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Tracing phylogenetic relationships in the family Gryllotalpidae

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Abstract

We propose a hypothesis of relationships in a subset of the mole cricket family (Gryllotalpidae), based on morphology and call type. Living and preserved specimens of six species were examined and a literature analysis conducted, as preliminary steps in a comparative study of this family, known world-wide in tropical and temperate regions. In the literature, 76 species in 5 extant genera are described; we included in our analysis 34 species from four genera for which the most complete morphological data were available. All analyses were rooted by the outgroup method, with *Gryllus texensis* Cade & Otte as the outgroup and the presence of mole-like digging forelimbs as the synapomorphic character diagnosing the ingroup. Seven other characters in the analysis were restricted to discrete traits for a total of 8 characters in the analysis. Phylogenetic analyses of the complete data set yielded >15,000 trees to which we applied various consensus analyses by PAUP without high levels of resolution. The Adams method, however, revealed a resolved group of 14 ingroup taxa from four genera, but mostly from the genus *Gryllotalpa*, that we subjected to re-analysis with PAUP. Two equally parsimonious trees were roughly organized into clades by call type. Our hypothesis supports previous work that has placed the genus *Scapteriscus* in a separate subfamily and other work that suggested the New Zealand endemic, *Triamescaptor aotea* Tindale, is more closely related to two Australian species of *Gryllotalpa* than to *Gryllotalpa* species as a whole. Additional field studies of songs of this family and addition of characters based on molecular data are important to resolving relationships suggested by our hypothesis.

Key words

Gryllotalpa, phylogeny, call type

Introduction

Mole crickets in the family Gryllotalpidae are distributed throughout temperate and tropical regions. These insects are best known for their digging forelimbs and singing from specialized burrows in the soil (Bennet-Clark 1970, 1987; Daws *et al*. 1996). Mole crickets are also notable because some females produce sounds (Petrunkewitsch & von Guaita 1901; Baumgartner 1905, 1910; Tindale 1928; Zhantiev & Korsunovskaya 1973; Nickle & Carlysle 1975; Ulagaraj 1976; Townsend 1983; Hoffart *et al*. 2002), and members of at least four genera exhibit some degree of maternal care (Gwynne 1995).

The genus *Neocurtilla* is known from six (Eades 2002) or nine (Otte & Alexander 1983) New World species, and *Gryllotalpella* is represented by two species native to South America (Otte & Alexander 1983, Eades 2002). *Triamescaptor* is endemic to New Zealand and represented by a single species (Otte & Alexander 1983). *Scapteriscus* is represented by 10 to 12 species native to South America (Otte & Alexander 1983, Eades 2002). Three of these species have been introduced to the United States (Walker & Moore 2002) and two more to Puerto Rico (Forrest 1983, Nickle & Castner 1984). There are also two species of *Scapteriscus* known from Malaysia (Townsend 1983, Eades 2002). The genus *Gryllotalpa* is known as an exclusively Old World genus (Townsend 1983), distributed throughout temperate and tropical regions of Europe, Africa, Asia and Australia (Otte & Alexander 1983), but there are two rare native species in North America, the prairie mole cricket, *Gryllotalpa major* Saussure, and the knife mole cricket, *G. cultriger* Uhler (Walker & Moore 2002). The genera *Pterotriamescaptor* and *Palaeoscapteriscops* are newly described since 1991 and are represented by one species each in the fossil record, with no known extant species (Eades 2002).

The number of species in the family has been variously reported as 46 (Otte & Alexander 1983), approximately 70 (Walker 1997), and 76 (Eades 2002). Nevo *et al*. (2000) state that there are 6 genera and 65 species without further comment or citation. A literature analysis identified a total of 78 species grouped in seven genera in the family (Tindale 1928, Kushnir 1952, Ortiz 1958, Bennet-Clark 1970, Baccetti & Capra 1978, Forrest 1983, Popov *et al*. 1974, Walker & Carlysle 1975, Otte & Alexander 1983, Townsend 1983, Nickle & Castner 1984, Semlitsch 1986, Broza *et al*. 1998, Walker 1997, Walker & Moore 2002, Eades 2002). The most comprehensive list is in the Orthoptera Species File Online, Version 2 (Eades 2002).

