Review of the *Allonemobius fasciatus* (Orthoptera: Gryllidae) Complex with the Description of Two New Species Separated by Electrophoresis, Songs, and Morphometrics

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ABSTRACT The *Allonemobius fasciatus* (De Geer) complex, a group of closely related ground crickets, has proven recalcitrant to analysis by traditional methods of museum taxonomists. Here we formally describe two new species (*A. walkeri* and *A. fultoni*), reinstate the species status of *A. socius* (Scudder), and provide an electrophoretic key to the complex. In addition, we describe male calling song, habitat, life cycle, and geographic distribution of each species in the complex, and we compare the species morphometrically.

FULTON (1931, 1933, 1937) recognized three subspecies or forms ("physiologically distinct") of *Allonemobius fasciatus* (De Geer) (formerly in *Nemobius*): *A. f. fasciatus*, *A. f. socius* (Scudder), and *A. f. tinnulus* (Fulton), but he did not treat them as distinct species. For many years members of the *Allonemobius fasciatus* group remained enigmatic and were often confused with each other. Alexander & Thomas (1959) emphasized that identification based solely on morphology is largely unreliable. They attempted to resolve the long-standing confusion in the *A. fasciatus* group by employing several types of evidence, including some morphology and ecology, but especially male songs, for differentiating the species. After extensive examination of thousands of specimens, including the type material of all taxa concerned, Alexander & Thomas (1959) redefined the *A. fasciatus* complex. They synonymized the subspecies *A. fasciatus socius* under the name *A. fasciatus*, described *A. fasciatus fasciatus* (auctt., nec De Geer) as new (*A. allardi*), and raised *A. fasciatus tinnulus* to specific rank (*A. tinnulus*). However, this picture of the *A. fasciatus* complex was recently changed by Howard (1982, 1983), who presented electrophoretic evidence that *A. fasciatus* is composed of two cryptic species and that *A. allardi* consists of three. The status of *A. tinnulus* was unaffected by Howard's work. Thus, instead of three species in the eastern United States, the complex consists of at least six.

One of the two cryptic species of *A. fasciatus* is widely distributed in the northeastern United States, and the other is widely distributed in the southeast (Howard 1982, 1983; Fig. 1). Based on the type locality (Pennsylvania) of *A. fasciatus* (De Geer 1773), Howard (1983) suggested that the northeastern species should be named *A. fasciatus*. He applied the name *A. socius* to the southeastern species based on the type specimen from Georgia described by Scudder in 1877. Of the three cryptic species in *A. allardi*, Howard (1983) applied binomial nomenclature only to the northeastern one, which he called *A. allardi* (sensu Alexander & Thomas 1959). He referred to the two central eastern species as *A.* y and *A.* z.

In this paper we review the *A. fasciatus* complex and formally describe the two new species left unnamed by Howard (1982, 1983). Among the traits described for each species are diagnostic biochemical characters, morphological characters, male calling songs, habitat utilization patterns, and life history patterns.

Materials and Methods

Calling Songs. We collected all crickets used for song analysis during August of 1981 (sites in Table 1). After collection, we identified each male to species by removing a hind femur and assessing its phenotype at three loci coding for soluble enzymes (see electrophoretic key section). If any ambiguity existed as to specific identity, a possibility in areas of overlap between *A. socius* and *A. fasciatus*, the cricket was not used for song analysis. After identification, males were placed individually into petri dishes (20 by 100 mm) supplied with food (Purina Cat Chow) and water (wet cotton).

We recorded calling songs in a soundproof room at 23–25°C using an open-reel tape recorder (Crown 800) and a microphone (Sennheiser). We measured the dominant frequency of a song on a spectrum analyzer (Unigon [Uniscan] Model 4500). The temporal pattern of a song was monitored on an oscilloscope (Tektronix 5111 Dual Trace) with dual trace amplifier (5A26) and time base amplifier (5B10N). A differential amplifier (Tektronix

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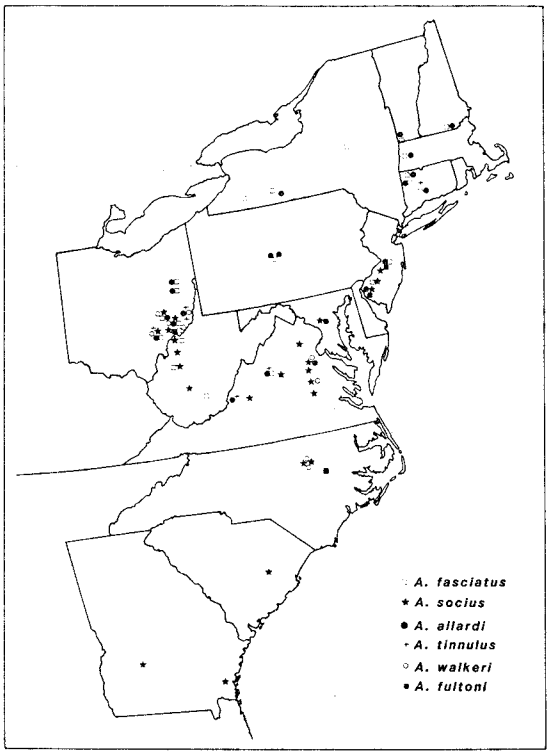

Fig. 1. Distributions of *A. fasciatus* complex species in the eastern United States based on populations examined electrophoretically.

AM 502) with the high pass filter set at 100 Hz was used to filter out low-frequency background noise in the analysis of temporal patterns. All songs analyzed were at least 30 s long.

Morphology. After an extensive search for characters, we concluded that the following measurements would be most demonstrative. Males: body length (Lb); maximal length of pronotum (Lp); maximal width of pronotum (Wp); length of hind femur (Lf); right tegmen distances as in Fulton (1931, Fig. 2A), that is, stridulatory vein from mesal origin to ulnar vein (Tg1), distance from ulnar vein to lateral border of dorsal tegmen surface (Tg2), distance from stridulatory vein to apex (posterior edge) of tegmen (Tg3). Females: Lb, Lp, Wp, Lf, length of ovipositor shaft (Lo). File teeth counts were obtained from at least 10 male specimens of each species.

