CHAPTER 30

Gryllotalpinae: Mole Crickets

Mole crickets are such peculiar crickets that they are usually ranked as a family of crickets (Gryllotalpidae) rather than as a subfamily. Approximately 70 species, placed in 5 genera, occur throughout the world's temperate and tropical regions. In North America there are 7 species, including 4 that are immigrants.

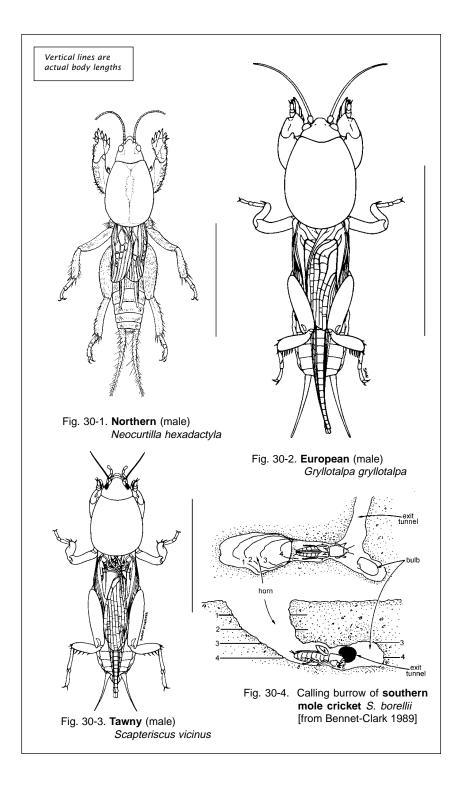
Identification: (Fig. 30-1,2,3) (19-50 mm) No other crickets have mole-like forelegs. Antennae shorter than body; foretibia with two or four strong blade-like projections; first two segments of foretarsus developed into blades; body cylindrical and covered with short dense pubescence; hindfemur not reaching tip of abdomen.

Burrowing: Mole crickets spend nearly all their lives underground. They occupy extensive tunnel systems within which they can move, forward or backward, with great speed—as can be demonstrated by allowing one to tunnel in damp sand in a container with a transparent bottom (such as a glass bowl or clear plastic dish). When dug up, they do not leap away like other burrow-inhabiting crickets but dig their way back underground with powerful strokes of the forelegs. The dirt is simply forced aside. Other burrowing crickets have much slower digging techniques. Short-tailed crickets (*Anurogryllus*), for example, carry dirt away one mouthful at a time. Mole crickets often tunnel immediately beneath the surface and leave trails of pushed-up soil that resemble, in miniature, the surface tunnels of mammalian moles. The burrowing techniques of mole crickets restrict them to sandy, friable, or nearly saturated soils.

Flight: Although mole crickets appear heavy and clumsy, many are capable fliers. In some species all individuals have the long hindwings necessary for flight. In others, some or all individuals have short hindwings and cannot fly. Capturing mole crickets as they end their flights at conspecific calls or at bright lights is far easier than extracting them from soil.

Food: Mole crickets eat both plant and animal matter, with some species being mostly herbivorous and others mostly carnivorous. Three of our species damage lawns, pastures, and crops, mostly by feeding on roots and leaves but also by cutting roots and uprooting seedlings as they tunnel.

Oviposition and social behavior: Female mole crickets lack an external ovipositor and lay eggs in their burrows or in special chambers that they then seal off. The females of northern and European mole crickets stay with their eggs and young nymphs. It is not known when the relationship is



