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Zoogeography of mole crickets (Orthoptera: Gryllotalpidae)
in the West Indies

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Zoogeography of mole crickets (Orthoptera: Gryllotalpidae) in the West Indies

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Abstract. Four species of mole crickets (Orthoptera: Gryllotalpidae) are known from the West Indies: *Neocurtilla hexadactyla* (Perty), *Scapteriscus abbreviatus* Scudder, *S. didactylus* (Latreille), and *S. imitatus* Nickle and Castner. All are adventive (not native). We document their distributions in West Indian islands/countries by use of records from the literature and examination of specimens. *Scapteriscus abbreviatus* has been suggested to have arrived in, and been transported about the West Indies in ship ballast (immigration). Based on records of arrival in various parts of the West Indies and the species' inability to fly, this suggestion seems reasonable. *Scapteriscus imitatus* apparently was released in Puerto Rico as a result of mistaken identification (introduction – arriving with assistance from humans – although inadvertent), and has not expanded its range in the West Indies. Although the principal mode of dispersal for the other two species also has been suggested to be ship ballast, we present an alternative based on flight which would seem at least equally as plausible. We suggest that *S. didactylus* could have dispersed by flight from South America through the Lesser Antilles; likewise *N. hexadactyla* probably from the Yucatan Peninsula to Cuba, and from South America northward through the Lesser Antilles, in at least some localities assisted by wind. Our zoogeographical alternative, if correct, means that the natural range expansions of these latter two species began very long ago and without human assistance – they were not introduced recently to the West Indies.

Key words. *Neocurtilla*, *Scapteriscus*, Greater Antilles, Lesser Antilles, West Indies, North America

Introduction

Given the small number of species of mole crickets in the West Indies, it is remarkable that so much confusion exists about their specific identities, origins, means of dispersal, and distributions. The names (current names bolded) that have been applied, rightly or wrongly, to species in the West Indies are *Gryllotalpa hexadactyla* Perty [= ***Neocurtilla hexadactyla*** (Perty)], *Gryllotalpa borealis* Burmeister [= ***Neocurtilla hexadactyla*** (Perty)], *Gryllotalpa didactyla* Latreille [= ***Scapteriscus didactylus*** Latreille)], *Gryllotalpa variegata* Burmeister [= ***Scapteriscus variegatus*** (Burmeister)], ***Scapteriscus abbreviatus*** Scudder, ***Scapteriscus vicinus*** Scudder, and ***Scapteriscus imitatus*** Nickle and Castner. Several of these species' records are the result of misidentifications in the taxonomic and economic entomology literature. The consequence is that anyone attempting to mine the older literature (pre-1980s) and even a few more recent contributions for its behavioral, ecological, and pest-management content is likely to become confused. In fact, only four species currently occur there, and all arrived from somewhere else.

Walker and Nickle (1981) interpreted the colonization of the southeastern USA by South American *Scapteriscus* mole crickets. Nickle and Castner (1984) concentrated on *Scapteriscus* specimens in Puerto Rico and the US Virgin Islands. From those two papers, emerged a partial zoogeographical history, complete for *Scapteriscus* mole crickets in the USA at the time, but incomplete for the West Indies and for *Neocurtilla*. These authors, appropriately, relied entirely upon specimens they had examined in some museum collections, to verify the data. Unfortunately, the specimens they examined failed to explain the whole zoogeographical story. Subsequently, Otte and Perez (2009) listed the distribution of mole crickets in the Caribbean briefly, but their failure to list *Neocurtilla hexadactyla* as being present and listing of *Scapteriscus vicinus* as being present, despite a lack of evidence, render their list suspect. In this paper,

we bring the distribution of the species of mole crickets in the West Indies up to date. Older publications are reexamined and reinterpreted, and information from newer ones is added, allowing a fuller examination of the zoogeographical story. We suggest plausible explanations for the arrival of mole cricket species in the West Indies, and their subsequent dispersal throughout the islands, based on the accumulated data.

Occurrence and Distribution of Mole Crickets in the West Indies

We documented, as well as possible, the year in which each mole cricket species was first recorded for each West Indian island/country. The first record was either the earliest date of collection (if that could be determined) or the earliest date of a report in the literature. We examined specimens from four collections: ANSP (Academy of Natural Sciences of Philadelphia); FSCA (Florida State Collection of Arthropods); ICTA (Imperial College of Tropical Agriculture, now part of the University of the West Indies), Trinidad; and NHM (Natural History Museum), London. Specimens in museums are inadequate to explain presence much before the 20th century, so the published works of many authors were scrutinized and in some instances reinterpreted. All of the records provided by Brunner von Wattenwyl and Redtenbacher (1892), Brunner von Wattenwyl (1893), Walker and Nickle (1981), and Nickle and Castner (1984), supplemented by Nickle and Frank (1988) and Nickle (1992, 2003), are here accepted.

We acknowledge that even when a date of collection is provided, the species may have been present longer or much longer, because it may have been years after a species arrived that a collector detected and collected specimens. Some West Indian islands still have no published records of mole crickets, although it would be surprising if any but the smallest and/or northernmost islands (e.g., Cayman Islands and some of the Bahamas) has no species of mole crickets. Some collections for which we have not gained access may reveal earlier records for certain islands (e.g., Barbados).

We also acknowledge that “gaps” in the distribution of mole crickets can occur for several reasons apart from true absence or inadequate collection. A species once occupying an area may subsequently have disappeared from the area. One example from the southeastern USA is *Scapteriscus abbreviatus*, which colonized southeastern Georgia by 1904, but has not been observed in Georgia at least since 1988 (W. G. Hudson, pers. comm.) for unknown reasons. The species now occurs in many places farther south, at least along most of the eastern coast, southwestern coast, and a few inland sites in Florida. A species may have dispersed to an area, but failed to establish there, perhaps because it was intercepted at or after arrival. Individuals of two Neotropical mole cricket species somehow arrived in Switzerland, but failed to establish (Nickle and Castner 1984). One specimen of the European mole cricket *Gryllotalpa gryllotalpa* (L.) (in FSCA) was reported to have been collected in 1924 at Belle Glade, Florida (Nickle and Castner 1984), but the species does not have a Florida population. Perhaps individuals arrived in Belle Glade by rail from the northeastern USA, where the species is established; or perhaps the specimen was mislabeled.