The character data were analyzed on a mainframe computer (IBM 4341-II) (running VM-SP3), using the SAS Institute (1982) statistical package. We first experimented with discriminant and principal components analysis, on both raw data and certain ratios, but neither method gave notably better separation of the several taxa than did simpler techniques. Accordingly, we chose to portray species differences graphically (Fig. 2) using analysis of variance (ANOVA) statistics (specifically, probabilities from Duncan's [1975] multiple range test [$\alpha = 0.05$], with species as the class variable).

Abbreviations. The following institutional abbreviations are used: YPM, Peabody Museum of Natural History, Yale University; USNM, National Museum of Natural History; PANS, Academy of Natural Sciences of Philadelphia.

Results

The description of each species is divided into these categories: color and pattern; stridulatory file teeth number (range, mean, and number of specimens examined); morphometrics of males and females including range, number, and location of specimens examined (in brackets, mean values in parentheses); and biological notes, including comments on habitat, phenology, and distribution.

Allonemobius walkeri Howard & Furth, n. sp.

Color/Pattern. Head pattern and coloration as in *A. allardi* (Alexander & Thomas 1959) with three separate black stripes obscured at base (nearest anterior border of pronotum); pronotum laterally bordered with yellow band (not visible from above), sublaterally with wide black band, medially with yellowish band of irregular width (both visible from above), disc of pronotum with mottled irregular pattern of light and dark brown (variable); legs lighter brown; abdominal venter primarily light brown, especially mesally; dorsal half of abdomen black; male tegmen brown with basal third darker, especially on both sides of base and apex of stridulatory vein, along mesal edge of wing from base until more than half its length.

Stridulatory File Teeth Number. 183–208 (mean, 195; *n*, 11); differing significantly from *A. allardi* (208) and *A. fultoni* (157).

Morphometrics (nearest 0.1 mm).

Males [18: localities given below]:		Females [17: localities given below]:	
Lb = 9.9–11.7	(10.6)	Lb = 9.2–11.7	(11.2)
Lp = 2.0–2.5	(2.2)	Lp = 2.3–2.6	(2.5)
Wp = 2.9–3.5	(3.2)	Wp = 3.2–3.5	(3.4)
Lf = 7.0–8.1	(7.5)	Lf = 7.7–8.7	(8.3)
Tg1 = 1.3–1.5	(1.3)	Lo = 8.1–10.5	(9.4)
Tg2 = 1.2–1.5	(1.4)		
Tg3 = 3.9–5.0	(4.5)		

The males of *A. walkeri* are significantly larger in all seven measured characters than males of *A. fultoni* and *A. allardi*. The females of *A. walkeri* are significantly larger than females of *A. fultoni* and *A. allardi* in Lp, Wp, and Lo, but differ from females of *A. allardi* only in Lf.

Type Data. Holotype ♂, USA: Ohio, Noble County, Macksburg, 17-IX-1983, Howard (electrophoresis code MBO #8) (deposited in YPM). Allotype ♀, USA: Ohio, Morgan County, Reinersville,

Table 1. Calling song characteristics of five North American *Allonemobius* species

Species (each individual listed separately)[a]	Collection site[b]	Temp of recording (°C)	Dominant frequency (Hz)	$\bar{x}$ chirp or trill length (s)	SE	$\bar{x}$ interval between chirps or trills (s)	SE	$\bar{x}$ pulse rate (per second)	SE
A. *all* 1	Noble, Ohio	24.0	8,160	10.7	±6.0	0.6	±0.13	13.2	±0.1
A. *all* 2	Noble, Ohio	24.0	7,200	3.1	±0.3	0.6	±0.03	14.5	±0.2
A. *all* 3	Litchfield, Conn.	24.0	7,200	3.7	±0.8	0.4	±0.05	14.5	±0.2
A. *all* 4	Litchfield, Conn.	24.0	7,440	9.5	±1.3	1.0	±0.16	16.0	±0.2
A. *ful*	Salem, N.J.	24.0	6,640 7,040	5.3	±0.1	3.3	±0.32	22.0	±0.1
A. *wal* 1	Noble, Ohio	23.5	6,720	12.0	±3.5	0.3	±0.05	24.0	±0.1
A. *wal* 2	Noble, Ohio	23.5	7,680	32.2	±0.7	0.5	±0.04	24.6	±0.2
A. *wal* 3	Washington, Ohio	23.0	6,960	26.0	±3.2	0.4	±0.10	25.2	±0.2
A. *fas* 1	Washington, Ohio	24.0	7,920	0.09	—	0.38	±0.01	89.6	±1.2
A. *fas* 2	Washington, Ohio	24.0	7,200	0.10	—	0.41	±0.03	97.6	±2.4
A. *fas* 3	Wood, W.Va.	24.0	7,120	0.09	—	0.56	±0.03	89.1	±0.2
A. *fas* 4	Mercer, N.J.	24.5	7,920	0.10	—	0.38	±0.01	92.6	±2.4
A. *fas* 5	Mercer, N.J.	24.5	8,080	0.11	—	0.56	±0.02	89.1	±1.8
A. *soc* 1	Washington, Ohio	23.0	7,680	0.10	—	0.22	±0.01	91.3	±0.8
A. *soc* 2	Washington, Ohio	23.0	7,680	0.10	—	0.17	—	92.1	±1.3
A. *soc* 3	Washington, Ohio	23.0	7,920	0.12	—	0.24	—	97.4	±1.9
A. *soc* 4	Camden, N.J.	24.5	7,040	0.09	—	0.30	±0.01	101.0	±0.9
A. *soc* 5	Salem, N.J.	24.5	7,920	0.08	—	0.32	±0.01	95.2	±1.9

[a] A. *all*, A. *allardi*; A. *ful*, A. *fultoni*; A. *wal*, A. *walkeri*; A. *fas*, A. *fasciatus*; A. *soc*, A. *socius*.
[b] Collection site localities are identified by county and state.