Comprehensive taxonomic analyses are available for species from Africa (Townsend 1983), Australia (Otte & Alexander 1983), and the United States (Walker & Moore 2002). However, the types of data provided are not suited to a large-scale analysis of the family because of the variation in morphological characters chosen in the species descriptions. For example, Townsend (1983) chose details of the stridulatory file and venation of the male forewing to define species, but descriptions of those characters were not always available for species documented by other sources. Many of the available data are morphological measurements of museum specimens, together with locality taken from the type specimen, data for species where habitat or descriptions of the calling song or burrow are unknown. Bennet-Clark (1970) has found the song and burrow system to be characteristic of mole cricket species, but these details are not documented for many named species, and virtually all life cycles are unknown (but see Semlitsch 1986). Thus, the task of developing inclusive hypotheses across mole cricket taxa for such things as selection for variations in morphology and behavior is constrained by the inability to extrapolate from the data available, as well as by the dearth of data for many species.

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Behavioral traits can be used in the same way as morphological ones to study evolutionary relationships (Wenzel 1992), but behavioral data are rarely available. What we do know of mating systems suggests divergence among taxonomic groups: *Gryllotalpa major* males, rare natives of the grasslands of North America, display in leks to attract flying females (Hill 1999), while *Scaptericus* species, introduced to the United States from South America, form mating sprees (Walker 1983). *Gryllotalpa major* males are able to detect and respond to soil vibrations produced by calling neighbors (Hill & Shadley 1997, 2001), and *N. hexadactyla* from North America communicates through the soil from a closed burrow to attract females for mating (Forrest 1983). The possibility that this communication is accomplished through vibration rather than airborne sound has not been explored for *N. hexadactyla*, but a species of *Gryllotalpa* from France produces vibrations that can be detected at a distance of 20 cm (Bennet-Clark 1970).

The present paper describes preliminary results of a comparative study initiated to determine the evolution of the unique, as well as the variant, behaviors found in the Gryllotalpidae. Our analysis was limited to 34 species from 4 genera of the Gryllotalpidae for which comparable morphological data were available and is based on 7 morphological characters and the call.

Table 1. Thirty-four species from 4 genera of the Gryllotalpidae included in our phylogenetic analysis with PAUP version 4.0 beta 5.

Species	Authority	Location *Introduced
Outgroup=*Gryllus texensis*	Cade & Otte	South-central North America
Gryllotalpa major	Saussure	South-central North America
Gryllotalpa cultriger	(Uhler)	North America
Gryllotalpa africana	Beauvois	Africa, Middle East, Hawaii*
Gryllotalpa bulla	Townsend	Central and East Africa
Gryllotalpa debilis	Gerstaecker	Tropical Africa
Gryllotalpa devia	Saussure	South Africa
Gryllotalpa robusta	Townsend	Africa south of the Sahara, Canary Islands
Gryllotalpa rufescens	Chopard	Central Africa
Gryllotalpa parva	Townsend	Equatorial and Southern Africa, Madagascar
Gryllotalpa brevilyra	Townsend	Central Africa
Gryllotalpa pluridens	Townsend	Central Africa
Gryllotalpa spissidens	Townsend	West African rainforest, Cameroon
Gryllotalpa marismortui	Broza, Blondheim & Nevo	Israel
Gryllotalpa tali	Broza, Blondheim & Nevo	Israel
Gryllotalpa vineae	Bennet-Clark	Europe
Gryllotalpa gryllotalpa	(Linnaeus)	Europe, North America*
Gryllotalpa monanka	Otte & Alexander	Australia
Gryllotalpa coarctata	Walker, F.	Australia
Gryllotalpa pilosipes	Tindale	Australia
Gryllotalpa inermis	Chopard	Australia
Gryllotalpa australis	Erichson	Australia
Gryllotalpa brachyptera	Tindale	Australia
Gryllotalpa babinda	Otte & Alexander	Australia
Gryllotalpa pluvialis	Mjöberg	Australia
Gryllotalpa nitidula	Serville	Australia
Gryllotalpa oya	Tindale	Australia
Gryllotalpa howensis	Tindale	Australia
Neocurtilla hexadactyla	Perty	North America, South America*
Scapteriscus vicinus	Scudder	South America, North America*
Scapteriscus borelli	Giglio-Tos	South America, North America*
Scapteriscus abbreviatus	Scudder	South America, North America*
Scapteriscus didactylus	(Latreille)	South America, Puerto Rico*
Scapteriscus imitatus	Nickle & Castner	Brazil, Puerto Rico*
Triamescaptor aoeta	Tindale	New Zealand

