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A history of mole crickets (Orthoptera: Gryllotalpidae) in Puerto Rico

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A history of mole crickets (Orthoptera: Gryllotalpidae) in Puerto Rico

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Abstract. Published claims in 1887-1903 that the mole cricket *Neocurtilla hexadactyla* (Perty) occurs in Puerto Rico all seem to be derived from a misidentification made by Agustín Stahl, a medical practitioner and collector of natural history objects, published in 1882. That species does not seem now to occur in Puerto Rico and almost certainly never did. However, the opportunity still exists for it to colonize by wind-assisted flight from islands to the southeast just as we believe did the mole cricket *Scapteriscus didactylus* (Latreille) as an immigrant. Stahl evidently mistook the latter for the former. According to some subsequent authors, he also stated that it (the mole cricket now believed to be *S. didactylus*) arrived in the port of Mayagüez in a cargo of guano about 1850 from Peru and thus colonized Puerto Rico. We found no verification for that story, and we doubt it. The first detection of the presence of *S. didactylus* in Puerto Rico may have been by a French expedition in 1797, but this species may have been present much earlier. Two other species of *Scapteriscus* were later detected in Puerto Rico. One, *S. abbreviatus* Scudder, was detected in 1917 and likely arrived as a contaminant of ship ballast some time earlier, perhaps at the port of Mayagüez. The other, *S. imitatus* Nickle and Castner, was detected about 1940 and seems to have been introduced inadvertently, as a result of mistaken identity. In broad terms, *S. didactylus, S. abbreviatus,* and *S. imitatus* are adventive species (meaning they arrived from somewhere else and are not native) in Puerto Rico. The vernacular name 'changa' in Puerto Rico is owned by *S. didactylus*, which is called 'West Indian mole cricket' in the English-speaking Caribbean. Historical accounts suggest that populations of *S. didactylus* and of two pest *Phyllophaga* spp. (Coleoptera: Scarabaeidae) surged after 1876/1877 and declined after 1920. This coincidence suggests that the cause may have been the same. The cause of the rise might conceivably have been introduction of the mongoose *Herpestes javanicus* (E. Geoffroy St. Hilaire) in 1877 (because it may have destroyed vertebrate predators) and the cause of the decline might conceivably have been introduction of the toad *Bufo marinus* L. in 1920, because it is a predator of *Phyllophaga* and *Scapteriscus*.

Resumen. Toda la información publicada durante los años 1887-1903 que indica que el grillotopo *Neocurtilla hexadactyla* (Perty) se encontraba en Puerto Rico, parece derivarse de una identificación incorrecta publicada en el 1882 por Agustín Stahl, médico y colector de objetos de historia natural. Aparentemente dicha especie no se encuentra ahora en Puerto Rico y seguramente nunca existió en la isla. Sin embargo, aún existe la posibilidad de que podría colonizarla mediante vuelo ayudado por el viento, desde las islas del sureste, como creemos que ocurrió con otro grillotopo inmigrante, *Scapteriscus didactylus* (Latreille). Stahl evidentemente confundió la primera especie con la segunda. Según otros autores, él mencionó también que el grillotopo (que ahora creemos es *S. didactylus*) llegó cerca del 1850 al puerto de Mayagüez en un cargamento de guano proveniente del Perú, y, por lo tanto, colonizó Puerto Rico. No encontramos ninguna verificación de esa historia, y por eso la dudamos. La primera detección de la presencia de *S. didactylus* en Puerto Rico pudo haber sido realizada por una expedición francesa en 1797, pero esta especie pudo haber estado presente mucho antes. Dos otras especies de *Scapteriscus* se detectaron en Puerto Rico más tarde. Una, *S. abbreviatus* Scudder, se detectó en 1917 y probablemente llegó