***Neocurtilla hexadactyla* (Perty) 1832** [= *Gryllotalpa hexadactyla* Perty 1832, = *Gryllotalpa borealis* Burmeister 1838 (an old-established synonymy)]

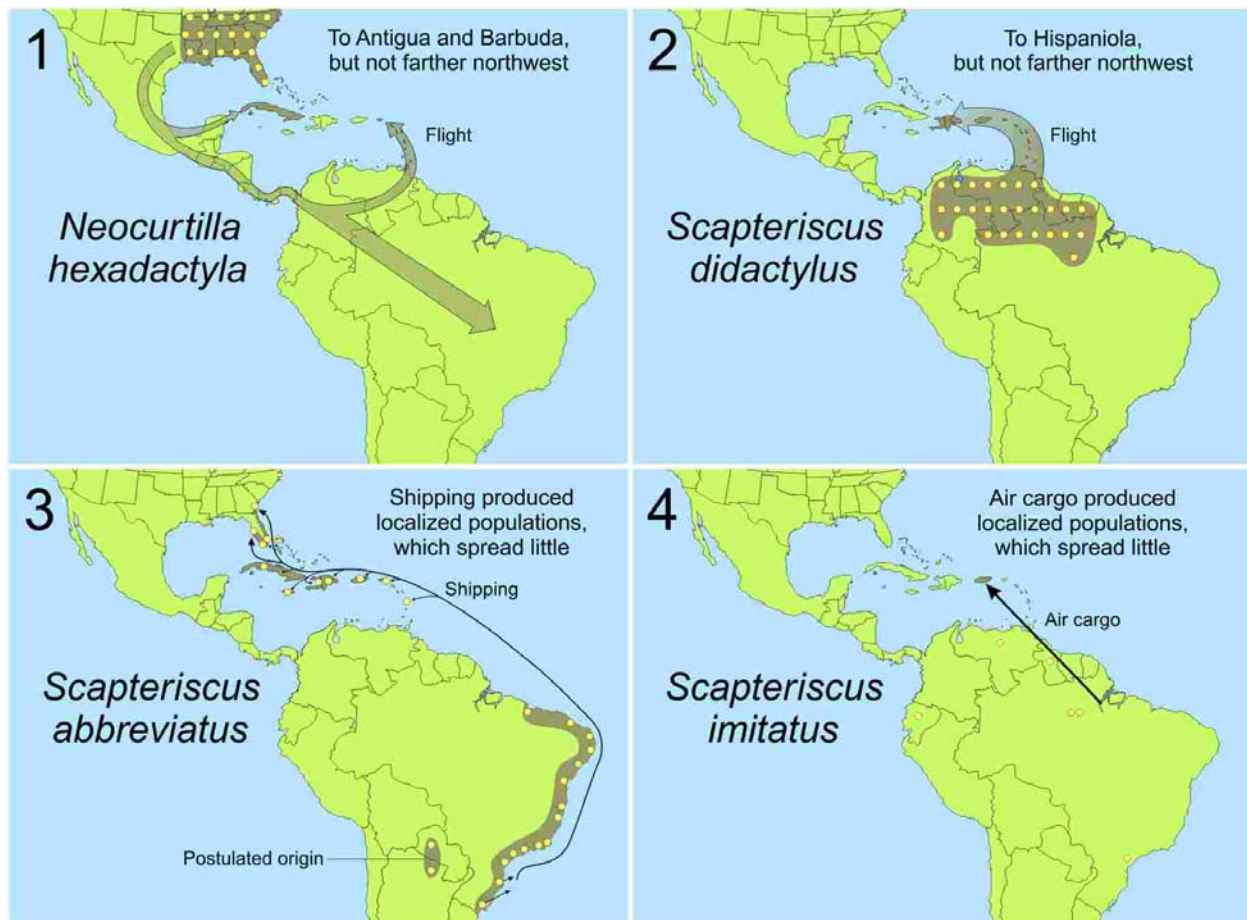
This is the only mole cricket in the West Indies having four fixed tibial dactyls (Fig. 5) in the West Indies to the present. West Indian adults have long flight wings (Fig. 9). Many Florida adults have short flight wings and cannot fly (Fig. 10). This species seems to be a very minor pest in the West Indies and Florida, perhaps because of its diet and habitat, neither of which is fully understood. The species' distribution in the West Indies:

Trinidad and Tobago: Trinidad – **1906** (Bruner 1906).

Grenada – **1893** (Brunner von Wattenwyl 1893), see also Woodruff et al. (1998) and Frank et al. (2002).
St. Vincent – **1892** (Brunner von Wattenwyl and Redtenbacher 1892).

Barbados – **1953** (Tucker 1953).

St. Lucia – **1888** (specimen in NHM labeled Fort Castries St. Lucia W.I. Feb. 88, examined by J.H. Frank in September 2011 and identified as *N. hexadactyla*).



Figures 1-4. 1) Proposed dispersal pathways of *Neocurtilla hexadactyla*. 2) Proposed dispersal pathway of *Scapteriscus didactylus*. 3) Proposed dispersal pathway of *Scapteriscus abbreviatus*. 4) Dispersal pathway of *Scapteriscus imitatus* to Puerto Rico.

Martinique – **2009** (Anon. 2009) a clear photograph, taken in October 2009 of a living adult of this species, undoubtedly many years after the arrival of the species in that island.

Dominica – **1899** (specimen in NHM labeled Dominica 99-119 examined by J.H. Frank in September 2011 and identified as *N. hexadactyla*).

Guadeloupe – **1839*** (Audinet Serville 1839), repeated by Saussure (1894).

Montserrat – **1904** (Rehn 1905 as *N. hexadactyla*, based on a specimen collected there in 1904 by H. A. Ballou, now in ANSP, photographed there by J.A. Weintraub in 2010 and from the photograph confirmed as *N. hexadactyla* by J.H. Frank).