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Materials and Methods

Living specimens of the prairie mole cricket, *G. major*, were obtained as part of our long-term field study of the reproductive ecology of this species in northeastern Oklahoma, USA. Live individuals of four other species (short-winged mole cricket, *Scapteriscus abbreviatus* Scudder; tawny mole cricket, *S. vicinus* Scudder; southern mole cricket, *S. borelli* Giglio-Tos; northern mole cricket, *N. hexadactyla*) were donated from the lab of Dr. Thomas J. Walker at the University of Florida, USA. Preserved specimens of the New Zealand mole cricket, *Triamescaptor aotea* Tindale, were provided by Dr. Phil Sirvid of the Museum of New Zealand Te Papa Tongarewa. Our observations and measurements of these specimens were added to details gleaned from a literature survey of the family.

Thirty-four species from among the 78 identified from the literature were selected for this study (Table 1). Species with insufficient, or no, morphological or song data available were excluded from the analysis. All analyses were rooted by the outgroup method using data from *Gryllus texensis* Cade & Otte (Cade & Otte 2000), a common member of the family Gryllidae, which we collected locally in Tulsa, Oklahoma, USA. The family Gryllidae has been identified as the sister taxon for the Gryllotalpidae in previous phylogenetic analyses (Gwynne 1995) and the two have been associated in the past as a common family of insects (Walker & Moore 2002).

The presence of mole-like digging forelimbs was the synapomorphic character that diagnosed the ingroup of mole crickets. The other 7 characters chosen to build a coding matrix were restricted to discrete traits or continuous measurement data converted to discrete character data (see Grandcolas *et al*. 1994), used to identify taxonomic groups primarily by Otte and Alexander (1983): number of dactyls, condition of tibial tympanum, presence or absence of ocelli, presence or absence of inner subapical spurs of the hindtibae, type of call, presence or absence of hindwings, and relative length of hindwings. Nonapplicable characters (*i.e.*, relative length of hindwings when hindwings were absent) were coded as missing data (see Gwynne 1995). The Phylogenetic Analysis Using Parsimony (PAUP) program version 4.0 beta 5 (Swofford 2001) and MacClade 4.0 (Maddison & Maddison 2000) were used for parsimony analyses. Searches were conducted using the heuristic search or branch and bound option in PAUP.