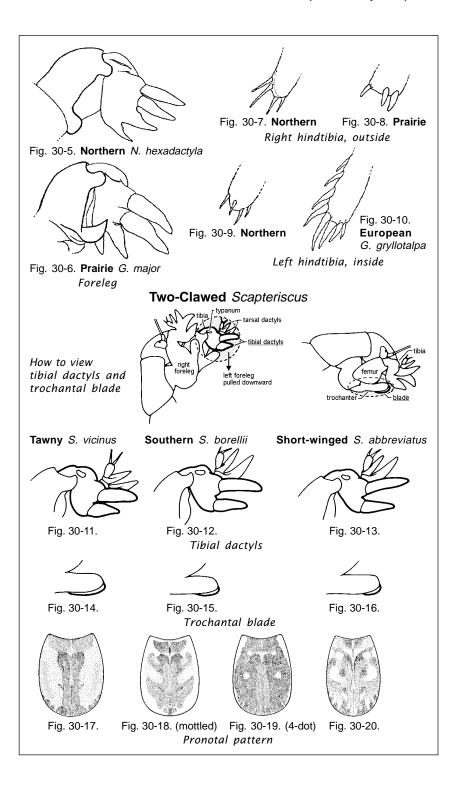
terminated nor to what extent the mothers provide protection and food. Mole crickets have anal glands from which some can expel a sticky liquid that may thwart insect predators such as ants.

Mating occurs within the burrow, and the male's courtship song can be heard issuing from the ground during the day as well as at night. Observations in glass-sided burrows reveal that the male sometimes enlarges the burrow to give the female room to mount. In at least one species, the northern mole cricket, matings are initiated tail-to-tail with the male lying on his back! A female may mate several times with the same male at intervals of 10 or 15 minutes, but once she no longer responds to the male's courtship, the pair fights and one leaves the burrow system. Perhaps in the wild the male leaves or is driven away, with the female taking over the tunnel system for egg laying.

Life cycles: Mole crickets generally require a year or more to develop, and they overwinter in all stages except the egg and small nymph. The only populations that have more than one generation per year are southern and short-winged mole crickets in south Florida. Two-year life cycles have been documented for the northern mole cricket in the Carolinas. Longer life cycles seem likely for more northern populations and for larger mole crickets, but these have not been studied.

Acoustic behavior: Since soil transmits sound poorly, crickets that remain earthbound are unlikely to use sound for long range communication. Indeed, the calling of mole crickets seems to be directed largely or entirely to those that are flying. In the two European and three U.S. species that have been most thoroughly studied, males construct special burrows for calling (Fig. 30-4). These have horn-shaped openings to the outside and are of appropriate dimensions and design to augment the sound and project it skyward. Calling to the sky would make little sense except that in these species females fly prior to mating and can locate mating partners by flying to the source of calls. Such a link between flying and calling is evident in the three species of two-clawed mole crickets (*Scapteriscus*). The two that fly project their calls upward, and flying conspecifics land at or near the calls. The one that cannot fly does not call, though it retains a courtship song.

Sound production by female mole crickets is somewhat a mystery. On rare occasions, when in contact with other mole crickets, females have been heard making sounds as they rub their wings together. S.M. Ulagaraj tape recorded and analyzed such sounds of a female tawny mole cricket. D.A. Nickle and T.C. Carlysle found toothed crossveins that may function in stridulation on the upper surface of the left forewing of females of tawny and southern mole crickets. They also reported male-like files (beneath the right forewing) in females of European and prairie mole crickets and summarized what was known of female sound production. Females seem to produce sounds during aggression or defense.



Mole Crickets 5

Two aspects of hearing in mole crickets are puzzling. Firstly, the young nymphs of two-clawed mole crickets have perfectly-formed, completely exposed tympana. In other crickets, the tympana are not evident in the early instars and are fully developed only in the adult. Dave Yager, in a pilot study, established that some southern mole cricket nymphs had hearing similar to, but generally less sensitive than, the adult. The function and exact nature of precocious hearing in mole crickets are unexplored. Secondly, all songs of mole crickets have dominant frequencies of less than 5 kHz, yet Nobuo Suga determined that the northern mole cricket (or a close Amazonian relative) hears best at 20-30 kHz. The specimens he studied had flown to lights. Mole crickets that fly may have their hearing evolutionarily tuned to detect the ultrasonic pulses of insectivorous bats.