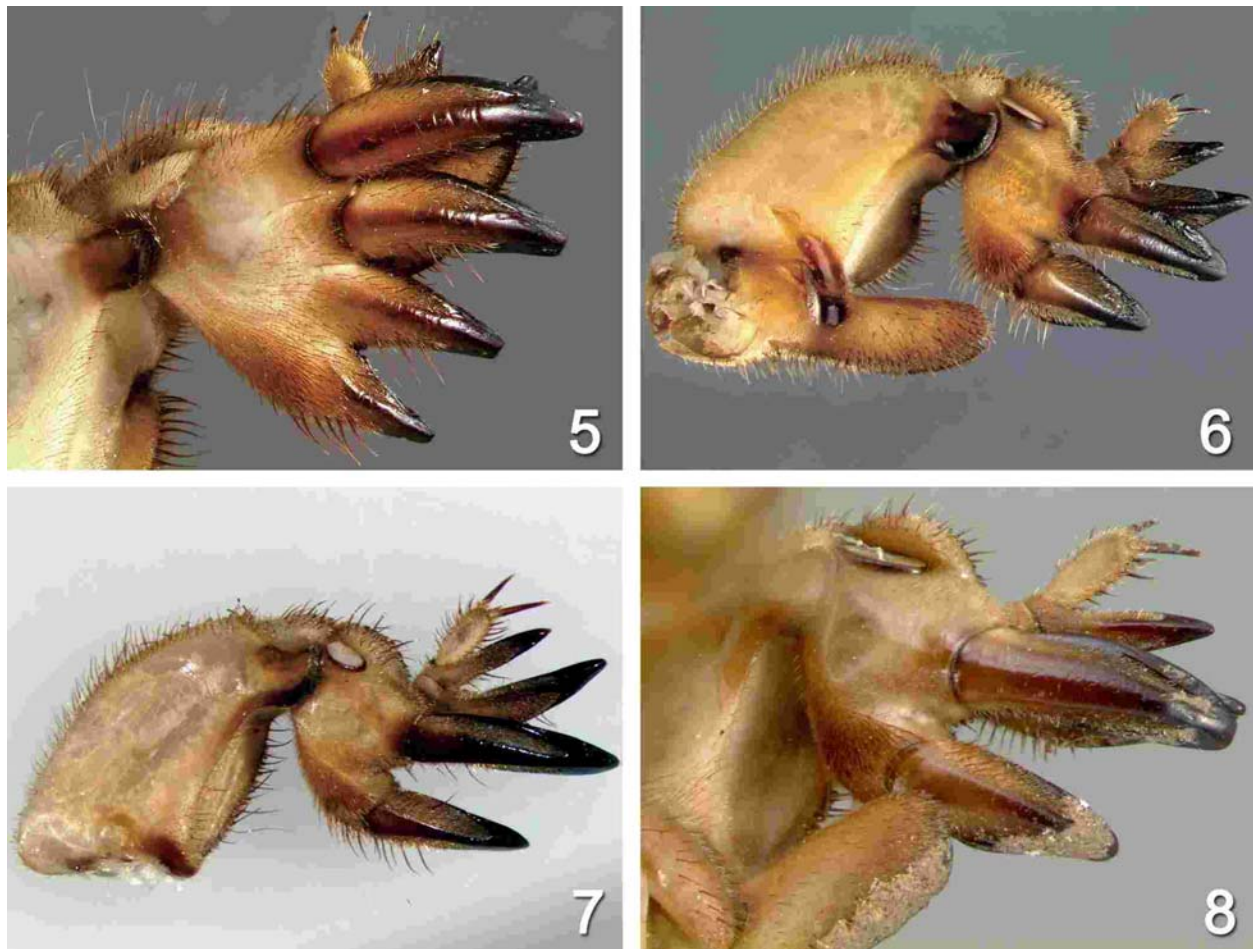
Antigua and Barbuda: Antigua – **1918** (Caudell 1922); Barbuda – 1899 (specimen in NHM labeled Barbuda Gregory 99.164 examined by J.H. Frank in September 2011)

Puerto Rico – **1925-1926** (specimen in NHM labeled Porto Rico 1925-1926 H.E. Box, Pres. by Imp. Inst. Ent. Brit. Mus. 1930-336, examined by J.H. Frank in 2011, comments below).

Cuba – **1857*** (Guérin-Méneville 1857) (also, Saussure 1874 reported that he had specimens of *G. borealis* from Cuba), see also Zayas 1974 for indication of its continued presence.

* Note that the records from Guadeloupe and Cuba stand out as being earlier than the others, thanks to studies by European taxonomists.

Frank et al. (2007) found no evidence for the existence of *Neocurtilla hexadactyla* in Puerto Rico. Now we see (above) that a specimen exists. Its collector, Harold E. Box, was a British entomologist who moved to the New World tropics after spending years in East Africa. In 1925-1927 he was employed by Central Aguirre, a sugarcane plantation in southern Puerto Rico. Because of his employment history, it