Results

Phylogenetic analyses of the complete data set yielded >15,000 trees to which various consensus analyses by PAUP (strict, majority rule, Adams) were applied. The Adams method revealed a resolved group of 14 ingroup taxa mostly from the genus *Gryllotalpa*. This resulted in a re-analysis with PAUP on this subset of taxa. Two equally parsimonious trees (L=12 steps, C.I.=1.00) containing 14 species in 4 genera roughly organized into clades by call type (Fig. 1). The coding matrix for these species is given in Table 2. Although several sets of taxa are not distinguishable by the matrix used in this

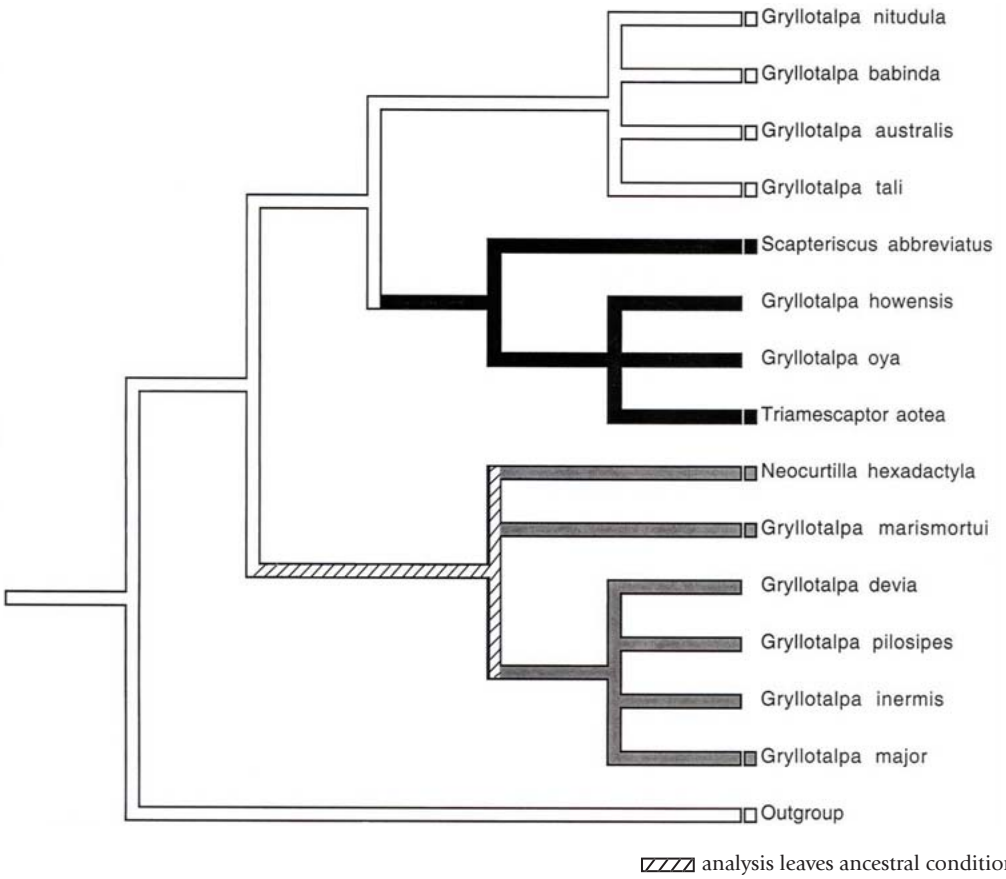


Fig. 1. One of the equally parsimonious trees (L=12, C.I.=1.00). *Gryllus texensis* is the outgroup taxon. Unshaded branches indicate the clade of trilling species. The dark-shaded branches indicate a clade of wingless, or reduced-winged, taxa. The gray-shaded branches indicate three chirping species and three of unknown call grouped with *Gryllotalpa major* because of a lack of subapical spurs on the dorsal hindtibiae.

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analysis (see Fig. 1), multiple representatives of each group were included in order to allow for a broader taxonomic assessment. The only difference in the trees resolved from the analysis was the placement of *G. marismortui* Broza, Blondheim & Nevo, which was a basal member in Fig. 1, and a clade member with the four other *Gryllotalpa* species on the adjacent branch in the alternative tree (not shown).

