

## *Allonemobius shalontaki*, a New Cryptic Species of Ground Cricket (Orthoptera: Gryllidae: Nemobiinae) from the Southwestern United States

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**ABSTRACT** A new species of ground cricket in the genus *Allonemobius* (Hebard) is described from the southwestern United States. Like many singing Orthoptera, this species is morphologically cryptic and most easily distinguished from related species by using molecular characters and male calling song traits. We describe *Allonemobius shalontaki* as a new species and present data suggesting its reproductive isolation from congeneric species. *Allonemobius shalontaki* exhibits a unique male calling song and possesses a distinct allozyme genotype. Additionally, we present an electrophoretic key to the genus and propose phylogenetic relationships among species.

**KEY WORDS** *Allonemobius*, calling song, Nemobiinae, Orthoptera, phylogeny

Among the singing Orthoptera many closely related, reproductively isolated species are divergent in ecological and sexual traits yet exhibit little or no morphological divergence. Species with these characteristics are known as cryptic species and pose particular problems for taxonomy (Alexander 1962, Walker 1964). Frequently among these groups, new species are recognized not by museum specimens but rather by detailed ecological and behavioral observations. For example, crickets of the genus *Allonemobius* (Hebard) were initially constrained to a single species (DeGeer 1773; Alexander and Thomas 1959, Vickery and Johnstone 1970). Intense study by Fulton (1931, 1933, 1937) revealed physiological distinctions between populations that lead to the eventual description of several unique species (Alexander and Thomas 1959). Despite these intense ecological, behavioral, and morphological studies, additional cryptic species were found after detailed genetic work (Howard 1983, Howard and Furth 1986).

All members of the genus *Allonemobius* are small, ground-dwelling omnivores with most species distributed broadly across eastern North America. They have become well known through their role in the description of major patterns and processes in ecology and evolution. Species in this genus have been used to elucidate the process of speciation (Gregory and Howard 1993, 1994; Gregory et al. 1998; Doherty and Howard 1996; Veech et al. 1996; Howard et al. 1998), sexual selection (Howard and Gregory 1993; Gregory and Howard 1996; Fedorka and Mousseau 2002a,b), sexual conflict (Fedorka and Mousseau 2004), mating system evolution (Sadowski et al. 2002), genetic dif-

ferentiation (Chu and Howard 1998, Mousseau and Howard 1998, Roff and Mousseau 1999, Roff et al. 1999), life history evolution (Tanaka and Brookes 1983, Bradford and Roff 1995, Carrière et al. 1997, Roff and Bradford 2000, Olvido et al. 2003), hybrid zone dynamics (Howard 1986, Howard and Waring 1991, Howard et al. 1993, Chu et al. 1995), competition and habitat selection (Howard and Harrison 1984a, 1984b), and reproductive protein evolution (W.E.B., unpublished data). Their role as important study systems may be because of their abundance. Indeed, these species have been studied most intensively along the eastern coast of North America where they are perhaps the most abundant singing orthopteran. However, most species in this genus are rarely encountered and relatively unknown. The majority of work on this genus has focused on the three species exhibiting the highest abundance on the east coast: *Allonemobius fasciatus* (De Geer), *Allonemobius socius* (Scudder), and *Allonemobius allardi* (Alexander & Thomas). Unfortunately, other members of this genus remain in their shadow.

Although little work has been done outside of eastern North America, the presence of geographic barriers and diverse habitats in western North America, suggests that there may be many undiscovered isolated populations in the west. We know of only two taxonomic studies of *Allonemobius* in the west; Vickery and Johnstone (1970) collected extensively across Canada, and Weibel (1996; see also Weibel and Howard 2000a,b) sampled *Allonemobius* across the western United States. Weibel (1996) discovered several new populations that she suggested were composed of new species. Her work suggests that at least

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some species of *Allonemobius* remain to be discovered. Herein, we describe one such species.

### Materials and Methods

In August 1999, W.E.B. collected crickets at the Confederate Memorial Museum and rest stop along U.S. Hwy. 69 in Atoka, OK, and south of Salado, TX, at mile marker 283 on Interstate Hwy. 35. The Atoka collection was transported back to the laboratory alive and used for calling song, genetic, and morphological analyses. The Salado collection was immediately frozen in liquid nitrogen, transported back to the laboratory, and transferred to  $-80^{\circ}\text{C}$  until used for genetic analyses.

Genetic analysis of individual crickets was performed using allozyme electrophoresis. Electrophoretic analysis was based on 14 enzyme loci, including isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), hexokinase (HK), aspartate aminotransferase (AAT), esterase-1 (EST-1), phosphoglucose isomerase (PGI), 6-phosphogluconate dehydrogenase (6-PGD), malic enzyme (ME), phosphoglucomutase (PGM), mannose-6-phosphate isomerase (MPI), acid phosphatase (ACP),  $\alpha$ -glycerophosphate dehydrogenase ( $\alpha$ -GPD), glucose-6-phosphate dehydrogenase (G6PD), and general protein (GP). A single hind leg was removed from each cricket and analyzed as in Howard (1982).