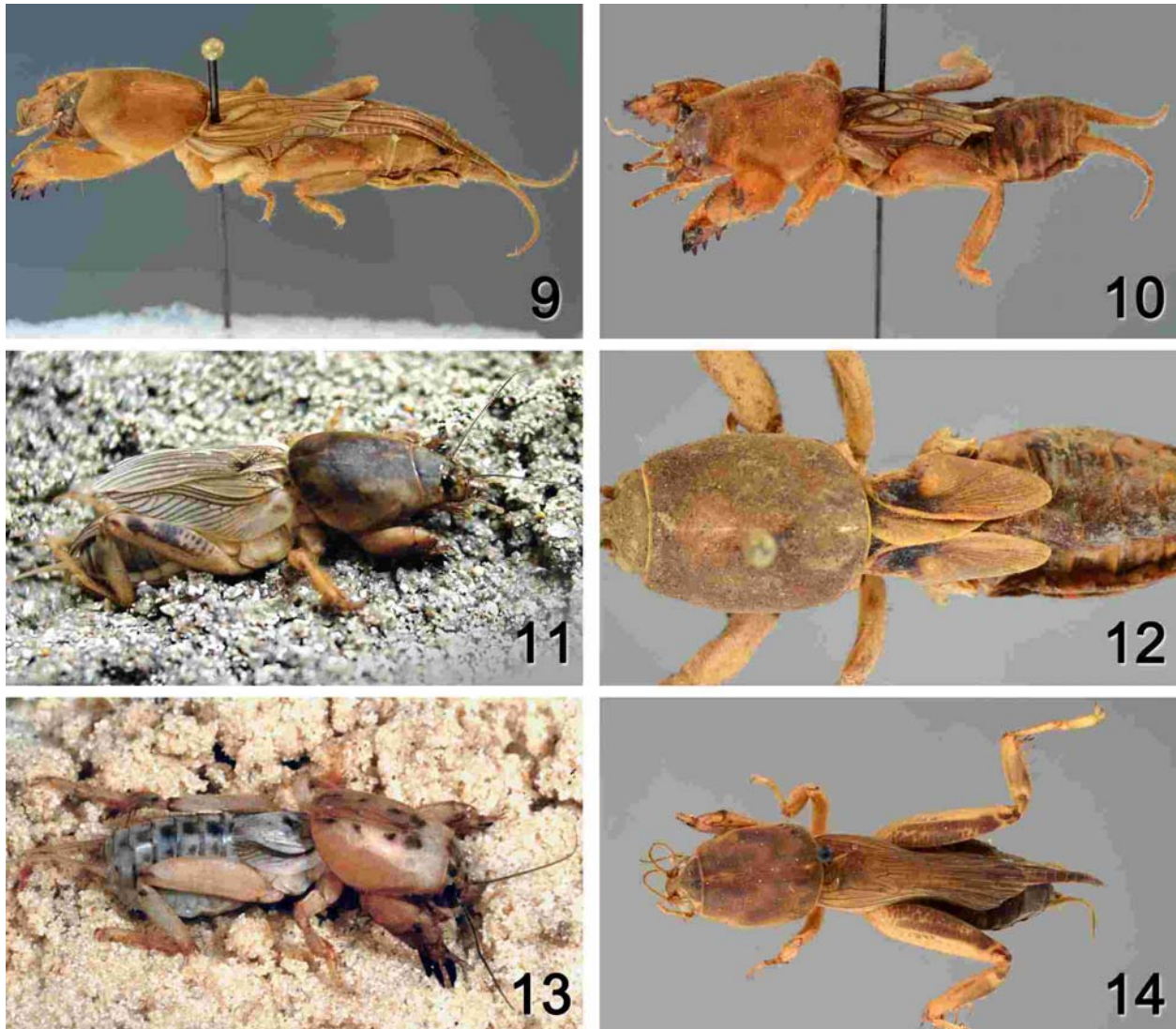


Figures 5-8. Gryllotalpid dactyls. **5)** *Neocurtilla hexadactyla*. Four fixed tibial dactyls. **6)** *Scapteriscus didactylus*. Two fixed tibial dactyls separated at the base. **7)** *Scapteriscus abbreviatus*. Two fixed and widely separated dactyls (the trochantal blade is broken off). **8)** *Scapteriscus imitatus*. Two fixed tibial dactyls separated at the base.

was natural that he would send unusual specimens to the Imperial Institute of Entomology in London. How was it possible that he would find a specimen of *N. hexadactyla* in Puerto Rico when thousands of other mole crickets examined in that island failed to produce one? Discounting the possibility of erroneous labeling, one possible explanation is an extraordinary weather event. Because adults are long-winged in most parts of the species' range and can fly readily (Frank et al. 2007), they are candidates for wind dispersal. The intense hurricane "San Liborio" entered the Caribbean at Martinique and then hit southern Puerto Rico on 23-24 July, 1926, killing 25 persons. The mole cricket found by Box may have arrived in Puerto Rico by wind-assisted flight from Martinique or nearby island. It seems that the species did not establish a population in Puerto Rico as a consequence (evidence in Frank et al. 2007). Extreme long-distance wind-assisted flight of Orthoptera is evidenced by desert locusts (*Schistocerca gregaria* [Forskåll]) found in Antigua, Barbados, Dominica, Martinique, St. Kitts, St. Lucia, St. Vincent, Trinidad and Suriname in October 1988 (Kevan 1989, Ritchie and Pedgley 1989). After crossing the Atlantic, desert locusts also failed to establish a West Indian population.

Scapteriscus didactylus (Latreille) 1804 [= *Gryllotalpa didactyla* Latreille 1804]

Adults and nymphs have two fixed tibial dactyls which are well separated at the base (Fig. 6). Adults are long-winged (Fig. 11) and can fly. They are attracted readily to incandescent light. Large nymphs have short flight wings, darkly colored at the base, but these are displayed above the tegmina (Fig. 12), rotating to their adult position below the tegmina at final molt. It is the large nymphs of this species that



Figures 9-14. Gryllotalpid habitus. **9** *Neocurtilla hexadactyla*. Habitus of an adult (from Grenada) with long flight wings. The cerci are prominent. **10** *Neocurtilla hexadactyla*. Habitus of an adult (from Florida) with short flight wings, barely protruding behind the tegmina. **11** *Scapteriscus didactylus*. Habitus of an adult (from Puerto Rico). **12** *Scapteriscus didactylus*. Habitus of a large nymph (from Trinidad) with short flight wings, darkly colored at the base, and dorsal to the tegmina before wing reversal. **13** *Scapteriscus abbreviatus*. Habitus of an adult (from Florida) with truncate apices of the tegmina. **14** *Scapteriscus imitatus*. Habitus of an adult (from Puerto Rico).

have been confused by a few authors with *S. variegatus* [a Central American species known from Guatemala south to Costa Rica (Nickle 2003)].

This species was documented as a pest in St. Vincent in 1837. It is by far the major pest mole cricket in the West Indies, and was cited as a pest there by Harris (1862) who, unfortunately, did not name the islands from which he had received reports of damage [although perhaps he merely cited Kirby and Spence (1846)]. When pest *Scapteriscus* mole crickets arrived in Georgia and Florida (USA) at the end of the 19th century, they (actually three species of them together) were wrongly assumed at the time to be this one species (e.g., Worsham and Reed 1912). The individual identities and origins were sorted out by Walker and Nickle (1981): Florida's pest mole cricket problem did not, after all, result from arrival of *S. didactylus* from the West Indies, but from *S. abbreviatus*, *S. borellii*, and *S. vicinus* from southern South America, and was largely solved by importation of biological control agents from southern South America (Frank and Walker 2006).

Works by Barrett (1902) and Zwaluwenberg (1918) provide good accounts of the behavior, development, and economic effect of *S. didactylus*. The biological campaign against it in Puerto Rico (e.g., Wolcott 1938, 1941) provides much useful information. Unfortunately, many publications after Rehn and Hebard (1916) give its name erroneously as *S. vicinus* because of an error of taxonomic judgment by those authors. This error influenced identifiers at museums and Wolcott and other agricultural entomologists in the West Indies to make the same error. The species' distribution in the West Indies:

Trinidad and Tobago: Trinidad – **1901** (Anon. 1901 as *G. didactyla*) – 1906 (Bruner 1906 as *S. didactyla*) – 1909 (Nickle and Castner 1984) – 1929 (Allan 1929, including a detailed species description of *S. didactylus* and statement that he had not encountered *S. vicinus*).