The clade containing *Gryllotalpa nitidula* Serville, *G. babinda* Otte & Alexander, *G. australis* Erichson and *G. tali* Broza, Blondheim & Nevo is diagnosed by a trilling advertisement call. *Scapteriscus abbreviatus* and *T. aotea* have no advertisement call, and the calls of *Gryllotalpa howensis* Tindale and *G. oya* Tindale are unknown. This clade is defined by absent or reduced hindwings. The larger clade including these 8 might be called 'non-chirping', because the alternative clade includes 3 species (*N. hexadactyla*, *Gryllotalpa marismortui* and *G. major*) with a chirping advertisement call and 3 (*Gryllotalpa devia* Saussure, *G. pilosipes* Tindale, and *G. inermis* Chopard) whose calls are unknown. These last 3 species with call unknown are grouped with *Gryllotalpa major* because of the lack of subapical spurs on the dorsal hindtibiae.

When we analyzed the data set without the 'call' character, 12 equally parsimonious trees were resolved. The 3 species with call unknown were still included in the clade with *Gryllotalpa major*, but the other 2 chirping species were either completely unresolved (*N. hexadactyla*), or alternatively grouped with *G. major* or unresolved (*G. marismortui*). Likewise, the 4 trilling species were grouped as a clade in 9 of the 12 equally parsimonious trees, while the other 3 had *Gryllotalpa tali* more closely related to the *G. howensis*–*G. oya*–*T. aotea* clade.

Discussion

Communication in the Ensiferan Orthoptera is of great interest to many biologists (Gwynne 1995), and our limited phylogeny of the Gryllotalpidae yields a hypothesis of relationships based on type of call. The most common signals in crickets today are trills (Otte 1992), which probably represent the ancestral condition (Alexander 1962, Otte 1992), and 18 of the species in our literature analysis for which calls were described produce trills. At least 4 species of mole crickets world-wide produce a chirping call (Nevo & Blondheim 1972, Otte & Alexander 1983, Walker & Figg 1990, Broza *et al*. 1998, Hill 2000, Hoffart *et al*. 2002), and 3 of those (*Gryllotalpa marismortui*, *G. major* and *N. hexadactyla*) were grouped as a clade in our hypothesis. The other chirping species, the Australian *Gryllotalpa pluvialis* Mjöberg, was omitted from our analysis because it was not part of the consensus tree identified by analysis with the Adams method.

The predictions of our hypothesis correspond to suggestions made in previous taxonomic analyses. Tindale (1928) suggested that *Triamescaptor* was more closely related to *Gryllotalpa australis*

Table 2. Coding matrix for the 14 ingroup taxa subset (see Fig. 1 and text). S/A=subapical; ?=missing data. Sources: 1) Otte & Alexander 1983, 2) Walker & Moore 2002, 3) Hill, pers. obs., 4) Walker & Carlysle 1975, 5) Townsend 1983, 6) Broza *et al*. 1998, 7) Nickle & Castner 1984, 8) Tindale 1928, 9) Cade & Otte 2000.

Species	Forelimbs	Dactyls	Tympanum	Ocelli	S/A Spurs	Call	Hindwings	HW Length	Sources
Outgroup= *Gryllus texensis*	Absent	?	?	Present	Present	Trill	Present	Longer than FW	9,
Gryllotalpa oya	Present	Four	Covered	Absent	Present	?	Absent	?	1,5
Gryllotalpa howensis	Present	Four	Covered	Absent	Present	?	Absent	?	1,5
Triamescaptor aotea	Present	Three	Absent	Absent	Present	Absent	Absent	?	7,8
Scapteriscus abbreviatus	Present	Two	Exposed	Present	Present	Absent	Present	Shorter than FW	2,3,4,5,7
Gryllotalpa australis	Present	Four	Covered	Present	Present	Trill	Present	Shorter than FW	1,5
Gryllotalpa babinda	Present	Four	Covered	Present	Present	Trill	Present	Shorter than FW	1,5
Gryllotalpa nitidula	Present	Four	Covered	Present	Present	Trill	Present	Shorter than FW	1,5
Gryllotalpa tali	Present	Four	Covered	?	?	Trill	Present	Shorter than FW	5,6
Gryllotalpa major	Present	Four	Covered	Present	Absent	Chirp	Present	Longer than FW	2,3,5,7
Gryllotalpa pilosipes	Present	Four	Covered	Present	Absent	?	Present	Longer than FW	1,5
Gryllotalpa inermis	Present	Four	Covered	Present	Absent	?	Present	?	1,5
Gryllotalpa devia	Present	Four	Covered	?	Absent	?	?	?	5,
Gryllotalpa marismortui	Present	Four	Covered	Present	?	Chirp	Present	Longer than FW	5,6
Neocurtilla hexadactyla	Present	Four	Covered	Present	Present	Chirp	Present	Longer than FW	2,3,4,5,7