Morphological analyses were performed on crickets from Atoka that had been previously identified by electrophoretic and calling song analysis. Eight morphological traits were measured, including shared and sex-specific characters. These characters were chosen to match those used by Howard and Furth (1986) in describing other members of the genus. For both sexes, we measured the body length (Lb), pronotum length (Lp), pronotum width (Wp), and hind femur length (Lf). For males, we measured characters of the tegmen as these characters may affect calling song. Tegmen characters were measured as in Fulton (1931) and Howard and Furth (1986) and included the stridulatory vein measured from the mesal origin to the ulnar vein (Tg1), the distance from the ulnar vein to the lateral border of dorsal tegmen surface (Tg2), and the distance from the stridulatory vein to the apex of the tegmen (Tg3). For females, we measured the length of the ovipositor (Lo).

To record male calling songs, males were individually isolated in 17- by 12- by 6-cm plastic boxes with mesh covers. Songs were recorded using a Realistic Cardioid dynamic microphone and a Sony MZ-R50 recorder at 22–24°C. Songs were analyzed using the Canary software (Cornell Laboratory of Ornithology, Ithaca, NY; Charif et al. 1995). By isolating individual males, we ensured that songs produced were not in response to stimulus from females or other males; as a result, the songs recorded are calling songs and not courtship or aggressive songs.

Phylogenetic analyses were performed to assess the relationship of newly collected crickets to the remaining members the genus *Allonemobius* by using programs in PHYLIP (Felsenstein 2004). The data used in

Table 1. Allele frequency of new populations with number of individuals in parentheses

Locus	Allele	Salado, TX	Atoka, OK
MDH	1.6	0.9 (9)	1.0 (22)
	1.0	0.1 (9)	
HK	1.0	1.0 (8)	1.0 (15)
IDH	1.5	0.9 (9)	1.0 (21)
	1.0	0.1 (9)	
ME	1.0	1.0 (9)	1.0 (22)
AAT (GOT)	2.0	0	0.14 (18)
	1.0	0.69 (7)	0.86 (18)
	0.8	0.31 (7)	0
PGI	1.6	0	0.02 (22)
	1.17	0.5 (1)	0.93 (22)
EST-1	1.0	0.5 (1)	0.05 (22)
	1.1	0.13 (8)	
	0.9	0.5 (8)	
G-PCD	0.8	0.31 (8)	
	0.8	0.06 (8)	
PGM	1.0	1.0 (8)	1.0 (22)
PGM	1.0	1.0 (9)	1.0 (22)
MPI	1.0		1.0 (9)
G6PD	1.0		1.0 (1)
ACP	1.0		1.0 (5)
$\alpha$ -GPD	1.0		1.0 (5)
GP	1.0		1.0 (5)

Allele names are based on the starch electrophoretic mobility of the allele relative to that of the most common allele in *A. fasciatus*.

these analyses included both the electrophoretic data mentioned above as well as data previously published by Howard (1983). Pairwise genetic distances were estimated using the methods of Nei (1972), Cavalli-Sforza and Edwards (1967), and Reynolds et al. (1983). Pairwise distances were used to reconstruct phylogenetic relationships by using both least squares and minimum evolution methods with and without the assumption of a molecular clock in the FITCH and KITCH programs. Neighbor-joining and unweighted pair-group methods with arithmetic average methods were used with the NEIGHBOR program. Data sets were resampled 1000 times to generate bootstrap support using SEQBOOT, and consensus trees were obtained using CONSENSE.

### Results

We genetically analyzed a total of 31 crickets from the two collections (22 from Atoka, OK, and nine from Salado, TX) for 14 electrophoretic loci. Most loci are invariant and have alleles typical of the *A. fasciatus* species group (Table 1). However, two allozyme loci are fixed for novel alleles in one population. These novel alleles occur at high frequencies in the other population. A third locus exhibits variation in both populations, with high frequency alleles that are rare within the *A. fasciatus* group. In the Atoka population, the allele for the MDH enzyme is fixed and migrates at 1.6 times the distance as the most common allele in *A. fasciatus*. Similarly, the IDH locus is fixed for a novel allele in the Atoka population, which migrates 1.5 times the distance as the most common allele in *A. fasciatus*. The PGI locus was only well sampled in the Atoka population. Here, an allele migrating 1.17