Grenada – **1893** (Brunner von Wattenwyl 1893, cited also by Woodruff et al. 1998) – 1905 (Nickle and Castner 1984) – 1990 (Frank et al. 2002).

St. Vincent – **1837*** (A letter from Mr. M'Barnet [presented by Johnstone 1837] stated that he believed “the mole cricket” “has always I believe been known in the West Indies.” That it was a species destructive to agriculture is clear from the words of Mr. M'Barnet. This mole cricket was named as *Grylotalpa didactyla* by Kirby and Spence (1846 p. 136) – 1892 (Brunner von Wattenwyl and Redtenbacher 1892 as *S. didactylus*) – 1901 (Anon. 1901 as *G. didactyla*).

Barbados – **1903** (Rehn 1905 as *S. variegatus* !) – 1953 (Tucker 1953, as *S. variegatus* !) – see previous comments concerning *S. variegatus*.

St. Lucia – **1889** (Two specimens in NHM labeled “Santa Lucia G.A. Ramage June 1889 97-67” examined by J.H. Frank in September 2011 – G. A. Ramage, a collector of natural history specimens, is known to have been in the island of St. Lucia, West Indies, in 1889 (Smith 1889) despite the unusual spelling of the name of the island) – 1896 (Saussure 1896 cited by Rehn 1905 as *S. variegatus* !) – 1901 (Anon. 1901 as *G. didactyla*) – 1904 (Crawford Exp. St. Lucia 1904-156, specimen in NHM examined by J.H. Frank in September 2011) – 1941 (specimen borrowed from ICTA and examined by J.H. Frank in 2004) – 1973 (Nickle and Castner 1984 examined a specimen from St. Lucia collected in 1973).

Martinique – **1952** (Nickle and Castner 1984).

Dominica – **1901** (Anon. 1901 as *G. didactyla*) – 1933 (Nickle and Castner 1984, specimen examined and identified as *S. didactylus*).

Guadeloupe – **2011** (Meurgey 2011).

St. Christopher-Nevis: St. Kitts – **1903** (Anon. 1903 as *S. didactylus*) – 1941 (Wolcott 1941, as *S. vicinus* !).

US Virgin Islands, St. John and St. Thomas – **1979** both islands (Ivie and Nickle 1986).

Puerto Rico – **1797*** (Frank et al. 1987, 2007 with explanation) – 1892 (Brunner von Wattenwyl and Redtenbacher 1892 as *S. didactylus*, later misrepresented by others first as *N. hexadactyla* ! and still later as *S. vicinus* ! (see Frank et al. 2007 for explanation).

Haiti – **1892** (Brunner von Wattenwyl and Redtenbacher 1892).

Dominican Republic – **1986** (Frank et al. 1987).

*Note that the records from Puerto Rico and St. Vincent stand out as being much earlier than for any other *Scapteriscus* species mentioned here. The letter by Mr. M'Barnet mentioned above stresses the antiquity of the presence of this species at least in the Lesser Antilles.

Scapteriscus abbreviatus Scudder 1869

Adults and nymphs have very widely separated tibial dactyls (Fig. 7). Adults are short-winged, and the apices of the tegmina are truncate (Fig. 13). This species is a pest of highly managed turf (golf courses) in coastal southern Florida and St. Croix, and a minor pest (because of its restricted range) of crops elsewhere. The species' distribution in the West Indies:

Guadeloupe – **1938** (Nickle and Castner 1984).

Jamaica – **1926** (Gowdey 1926, misidentified as *S. didactylus* !) – see Frank and Walker (2003), who identified specimens from the Institute of Jamaica as *S. abbreviatus*, for explanation.

US Virgin Islands: St. Croix – **1918** (Zwaluwenburg 1918 p. 6, misreported as “the changa”, the vernacular name bestowed on *S. didactylus* in Puerto Rico !) – year? (Miskimen and Bond 1970 as

probably *S. abbreviatus*) – 1940 (Nickle and Castner 1984 as *S. abbreviatus*) – (Ivie and Nickle 1986 discounted presence of any species other than *S. abbreviatus*) – 1991 (Frank and Keularts 1996: fresh specimens of *S. abbreviatus* collected and identified with explanation of history).

Puerto Rico – **1910** (one specimen in NHM labeled “Antilles P. Rico 1910-339” examined by J.H. Frank in September 2011 and identified as *S. abbreviatus* – 1917 Wolcott (1924) as *S. abbreviatus* – 1920 Nickle and Castner (1984) as *S. abbreviatus*).

Haiti – **1929** (Nickle and Castner 1984).

Cuba – **1906** (Cook 1906, misidentified as *S. didactylus* ! and Rehn 1909 consequently listed as *S. didactylus* !) – (Bruner 1940, with an unequivocal photograph, as *S. abbreviatus*) – (Zayas 1974 as *S. abbreviatus*) – (Ruíz Baliú and Fernández Iriana 1996, as *S. abbreviatus*). Nickle (2003) stated that *S. abbreviatus* may have been present in Cuba “perhaps as early as 1750” but provided no evidence – the earliest reference he cited is Saussure 1874, but Saussure does not mention the presence of this species in Cuba).

Bahamas: New Providence Island, Nassau – **1922?** (Caudell 1922 as *S. abbreviatus*; the specimen examined by Caudell, supposedly collected by W. M. Mann in Nassau sometime before 1922, and now in the US National Museum of Natural History) – this is curious because W.M. Wheeler is known to have collected on New Providence in May 1904, whereas his student W.M. Mann collected on other Bahamian islands (Andros and Mangrove Cay) in May-June 1917 – Nickle and Castner (1984) re-examined the specimen and confirmed its identity but added no details – it is even more curious because of a specimen in the University of Iowa collection mentioned by Caudell (1922) as being labeled as *S. variegatus* and B 1047.013 but identified by him (Caudell) as *S. abbreviatus*, collector and collection locality unknown (see below).

***Scapteriscus imitatus* Nickle and Castner 1984**

Its foreleg, showing spacing of the two fixed dactyls (Fig. 8); and its habitus (Fig. 14), showing it as a smaller, darker, and more slender mole cricket, distinguish it from *S. didactylus*. It has no recognized pest status. The species’ distribution in the West Indies:

Puerto Rico – **ca. 1940** (Nickle and Castner 1984, although the first Puerto Rican specimen they saw was collected in 1982). It seems now to be restricted to a small area in northwestern Puerto Rico (Frank et al. 2007).