State Route 78, 17-IX-1983, Howard (electrophoresis code MCO #24) (YPM). Paratypes: USA: 4 ♂♂, Ohio, Noble County, Macksburg, 22-VIII-1981, Howard (calling song #61, 62, 63, 65); 2 ♂♂, Ohio, Washington County, North Marietta, 22-VIII-1981, Howard (calling song #66, 67); 7 ♂♂, 12 ♀♀, same data as holotype (electrophoresis code MBO #1, 2, 4, 5, 6, 7, 9, 14, 18, 36, 45, 46, 47, 49, 52, 53, 54, 55, 56); 4 ♂♂, 4 ♀♀, same data as allotype (electrophoresis code MCO #22, 23, 25, 26, 27, 28, 30, 32). Most paratypes are deposited at YPM, but 2 ♂♂ and 2 ♀♀ are also deposited at both USNM and PANS.

Biological Notes. *Allonemobius walkeri* is the species Howard (1983) designated as *A.* y. It is named in honor of Thomas J. Walker of the University of Florida, Gainesville, the first person to recognize the calling song differences between this species and *A. allardi*.

A. walkeri is a relatively rare cricket. Even Ful-

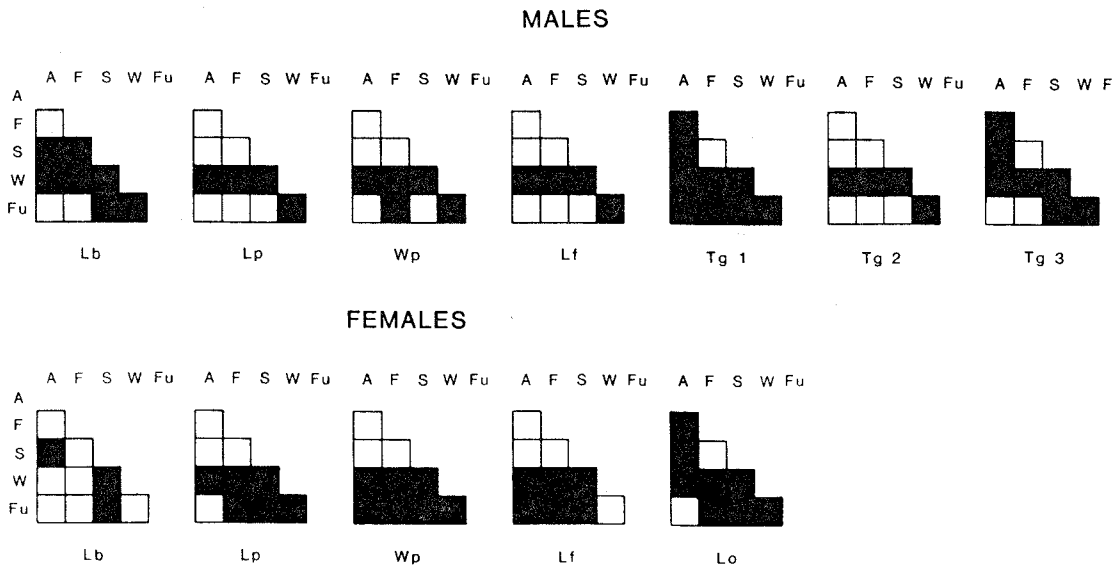

Fig. 2. Graphic summary of statistical results of morphometric analyses of *Allonemobius*. Black cell in matrix, the two taxa differ significantly. White cell in matrix, taxa do not differ significantly. A, *A. allardi*; F, *A. fasciatus*; S, *A. socius*; W, *A. walkeri*; Fu, *A. fultoni*.

ton, who lived in North Carolina, did not suspect the presence of this species. He did recognize a southern counterpart of *A. allardi* (Fulton 1931, 1933, 1937), but his description of the habitat and male calling song of this southern cricket indicates that he was dealing with *A. fultoni*, not *A. walkeri*. The geographic distribution of *A. walkeri* based on populations studied electrophoretically is given in Fig. 1.

A. walkeri inhabits dry grassy fields and pastures. In southeastern Ohio, where its range overlaps that of *A. allardi*, we have never collected one species without also collecting the other. Available evidence indicates that *A. walkeri* is a univoltine, egg-overwintering species. In an extensive collecting trip through Virginia, North Carolina, South Carolina, and Georgia in late June of 1980, we collected many *A. socius* adults but found no trace of *A. walkeri*. In a less extensive trip in September of 1980, *A. walkeri* adults were found at two sites in North Carolina and two sites in Virginia. Fulton never heard a trilling *Allonemobius* in the early summer.

The male calling song of *A. walkeri* can be categorized as an irregularly broken trill (Table 1). In the laboratory, pulses were delivered at the rate of 24–25 per second at 23–23.5°C.

Allonemobius fultoni Howard & Furth, n. sp.

Color/Pattern. Color, pattern of head, pronotum, abdomen, and tegmen essentially as in *A. walkeri*.

Stridulatory File Teeth Number. 140–174 (mean, 157; *n*, 10), differing significantly from *A. walkeri* (195) and *A. allardi* (208).

Morphometrics (nearest 0.1 mm).