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and *G. oya* than to members of the genus *Gryllotalpa* in general, and the genus *Scapteriscus* is sometimes placed in a separate subfamily from the other genera of mole crickets (Townsend 1983). These opinions are consistent with our hypothesis.

Townsend (1983) argued that presence or absence of subapical spurs on the hindtibiae is an unreliable character at both the specific and generic levels. However, he used this same character to distinguish between *Gryllotalpa devia* and *G. rufescens* Chopard in his taxonomic key (Townsend 1983). The three species grouped with *G. major*, based on the absence of subapical spurs, are notable for living in marginal habitats. *G. devia* is from the Cape of Good Hope and Lesotho in Africa, "Apparently associated with drier regions than is usual for mole-crickets" (Townsend 1983, p. 186), and *G. pilosipes* and *G. inermis* are from xeric locales in Australia (Otte & Alexander 1983). *G. marismortui*, the Dead Sea mole cricket (it produces chirps), is also found in marginal habitat in dry, highly saline soils (Broza *et al.* 1998). We have previously hypothesized a relationship between call type and habitat in the evolution of the chirping North American natives, *G. major* and *N. hexadactyla* (Hoffart *et al.* 2002), and Morton (1975) found the only chirping species in his vireo study came from the most open habitat. Selection for communication in an open habitat may have contributed to a chirping call type in these species (see Römer 1993), but chirping should also be less energetically expensive than trilling (Prestwich & Walker 1981, Hill 1998). This would benefit *G. major*, which lives at the colder and drier extemes of the range of the Gryllotalpidae in North America. Future work that identifies the unknown songs within the Gryllotalpidae, particularly those of the three species in our chirping clade with unknown songs, will support or refute the hypothesis represented by our tree.

Likewise, additional work will reveal whether *Gryllotalpa howensis* and *G. oya* have, like the other two members of our hypothetical clade, no advertisement call . *G. howensis* has no hindwings but does have short elytra with nine stridulatory teeth (Tindale 1928). *G. oya* has no hindwings, but neither Tindale (1928) nor Otte & Alexander (1983) commented on a stridulatory file, merely stating that the forewings were shorter than the pronotum. *Triamescaptor aotea* is completely wingless with no trace of a stridulatory apparatus (Tindale 1928), but the short forewings of *S. abbreviatus* do have a stridulatory file, and males do sing a courtship song, even though there is no advertisement call (Walker & Carlysle 1975). This condition fits the model tested by Desutter-Grandcolas (1997a) that predicted the advertisement call would be lost before the courtship song in a progression of reduced communication. Still, the relationship between evolution of cricket communication and the stridulatory apparatus is unexpectedly complex (Desutter-Grandcolas 1997a, 1997b). Clearly more field studies of the songs, or lack of songs, of species are of great importance in resolving relationships suggested by our hypothesis.

Phylogenies are hypotheses about evolutionary relationships that can be tested and refined (Gwynne 1995). Our plans are to continue to refine this preliminary phylogeny through addition of molecular characters and to expand it to include more species from throughout the world as additional morphological and behavioral characters become known.

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