Records of two other species in the West Indies appear to be erroneous. All of the published records of *Scapteriscus vicinus* in the West Indies seem to be based on misidentification. A few erroneous records of occurrence in the West Indies of *S. variegatus* exist. Barbados (1903; Rehn 1905): “Barbados. July 10, 1903. (H. A. Ballou). [No. 224]” One male.” “This specimen has the wings shorter than the tegmina, in this resembling *S. abbreviatus* Scudder, which, however, has the tegmina of a very different shape. The species (*S. variegatus*) has been recorded from St. Lucia by Saussure.” Rehn (loc cit.) believed this to be an adult of a short-winged mole cricket that was not *S. abbreviatus*. It is almost certainly a large nymph of *S. didactylus*, however (see Fig. 10 and explanation below). Barbados (1953; Tucker 1953): “*Scapteriscus variegatus* Burmeister – Specimens taken under a dripping tap, also in a muddy situation.” This record was reported uncritically by Bennett and Alam (1985), pers. comm. from F.D. Bennett to J.H. Frank on 7 Feb 2011. St. Lucia (1896; Saussure 1896): Cited by Rehn (1905). This probably is another misidentification of a nymph of *S. didactylus*, which is reported from that island by Nickle and Castner (1984). This erroneous record may be what led Rehn (1905) to misidentify a *S. didactylus* nymph from Barbados, another of the Windward Islands. Locality unknown, University of Iowa, “*Scapteriscus variegatus*, B 1047. 013.” The specimen was later identified by Caudell (1922) as *S. abbreviatus*. Its origin is obscure, but perhaps the West Indies.

The records of *Scapteriscus variegatus* (Burmeister) from Barbados need further mention. The identity of a specimen discussed by Rehn (1905) as having been collected by H. A. Ballou in Barbados in 1903 is unclear. Rehn (1905) stated that the wings are shorter than the tegmina, which are “of a very different shape” from those of *S. abbreviatus*, and he attributed it to “*S. variegatus* (Burmeister).” Caudell (1922) commented on Rehn’s interpretation, but drew no new conclusion. Tucker (1953) mentioned two specimens from Barbados that he attributed to this same species. “Short-winged” mole cricket specimens from

elsewhere, Trinidad, suggest another interpretation. Final instar nymphs of *S. didactylus* have developing flight wings as long as 40% of the length of the abdomen. In repose, these wings are dorsal to, and longer than the tegmina; not until the nymphs molt to the adult stage do the tegmina rotate to assume the dorsal position seen in the adult, a phenomenon known in Orthoptera as wing reversal. [An instance of this in instar VI of *Schistocerca americana* (Drury) is illustrated by Capinera 1993.] At first glance, it thus appears that the flight wings are the tegmina – but their apices are pointed, unlike the truncate tegmina of *S. abbreviatus*, and their venation is unlike that of tegmina. Furthermore, the bases of the flight wings are darkly pigmented in *S. didactylus* nymphs as the basal venation of the tegmina of *S. variegatus* was reported to be (Nickle 2003). It is likely, therefore, that Rehn (1905) mistook a large nymph of *S. didactylus* (Fig. 10) as an adult of *S. variegatus*; if the specimen examined by Rehn was returned to the collection of the Department of Science and Agriculture in Barbados as seems probable, this would also account for the listing of *S. variegatus* by Tucker (1953) in that island without mention of *S. didactylus*. This scenario makes sense in that *S. didactylus* is known from the neighboring islands of Dominica, Grenada, Martinique, St. Lucia, St. Vincent and Trinidad, whereas no specimens of a short-winged (adult) mole cricket from those islands have been found there.

We plotted the first records of occurrence (rank) on West Indian islands against the distances of the islands from South America (rank). The relationships for the two widespread species capable of flight are shown in Fig. 15A, B. The similarity of these relationships is not surprising, as extensive collection in one area is likely to have revealed both species, even if one or both species initially were misidentified. Neither the strong tendency for earlier records to be nearer South America, nor the apparent division of islands into separate “groupings” is readily explainable, based on the historical record. It is possible, for instance, that British entomologists based perhaps in Barbados searched systematically for pests south to north in the Lesser Antilles, but we have not encountered any statement to that effect. That these two relationships parallel our proposed dispersal pathways for the species (see below) may be entirely fortuitous, but the matter would seem to warrant further examination. The relationship for the flightless species is shown in Fig. 15C.

Zoogeography

The zoogeography of mole crickets in the West Indies hinges on the likelihoods of two principal dispersal mechanisms, hitchhiking and flying, for three of the four species. We exclude further consideration of *Scapteriscus imitatus*, which, in the strictest sense, is the only West Indian mole cricket rightly called “introduced.” This species is thought to have been transported deliberately to Puerto Rico and released, in the belief that it was *S. didactylus* (which already occurred in Puerto Rico), during an attempt to introduce the parasitoid wasp *Larra bicolor* F. as a biological control agent for *S. didactylus* (Nickle and Castner 1984). It is recorded from nowhere else in the West Indies. We begin with two simple premises, that the distributions of flying species tend to be attributable to flight, and the distributions of non-flying species to some other means of dispersal. Thus, we suggest that the principal mode of dispersal of *Neocurtilla hexadactyla* and *S. didactylus* among the West Indian islands was flight, and that the principal mode for *S. abbreviatus* was hitchhiking. Although possible, we discount the likelihood of passive aerial dispersal by *S. abbreviatus*, because of its size. These suggestions contrast with the suggestions of Nickle and Castner (1984) and Nickle (2003) that the distributions of all three species in the West Indies were the result of hitchhiking. Although no clear resolution of this disagreement may be possible, even with genetic data, we attack the problem by comparing the distributions of non-flying and flying species, including species not found in the West Indies, but adventive to North America (*S. borellii*, *S. vicinus*).