Males [12: localities given below]:		Females [8: localities given below]:	
Lb = 8.7–10.5	(9.7)	Lb = 10.0–11.9	(10.9)
Lp = 1.8–2.1	(1.9)	Lp = 2.0–2.7	(2.3)
Wp = 2.6–3.0	(2.8)	Wp = 3.0–3.5	(3.1)
Lf = 6.3–7.5	(6.8)	Lf = 7.4–8.9	(7.9)
Tg1 = 0.7–1.2	(1.0)	Lo = 7.9–9.6	(8.6)
Tg2 = 1.1–1.4	(1.2)		
Tg3 = 3.2–4.4	(3.7)		

The males are significantly smaller in all measurements than males of *A. walkeri*, but only the Tg1 is significantly smaller than in males of *A. allardi*. The females are significantly smaller than females of *A. walkeri* in all measurements (except Lb). Females are somewhat larger than those of *A. allardi* in Wp and distinctly so for Lf (see Fig. 2).

Type Data. Holotype ♂, USA: New Jersey, Salem County, New Jersey Turnpike, Clara Barton Service Area, 12-VIII-1981, Howard (deposited in YPM). Allotype ♀, USA: New Jersey, Salem County, New Jersey Turnpike, Clara Barton Service Area, 12-VIII-1981, Howard (YPM). Paratypes: USA: 9 ♂♂, 3 ♀♀, same data as holotype; 2 ♂♂, 4 ♀♀, New Jersey, Salem County, New Jersey Turnpike, Clara Barton Service Area, 23-IX-1983, Furth (electrophoresis code SEM #60, 61, 67, 70, 75, 84). Most paratypes are deposited at YPM. At least 1 ♂ and 1 ♀ are also deposited at both PANS and USNM.

Biological Notes. *Allonemobius fultoni* corresponds to the species that Howard (1983) designated as *A.* z. It is named for the late B. B. Fulton from North Carolina State University, who, in the 1930's, suspected evolutionary divergence between northern and southern populations of *A. allardi* based on habitat differences.

The distribution of *A. fultoni* is not well known. We have collected it from only three sites, two in southern New Jersey and one in North Carolina (Fig. 1). However, Fulton reported finding a species in South Carolina resembling *A. fultoni* in song and habitat association patterns, so it is likely that *A. fultoni* occurs farther south and west than shown in Fig. 1.

We have only found *A. fultoni* in wet grassy areas, either near marshes or in deep shade. Like *A. walkeri*, it seems to be relatively rare. Our largest collection from southern New Jersey numbered fewer than 20 individuals.

A. fultoni appears to be a univoltine, egg-overwintering species (Fulton 1933, 1937). An intensive effort to find adults during a trip through Virginia, North Carolina, South Carolina, and Georgia in late June 1980 was unsuccessful.

Thus far, we have only analyzed the recorded calling song of one *A. fultoni* male (Table 1), but its song proved to be quite distinctive from the songs of *A. allardi* and *A. walkeri*. The trill was broken at regular intervals for a fairly set period of time; the pulse rate within the trill was intermediate between that of *A. allardi* and *A. walkeri* (Table 1); and the trill began at a frequency of ca. 6,640 Hz but, about halfway through, abruptly shifted to a frequency of ca. 7,040 Hz. The lower frequency did not totally disappear subsequently, but its intensity was considerably reduced.

Allonemobius allardi (Alexander & Thomas)

Color/Pattern. Head pattern with longitudinal stripes indistinct at base but distinct (variable) apically, on vertex between eyes.

Stridulatory File Teeth Number. 190–228 (mean, 208; *n*, 12). Alexander & Thomas (1959) give a range of 165–200 for *A. allardi*.

Morphometrics (nearest 0.1 mm).

Males: 10, Connecticut; 1, New Jersey; 8, Ohio = 19

Females: 10, Connecticut; 3, New Jersey; 10, Ohio = 23

Males:	Females:
Lb = 9.2–11.2 (11.0)	Lb = 8.9–12.9 (10.9)

Lp = 1.6–2.2	(1.8)	Lp = 1.8–2.5	(2.1)
Wp = 2.2–3.3	(2.7)	Wp = 2.4–3.4	(2.9)
Lf = 5.3–7.8	(6.4)	Lf = 5.9–8.0	(7.1)
Tg1 = 1.0–1.4	(1.1)	Lo = 7.0–9.0	(8.1)
Tg2 = 1.0–1.5	(1.2)		
Tg3 = 3.2–4.9	(3.8)		

Biological Notes. Throughout its known range (Fig. 1), *A. allardi* occurs in a wide range of grassy areas, avoiding only wetter parts of these habitats, such as low-lying land adjacent to ponds and streams (Fulton 1931, 1937, Alexander & Thomas 1959). Interspecific competition with *A. fasciatus*, oviposition preference, and effects of the physical environment do not appear to influence its pattern of habitat association (Howard & Harrison 1984a,b).

A. allardi is a univoltine, egg-overwintering species (Fulton 1931, 1937, Alexander & Thomas 1959). In Connecticut, the earliest song record we have for *A. allardi* is 20 July, in Meriden. Adults reach their peak abundance from the middle of August through the middle of September, beginning a gradual decline thereafter. Generally, only a few males can be heard singing in early November.

We have analyzed the calling songs of four *A. allardi* males (Table 1). At 24°C, the pulse rate within the trill was 13–16 per second. In describing the calling song of *A. allardi*, Alexander & Thomas (1959) relied on recordings of 14 individuals from six locations in Illinois, Ohio, Pennsylvania, and New Hampshire. The pulse rates they reported correspond well with those we found for *A. allardi*.

Allonemobius tinnulus (Fulton)

Color/Pattern. General coloration lighter (than *A. allardi*, *A. fasciatus*, *A. socius*, *A. walkeri*, *A. fultoni*), yellow or orange (especially head, legs, tegmen); without distinct stripes on head, rarely with faint indication of nonbristled striped areas (only between eyes) (see Fig. 2 of Alexander & Thomas [1959]); lateralmost edge or crease (as seen from above) of male tegmen very light (white).

Stridulatory File Teeth Number. 187–239 (Fulton 1931).

Morphometrics. (All specimens are from PANS, and most were mentioned and measured by Fulton [1931] in his original description. To remain consistent with Fulton, cities are included in the locality description.)