antes como un contaminante del lastre en barcos, tal vez en el puerto de Mayagüez. La otra especie, *S. imitatus* Nickle y Castner, se detectó alrededor de 1940 y parece haber sido una introducción accidental, como resultado de una identificación errónea. *S. didactylus, S. abbreviatus, y S. imitatus* se consideran especies no nativas que llegaron de otro lugar a Puerto Rico. En Puerto Rico el nombre vulgar 'changa', pertenece a *S. didactylus*, conocida como 'West Indian mole cricket' en inglés caribeño. Cuentos históricos sugieren que las poblaciones de *S. didactylus* y de dos especies de la plaga *Phyllophaga* (Coleoptera: Scarabaeidae) aumentaron después de 1876/1877 y disminuyeron después de 1920. Esta coincidencia sugiere que la causa pudo haber sido la misma en ambos casos. El aumento posiblemente se debió a la introducción de la mangosta, *Herpestes javanicus* (E. Geoffroy St. Hilaire), en 1877. Esta última tal vez destruyó depredadores vertebrados. La disminución posiblemente se debió a la introducción del sapo, *Bufo marinus* L. en 1920, el cual es un depredador de *Phyllophaga* y de *Scapteriscus*.

Introduction

The main purpose of this account is to clarify the contorted history of mole crickets in Puerto Rico. A secondary purpose is to clear the mole cricket *Neocurtilla hexadactyla* (Perty) from charges that it is, or has been, a pest in Puerto Rico, or even that it occurs in Puerto Rico.

Neocurtilla hexadactyla was originally described from Brazil in 1832 under the name *Gryllotalpa hexadactyla*. It was also described in 1838 under the name *Gryllotalpa borealis* Burmeister (a synonym) from North America. In 1906 it was made the type species of the genus *Neocurtilla* Kirby. Although it was originally described from South America, we believe it to be native to North America and to be adventive in Central America and South America. Although brachypterous (thus flightless) adults predominate in Florida, long-winged adults are abundant in South America and the Lesser Antilles. Flight is its most likely means of dispersal, because it is not synanthropic and occupies cultivated soils only to a very limited extent. In the West Indies, it is known from Cuba and several of the Lesser Antilles as far north as Antigua (Brunner and Redtenbacher 1892). Below we refer to *N. hexadactyla*, regardless of whether the cited author used the name *G. hexadactyla*.

The major reason for our belief that *N. hexadactyla* is native to North America is its wide distribution there and specialist natural enemies. Specialist natural enemies of *N. hexadactyla* are *Larra analis* F. (Hymenoptera: Sphecidae) and *Steinernema neocurtillae* Nguyen and Smart (Rhabditida: Steinernematidae), which are known only from the U.S.A.

Claims of the presence of *N. hexadactyla* in Puerto Rico have been clouded by repetition of an erroneous identification in which *N. hexadactyla* was confused with members of the genus *Scapteriscus*. In reality, *Scapteriscus* and *Neocurtilla* are separate at least at the tribal level (some authors claim subfamilial level) and specimens are easy to distinguish. However, knowledge of mole cricket identification and classification by entomologists not involved in orthopteran taxonomy was very inadequate until far into the 20th century. Faulty taxonomy caused confusion in the early 20th century. Here, we examine published statements that it occurs or occurred in Puerto Rico. Until now, claims of the presence of *N. hexadactyla* in Puerto Rico have been virtually ignored rather than examined critically. We also review records of >1,500 mole cricket specimens collected in Puerto Rico.

'A relative of *Gryllotalpa gryllotalpa* (L.)'

The first record of a mole cricket in Puerto Rico seems to date from a French expedition in 1797, in which the presence of a mole cricket species was reported by Ledru (1957, originally published in French in 1810). At the end of the 18th century, only one mole cricket species had been described anywhere in the world, and it was the European species now known as *Gryllotalpa gryllotalpa* (L.). According to Ledru, one or more specimens of "*Achaeta grillotalpa* Fab., como una cuarta parte más pequeña" (*Achaeta grillotalpa* Fab., about a fourth smaller) were collected by the expedition and deposited in the museum now known as Muséum National d'Histoire Naturelle in Paris. We take Ledru's words to indicate that he thought the specimen(s) belonged to some undescribed mole cricket species other than *G. gryllotalpa*, and with adults considerably smaller. We tentatively believe for reasons given below that the species encountered in 1797 was *Scapteriscus didactylus* (Latreille) (Frank et al. 1987). What a shame that Ledru, or the entomologists with whom he worked, failed to show the specimen(s) to Latreille, who, in Paris, had published descriptions of mole crickets from South America, including *S. didactylus* (Latreille 1804).

Table 1. A Chronology of Arrival and Subsequent Mention of Mole Crickets in Puerto Rico.