All species of *Scapteriscus* in North America were presumed to have arrived as contaminants of ship’s ballast (Walker and Nickle 1981). They were not introduced, in the strictest sense, but rather were hitchhikers [stowaways] and may be considered immigrants (see Zimmerman 1948, Frank and McCoy 1990). *Scapteriscus vicinus* Scudder 1869 is native to temperate South America. It likely arrived at its sole port of entry into the USA, Brunswick, Georgia (1899), after a long and direct sea voyage from the Río de la Plata (Argentina and/or Uruguay). From its port of entry, the species spread slowly north on the coastal plains to North Carolina and south to Florida (1919), and eventually west to Texas (1996; Reinert and Drees 2007). *Scapteriscus borellii* Giglio-Tos 1894 [= *S. aletus* Rehn and Hebard 1916

(synonymy due to Nickle 1992)] also is native to southern South America, and like *S. vicinus*, likely arrived in the USA from the Río de la Plata. Apparently, the species spread out from four southeastern seaports (Brunswick, Georgia; Charleston, South Carolina; Mobile, Alabama; and Port Arthur, Texas) in the early 20th century (Walker and Nickle 1981). First records of occurrence are: Georgia = 1904, South Carolina = 1915. Alabama = 1919; Florida = 1924, Texas = 1925, Louisiana = 1926, Mississippi = 1926, and North Carolina = 1927. Subsequently, it has been recorded from western Arizona (1987; Nickle and Frank 1988); Los Angeles County, California (2007; Arakelian 2008); and the Mapimi Biosphere Reserve, Chihuahua, Mexico (2005; Rivera-García 2006). In contrast to these flying species, the dispersal of *S. abbreviatus* in North America has been restricted. The earliest record is from Tampa, Florida (1899), with subsequent records from Miami, Florida (1902), Brunswick, Georgia (1904), and Key West, Florida (1905). The species may have arrived in ship's ballast from Montevideo or Buenos Aires (Walker and Nickle 1981). Since the early 20th century, additional records seem to come only from Florida. Of course, the restricted distribution of *S. abbreviatus*, compared to the other North American species, may be for reasons other than its inability to fly. For example, it seems to prefer coastal areas over inland (pers. obs.). Although its origin may be inland Argentina or Paraguay (Walker and Nickle 1981), *S. abbreviatus* extended its range northward along the coast of eastern Brazil, attaining at least 20 seaports from Brazil's southernmost state to the mouth of the Amazon (Fowler 1987).

Nickle and Castner (1984) speculated that *Scapteriscus abbreviatus* first arrived from South America in one or more West Indian islands, and secondarily dispersed to North America, but the data from North America do not support this speculation. The earliest adventive [arrived from somewhere else (Frank and McCoy 1990, Wheeler and Hoebeke 2009)] record outside South America is from North America (Tampa, Florida, 1899), and the first record in the West Indies is from only slightly later (1906). The earliest North American records for *S. borellii* (1904) and *S. vicinus* (1899) also are from the same time period. We suggest that all of these species were transported as contaminants of ship's ballast from ports in South America to ports in North America and, in one case, to ports in the West Indies. *Scapteriscus abbreviatus* may have been transported from one

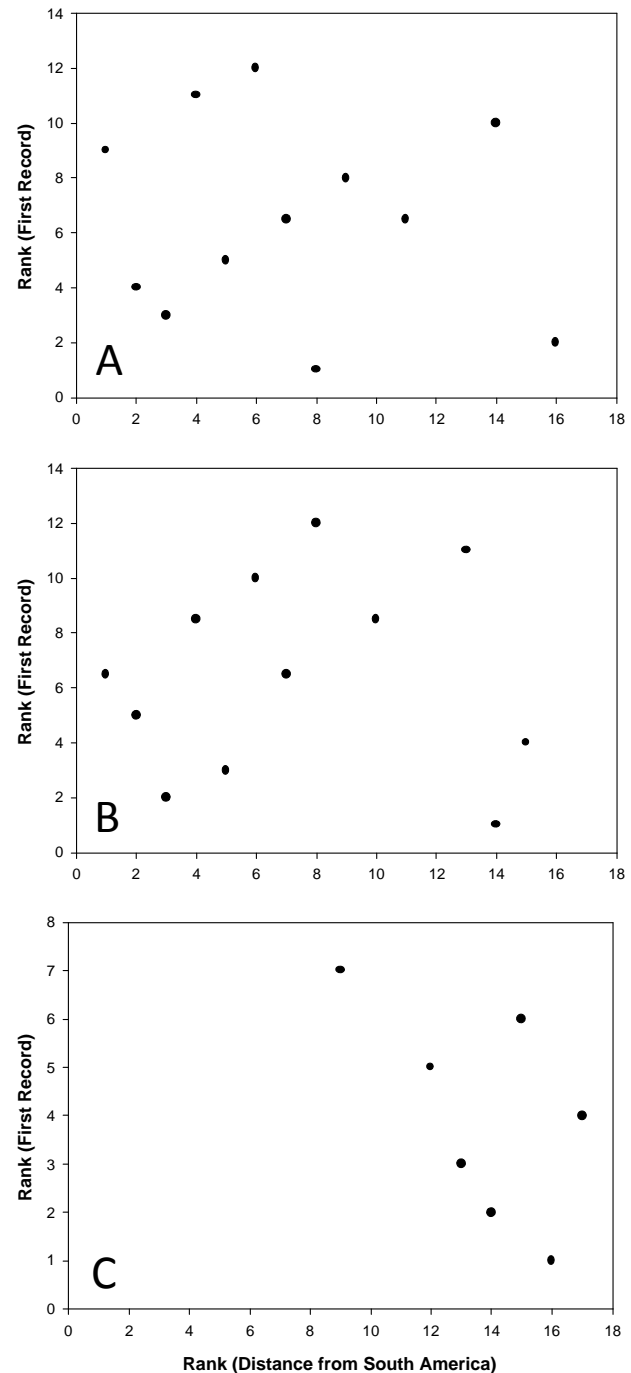


Figure 15. Relationships of first record of occurrence (rank) with distance from South America (rank). Distance increases from left to right. Along the distance axes, 1 = Trinidad/Tobago, 2 = Grenada, 3 = St. Vincent, 4 = Barbados, 5 = St. Lucia, 6 = Martinique, 7 = Dominica, 8 = Guadeloupe, 9 = Montserrat, 10 = St. Kitts/Nevis, 11 = Antigua/Barbuda, 12 = Jamaica, 13 = US Virgin Islands, 14 = Puerto Rico, 15 = Hispaniola, 16 = Cuba, 17 = Bahamas. (A) *Neocurtilla hexadactyla*, (B) *Scapteriscus didactylus*, (C) *Scapteriscus abbreviatus*.

or more of numerous Brazilian seaports to North America, to Guadeloupe, and to the Greater Antilles, as illustrated in Fig. 3. The absence of *S. borellii* and *S. vicinus* in the West Indies suggests either that they never arrived there – perhaps because they were transported only by ships sailing directly from southern South America to North America – or that they arrived there and could not colonize or subsequently went extinct locally. Nickle (2003) suggests that *S. vicinus* may not have become established in the West Indies because it is not adapted for a tropical climate; yet Nickle and Castner (1984) record it for Magdalena, a tropical coastal province of Colombia. Likewise, Nickle (2003) cites the presence of *S. borellii* in many tropical states of Brazil, and in Colombia and Venezuela. These species could have failed to colonize West Indian islands for reasons other than tolerance for tropical conditions.