Table 2. Summary of morphological characteristics in the genus *Allonemobius*

Species	Sex	Lb	Lp	Wp	Lf	Lo	Tg1	Tg2	Tg3	Citation
<i>A. shalontaki</i>	Male (n = 7)	11.9 (11-13)	2.1 (1.9-2.2)	3.2 (2.7-3.7)	6.9 (6.0-7.5)		1.0 (8.0-11)	1.4 (1.3-1.7)	3.9 (3.0-4.6)	This study
	Female (n = 11)	10.8 (10-12)	2.3 (2.1-2.5)	3.4 (3.0-3.8)	7.5 (7.0-8.0)	7.6 (7.0-8.5)				
<i>A. socius</i>	Male	9.1	1.8	2.7	6.4		1.0	1.1	3.5	Howard and Furth (1986)
	Female	10.0	2.1	2.9	6.8	6.9	-			
<i>A. fasciatus</i>	Male	9.8	1.8	2.6	6.3		0.9	1.1	3.5	Howard and Furth (1986)
	Female	10.7	2.1	2.9	6.9	7.3				
<i>A. allardi</i>	Male	11.0	1.8	2.7	6.4		1.1	1.2	3.8	Howard and Furth (1986)
	Female	10.9	2.1	2.9	7.1	8.1	1.2	1.2	3.5	Howard and Furth (1986)
<i>A. tinnulus</i>	Male	8.7	1.8	2.7	6.3		1.2	1.2	3.5	Howard and Furth (1986)
	Female	9.4	2.1	2.9	7.1	8.2	1.3	1.4	4.5	Howard and Furth (1986)
<i>A. walkeri</i>	Male	10.6	2.2	3.2	7.5	9.4				
	Female	11.2	2.5	3.4	8.3					
<i>A. fultoni</i>	Male	9.7	1.9	2.8	6.8		1.0	1.2	3.7	Howard and Furth (1986)
	Female	10.9	2.3	3.1	7.9	8.6				
<i>A. sparsalsatus</i>	Male	-	2.2	-	7.1					Fulton (1930)
	Female	-	2.4	3.4	7.7	6.8				
<i>A. maculatus</i>	Male	7.4	1.8	2.5	5.7					Hebard (1913)
	Female	8.3	2.0	2.6	6.3	6.2				
<i>A. griseus</i>	Male	7.2	1.6	2.1	5.2					Hebard (1913)
	Female	8.1	1.8	2.3	6.3	8.0				

Data are presented as mean values along with citations from which the data are drawn. The range of variation is presented in parentheses for *A. shalontaki*.

times the distance as the most common allele in the *A. fasciatus* group was common.

The Salado population, however, seems to consist of two genotypic classes along with potential advanced backcross individuals. The Salado collection has one individual that seems to be a member of a recently discovered yet undescribed species, *A. sp. nov. TX* (Traylor et al., unpublished data; Marshall 2004). This individual is homozygous at IDH, MDH, and AAT for the 1.3, 1.0, and 2.0 alleles, respectively. The other eight individuals from Salado are homozygous for the same novel alleles found in Atoka at the MDH and HK loci (1.6 and 1.0, respectively). Six of these eight individuals are also homozygous for the novel IDH allele found in Atoka (namely, the 1.5 allele). However, the remaining two individuals are heterozygous at IDH (carrying both the 1.5 and 1.3 alleles). That is, all individuals in Salado are genotypically identical to the crickets from Atoka except three crickets. One of these three is a member of *A. sp. nov. TX*. The remaining two crickets are genotypically identical to Atoka crickets at all loci except IDH where they are heterozygous for the Atoka allele and the *A. sp. nov. TX* allele.

We measured morphological characters of a sample of individuals from Atoka that were previously identified by song analysis and genotyped by electrophoretic analysis. Morphological data are presented in Table 2 (and in Diagnosis below). The clear pattern is that these crickets are larger than *A. fasciatus* or *A. socius* (Table 2). Other than body size, these crickets seem similar to *A. fasciatus* and *A. socius*, including similar head coloration, one of the most variable characters in this genus of cryptic species.

Calling songs were recorded from 18 field-collected crickets from the Atoka population. These crickets exhibited a unique male calling song that lies outside the range of variation of all known *Allonemobius* species. The song is characterized as a relatively long chirp (or short trill) that crescendos through the length of the chirp (Fig. 1). That is, the chirp lasts between 720 and 770 ms with a dominant frequency of 8 kHz and exhibits a unique pattern of increasing amplitude (sound pressure) through the chirp (Fig. 1B and C). Chirps are regularly timed occurring  $\approx 0.6$  s apart (Fig. 1A) and are composed of  $\approx 50$  pulses. Although chirps are regularly timed, the song is complex at the level of the chirp. Individual chirps have a temporal structure as there is variation in the rate of the crescendo within chirps (Fig. 1B). Specifically, the amplitude increases 22% by 0.4 s into the song, and another 60% by the end of the song. The song is further complicated by variation in pulse duration and pulse rate. The final 10 to 11 pulses of each chirp are longer and occur at a slower rate than the first 40 pulses. Moreover, these last pulses vary little in amplitude such that the additional 60% increase in amplitude occurs before these last pulses (Fig. 1B). The initial 40 pulses have an average pulse rate of 69 pulses per second, whereas the final pulses have an average pulse rate of 45.6 pulses per second. Finally, the last ten pulses exhibit frequency modulation with a rapid rise