1797 or much earlier, *Scapteriscus didactylus* arrived by flight from islands to the southeast as an immigrant (it was not introduced). Its population spread gradually.

1892 Brunner and Redtenbacher (1892) documented the presence of *S. didactylus* in Puerto Rico.

1895 or earlier, *S. didactylus* was named 'la changa' and, by population spread, it became very damaging to seedlings of cultivated plants. It was misidentified as *Neocurtilla hexadactyla* by Stahl (1882), Gundlach (1887), and Busck (1902). Barrett (1902) described its behavior, correctly naming it *Scapteriscus didactylus*, and expressly doubting a story, supposedly recounted by Stahl that it had been "introduced in guano to Mayagüez from Peru about 1850."

1917 or earlier, *Scapteriscus abbreviatus* arrived, probably as a hitchhiker in ship ballast. Its population remained localized in parts of the north coast and west coast.

1918-1938, Zwaluwenburg (1918) published on the behavior of *Scapteriscus didactylus*, (misnamed as "*S. vicinus*"), but its population began to decline after 1920. Wolcott published his first and second catalogues (1924a, 1936) listing *S. abbreviatus* and '*S. vicinus*.'

1938-1942, Wolcott, Martorell and colleagues introduced a parasitoid wasp, *Larra bicolor*, from Amazonian Brazil, against *S. didactylus* (still called '*S. vicinus*' in Puerto Rico).

1942 or earlier, *Scapteriscus imitatus* was captured in northwestern Puerto Rico. This species, from northern South America, never before detected in Puerto Rico, was assumed introduced by error of Wolcott and Martorell's biocontrol campaign against *S. didactylus*, and still exists (Nickle and Castner 1984).

1942-present, little was written in Puerto Rico about problems caused by mole crickets. Wolcott (1948) published his third (final) catalogue.

1984-present, in taxonomic and distributional papers, Nickle and Caster (1984) pointed out the correct names for the *Scapteriscus* species in Puerto Rico and provided a key, and Castner and Fowler (1984) provided a distributional map for them in Puerto Rico. Many economic entomologists in Puerto Rico paid no attention and continued to use the name *S. vicinus* for 'la changa' while ignoring existence of two other species of *Scapteriscus*.

1987, presence of a mole cricket, probably *S. didactylus*, in Puerto Rico by 1797 was again pointed out from examination of the literature (Frank et al. 1987).

Now, existence of the mole cricket *Neocurtilla hexadactyla* in Puerto Rico is expressly denied. There are just three mole cricket species in Puerto Rico: *Scapteriscus abbreviatus*, *S. didactylus* ('la changa'), and *S. imitatus*. We introduced and established a second specialist biological control agent (*Steinernema scapterisci* Nguyen and Smart, Rhabditida: Steinernematidae) in 2001 against *S. didactylus*.

Only specimens from the Muséum National d'Histoire Naturelle, if they have appropriate labels or documentation, can fully validate this concept. We have not been able to find the specimen(s) in Paris.

'*Neocurtilla hexadactyla* (Perty)'

Agustín Stahl (1882), a Puerto Rican medical practitioner in the town of Bayamón, and collector of natural history objects, reported specimens of *N. hexadactyla* in his collection, from Trinidad and Puerto Rico. He did not state how the identification was made, nor did he give any information about behavior or collection locality. Unfortunately, Stahl's insect collection was poorly maintained, and we know of no surviving specimens; none of his mole cricket specimens is in the major insect collection in Puerto Rico.

Johann (Juan) Gundlach (1887), a Cuban resident and collector of natural history objects, who visited Puerto Rico thrice, in 1873, 1875-1876, and 1881, reported *N. hexadactyla* as a pest in the vicinity of Mayagüez, and often attracted to lights of houses (presumably adults can fly). He stated that his orthopteran specimens were shipped to Berlin and then were examined and identified by Henri Saussure (an orthopteran expert in Geneva) and named in a letter, which was sent indirectly (via Berlin) to Gundlach. He stated that his paper reproduces Saussure's identifications, except that he (Gundlach) identified specimens of some species with which he was familiar in Cuba, and he mentioned (correctly) that *N. hexadactyla* occurs in Cuba. He also admitted contact with Stahl, and we know (above) that Stahl had identified Puerto Rican mole cricket specimens as belonging to '*N. hexadactyla*.' Thus, Gundlach may have based his use of the name *N. hexadactyla* on (a) his own (mis)identification, or (b) Stahl's (mis)identification. We have not been able to find in Cuba a letter from Saussure identifying Puerto Rican Orthoptera collected by