Remarks: The so-called "pygmy mole crickets" (Tridactylidae), once assumed to be closely related to mole crickets are now placed in a different suborder of Orthoptera (Caelifera). The sharing of mole-like features by these two insect groups is a result of evolutionary convergence rather than their having a mole-like common ancestor. Pygmy mole crickets are less than 10 mm and their forelegs have no tibial tympanum or tarsal blades.

References: Alexander & Otte 1967 (mating); Baumgartner 1910 (anal glands; female song); Bennet-Clark 1989 (acoustic burrows); Castner & Nation 1986* (cuticular lipids); Hayslip 1943 (life histories); Lawrence 1982 (pitfall); Nation 1983 (gut); Nguyen & Smart 1992 (nemas); Nickle & Carlysle 1975 (female files); Nickle & Castner 1984* (origins); University of Florida 1979-96 (reports); Walker 1984 (bulletin).

Key to genera

1	Foretibia with two blade-like projections (Fig. 30-11)
1'	Foretibia with four blade-like projections (Fig. 30-5).
2(1')	Forefemur with blade-like lobe (Fig. 30-6); apex of hindtibia armed with 7 spurs, 4 on inside and 3 on outside (Fig. 30-8, 10)
2'	Forefemur lacking blade-like lobe (Fig. 30-5); apex of hindtibia armed with 8 spurs, 4 on inside and 4 on outside (Fig. 30-7, 9)

Neocurtilla: Northern Mole Cricket

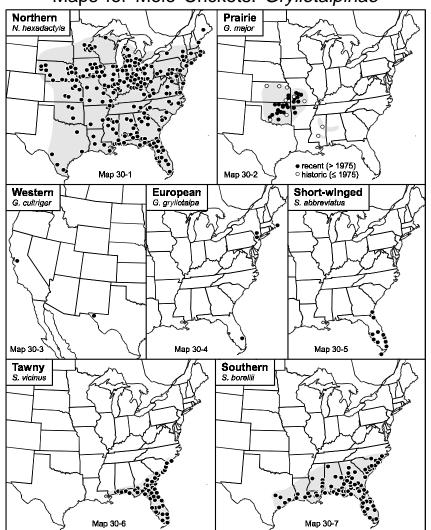
NORTHERN MOLE CRICKET: Neocurtilla hexadactyla Map 30-l

Identification: (Fig. 30-1) (19-33 mm) Basal projection of fore femur lobe-like (Fig. 30-5); hind tibia with eight spines at apex, four on inside and four on outside (Fig. 30-7,9).

Habitat: Margins of lakes and streams; low, mucky ground.

Season: Adults occur nearly year-round. Song period July-Sept. in southern Michigan; July-Nov. at Raleigh, N. Car.; and Jan.-Aug. at Gainesville, Fla. In central Florida, northern mole crickets have a one year life cycle and overwinter as adults. In North and South Carolina the life cycle is two years, with the first winter passed as mid juveniles and the second as adults.

Maps for Mole Crickets: Gryllotalpinae



Mole Crickets 7

Farther north—e.g., in Michigan—more than two years may be required, but no one has investigated.

Song: (Song 30-1) Rhythmic, low-pitched chirps from the ground at ca. 2-3 ch/s, 8-16 p/ch, 1.7 kHz, 58 p/s. No acoustical burrow is known. Calling occurs afternoons as well as evenings. Neighbors do not synchronize or alternate their chirps. The courtship song of the southern mole cricket is similar but higher in pitch (2.8 kHz) and chirp rate (3-4 ch/s).

Similar species: (1) Prairie mole cricket—35-50 mm long; basal projection of femur blade-like (Fig. 30-6). (2) European mole cricket—36-46 mm long; hind tibia armed above with three or four long spines (Fig. 30-10).

Remarks: In the Carolinas this species may mate in the fall (when singing occurs) with the females storing the sperm until they lay eggs the following spring. In Florida, most singing is in the spring and probably immediately precedes egg-laying.

Individuals from peninsular Florida average smaller than those from farther north. This difference may be indicative of a one-year life cycle in the south compared with a two- or three-year life cycle in the north.