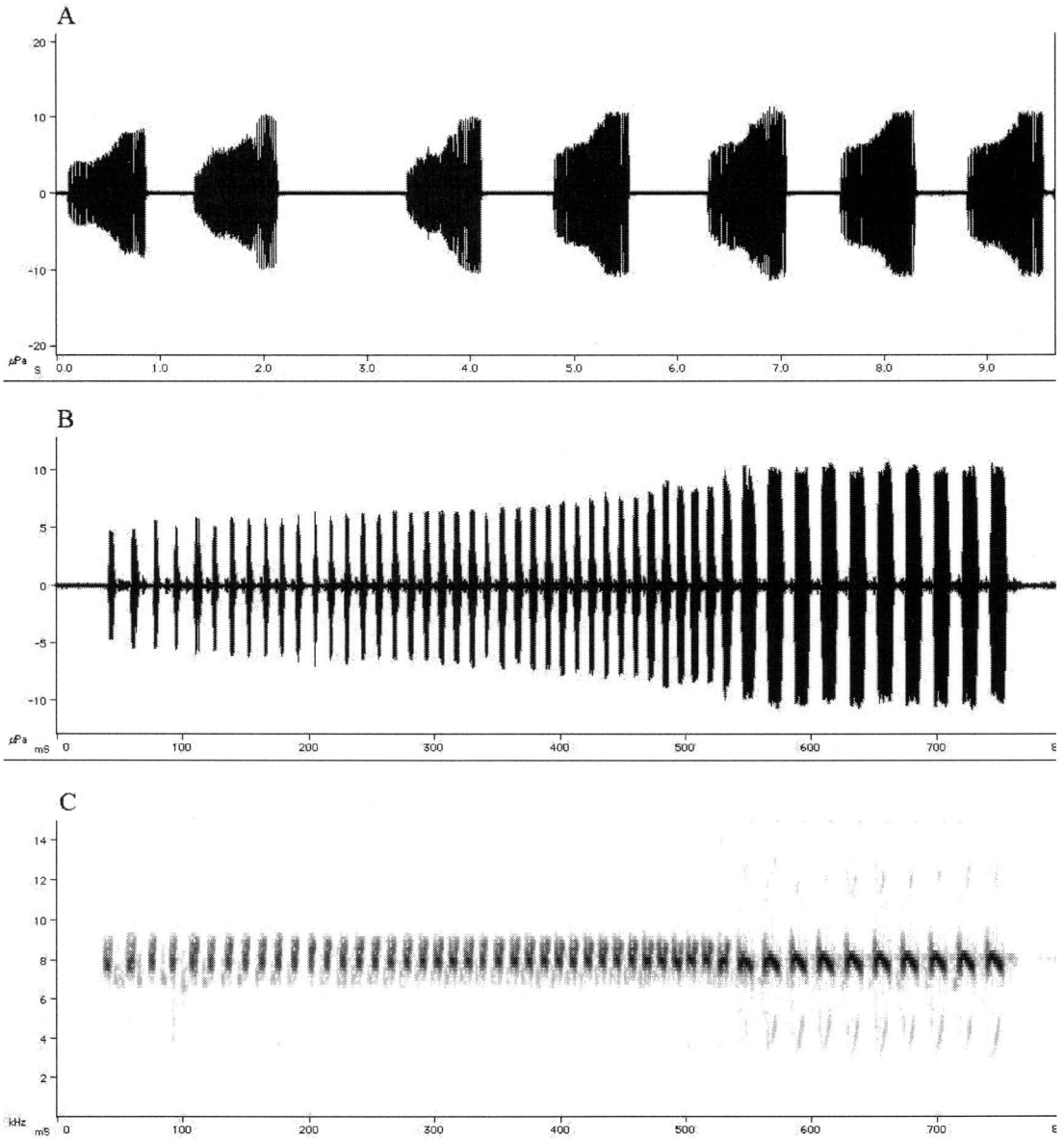


Fig. 1. Representative male calling song of *A. shalontaki* from Atoka, OK, recorded at 22°C. (A). Waveform depicting 9 s of male calling song. (B). Detailed waveform view of one chirp (or trill) lasting <0.8 s and depicting a crescendo in amplitude through the course of the chirp as well as a decrease in pulse rate toward the end of the chirp. (C). Spectrogram of the same chirp as in B, indicating the dominant frequency of 8 kHz.

followed by a slower decline in frequency not detectable within the initial 40 pulses (Fig. 1C).

*Allonemobius shalontaki* Braswell, n. sp.

Choctaw ground cricket

**Type Data.** HOLOTYPE: 1 ♀ was collected by W.E.B. VIII-1999 at Confederate Memorial Museum and rest stop along U.S. Hwy. 69 in Atoka, OK, USA, and is deposited in the Florida State Collection of Arthropods. PARATYPES: Additional specimens col-

lected by W.E.B. from same area as holotype are housed in the Florida State Collection of Arthropods and in the New Mexico State University entomology collection (accession nos. 26267–26274).