Males: 1 paratype, North Carolina (Raleigh); 1, Iowa (Mt. Pleasant); 1, Virginia (Falls Church) = 3

Females: 1 paratype, North Carolina (Raleigh); 1, Iowa (Mt. Pleasant); 1, Illinois (Hillary) = 3

Males:	Females:
Lb = 8.1–9.2 (8.7)	Lb = 9.0–10.2 (9.4)
Lp = 1.7–1.9 (1.8)	Lp = 2.1 (2.1)
Wp = 2.4–2.9 (2.7)	Wp = 2.8–3.0 (2.9)
Lf = 5.8–6.9 (6.3)	Lf = 6.9–7.4 (7.1)
Tg1 = 1.1–1.3 (1.2)	Lov = 7.4–9.4 (8.2)
Tg2 = 1.1–1.3 (1.2)	
Tg3 = 3.2–3.9 (3.5)	

Morphometrics (Fulton 1931):

Tg1 = 1.2–1.5	Lf = 5.4–7.8
Tg2 = 1.1–1.4	Lo = 6.2–8.8
Tg3 = 3.4–4.2	

Because of the small sample size, *A. tinnulus* was not included in Duncan's (1975) multiple range tests.

Biological Notes. The electrophoretic work of Howard (1982, 1983) did not change the conception of *A. tinnulus* developed by Fulton (1925, 1931, 1933) and by Alexander & Thomas (1959). Howard examined four *A. tinnulus* populations from Connecticut, Ohio, and Virginia, and all were extremely similar electrophoretically. As predicted by Fulton (1931) and Alexander & Thomas (1959), this species appears to be closely related to *A. allardi* (Howard 1982, 1983).

The distribution of *A. tinnulus* (based on populations characterized electrophoretically) is shown in Fig. 1. This is probably a very incomplete range map. Fulton (1931, 1937) reported finding *A. tinnulus* as far west as Iowa and as far south as North Carolina. Alexander & Thomas (1959) reported the occurrence of *A. tinnulus* in southern Maine, Minnesota, Georgia, Alabama, and Mississippi.

A. tinnulus appears to be an open woodland and forest border inhabitant (Fulton 1933, 1937, Alexander & Thomas 1959). We have not collected it in dense forest or in open grassland away from the edge of woods. Although sometimes abundant, it does not seem to achieve the tremendous population densities sometimes exhibited by *A. allardi* and *A. fasciatus*.

A. tinnulus is a univoltine, egg-overwintering species (Fulton 1931, 1937, Alexander & Thomas 1959). The first adults appear in late July or early August and, at least in the northeastern United States, the last males can be heard singing in early November. The male calling song of *A. tinnulus* is a clear musical trill resembling that of *A. allardi*, but with the pulses delivered at a slower rate. We have not analyzed any recorded *A. tinnulus* songs, but Alexander & Thomas (1959) reported that, at the same temperature, the calling songs of *A. allardi* and *A. tinnulus* differ by 6–10 pulses per second.

Allonemobius fasciatus (De Geer)

Synonymy. (A more detailed synonymy can be found in Hebard [1913] and Vickery & Johnstone [1973].)

Gryllus fasciatus De Geer (1773: 522).
Nemobius fasciatus Scudder (1862: 430–431).
Allonemobius fasciatus Vickery & Johnstone (1970: 1746).

Color/Pattern. Head with dark longitudinal stripes from base onto vertex between eyes.

Stridulatory File Teeth Number. 113–144 (mean, 131; *n*, 10). Alexander & Thomas (1959) give a range of 101–145 for *A. fasciatus*.

Morphometrics (nearest 0.1 mm).

Males: 6, New Hampshire; 4, Connecticut; 2, New Jersey = 12

Females: 5, New Hampshire; 4, Connecticut; 3, Vermont = 12

Males:		Females:	
Lb = 8.8–10.4	(9.8)	Lb = 9.9–11.9	(10.7)
Lp = 1.7–2.0	(1.8)	Lp = 1.8–2.5	(2.1)
Wp = 2.4–3.0	(2.6)	Wp = 2.5–3.1	(2.9)
Lf = 5.7–7.1	(6.3)	Lf = 6.4–7.8	(6.9)
Tg1 = 0.8–1.0	(0.9)	Lo = 6.5–8.1	(7.3)
Tg2 = 1.0–1.2	(1.1)		
Tg3 = 3.3–4.0	(3.5)		

Biological Notes. *Allonemobius fasciatus* is a grassland inhabitant, achieving remarkably high population densities in low-lying pasture land and the edge of ponds and streams (Alexander & Thomas 1959, Howard & Harrison 1984a,b).

Throughout its known range (Fig. 1), *A. fasciatus* is univoltine and egg-overwintering (Alexander & Thomas 1959; Vickery & Johnstone 1973; D.J.H., unpublished data). In New England, nymphs begin to emerge in early June and adults are abundant by mid-August. By mid-November singing has ceased in the field.

We analyzed the recorded calling songs of five *A. fasciatus* males (Table 1). The song of *A. fasciatus* would be classified as a long chirp (Alexander 1962) and is very similar to the song of *A. socius*. The only difference we could detect was in the length of the interchirp interval. The songs of *A. fasciatus* males had slightly longer intervals than those of *A. socius* males (Table 1).