Gundlach. We have found no mention of *N. hexadactyla* occurring in Puerto Rico in any publication by Saussure or any other European specialist in Orthoptera. For example, Saussure (1896) lists *N. hexadactyla* as occurring in Cuba and Guadeloupe, but does not mention Puerto Rico. (But see our section on *S. didactylus*).

López Tuero (1895) explained the pest status of a mole cricket he called simply 'la changa' and 'el grillotalpa' without using a scientific name. He noted extensive damage caused by "this terrible animal" to seedling plants of rice, tobacco, maize (corn), vegetables, and sugarcane. He also noted that this mole cricket was captured in light traps, to which it must have flown, so must be capable of flight.

Busck (1900) wrote of his encounter with '*N. hexadactyla*' in Puerto Rican tobacco fields where it was "very abundant and very damaging." He stated that it was "named for me by Dr. Stahl in Bayamón, having been introduced within his recollection." Rehn (1903) cites only Scudder (1901), and Scudder (1901) cites only Busck (1900) as the source of information about '*N. hexadactyla*' in Puerto Rico. These misidentifications rest on a misinterpretation by Stahl (1882) of the identity. Specimens collected by Busck in 1899, now in the U.S. National Museum of Natural History, were re-examined and found to belong to *S. didactylus* by Nickle and Castner (1984).

Scapteriscus didactylus (Latreille)

Brunner and Redtenbacher (1892), in a taxonomic work on Orthoptera from the island of St. Vincent, list *S. didactylus* as occurring on several additional islands. They name Puerto Rico as one of these islands, and they state "coll. Brunner", indicating that voucher specimens of *S. didactylus* from Puerto Rico were in Brunner's collection (in Vienna). Although they report *N. hexadactyla* from St. Vincent, they do **not** list it as occurring in Puerto Rico. The collector of the *S. didactylus* specimens in Brunner's collection from Puerto Rico was not stated. They might even have been specimens collected by Juan Gundlach in 1873-1881, and named by the latter (1887) as '*N. hexadactyla*.'

Barrett (1902) provided the first detailed account of the development and behavior of *S. didactylus* because it had become a major pest. His objective was improved control methods.

Thus, *S. didactylus* is likely to have been the mole cricket species encountered in Puerto Rico during a French expedition in 1797 (Frank et al. 1987). This is because no specimens of any other mole cricket species, collected in Puerto Rico before 1900, have been confirmed to exist, nor is there a pre-1900 publication by a taxonomist specializing in Orthoptera confirming existence of any species other than *S. didactylus* there. The mole crickets encountered by Gundlach (1887) and López Tuero (1895) could not have been *S. abbreviatus* Scudder, because those authors indicated that adults can fly, whereas *S. abbreviatus* cannot do so.

'*Scapteriscus vicinus* Scudder'

Rehn and Hebard (1916), prominent U.S. orthopteran taxonomists, pronounced that they "were satisfied that the species found abundantly in the southeastern United States, the West Indies and portions of South America, and which has been frequently recorded as *S. didactylus*, represents instead [*S.*] *vicinus* of Scudder." Thenceforward, from 1916, Puerto Rican entomologists (and those in the Lesser Antilles) began using the name '*Scapteriscus vicinus*' for 'la changa.' This interpretation was later shown to be wrong; Chopard (1968) accepted that West Indian populations belong to *S. didactylus*, not to *S. vicinus*; Nickle and Castner (1984) distinguished *S. didactylus* and *S. vicinus* in a key: the species is correctly *S. didactylus* for West Indian specimens, but not those from the southeastern United States. The correction was ignored by applied entomologists in Puerto Rico almost through the end of the 20th century.

Zwaluwenburg (1918) outdid Barrett (1902) by writing a lengthier account of 'the changa or West Indian mole cricket', which he called '*S. vicinus*' and described its development, behavior, and the extensive damage it caused to various crops.