**Color and Pattern.** Head with dark longitudinal stripes from base onto vertex between eyes, as in *A. fasciatus*, and *A. socius*.

**Morphometrics.** Morphological measurements (in millimeters) are presented in Table 2. Average body length is greater in males (11.9 mm) than in females (10.8 mm). However, females are larger in all other

measurements, including pronotum length and width, and femur length (Table 2).

**Biological Notes.** *A. shalontaki* was first collected within the Choctaw Nation at Atoka, OK. Therefore, the species is named in honor of the Choctaw Nation. The specific epithet *shalontaki* means “cricket” in the Choctaw language.

Like many of its congeners in eastern North America, *A. shalontaki* is an inhabitant of short grasslands. It is likely a more drought-tolerant species than its congeners; however, the two localities in which this cricket has been found were watered lawns.

**An Electrophoretic Key to *Allonemobius* Species, by Using *A. fasciatus* as a Standard**

- 1. MDH migrates the same distance as standard . . . 3  
MDH migrates farther than standard . . . . . 2
- 2. MDH migrates 1.3 times the distance of standard . . . . . 4  
MDH migrates 1.6 times the distance of standard . . . . . *A. shalontaki*
- 3. HK migrates the same distance as standard . . . . .  
. . . . . *A. fasciatus*  
HK migrates 0.8 times the distance of the standard . . . . . *A. socius*
- 4. ME migrates the same distance as standard . . . 5  
ME migrates faster or slower than standard . . . 8
- 5. IDH migrates at least 1.8 times the distance of the standard . . . . . 6  
IDH migrates no >1.5 times the distance of standard . . . . . 7
- 6. HK migrates the same distance as standard . . . . .  
. . . . . *A. allardi*  
HK migrates 1.3 times the distance of standard . . . . .  
. . . . . *A. timmulus*
- 7. HK migrates the same distance as standard . . . . .  
. . . . . *A. fultoni*  
HK migrates 1.3 times the distance of standard . . . . .  
. . . . . *A. walkeri*
- 8. ME migrates slower than standard . . . . .  
. . . . . *A. maculatus*  
ME migrates faster than standard . . . . . *A. griseus*

**Discussion**

We present data supporting species status of the crickets we have named *A. shalontaki*. The data sets we present are of varying importance in supporting species status. For example, morphological data suggest that although *A. shalontaki* is larger than other members of the *A. fasciatus* species group, it is generally indistinguishable from these species. However, because body size measurements of other *Allonemobius* species are from published results rather than sympatric, or even western, populations it is impossible to know whether size variation is because of divergence or environmental variation.

Electrophoretic data, however, suggest that *A. shalontaki* represents a unique gene pool from other *Allonemobius* species. At a minimum, the IDH locus in *A. shalontaki* is fixed for an allele unknown within the

*A. fasciatus* clade, and the MDH allele is novel to the entire genus (Table 1). Although the lack of genotypically distinct sympatric congeners poses a theoretical problem to the utility of genetic divergence as a sign of reproductive isolation, extensive work has shown this pattern to be a robust method for identifying cryptic species (Howard and Furth 1986, Howard et al. 1998).

Although allozyme divergence represents persuasive data supporting species status of *A. shalontaki*, the extreme divergence in calling song makes explanations other than reproductive isolation unlikely. Although studies of female calling song preference have not been performed, it is unlikely that such divergent calling songs (let alone electrophoretic variants) could remain intact if these crickets were exchanging genes with any known *Allonemobius* species. In addition to supporting species status, male calling song likely acts as a prezygotic isolating barrier. Although mating studies have not been performed to confirm reproductive isolation, morphological, electrophoretic, and calling song analyses all indicate a lack of gene flow with previously described species. As a result, we feel confident in naming *A. shalontaki* as a new species.

Electrophoretic data suggest two possibilities regarding the Salado population. Either *A. shalontaki* exhibits allelic variation at the IDH locus and is not fixed for the 1.5 allele as suggested by the Atoka population, or *A. shalontaki* and *A. sp. nov. TX* have exchanged genes at sometime in the, perhaps recent, past. Although these two possibilities are not mutually exclusive, indirect evidence does make some predictions. Given that these species co-occur in Salado, it seems reasonable to suggest that at least limited hybridization is or has occurred between these two species. Additional work is required to differentiate between these two possibilities.