Table 2. Buffer and stain recipes for horizontal starch gel electrophoresis

Buffers

Malate dehydrogenase and hexokinase (buffers from Whitt [1970])
- Gel buffer: 1:60 dilution of stock solution
- Electrode buffer: 1:20 dilution of stock solution
- Stock solution: 0.75 *M* Tris, 0.25 *M* citric acid, pH 6.5

Isocitrate dehydrogenase-1 (buffers from Selander et al. [1971])
- Gel buffer: 0.023 *M* Tris, 0.005 *M* citric acid, pH 8.0
- Electrode buffer: 0.687 *M* Tris, 0.157 *M* citric acid, pH 8.0

Stain recipes

Malate dehydrogenase
- 45 ml 0.1 *M* Tris/HCl, pH 8.5
- 5 ml substrate
- 25 mg nicotinamide adenine dinucleotide
- 20 mg nitro blue tetrazolium
- 1 mg phenazine methosulfate
- Substrate: 13.4 g malic acid in water, adjusted to pH 7.0 with $NaCO_3$, volume to 100 ml

Hexokinase
- 50 ml 0.1 *M* Tris/HCl, pH 8.5
- 10 mg nitro blue tetrazolium
- 25 mg nicotinamide adenine dinucleotide phosphate
- 25 mg adenosine triphosphate
- 20 mg $MgCl_2$
- 45 mg glucose
- 40 units glucose-6-phosphate dehydrogenase
- 2 mg phenazine methosulfate

Isocitrate dehydrogenase-1
- 50 ml 0.2 *M* Tris/HCl pH 8.0
- 7.5 mg isocitric acid
- 50 mg $MgCl_2$
- 10 mg nicotinamide adenine dinucleotide phosphate
- 10 mg nitro blue tetrazolium
- 2 mg phenazine methosulfate

Allonemobius socius (Scudder), new status

Synonymy. (For a more detailed synonymy up to 1913 see Hebard [1913].)

Nemobius socius Scudder (1877: 37).
Nemobius fasciatus socius Rehn & Hebard (1911: 596); Hebard (1913: 421); Fulton (1931: 212).
Nemobius fasciatus Alexander & Thomas (1959: 592).
Pteronemobius fasciatus socius Chopard (1967: 175).
Allonemobius fasciatus Vickery & Johnstone (1973: 626–627).

Color/Pattern. Head pattern with longitudinal stripes as in *A. fasciatus*.

Stridulatory File Teeth Number. 122–149 (mean, 134; *n*, 11).

Morphometrics (nearest 0.1 mm).

Males: 4, Georgia; 5, New Jersey; 2, North Carolina; 2, South Carolina; 1, Virginia; 1, Maryland = 15

Females: 4, Georgia; 11, New Jersey; 2, North Carolina; 2, South Carolina; 1, Virginia; 1, Maryland = 21

Males:		Females:	
Lb = 8.2–10.1	(9.1)	Lb = 8.3–11.5	(10.0)
Lp = 1.6–2.2	(1.8)	Lp = 1.7–2.5	(2.1)
Wp = 2.3–3.1	(2.7)	Wp = 2.5–3.3	(2.9)
Lf = 5.5–7.4	(6.4)	Lf = 6.0–8.1	(6.8)
Tg1 = 0.8–1.0	(1.0)	Lo = 5.7–8.3	(6.9)
Tg2 = 1.0–1.2	(1.1)		
Tg3 = 3.2–4.1	(3.5)		

Biological Notes. The geographic distribution of *A. socius* based on electrophoretic evidence is shown in Fig. 1. Again, this is a conservative range map and it seems likely from the work of Fulton (1931) and Alexander & Thomas (1959) that *A. socius* occurs farther south and west than shown here.

A. socius is typically associated with wet grassy areas similar in appearance to those inhabited by *A. fasciatus* in the north. It is the only recognized species in the *A. fasciatus* complex that is not strictly univoltine. Fulton (1937) demonstrated that in the coastal plain of North Carolina *A. socius* has two generations, the first maturing before the mid-

Table 3. Mean allele frequencies in populations of *A. fasciatus* complex species[a]

Allele		*all*	*tin*	*ful*	*wal*	*fas*	*soc*
Mdh	*n*[b]	62	38	18	14	53	42
	b	1.00	1.00	1.00	1.00	—	—
	c	—	—	—	—	1.00	1.00
Hk	*n*	53	36	18	15	50	52
	c	0.01	0.95	—	—	—	—
	d	—	—	—	1.00	—	—
	e	0.99	0.05	0.88	—	—	—
	f	—	—	—	—	1.00	0.02
	g	—	—	—	—	—	—
	h	—	—	0.12	—	—	0.98
Idh-1	*n*	54	36	18	15	53	49
	b	0.02	0.21	—	—	—	—
	c	0.34	0.41	—	—	—	0.21
	d	0.61	0.66	—	—	—	0.44
	e	0.02	—	—	—	—	0.21
	f	—	—	—	—	—	—
	g	—	—	1.00	0.25	—	—
	h	—	—	—	0.75	—	—
	i	—	—	—	—	1.00	0.12

[a] *all*, *A. allardi*; *tin*, *A. tinnulus*; *ful*, *A. fultoni*; *wal*, *A. walkeri*; *fas*, *A. fasciatus*; *soc*, *A. socius*.
[b] Represents mean number of loci sampled in a population.

dle of June and the second maturing in late August. Farther south, *A. socius* may breed continuously (Alexander & Thomas 1959). A question of interest is whether *A. socius* is univoltine in the northern part of its range. To answer this question we collected crickets from 15 localities stretching from southern New Jersey to Richmond, Va., on 26 and 27 June 1981. The northernmost population containing adults was from Caroline County, Va., and it was not until Richmond, Va., that adults predominated in a sample. Thus, it seems that coastal plain populations of *A. socius* north of Caroline County, Va., were univoltine in 1981.

An Electrophoretic Key

Because identification of members of the *A. fasciatus* complex on the basis of morphological differences is often unreliable, we present here electrophoretic techniques and a key that can be used for distinguishing species. Berlocher (1980) presented the ideas behind such a key well. Briefly, discrimination is based on the fact that most species of this complex differ at one or more genes coding for soluble enzymes and these differences can be detected by gel electrophoresis.