C.E. Smith studied a wasp (*Larra analis*) that hunts northern mole crickets by entering their burrows. Unless thwarted by the sticky slime ejected by the mole cricket, the wasp paralyzes the mole cricket with stings and attaches an egg to it. The mole cricket quickly recovers from the attack and resumes normal activity, but the egg becomes a larva that feeds on and eventually kills its host.

Northern mole cricket males apparently call from closed burrows rather than from structures that direct the sound upward. Such calling is safer than calling at the bottom of an open horn and may be more effective in attracting flightless females, which must travel on the surface or through the burrow system to reach the calling male. In museum collections about half the females have long wings, but many of these are individuals that had flown to light, thereby biasing the sample in favor of long wings.

This species occurs in South America, but may not be native there. Its abundance in temperate South America, as judged from light trap catches, is like our pest mole crickets rather than our populations of northern mole crickets. On the other hand, our pest mole crickets are much less abundant in their South American homeland than they are in their adopted home. This switch in roles may be due to the introduced mole crickets leaving specialized natural enemies behind. In keeping with this, *Larra analis* attacks northern mole crickets, but not our pest species, and does not occur in South America.

References: DeWitt 1978 (collecting); Fulton 1951 (life history); Semlitsch 1986 (life history); Smith 1935 (*Larra*); Suga 1968 (hearing).

Songs	of	Mole	Crickets:	Gr	yllotal	pinae
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Song 30-1 Northern	Neocurtilla hexadactyla	1.7 kHz 1 sec.					
1111111111	. (440)460	1400100100					
2 Prairie	Gryllotalpa major (65°F)	2.0 kHz 1 sec.					
abilimonds	andalahlin)	ofeilittilitie					
3 European	Gryllotalpa gryllotalpa	1 .6 kHz 1 sec.					
	(no recording available)						
4 Western	Gryllotalpa cultriger						
	(song not known)						
5 Southern	Scaptericus borellii	2.6 kHz 1 sec.					
444444444444444444444444444444444444444							
6 Tawny	Scaptericus vicinus	3.2 kHz 1 sec.					

Gryllotalpa: Seven-spurred Mole Crickets

Three species of this genus occur north of Mexico. One is an immigrant from Europe, established in New Jersey; another is restricted to remnants of tall grass prairie; and the third is barely known.

Identification: (Fig. 30-3) (26-50 mm) Four blade-like fingers on each foretibia; auditory tympanum covered. Forefemur with blade-like lobe (Fig. 30-6). Hindtibia usually armed along upper inner margin with three or four long spines (Fig. 30-10).

PRAIRIE MOLE CRICKET *Gryllotalpa major*

Map 30-2

Identification: (35-50 mm) Basal projection of fore femur blade-like (Fig. 30-6); hind tibia with seven spines at apex, four on inner and three on outer side (Fig. 30-8,10).

Habitat: Relicts of tall grass prairie.

Season: Nothing is known of the life cycle except that adults are active in spring as early as 28 March and as late as 8 June. Two adults collected 20 October are the only evidence that adults are active at other seasons. Comparisons with other large mole crickets suggest that the first winter is spent as a small to medium nymph and that further development requires a year or more.

Mole Crickets 9

Song: (Song 30-2) A loud *beep*, *beep*, *beep* reminiscent of some fire alarms; regular, brief chirps issuing from a well-formed acoustical burrow; ca. 2-3 ch/s, 13-35 p/ch, 2.0 kHz, 120 p/s. Calling begins ca. at sunset and lasts for ca. 1 h. The distinctive song of the prairie mole cricket, which can be heard as far away as 400 m, has greatly facilitated the mapping of its current distribution. The song of the northern mole cricket is much less intense, and although its chirp rhythm is similar, its chirps have half the pulses at half the pulse rate.

Similar species: Northern mole cricket—19-33 mm; basal projection of fore femur lobe-like (Fig. 30-5).