In an attempt to understand the evolutionary relationships within the genus *Allonemobius*, we reconstructed phylogeny by using genetic distance estimated from electrophoretic data (Table 3). We found that tree topology was resilient to both the method of reconstruction and genetic distance estimators. Most methods revealed *A. shalontaki* as basal to the *A. fasciatus*-*A. socius* clade (Fig. 2). Indeed, only two of the 18 methods, least squares (with a molecular clock) and unweighted pair-group method with arithmetic average methods by using Reynolds genetic distance, placed *A. shalontaki* differently. These two methods place *A. shalontaki* basal to both the *A. fasciatus* and *A. allardi* clades, e.g., ((((*fasciatus*, *socius*), ((*allardi*, *timulus*), *walkeri*), *fultoni*)), *shalontaki*), *griseus*), *maculatus*). Although all of these analyses are based on a small data set and exhibit moderate bootstrap support, they demonstrate the interspecific relationships within the genus and are largely consistent with previous work on the genus (Howard 1983). Thus, these analyses pose viable hypotheses regarding the placement of *A. shalontaki*. Additional data are required to assess the evolutionary relationships

Table 3. Summary of pairwise genetic distance among *Allonemobius* species by using nine loci

	<i>shalontaki</i>	<i>allardi</i>	<i>tinnulus</i>	<i>fultoni</i>	<i>walkeri</i>	<i>fasciatus</i>	<i>socius</i>	<i>maculatus</i>	<i>griseus</i>
<i>shalontaki</i>	***	0.602	0.600	0.400	0.508	0.406	0.580	1.200	0.765
<i>allardi</i>	0.376	***	0.129	0.203	0.402	0.608	0.447	0.953	0.767
<i>tinnulus</i>	0.371	0.104	***	0.343	0.400	0.606	0.466	0.824	0.765
<i>fultoni</i>	0.251	0.089	0.206	***	0.308	0.606	0.608	1.000	0.565
<i>walkeri</i>	0.352	0.203	0.198	0.203	***	0.606	0.608	1.000	0.673
<i>fasciatus</i>	0.254	0.380	0.375	0.409	0.390	***	0.325	1.000	0.971
<i>socius</i>	0.367	0.292	0.285	0.370	0.351	0.204	***	1.123	0.974
<i>maculatus</i>	1.083	0.756	0.585	0.796	0.777	0.789	1.008	***	1
<i>griseus</i>	0.579	0.550	0.544	0.397	0.519	0.809	0.771	0.793	***

Nei's distance is presented below the diagonal and Cavalli-Sforza's distance is presented above the diagonal.

within this genus and such analyses, based on DNA sequence, are underway (W.E.B., unpublished).

Although most species in the genus *Allonemobius* are morphologically cryptic, many were recognized to be "physiologically distinct" (Fulton 1931, 1933, 1937) before their eventual description as distinct species (Alexander and Thomas 1959). Unlike these species, *A. shalontaki* was not previously recognized. Although *A. shalontaki* cannot be identified morphologically, males can be easily identified by calling song. There-

fore, it seems that the lack of recognition of this species is because of a lack of work in the west rather than its cryptic nature. Identification of *A. shalontaki* and an as yet undescribed species from Texas (Traylor et al., unpublished data; Marshall 2004) along with two potential new species in the Dakotas (Weibel 1996) suggest that the genus *Allonemobius* may be much more diverse than currently recognized. It seems that we have only begun to sample the diversity of this genus and additional work in the west may be fruitful.

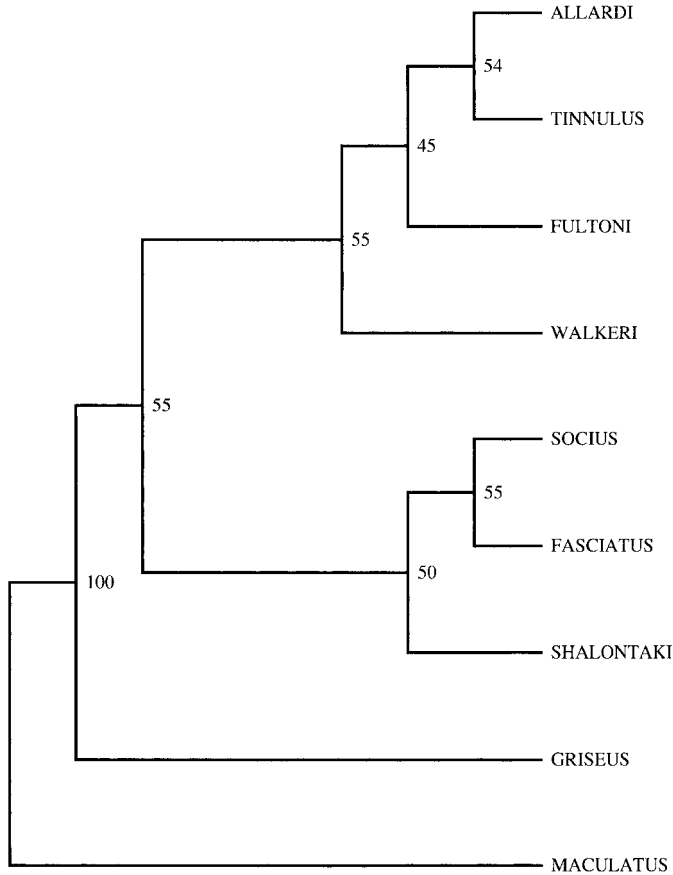


Fig. 2. Unweighted pair-group method with arithmetic average tree based on Cavalli-Sforza's estimate of genetic distance. Values at nodes are percentage of bootstrap support based on 1,000 replicates.