The key is based on banding patterns produced by the enzyme products of three loci examined under the horizontal starch gel electrophoresis conditions described in Table 2. Table 3 shows allele frequencies at the three loci for all species. The key is applicable to both nymphs and adults; no bands are stage-specific. One requirement for using the key is a good supply of *A. allardi*, which is the standard. We recommend that at least five *A. allardi* individuals be run on each gel with unknowns. This will allow the detection of the occasional *A. fasciatus* individual collected with *A. allardi* and permit the identification of the most common allele (d) at isocitrate dehydrogenase-1, the only locus used in this key for which *A. allardi* is highly polymorphic. Another requirement for using the key is live specimens or specimens killed by freezing and subsequently stored at −60°C or below.

The morning of a gel run crickets should be ground in an equal part of buffer (0.1 *M* Tris/HCl, pH 7.0). The homogenates are then used to soak two small filter paper rectangles, which are each placed into a slit in a different starch gel. Two gels are necessary because the three enzymes used in this key cannot be satisfactorily separated on one gel and electrode buffer system. After the gels have been run and slices stained, use of the key should permit the identification of most unknowns. For adults and late instars, a single hind leg will provide enough material for analysis and the remainder of the body can be pinned or, in the case of live specimens, used in other studies.

Key to *Allonemobius*

1. Malate dehydrogenase mobility same as standard 3
   Malate dehydrogenase mobility slower than standard 2
2. Hexokinase mobility same as standard or only slightly slower ..... *A. fasciatus* (De Geer)
   Hexokinase mobility much slower than standard ..... *A. socius* (Scudder)
3. Hexokinase mobility same as standard 5
   Hexokinase mobility faster than standard .. 4
4. Isocitrate dehydrogenase-1 mobility same as standard ..... *A. tinnulus* (Fulton)
   Isocitrate dehydrogenase-1 mobility slower than standard ..... *A. walkeri* (Howard & Furth)
5. Isocitrate dehydrogenase-1 mobility same as standard .. *A. allardi* (Alexander & Thomas)
   Isocitrate dehydrogenase-1 mobility slower than standard ..... *A. fultoni* (Howard & Furth)

Comments on Key

Couplet 2. Hexokinase is an anodally migrating enzyme that appears as a three-banded pattern in most individuals, and this seems to represent the homozygous phenotype (Howard 1982, Tabachnick & Howard 1982). Measuring relative to the middle band, *A. fasciatus* individuals typically migrate ca. 1 mm slower than *A. allardi* individuals. This is a difference difficult to discern without experience. The middle band of *A. socius* migrates ca. 5 mm slower than the middle band of *A. allardi* and the difference is easily visualized. The faster two bands of *A. socius* match the mobility of the slower two bands of *A. fasciatus* and, in areas where the two species overlap in distri-

bution, four-banded phenotypes occur. Four-banded phenotypes are also found at low frequency in *A. socius* populations adjacent to areas of sympatry. Interspecific crosses indicate that these phenotypes represent heterozygotes (D.J.H., unpublished data). Because of variable levels of hybridization between *A. fasciatus* and *A. socius* (Howard 1982, 1986), this key will not be useful for identifying individuals from areas where the two species co-occur (Fig. 1). In such cases, the banding patterns of several other enzyme loci must be characterized for the positive identification of "pure" *A. socius* or *A. fasciatus* individuals (Howard 1982, 1986).

Couplet 3. There is a small chance of error at this couplet. Usually, the phenotype of *A. tinnulus* is a three-banded pattern, with the middle band running ca. 5 mm faster than the middle band of *A. allardi* and the slower two bands having the same mobility as the faster two bands of *A. allardi.* However, ca. 5% of *A. tinnulus* individuals and 1% of *A. allardi* individuals have a four-banded phenotype, which appears to represent the heterozygote. The Hardy-Weinberg law leads to the expectation that 2 of 1,000 *A. tinnulus* will have the phenotype characteristic of *A. allardi* and that 1 in 10,000 *A. allardi* will have the phenotype characteristic of *A. tinnulus.*

Couplet 4. There are two zones of isocitrate dehydrogenase (*Idh*) activity in *Allonemobius*, and bands in these two zones appear to be under the control of separate genes. The zone closest to the origin (*Idh-2*) is monomorphic for the same band in all eastern *Allonemobius. A. tinnulus* and the standard, *A. allardi,* are polymorphic at the locus controlling variation in the faster moving zone (*Idh-1*). However, the predominant allele in both species is the same (Table 2), and the two less common alleles in *A. tinnulus* also occur in *A. allardi. A. walkeri* is also polymorphic at this locus, but both alleles code for enzymes with slower mobilities than those of *A. allardi.* Because this is a dimeric enzyme, heterozygotes have three bands.

Discussion

Fulton (1931), Alexander & Thomas (1959), Vickery & Johnstone (1973), and others have attempted to separate the species of *Allonemobius* based on a variety of morphological characters such as head and pronotum shape or pattern, hind femur length, proportion of tegmen parts, number of stridulatory file teeth, ovipositor length and apex shape, and male genitalia. Most morphological characters used by previous authors are too variable and overlap too much for distinguishing species (except to species group) in the *A. fasciatus* complex. The same is also true for most of the morphological characters that we studied, although some show significant differences in two species comparisons. The most reliable species indicators for the *A. fasciatus* complex appear to be male calling song characteristics, electrophoretic banding patterns, habitat, and collection locality.

Allonemobius allardi group

It is easy to understand why *A. allardi, A. walkeri,* and *A. fultoni* were regarded as a single species until recently. They are extremely similar in morphology, overlap to some degree in distribution (Fig. 1), and the two eastern central species (*A. walkeri* and *A. fultoni*) are comparatively rare. Consequently, even though each of the three species has a distinctive male calling song when analyzed with modern acoustic tools (Table 1), the songs were not recognized as different because workers have tended to restrict their attention to the northeastern United States, where only one species occurs. A notable exception is T. J. Walker, who first recognized the difference in calling song between *A. walkeri* and *A. allardi.* However, he did not publish his results because of their preliminary nature.