Remarks: This species was once much more widespread, but most of its former habitat has been converted to agriculture. Early records included prairie areas in Mississippi and Illinois (Map 30-2). Until recent studies revealed its habitat and characteristic song, it was largely known from occasional specimens taken at light.

References: Figg & Calvert 1987 (natural history); Vaughn et al. 1993 (Oklahoma sites); Walker & Figg 1990 (song; acoustic burrow).

EUROPEAN MOLE CRICKET: *Gryllotalpa gryllotalpa* Map 30-4

Identification: (Fig. 30-2) (36-46 mm) the only seven-spurred mole cricket occurring in the East.

Habitat: Moist, loose soils.

Season: Adults are present at all times of year. Calling and mating probably occur in May and June. In Spain, the European mole cricket has a two-year life cycle, spending the first winter as a juvenile and the next as an adult. Eggs are laid in spring.

Song: (Song 30-3; rate and frequency estimated from observations by H.C. Bennet-Clark in France) Low-pitched trill at 60 p/s issuing from several irregular openings in the ground (Bennet-Clark, France).

Similar species: Northern mole cricket—less than 30 mm; hind tibia unarmed except at apex.

Remarks: This cricket is wide-spread in Europe and was evidently imported into the United States in shipments of ornamental plants. It reached pest proportions at a nursery in Rutherford, NJ, in 1915-1918, and was collected in nearby Wallington as recently as 1960. Other U. S. records are from Nantucket, MA, Montgomery, NY, and Belle Glade, FL, and may not represent established populations.

Reference: Weiss & Dickerson 1918.

WESTERN MOLE CRICKET: Gryllotalpa cultriger

Map 30-3

Identification: The only mole cricket with four tibial claws known from the West; smaller (26-31 mm) than Prairie or European mole crickets (35-50 mm).

Song: Not known.

Remarks: Only three specimens have been reported from the United States: one each from El Paso, Texas; "California"; and Lone Mt. Cemetary, San Francisco. All were collected prior to 1900. At least two Mexican specimens are known, one being from Fuerte, Sinaloa.

Reference: Hebard 1935c.

Scapteriscus: Two-clawed Mole Crickets

Our three species in this genus are native to South America and first became established in North America more than 90 years ago, apparently from stowaways in ships' ballast.

Identification: (Fig. 30-3) (22-33 mm) Only two blade-like claws (*dactyls*) on each fore tibia (Fig. 30-11), auditory tympanum exposed. Foretrochanters bear an elongate, blade (Fig. 30-14). Hindtibia has 3-6 long spines along upper inner margin.

Life cycles: Two-clawed mole crickets require a year or less for a generation. In the colder parts of their ranges they overwinter only as adults and large nymphs. Eggs are laid in clutches of 25 to 60 in small ovoid chambers $(4 \times 3 \text{ cm})$ 9 to 30 cm below the surface.

Economic importance: Members of this genus are the most damaging crickets in the New World. In the southeastern United States tawny mole crickets are major pests of turf and pastures, causing annual losses of \$10's of millions. Short-winged mole crickets do the same type of damage but are much more restricted geographically. Southern mole crickets feed largely on animal matter and avoid established turf; however, they damage seedlings in newly planted lawns, gardens, and fields.

Biological control: The fact that our pest mole crickets were introduced and occurred in much greater numbers here than in their homeland suggested to University of Florida researchers that they might be controlled by classical biological control—i.e., by introducing natural enemies that had been left behind when they immigrated from South America. Of the enemies that proved promising because of their host specificity, three were successfully introduced, and two seem to be substantially reducing *Scapteriscus* populations: a nematode (*Steinernema scapterisci*) that kills the mole cricket by introducing a lethal microbe, and a tachinid fly (*Ormia depleta*) that homes on the calling songs of male mole crickets.

Flights: Large numbers of tawny and southern mole crickets fly during the early evening of warm days each spring. One result of such flights is that new lawns and fields are infested and pesticide-treated ones are reinfested. Another result is that females find mates by homing to the appropriate calling song and landing near the entrance to the caller's burrow.