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### References Cited

- Alexander, R. D. 1962. The role of behavioral study in cricket classification. *Syst. Zool.* 11: 53–72.
- Alexander, R. D., and E. S. Thomas. 1959. Systematic and behavioral studies on the crickets of the *Nemobius fasciatus* group (Orthoptera: Gryllidae: Nemobiinae). *Ann. Entomol. Soc. Am.* 52: 591–605.
- Bradford, M. J., and D. A. Roff. 1993. Bet hedging and the diapause strategies of the cricket *Allonemobius fasciatus*. *Ecology* 74: 1129–1135.
- Carrière, Y., S. Masaki, and D. A. Roff. 1997. The coadaptation of female morphology and offspring size: a comparative analysis in crickets. *Oecologia* 110: 197–204.
- Cavalli-Sforza, L. L., and A.W.F. Edwards. 1967. Phylogenetic analysis: analysis and methods. *Evolution* 32: 550–570.
- Charif, R. A., S. Mitchell, and C. W. Clark. 1995. Canary 1.12 user's manual. Cornell Laboratory of Ornithology, Ithaca, NY.
- Chu, J., and D. J. Howard. 1998. Genetic linkage maps of the ground crickets *Allonemobius fasciatus* and *A. socius* using RAPD and allozyme markers. *Genome* 41: 841–847.
- Chu, J., E. Powers, and D. J. Howard. 1995. Gene exchange in a cricket hybrid zone. *J. Hered.* 86: 17–21.
- DeGeer, C. 1773. *Memoires pour servir a l'histoire des insectes*, III. Hosselberg, Stockholm, Sweden.
- Doherty, J. A., and D. J. Howard. 1996. Lack of preference for conspecific calling songs in female crickets. *Anim. Behav.* 51: 981–990.
- Fedorka, K. M., and T. A. Mousseau. 2002a. Material and genetic benefits of female multiple mating and polyandry. *Anim. Behav.* 64: 361–367.
- Fedorka, K. M., and T. A. Mousseau. 2002b. Tibial spur feeding in ground crickets: larger males contribute larger gifts (Orthoptera: Gryllidae). *Fla. Entomol.* 85: 317–323.
- Fedorka, K. M., and T. A. Mousseau. 2004. Female mating bias results in conflicting sex-specific offspring fitness. *Nature (Lond.)* 429: 65–67.
- Felsenstein, J. 2004. PHYLIP (phylogenetic inference package) version 3.6. Distributed by author. Department of Genome Sciences, University of Washington, Seattle, WA.
- Fulton, B. B. 1930. A new species of *Nemobius* from North Carolina (Orthoptera: Gryllidae). *Entomol. News* 41: 38–42.
- Fulton, B. B. 1931. A study of the genus *Nemobius* (Orthoptera: Gryllidae). *Ann. Entomol. Soc. Am.* 24: 205–237.
- Fulton, B. B. 1933. Inheritance of song in hybrids of two subspecies of *Nemobius fasciatus* (Orthoptera). *Ann. Entomol. Soc. Am.* 26: 368–376.
- Fulton, B. B. 1937. Experimental crossing of subspecies in *Nemobius fasciatus* (Orthoptera). *Ann. Entomol. Soc. Am.* 30: 201–207.
- Gregory, P. G., and D. J. Howard. 1993. Laboratory hybridization studies of *Allonemobius fasciatus* and *A. socius* (Orthoptera: Gryllidae). *Ann. Entomol. Soc. Am.* 86: 694–701.
- Gregory, P. G., and D. J. Howard. 1994. A post-insemination barrier to fertilization isolates two closely related ground crickets. *Evolution* 48: 705–710.
- Gregory, P. G., and D. J. Howard. 1996. Multiple mating in natural populations of ground crickets. *Entomol. Exp. Appl.* 78: 355–356.
- Gregory, P. G., M. D. Remmenga, and D. J. Howard. 1998. Patterns of mating between two closely related ground crickets are not influenced by sympatry. *Entomol. Exp. Appl.* 87: 263–270.
- Hebard, M. 1913. A revision of the genus *Nemobius* (Orthoptera: Gryllidae) found in North America north of the Isthmus of Panama. *Proc. Acad. Natl. Sci. Phila.* 65: 394–492.
- Howard, D. J. 1982. Speciation and coexistence in a group of closely related ground crickets. Ph.D. dissertation, Yale University, New Haven, CT.
- Howard, D. J. 1983. Electrophoretic survey of eastern North American *Allonemobius* (Orthoptera: Gryllidae): evolutionary relationships and the discovery of three new species. *Ann. Entomol. Soc. Am.* 76: 1014–1021.
- Howard, D. J. 1986. A zone of overlap and hybridization between two ground cricket species. *Evolution* 40: 34–43.
- Howard, D. J., and D. G. Furth. 1986. Review of the *Allonemobius fasciatus* (Orthoptera: Gryllidae) complex with the description of two new species separated by electrophoresis, songs, and morphometrics. *Ann. Entomol. Soc. Am.* 79: 472–481.
- Howard, D. J., and P. G. Gregory. 1993. Post-insemination signaling systems and reinforcement. *Phil. Trans. R. Soc. Lond. B* 340: 231–236.
- Howard, D. J., and R. G. Harrison. 1984a. Habitat segregation in ground crickets: experimental studies of adult survival, reproductive success, and oviposition preference. *Ecology* 65: 61–68.
- Howard, D. J., and R. G. Harrison. 1984b. Habitat segregation in ground crickets: the role of interspecific competition and habitat selection. *Ecology* 65: 69–76.
- Howard, D. J., and G. L. Waring. 1991. Topographic diversity, zone width, and the strength of reproductive isolation in a zone of overlap and hybridization. *Evolution* 45: 1120–1135.
- Howard, D. J., P. G. Gregory, J. Chu, and M. L. Cain. 1998. Conspecific sperm precedence is an effective barrier to hybridization between closely related species. *Evolution* 52: 511–516.
- Howard, D. J., M. Reece, P. G. Gregory, J. Chu, and M. L. Cain. 1998. The evolution of barriers to fertilization between closely related organisms, pp. 279–288. *In* D. J. Howard and S. H. Berlocher [eds.], *Endless forms: species and speciation*. Oxford University Press, New York.
- Howard, D. J., G. L. Waring, C. A. Tibbets, and P. G. Gregory. 1993. Survival of hybrids in a mosaic hybrid zone. *Evolution* 47: 789–800.
- Marshall, J. L. 2004. The *Allonemobius-Wolbachia* host-endosymbiont system: evidence for rapid speciation and against reproductive isolation driven by cytoplasmic incompatibility. *Evolution* 58: 2409–2425.

