably *squamosum* have wide ranges in the western U.S. and northern Mexico. *C. exsanguis* is perhaps least likely of branch 18 to have western origins, particularly if occurring on both coasts north of peninsular Florida, but without further collecting along the Gulf coast neither origin is strongly supported.

Branch 18 includes four species found in eastern U.S. One pair (21) share a major shift in habitat preference from mesic and probably coastal conditions to arid continental habitats, interpreted as originating in a desert-dwelling ancestor. Both of these species are members of large desert groups and these branches would show further divisions if these additional species were included. The *comprehendens* complex is unique in demonstrating an additional grade of song complexity; specific characters are discussed in the species accounts. The complementary ancestral characteristic (mesic-coastal) is found in at least some members of all other groups but *Hoplosphyrum* (which is probably independently arid-adapted), the exceptions remaining definitely more mesic if not coastal in preference.

The remaining two species each show some derived characteristics with definitely ancestral alternates, *C. exsanguis* singing an unusually slow pulse rate for members of the *squamosum* group, while *quatrainum* groups chirps in uniform bursts of four. As no combining derived characters are known, three branches are split at this point. For each of these character sets the ancestral states are shared at least by the terrestrial scaly crickets. Members of the *bidens* complex (15, 16) as well as *C. slossoni* and *C. trigonipalpus* have invaded continental habitats but these remain mesic in character and these species presumably derive from more coastal and eastern ancestors.

The remaining group of three species, branch 11, may be separated by relative characteristics of the song, character set 23 in-



dicating a more derived condition than present in *C. ainiktos*. While an alternate derived set is unknown, the presence of but a single species possessing many unique characters in that branch makes it unnecessary. Were a second species very like *C. ainiktos* to be discovered it would be necessary to add a third branch at this point unless derived characters unified it with one of the existing branches. *C. slossoni* and *C. kelainopum* are separable by specific characters.

#### EPILOGUE

Several major problem areas remain, especially in understanding the relationships between populations in the *bidens* complex and expanding and refining the phylogenetic scheme to include new information, other New World species and groups, and relating them to those of other land masses and islands. Even after more than doubling the number of species and adding considerable new data we are hardly to the point of repeating Hebard's statement (1931:135) ". . . we believe that little new will subsequently be found [on mogoplistines] in the United States."

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