Some important features of the flights are not adequately understood. Males and mated females, as well as virgin females, often terminate their flights by homing to conspecific calling song, and the same individual may fly repeatedly over a period of several weeks. Available evidence suggests that many flights terminate near their starting points and that in heavily infested fields a minority of the males call each evening. Pair formation and sexual competition in these species deserve further study. Most flights probably involve more than colonizing new or better fields or finding a willing source of conspecific sperm. T.G. Forrest has shown that calling males vary greatly in their attractiveness to females. On an evening when one calling male attracts no female, another, calling nearby, may attract more than 20! (He cannot service this many— Forrest prevented them from reaching the male.) Male attractiveness correlates with loudness of the calling song. Loudness correlates with both male size and soil moisture, which in turn are indicative of male quality and habitat quality. Scientists have exploited the attractiveness of loud calls by broadcasting simulated mole cricket sounds more than 30 times as powerful as the loudest male—and have collected as many as 8000 mole crickets at a single source in a single evening.

References: Bennet-Clark 1987 (acoustical burrow); Castner 1984 (biocontrol); Forrest 1983 (songs & mate choice); Forrest 1986 (maternal investment); Forrest 1987 (developmental strategies); Forrest 1987 (sinistrality); Forrest 1991 (sound production); Forrest & Green 1991 (sexual selection); Fowler 1987 (biocontrol); Fowler 1989 (biocontrol); Frank 1994 (biocontrol); Hudson 1987 (instars); Hudson 1989 (sampling); Hudson & Nguyen 1989 (biocontrol); Hudson & Saw 1987 (spatial distribution); Hudson et al. 1988 (biocontrol); Kleya & Dodson 1978 (calling); Matheny 1981 (food); Matheny et al. 1983 (landing distribution); Ngo & Beck 1982 (mark & release); Nguyan & Smart 1990 (biocontrol); Nickerson et al. 1979 (acoustic burrows); Nickle 1992* (synonymy); Nickle & Frank 1988 (Arizona); Parkman & Frank 1992 (biocontrol); Parkman & Frank 1993 (biocontrol); Parkman et al. 1993 (biocontrol); Schuster & Price 1992 (damage); Ulagaraj 1975 (ecology); Ulagaraj 1976 (sound production); Ulagaraj & Walker 1973 (phonotaxis); Ulagaraj & Walker 1975 (phonotaxis); Walker 1982 (sound traps); Walker & Forrest 1989 (phonotaxis); Walker & Fritz 1983 (flights); Walker & Nation 1982 (sperm storage); Walker & Ngo 1982 (damage); Walker & Nickle 1981* (immigration); Walker et al. 1983 (flights); Walker et al. 1996 (parasitoid fly); Yager 1986 (hearing).

Identification: (25-32 mm) Tibial blades separated at base by space equal to at least half of basal width of a dactyl (Fig. 30-12). Viewed from rear, sharp lower edge of trochantal blade extending one-half to two-thirds distance from trochantal tip to junction with femur (Fig. 30-15). Forewings longer than pronotum; hindwings longer than abdomen.

Habitat: Wet or moist, sandy or mucky, open areas—including fields, lawns, and the margins of ponds and streams.

Season: One generation per year except in south Florida, where there are two. Some individuals overwinter as adults, but most do so as large nymphs. Eggs are laid in spring. Most calling is Feb.-July, but because adults are long-lived, some calling occurs year-round. Flights are heaviest in April, May, and June except in south Florida, where a second generation sometimes produces a flight peak in July or August.

Song: (Song 30-5) A low-pitched, ringing trill at 54 p/s that issues from a horn-shaped opening in the ground (Fig. 30-4) during the first 2 hours after sunset or, after heavy rains, later. The male's courtship song, sometimes produced for minutes from a closed burrow, resembles the calling song of the northern mole cricket (Song 30-1) but is higher pitched and slightly faster in chirp rate.