- Mousseau, T. A., and D. J. Howard. 1998. Genetic variation in cricket calling song across a hybrid zone between two sibling species. *Evolution* 52: 1104–1110.
- Nei, M. 1972. Genetic distance between populations. *Am. Nat.* 106: 283–292.
- Olvido, A. E., E. S. Elvington, and T. A. Mousseau. 2003. Relative effects of climate and crowding on wing polymorphism in the southern ground cricket, *Allonemobius socius* (Orthoptera: Gryllidae). *Fla. Entomol.* 86: 158–164.
- Reynolds, J. B., B. S. Weir, and C. C. Cockerham. 1983. Estimation of coancestry coefficient: basis for a short-term genetic distance. *Genetics* 105: 767–779.
- Roff, D. A., and M. J. Bradford. 2000. A quantitative genetic analysis of phenotypic plasticity of diapause induction in the cricket *Allonemobius socius*. *Heredity* 84: 193–200.
- Roff, D. A., and T. A. Mousseau. 1999. Does natural selection alter genetic architecture? An evaluation of quantitative genetic variation among populations of *Allonemobius socius* and *A. fasciatus*. *J. Evol. Biol.* 12: 361–369.
- Roff, D. A., T. A. Mousseau, and D. J. Howard. 1999. Variation in genetic architecture of calling song among populations of *Allonemobius socius*, *A. fasciatus*, and a hybrid population: drift or selection? *Evolution* 53: 216–224.
- Sadowski, J. A., J. L. Grace, and A. J. Moore. 2002. Complex courtship behavior in the striped ground cricket *Allonemobius socius* (Orthoptera: Gryllidae): does social environment affect male and female behavior? *J. Insect Behav.* 15: 69–84.
- Tanaka, S., and V. J. Brookes. 1983. Altitudinal adaptation of the life cycle in *Allonemobius fasciatus*. *Can. J. Zool.* 61: 1986–1990.
- Veech, J. A., J. H. Benedix, Jr., and D. J. Howard. 1996. Lack of calling song displacement between two closely related ground crickets. *Evolution* 50: 1982–1989.
- Vickery, V. R., and D. E. Johnstone. 1970. Generic status of some Nemobiinae (Orthoptera: Gryllidae) in northern North America. *Ann. Entomol. Soc. Am.* 63: 1740–1749.
- Walker, T. J. 1964. Cryptic species among sound-producing ensiferan Orthoptera (Gryllidae and Tettigoniidae). *Q. Rev. Biol.* 39: 345–355.
- Weibel, A. C. 1996. Distribution, population genetics and evolutionary relationships of the striped ground cricket (genus *Allonemobius*) across North America. M.S. thesis, New Mexico State University, Las Cruces, NM.
- Weibel, A. C., and D. J. Howard. 2000a. Discovery of new populations of striped ground crickets in western North America: distribution, subdivision, and introduction detected by allozyme data. *J. Entomol. Res. Soc.* 2: 1–25.
- Weibel, A. C., and D. J. Howard. 2000b. Canonical correlation of allozyme and morphological variation across distinct geological features in one species of striped ground crickets. *J. Entomol. Res. Soc.* 2: 15–29.

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