Wolcott (1924a, 1936, 1948), in successive catalogues of the Puerto Rican insect fauna, reported '*S. vicinus*' as a major pest there. Wolcott (1936) equated the 18th century specimen(s) listed by Ledru (1957) with '*S. vicinus*.' He also equated Stahl's and Gundlach's '*N. hexadactyla*' with '*S. vicinus*.' It is clear that Wolcott (1924a, 1936, 1948) had no knowledge of the existence of *N. hexadactyla* in Puerto Rico, and

was deluded into accepting '*S. vicinus*' as the correct name of the mole cricket commonly called 'la changa', which in reality is *S. didactylus*.

In fact, *S. vicinus* has not been shown to occur anywhere in the West Indies. Specimens referred to this species in the West Indian literature seem to belong to *S. didactylus*.

The guano story

Busck's (1900) statement of the information that he obtained from Stahl (that 'changa' mole crickets had been introduced to Puerto Rico within the latter's recollection) appears to be the first published claim that the 'changa' is not native to Puerto Rico. Barrett (1902) elaborated upon this story from Stahl, while expressly doubting it, although he did not give his reasons for doubt. This version of the story states that 'la changa' first arrived in Puerto Rico in 1850 in a shipment of guano from Peru to Mayagüez. We have not discovered a published statement by Stahl on this subject, so we assume that Stahl spoke about it to Busck and Barrett, or perhaps mentioned it in letters. The story was repeated by Zwaluwenburg (1918) and Wolcott (1948). Nickle (2003: 420) erred in attributing such a story to Ledru (1957), because Ledru wrote in the very early 19th century, whereas this story originated in the late 19th century. However, Wolcott (1936, introduction), explained that it must have been 'changa' mole crickets that the French expedition of 1797 encountered in Puerto Rico; it is thus strange that he (1948) included 'the guano story' in the main body of his text on mole crickets, without further discussion; he can hardly have simultaneously believed that the species was present in Puerto Rico in 1797 **and** first arrived from Peru in 1850.

Stahl was born on 22 January 1842 in Aguadilla, 22 km north of Mayagüez. He lived there until 1852, when he was sent to Germany for an education, returning with a doctorate in medicine in 1864. If mole crickets did indeed contaminate a shipment of guano arriving at Mayagüez in 1850, when Stahl was eight years old, how and when would he have obtained this information? He is reported as a child to have liked spending time on the seashore, boarding fishing boats despite reprimands from his father, in Aguadilla (Ceide 1960). This was a time when there was no agricultural inspection of incoming cargoes, and no insect collection (in which specimens could have been deposited) on the island. No matter whether he saw mole crickets or if the information was later passed down to him from the recollection of an employee of a shipping company, who happened to notice mole crickets in the cargo, or of a grower who bought some of the guano, this does nothing to prove the identity of the species in question. Nor does it prove that this was the date of its first arrival in Puerto Rico.

Chopard (1954, 1968) listed *N. hexadactyla, S. oxydactylus* (Perty), *S. tetradactylus* (Perty), and *S. vicinus* (but not *S. abbreviatus* or *S. didactylus*) as occurring in Peru. Nickle (2003) described an additional species present in Peru: *S. peruvianus* Nickle. This opens possibilities for any of five species to have arrived in Peruvian guano in Mayagüez in 1850. However, there seem to be no specimens to confirm that any of them has ever been present in Puerto Rico. Perhaps the Peruvian guano industry (beginning ca. 1840) exported guano to Puerto Rico before the Puerto Rican guano industry (beginning ca.1850) got under way. The latter was based on deposits on the island of Mona, only 72 km WSW of Mayagüez, and had earlier been hindered from development by a pirate menace (pirates used Mona as an operating base). But 'the guano story' is not reliable - it depends upon the recollection of Stahl in about 1900 of events that occurred 50 years before, when he was eight years old.

Perhaps mole crickets did sometime arrive in Mayagüez, the major port in western Puerto Rico. Ballast-laden ships arrived there in 1850. One of us (JHF) examined the record of U.S. ships arriving during the late 1840s to 1850, compiled by a U.S. consul, and preserved on microfilm in the library of the University of Puerto Rico at Mayagüez, but did not find guano listed as a cargo, nor any mention of mole crickets. But, mole crickets thus arriving as a contaminant of ballast were likely to have been *S. abbreviatus*, which occurs there, and at localities north toward Aguadilla, and on parts of the north coast.