Similar species: (1) Tawny mole cricket—tibial dactyls nearly touching at base (Fig. 30-11); (2) Short-winged mole cricket—forewings shorter than pronotum; hindwings concealed by fore wings.

Remarks: This species was long thought to be native, but analysis of early records revealed that it was first captured in the United States in 1904, near the port of Brunswick, Georgia. Subsequently it became established at other ports—Charleston, South Carolina, 1915; Mobile, Alabama, 1919; Port Arthur, Texas, 1925—and spread from these sites to occupy most of the southeastern states (Map 30-7). Those southern mole crickets introduced at Brunswick and Mobile had a mottled pronotal pattern (Fig. 30-18), whereas those at Charleston and Port Arthur had four light dots arranged in a trapezoid on the dark pronotal disk (Fig. 30-19). The two patterns initially spread from the separate sites of introduction, but today the mottled pattern is only in the vicinity of Mobile. The recent establishment of southern mole crickets along the Colorado River and in turf near Yuma, Arizona, raises the possibility that it will spread to other sandy well-watered areas throughout the Southwest.

The southern mole cricket is largely carnivorous and apparently does less damage to established grass than the next two, mostly herbivorous, species.

Map 30-6

Identification: (Fig. 30-3) (24-33 mm) Tibial dactyls nearly touching at base, separated by less than half basal width of a dactyl (Fig. 30-11). Viewed from rear, sharp lower edge of trochantal blade extending more than two-thirds distance from trochantal tip to junction with femur (Fig. 30-14). Pronotal pattern as in Fig. 30-17. Forewings longer than pronotum; hindwings longer than abdomen.

Habitat: Moist or well-drained, sandy soils in open areas—including fields, lawns, and roadsides.

Season: One generation per year Most individuals overwinter as adults, but some overwinter as large nymphs. Eggs are laid in spring. Most calling is Feb.-June, but because adults are long-lived, some calling occurs year-round. Flights are heaviest in March and April, but occur Feb.-June, Sept.-Dec.

Song: (Song 30-6) A loud, nasal trill at 137 p/s issuing from a horn-shaped opening in the ground (Fig. 30-4) during the first 90 minutes after sunset.

Similar species: Southern and short-winged mole crickets—tibial dactyls widely separated at base (Fig. 30-12, 13).

Remarks: This destructive insect was first recorded in the United States at Brunswick, Georgia, in 1899. It is native to South America and was perhaps transported in ballast from Buenos Aires or Montevideo. It is continuing to spread westward along the Gulf coast, and its ultimate distribution may include portions of Louisiana and Texas.

Two similar species occur in Puerto Rico, where mole crickets were accidentally introduced and became important pests by 1876. The tawny mole cricket was formerly believed to be one of the Puerto Rican species and was misleadingly called the "Puerto Rican mole cricket" or "changa"—the latter name being a vernacular Puerto Rican term for mole cricket.

SHORT-WINGED MOLE CRICKET

Scapteriscus abbreviatus

Map 30-5

Identification: (22-29 mm) Tibial dactyls slightly divergent, separated at base by space equal to at least half of basal width of a dactyl (Fig. 30-13). Viewed from rear, sharp lower edge of trochantal blade extending less than half distance from trocantal tip to junction with femur (Fig. 30-16). Pronotal pattern complex (Fig. 30-20). Forewings shorter than pronotum; hindwings concealed by forewings.

Habitat: Sandy soils near the coast; beaches, lawns, fields, and groves.

Season: All stages occur all year.

Song: No calling song. Males produce weak, 1-5 pulse chirps during courtship.

Similar species: Southern and tawny mole crickets—fore wings longer than pronotum; hind wings longer than abdomen (last stage juveniles have short wings, but hind wings are longer than fore wings).

Remarks: This species, like the previous two, is native to South America and was inadvertantly brought into southern ports about 1900. Since it cannot fly, its subsequent spread has depended on human transport, probably in manure, sod, and nursery stock. This could account for its spotty distribution and its restriction to suburban and agricultural areas. For unknown reasons almost all records are coastal.