The geographic distributions of the four species in the *A. allardi* group are given in Fig. 1. It is very likely that all four species have greater ranges than depicted in this figure, but we based this range map on populations that we have been able to analyze electrophoretically. Because differences in morphology are slight and it is difficult to distinguish male calling song differences by ear, we are reluctant to accept pinned specimens or listening records as evidence of occurrence.

There are significant morphological differences among the four species in the *A. allardi* group, although none is truly diagnostic for all four species. The character that comes closest to being diagnostic is restricted to males, namely number of stridulatory file teeth. This character is quite distinctive between *A. allardi–A. tinnulus* and *A. fultoni,* and between *A. fultoni* and *A. walkeri,* and somewhat so between *A. allardi–A. tinnulus* and *A. walkeri. A. walkeri* is the most divergent species in the *A. allardi* group. There is a significant difference between *A. walkeri* and either *A. allardi* or *A. fultoni* for all seven measured male characters. Female *A. walkeri* are almost as distinct as the males, differing from females of *A. allardi* in four of the five measured characters and from those of *A. fultoni* in three characters. Electrophoretically, *A. walkeri* is also the most divergent species in this group (Howard 1982, 1983).

A. tinnulus was not measured morphologically as extensively as the other three species and, therefore, was not included in the Duncan (1975) multiple range analysis; but from previously published accounts and current observations it can be distinguished by head and pronotum color, number of stridulatory file teeth, electrophoretic banding patterns, habitat, and male calling song characteristics.

The species concept most widely accepted by biologists is the biological species concept (Mayr

1982). Although various authors have chosen different ways to express this concept, a practical criterion for distinguishing species is lack of appreciable genetic exchange between sexually reproducing populations in nature. By this criterion there can be no doubt that *A. allardi*, *A. tinnulus*, *A. walkeri*, and *A. fultoni* are distinct species. The geographical range of each species overlaps those of the other three to at least a limited extent. Yet in areas of sympatry, electrophoretic analysis of diagnostic or close to diagnostic enzyme loci reveals no hybridization (Howard 1982, 1983).

Allonemobius fasciatus group

Howard (1982, 1983) retained the name *A. fasciatus* for the more northerly distributed of the two species formerly regarded as *A. fasciatus*. He did this because the type specimen was collected in Pennsylvania. Available evidence indicates that the northeastern species predominates in this state, but it is unfortunate that we do not have a more exact locality for the type specimen because the southern species may also occur in the southern part of Pennsylvania (Fig. 1). *A. fasciatus* can be distinguished from species of the *A. allardi* group by differences in head banding intensity (especially in live specimens), ovipositor length, stridulatory vein size and file teeth number, and male calling song. However, it cannot be differentiated from *A. socius* on morphological grounds. There appears to be a slight difference in the calling songs of these species (*A. fasciatus* males have slightly longer interchirp intervals than *A. socius* males [Table 1]), but until more individuals have been studied we urge caution in regarding this difference as diagnostic.

Perhaps the most useful criterion for separating pinned specimens of *A. fasciatus* and *A. socius* is collection locality. *A. fasciatus* is a northern species (Fig. 1), abundant in New England, New York, Pennsylvania, Ohio, and northern New Jersey. It seems likely that its range extends into southern Canada (Vickery & Johnstone 1973) and at least as far west as Iowa (Alexander & Thomas 1959). On the other hand, *A. socius* is a southern species that appears to reach its northern limit in southern New Jersey and southeastern Ohio (Fig. 1). The two species occur together in southeastern Ohio, West Virginia, the Blue Ridge of Virginia, and southern New Jersey.

Gel electrophoresis offers the best means of identifying living or frozen material. There is a fixed difference between the two species at one locus (hexokinase) and species-specific alleles at three others (see Table 3 and Howard [1982, 1983]).

A. fasciatus and *A. socius* are the only species in the *A. fasciatus* complex that hybridize to a measurable extent in areas of sympatry (Howard 1982, 1986). Moreover, laboratory crosses between these species are often successful in producing fertile hybrids that can be backcrossed to both parental species (Fulton 1937, Howard 1982, 1986). This raises the question of whether *A. fasciatus* and *A. socius* should be regarded as specifically distinct. Obviously, we believe the answer is yes. As Howard (1982, 1983) has shown, these taxa are genetically quite distinct, with abrupt discontinuities at several enzyme loci separating them. Furthermore, despite variable levels of hybridization and backcrossing in mixed populations, pure *A. fasciatus* or pure *A. socius* genotypes usually predominate (Howard 1982, 1986), indicating strong but not complete reproductive isolation. Introgression of alleles characteristic of one taxon into the other taxon is very limited, another bit of evidence that *A. fasciatus* and *A. socius* are genetically isolated and should be recognized as distinct species.

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Addendum

T. J. Walker, of the University of Florida, has tape recordings and tape-recorded specimens that extend the known range of *A. walkeri* as follows: ARKANSAS, Lee County, 19-VIII-1972 (1 tape). ILLINOIS, Pope County, 7-VIII-1967 (2 tapes, 1 specimen). LOUISIANA, Evangeline Parish, 13-VIII-1964 (2 tapes, 1 specimen); Claiborne Parish, 18-VIII-1972 (4 tapes, 2 specimens). MISSISSIPPI, Attala County, 30-VIII-1965 (1 tape); Holmes County, 29-VIII-1965 (2 tapes); Sharkey County, 29-VIII-1965 (2 tapes, 2 specimens); Warren County, 4-VIII-1966 (2 tapes). TENNESSEE, Cumberland County, 12-VIII-1966 (1 tape); Lake County, 27-VIII-1964 (2 tapes). TEXAS, Trinity County, 14-VIII-1964 (2 tapes, 1 specimen).

He extends the range of *A. fultoni* to include Alachua County, Fla., 17-IX-1968 and later (4 tapes, 2 specimens; heard August to October each year).

The tapes are in the Tape Library of the Department of Entomology, University of Florida. The specimens are in the Florida State Collection of Arthropods.

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