Hurricane stories

The hurricane story of 1876 was noted by Barrett (1902). Its gist is that 'la changa' did not become a serious problem in Puerto Rico until a hurricane in 1876 destroyed many birds that had been important predators of changas. Maybe there is some grain of truth in the story, but accounts of severe damage caused by mole crickets in the early decades of the 20th century suggest that mole crickets (*S. didactylus*)

were a problem not only in the aftermath of hurricanes. The 1876 hurricane story of Puerto Rico is preceded by one from the island of St. Vincent in the Lesser Antilles in which it was claimed that the hurricane of 1831 made 'the mole cricket' (presumed by Nickle and Castner 1984 and by us to be *S. didactylus*) a far more serious pest than it had been (Johnstone 1837, presenting a letter by Mr. M'Barnet of St. Vincent).

A mongoose story

Herpestes javanicus (E. Geoffroy-St. Hilaire) (Mammalia: Herpestidae) was introduced into Puerto Rico beginning in 1877 to control invasive Eurasian *Rattus* spp. (Mammalia: Rattidae) in sugarcane, but this mongoose is a generalist predator and attacks many organisms. Wolcott (1948) credited the mongoose introduction with reduction of populations of the ground-dwelling lizard *Ameiva exsul* (Cope) (Reptilia: Teiidae), which he claimed to be a major predator of 'May beetles' (*Phyllophaga* spp., Coleoptera: Scarabaeidae). Thus he attributed major damage to sugarcane and other crops by *Phyllophaga* larvae to a huge increase in *Phyllophaga* populations caused by a decline in *Ameiva* populations, in turn caused by introduction of *Herpestes*. Wolcott (1924b), in a paper on the diet of Puerto Rican lizards, stated: "Altho no changa happened to occur in the stomachs of any of the [*Ameiva*] examined, the readiness with which other Orthoptera are eaten would indicate that the absence of the changa is due merely to the accidents of collection, in that not sufficient specimen[s] were examined." Nobody seems to have considered that the mongoose introduction might likewise be blamed for the increase in mole cricket populations which was virtually simultaneous with the increase in *Phyllophaga* populations but has thus far been considered a separate issue. Henderson (1992), in considering extinctions and declines of West Indian amphibians and reptiles, suggested that introduction of *Herpestes* was just one of several factors (others were habitat destruction by humans, arrival of Eurasian rats as hitchhikers, and introduction of domestic cats and dogs) causing decline in some amphibian and reptile (including *Ameiva*) populations. Doubtless the mongoose destroyed other predators, including birds.

A toad story

The other generalist predator introduced into Puerto Rico was *Bufo marinus* L. (Amphibia: Bufonidae), in 1920. A dozen of these toads were obtained from Barbados by D.W. May, head of the USDA Agricultural Research Station in Mayagüez (now called the Tropical Agriculture Research Station) and released in the vicinity. "It was not until the value of the toad in the control of the changa and white grubs was generally apparent in the Mayagüez region that [May's] official announcement [in 1927] appeared" (Wolcott 1950). This acknowledgment of the role of the toad by Wolcott (1950) is very informative because of his attempted introduction of insect parasitoids targeted at *S. didactylus*.

Introduction of parasitoids against *S. didactylus*

Whatever the effects of *B. marinus* on populations of *S. didactylus,* Wolcott surely must have deemed them insufficient, because in the 1930s he began a campaign to introduce specialist parasitoids. This involved exploration in South America, and detection of *Larra bicolor* F. (Hymenoptera: Sphecidae) at Belém on the Amazon in Brazil. It culminated in the successful establishment of *L. bicolor* in Puerto Rico (Wolcott 1941). But nobody seems to have measured its effect, just as nobody seems to have measured the effect of *B. marinus*, on *S. didactylus*. That *S. didactylus* populations by 2001-present (as seen by us) are a fraction of those reported much earlier by López Tuero (1895), Barrett (1902), and Zwaluwenburg (1918) does not tell the cause of the decline. Cruz and Segarra (1992) do not mention *B. marinus* and suggest only that introduction of *L. bicolor* was partially successful in controlling *S. didactylus*. Damage by *S. didactylus* on irrigated sod farms, golf courses, and vegetable fields continues, and it was for that reason that we introduced *Steinernema scapterisci* Nguyen and Smart (Rhabditida: Steinernematidae) in 2001 (Leppla et al. 2005). Sugarcane, which had been a very important crop and heavily damaged by *S. didactylus* 100 years earlier, is now only a very minor crop.