The flying species in the West Indies display a quite different distributional pattern from those of any of the species we have discussed so far. *Neocurtilla hexadactyla* was described first from South America by Perty (in 1832 as *Gryllotalpa hexadactyla*) and soon thereafter from North America by Burmeister (in 1838 as *Gryllotalpa borealis*). In subsequent years, it became clear that *N. hexadactyla* is distributed from the eastern USA through Mexico, Central America and South America, and north from South America through the chain of the Lesser Antilles as far north as Antigua (Caudell 1922). The species has been known from Cuba since the mid-19th century (Guérin-Méneville 1857). Based on the distribution of the species' co-evolved specialist natural enemies *Larra analis* (F.) (Hymenoptera: Crabronidae) (see Menke 1992) and *Steinernema neocurtillae* Nguyen and Smart (Nematoda: Steinernematidae), which are known only from eastern North America, *N. hexadactyla* appears to be native to eastern North America, from southern Ontario to Florida, and west to Nebraska and Texas. *Scapteriscus didactylus*, on the other hand, is native to the northern part of South America (Colombia, Venezuela, Guyana, Suriname, French Guiana, and perhaps extreme northeastern Brazil).

General dispersal pathways from eastern North America via Mexico and Central America to South America – with a side-track from southeastern Mexico to Cuba – and from northern South America northward through the chain of islands of the Lesser Antilles have been elucidated (e.g., Rosen 1975, Figs. 2H and 3H). These general pathways appear to account well for the distribution of *Neocurtilla hexadactyla* (Fig. 1). Following one pathway, the species may have expanded its range northward from South America through the West Indies, colonizing island after island. It is known from as far north as Antigua, Barbuda, and Montserrat, but apparently so far has not been able to reach the British and US Virgin Islands, Puerto Rico, Hispaniola, or Jamaica in sufficient numbers to establish there. Perhaps Antigua, Barbuda, and Montserrat do not serve it well as stepping-stone islands (MacArthur and Wilson 1967) from which enough adults can reach islands to the northwest. The species' presence in one of the Greater Antilles, Cuba, may be a consequence of wind patterns, which allowed it to follow the common dispersal pathway from Mexico to Cuba. Hurricanes commonly move between the Yucatan and Florida via Cuba (including the 2005 Hurricane Wilma, the most intense hurricane ever recorded in the Atlantic Basin), perhaps taking flying organisms with them. *Scapteriscus didactylus* appears to have followed the same general dispersal pathway as *Neocurtilla hexadactyla*: northward from South America through the West Indies (Fig. 2). This species has not been detected in Cuba and, like *N. hexadactyla*, not in Jamaica either.

The early records of occurrence for the two flying species from throughout the West Indies – 1839 in Guadeloupe and 1857 in Cuba for *Neocurtilla hexadactyla* and 1837 in St. Vincent and 1797 in Puerto Rico for *Scapteriscus didactylus* – indicate that the species were present throughout the West Indies well before the heyday of ship traffic from South America. Although inter-island transport in ship's ballast at the end of the 19th century could have occurred, it does not appear that repeated colonization from South America during that time was the norm. It also does not seem coincidental that the first record of *S. abbreviatus* in the West Indies dates from 1906. Although the evidence indicates that these species had reached many islands by flight by the 18th or early 19th centuries, a possibility is that earlier ship traffic carried the species from South America throughout the West Indies, but we have found no literature on the subject. Perhaps *N. hexadactyla* and *S. didactylus* have been present long enough in some West Indian islands that they should now be considered naturalized.

If the zoogeographical explanations we have suggested are correct, then *Scapteriscus didactylus* may eventually arrive by wind-assisted flight in Jamaica, Cuba, and/or Florida. Florida's agricultural interests may be adequately protected because three biological control agents (*Larra bicolor*, *Ormia depleta* [Wiedemann], and *Steinernema scapterisci* Nguyen and Smart (see Frank and Walker 2006) have been

established to control other adventive *Scapteriscus* species, and are likely to be effective against *S. didactylus*. Material of these species could be sent to Cuba or Jamaica should *S. didactylus* arrive there. It also may be that *Neocurtilla hexadactyla* eventually will arrive by wind-assisted flight in the British and U.S. Virgin Islands, and then in Puerto Rico and the Dominican Republic, from islands to the southeast. These events should have no consequences for agriculture.

The following contrast succinctly expresses our arguments for how the adventive species of mole crickets arrived in the West Indian islands and North America. *Scapteriscus borellii* and *S. vicinus* (from southern South America to southeastern North America), *S. abbreviatus* (from eastern Brazil to West Indies and southeastern North America): required flight distances are too great (and, one species does not fly), and wind patterns are not suitable (winds do not blow north along the Brazilian coast) to produce the current distributions. Earliest records are from the vicinities of ports, and all are in 1899-1926, after increased trade near end of 19th century and while ship ballast was still solid (see Walker and Nickle 1981). Likely dispersal mechanism is hitchhiking. *Scapteriscus didactylus* (from Venezuela to Lesser Antilles and northward to Puerto Rico and Hispaniola); *Neocurtilla hexadactyla* (overland through Mexico and Central America to South America, and northward through Lesser Antilles, and from the Yucatan Peninsula to Cuba): required flight distances are feasible, and the directions of normal and hurricane winds are suitable (and, coincide with general dispersal pathways) to produce the current distributions. Earliest records are not restricted to ports and are very much earlier than 1899-1926. Likely dispersal mechanism is flight.

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there is also an edition with text in French, with date 1857 on its title page and with the information about *Gryllotalpa hexadactyla* on p. 353].

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