Scapteriscus didactylus, *S. abbreviatus*, and *S. imitatus*

Nickle and Castner (1984) established that *S. didactylus*, *S. abbreviatus*, and *S. imitatus* Nickle and Castner are the species of that genus that occur in Puerto Rico. The distribution of these three species was mapped by Castner and Fowler (1984).

Recent and new records

In the 1980s through 2003 (see specimens examined, below) western Puerto Rico was shown to contain three species of *Scapteriscus*, two of them with restricted distribution and one widespread, but no *Neocurtilla*.

All published statements (known to us) that *N. hexadactyla* occurs in Puerto Rico have been refuted. There is no recognition of its occurrence there in Wolcott's (1924a, 1936, 1948) catalogues. We examined collections of mole crickets in Puerto Rico.

In August 2003, there were 33 specimens of *S. didactylus* in the Museo de Entomología y Biodiversidad Tropical of the Estación Experimental Agrícola in Río Piedras, Puerto Rico. Labels indicated collection dates between 1912 and 1991. Indicated localities were Aguirre, Caguas, Carolina, Isabela, Fajardo, Mayagüez, Mazaruni, Río Piedras, Toa Alta, Utuado, and Vega Baja. No other gryllotalpid species were represented.

We examined almost 1500 mole cricket specimens collected from various localities by us in a USDA-TSTAR-funded 2001-2004 project: *S. abbreviatus*: Mayagüez, Boquilla, Playa Añasco, Aguada, and Playa Jobos, *S. didactylus* from the west (Aguada, Aguadilla, Boquilla, Isabela, Joyuda, Playa Añasco, Playa Boqueron, Playa Jobos, and San Germán), center (Jayuya), south (Ponce, Coamo Springs), and east (Puerto Maunabo, Punta Uvero) of Puerto Rico, and *S. imitatus* only from Playa Jobos. We encountered no specimens of *N. hexadactyla*, nor were any reported by Castner and Fowler (1984). Use of a synthetic calling song of *N. hexadactyla* and ultraviolet light by J.H. Frank at the USDA Tropical Agriculture Research Station in Mayagüez on numerous nights of January-February 2003 failed to attract any specimens of *N. hexadactyla* (cf. the ease with which adults were attracted to ultraviolet light in Grenada [Frank et al. 2002]). These collections lead us to declare that *N. hexadactyla* does not occur in Puerto Rico, and probably never has occurred there; declaration of its presence there was based upon a misidentification by Stahl (1882), repeated by Gundlach (1887), Busck (1900), Scudder (1901), and Rehn (1903), whose publications have pervaded the literature.

The arrival of mole cricket species in Puerto Rico

It is difficult to prove a negative - that *N. hexadactyla* does not occur in Puerto Rico - but we argue the contrary - nobody has yet provided supportable evidence that it does occur there. Our search for Puerto Rican specimens in Puerto Rico, and museums in San Juan, Havana and Paris, revealed none. Previous reports to the contrary are all erroneous and are refuted. The records of specimens examined merely provide additional confirmation and some evidence that the species has not become established in Puerto Rico since Wolcott's (1948) third catalog.

Hurricane winds in Puerto Rico typically arrive from the southeast. Then they continue west to Hispaniola, Cuba, or Jamaica (or at some point veer north toward the Bahamas and/or Florida). If such winds are avenues for dispersal of insects, then we may expect that some winged insects may be carried from the Lesser Antilles to Puerto Rico. A dispersal track from northern South America through the chain of islands of the Lesser Antilles to the Greater Antilles was propounded for many organisms by Rosen (1975), and *N. hexadactyla* and *S. didactylus* may well have followed it.

We speculate that the presence of *N. hexadactyla* in the Lesser Antilles is the result of flight by winged adults that dispersed northward from South America, colonizing island after island. We suggest that it has not been able to colonize Puerto Rico from the Lesser Antilles, due to distances too great for unassisted flight, and because the right combination of inseminated females in flight during strong winds blowing in the right direction has not yet occurred. Those circumstances may yet occur. The nearest island to the east from which it is reported is Antigua (Brunner and Redtenbacher 1892). It has not been reported from the US Virgin Islands (Ivie and Nickle 1986, Frank and Keularts 1996), although *S.*

abbreviatus and *S. didactylus* **have** been. Additional support for the viewpoint is that *N. hexadactyla* is not reported from Hispaniola (Haiti and the Dominican Republic), although *S. abbreviatus* and *S. didactylus* **have** been.

In contrast, we speculate that *Scapteriscus didactylus* **did** arrive by wind-assisted flight, from islands to the southeast, first in Puerto Rico and later in Hispaniola. The closest islands where it occurs to the southeast are St. John and St. Thomas in the US Virgin Islands, and farther afield several islands in the chain of the Lesser Antilles as far south as Trinidad. [It has **not** been found to occur in St. Croix (Ivie and Nickle 1986, Frank and Keularts 1996); Nickle (2003 p. 428) erred in stating that it has]. It therefore is an immigrant to all these islands, and arrived in Puerto Rico by natural range expansion by the end of the 18th century or earlier. It has not yet been able to expand its range westward (to Cuba and Jamaica) or northwestward (to the Bahamas and Florida) although such range expansion may yet occur.

In further contrast is the arrival in Puerto Rico of *S. abbreviatus*. A specimen collected in 1917 was the first to be reported, by Wolcott (1924a). As in Florida, USA (Walker 1985) and Brazil (Fowler 1987) this species occupies scattered coastal localities, which in Puerto Rico are in the north and west of the island. Having only short wings, it could not have arrived by flight. Most likely, it arrived as a hitchhiker contaminating ship ballast from eastern South America. Conceivably, it might have arrived as early as 1850 in Mayagüez and remained unrecognized by entomologists for decades.

In final contrast is the means of arrival of *S. imitatus*, in the early 1940s. This is the only one of Puerto Rico's three mole cricket species that was introduced (imported deliberately). Nevertheless, the introduction was inadvertent, as a result of faulty identification, as deduced by Nickle and Castner (1984). Wolcott (1941) found it difficult to transport adult *L. bicolor* wasps alive from Belém to Puerto Rico, so he exposed locally-caught (in Belém) mole crickets to the female wasps for parasitism. This allowed the successful transport of parasitized mole crickets, some of which were released in Puerto Rico. If some of those mole crickets were *S. imitatus* and the wasp eggs or larvae they bore died, then the presence of that species in Puerto Rico has a ready explanation.

These are three distinct means of arrival, which were widely separated in time. Flight is the natural means of dispersal of winged mole crickets, and it should be the first to be considered in interpreting distributional patterns. Flight from island to island may be possible depending upon distance and prevailing winds. For *S. didactylus* to arrive in Puerto Rico by flight in the 18th century or earlier seems possible because of the prevailing winds, and it is the preferred theory for lack of other evidence. Among the many mole cricket species present in South America, only *N. hexadactyla* and *S. didactylus* followed the island chain northward. Later, some dispersal by mole crickets in solid ship ballast (e.g., sacks of sand) was possible because of prevailing international trade routes. After that era, solid ballast was gradually replaced by liquid ship ballast, so that mode of dispersal was lost for mole crickets. Additionally, agricultural regulations made it harder and then virtually impossible to ship sands and soils from country to country, to prevent entry of agricultural pests as contaminants.

Errata

Frank et al. (2002) erred in stating that H. H. Smith was sent from England to Grenada to collect insects. In fact, Smith was a U.S. insect collector, hired by the British Association for the Advancement of Science to collect insects in Grenada and St. Vincent (Howard 1898).

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y Sistemática houses mole cricket specimens (*N. hexadactyla*) collected by Gundlach in Cuba but not Puerto Rico. We thank Edda Martínez, Linnette Rosado, and Nisael Nieves for much work in the field and laboratory. We thank Ron Cave, Frank Slansky, Jr. and Marc Branham, University of Florida, for critical reviews of our manuscript, and Ron Cave and Alonso Suazo for drafting a Resumen.

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