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

DANIEL J. HOward1 AND DAVID C. FUrTH1

Department of Zoology, Michigan State University, East Lansing, Michigan 48824

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.

Howard, D. J. (1982, 1983) recognized three subspecies or forms ("physiologically distinct") of *Al- lonemobius fasciatus* (De Geer) (formerly in Ne- mobius): *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 oth- er. Alexander & Thomas (1959) emphasized that identification based solely on morphology is large- ly 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 exten- sive examination of thousands of specimens, in- cluding 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* (auct., nec De Geer) as new (*A. allardi*), and raised *A. fasciatus* to specific rank *A. tinnulus*. However, this picture of the *A. fasciatus* complex was re- cently changed by Howard (1982, 1983), who pre- sented 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 com- plex 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). 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 (1985) applied bi- nomial 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* com- plex and formally describe the two new species left unnamed by Howard (1982, 1983). Among the traits described for each species are diagnostic bio- chemical 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 two loci coding for soluble en- zymes (see electrophoretic key section). If any am- biguity existed as to specific identity, a possibility in areas of overlap between *A. socius* and *A. fas- ciatus*, the cricket was not used for song analysis. After identification, males were placed individ- ually into petri dishes (30 by 100 mm) supplied with food (Purina Cat Chow) and water (wet cot- ton).

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 (Unison [Unicam] Model 4500). The temporal pattern of a song was monitored on an oscilloscope (Tektronix 5111 Dual Trace) with dual trace amplifier (SS200) and time base ampli- fier (SB10N). A differential amplifier (Tektronix...
Fig. 1. Distributions of \textit{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.

\textbf{Morphology.} After an extensive search for characters, we concluded that the following measurements would be most demonstrative. Males: body length ($L_b$); maximal length of pronotum ($L_p$); maximal width of pronotum ($W_p$); length of hind femur ($L_f$); right tegmen distances as in Fulton (1931, Fig. 2A, that is, stridulatory vein from mesal origin to ulnar vein ($T_g1$), distance from ulnar vein to lateral border of dorsal tegmen surface ($T_g2$), distance from stridulatory vein to apex (posterior edge) of tegmen ($T_g3$). Females: $L_b$, $L_p$, $W_p$, $L_f$, length of ovipositor shaft ($L_o$). File teeth counts were obtained from at least 10 male specimens of each species.

The character data were analyzed on a mainframe computer (IBM 4341-11) running VM-SPS, 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).

\textbf{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.

\textbf{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.

\textit{Allonemobius walkeri} Howard & Furth, n. sp.

\textbf{Color/Pattern.} Head pattern and coloration as in \textit{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), sublaterially with wide black band, medially with yellowish band of irregular width (both visible from above), disc of pronotum withotted irregular pattern of light and dark brown mottles, 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.

\textbf{Stridulatory File Teeth Number.} 183-208 (mean, 195, n, 11), differing significantly from \textit{A. allardi} 208 and \textit{A. fultoni} 157.

\textbf{Morphometrics (nearest 0.1 mm.).}

\begin{align*}
\text{Males} & \quad \text{Females} \\
\text{[18: localities given below]:} & \quad \text{[17: localities given below]:} \\
L_b & = 9.9-11.7 \quad (10.6) \quad L_b = 9.2-11.7 \quad (11.2) \\
L_p & = 2.0-2.5 \quad (2.2) \quad L_p = 2.3-2.6 \quad (2.5) \\
W_p & = 2.9-3.5 \quad (3.2) \quad W_p = 3.2-3.5 \quad (3.4) \\
L_f & = 7.0-8.1 \quad (7.5) \quad L_f = 7.7-8.7 \quad (8.3) \\
T_g1 & = 1.3-1.5 \quad (1.3) \quad L_o = 8.1-10.5 \quad (9.4) \\
T_g2 & = 1.2-1.5 \quad (1.4) \\
T_g3 & = 3.9-5.0 \quad (4.3)
\end{align*}

The males of \textit{A. walkeri} are significantly larger in all seven measured characters than males of \textit{A. fultoni} and \textit{A. allardi}. The females of \textit{A. walkeri} are significantly larger than females of \textit{A. fultoni} and \textit{A. allardi} in $L_p$, $W_p$, and $L_f$, but differ from females of \textit{A. allardi} only in $T_g1$.

\textbf{Type Data.} Holotype 5. USA: Ohio, Noble County, Macksburg, 17-FX-1983, Howard (electrophoresis code MBO #48) (deposited in YPM). Alloptype 5, USA: Ohio, Morgan County, Reinersville.
Table 1. Calling song characteristics of five North American \textit{Allonemobius} species.

<table>
<thead>
<tr>
<th>Species (each individual listed separately)</th>
<th>Collection site</th>
<th>Temp of recording (°C)</th>
<th>Dominant frequency (Hz)</th>
<th># of chirps/min</th>
<th># interval between chirps or trills (s)</th>
<th># pulse rate (per second)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. allardi</td>
<td>Noble, Ohio</td>
<td>24.0</td>
<td>8,100</td>
<td>10.7</td>
<td>±0.6</td>
<td>2.0 ± 0.3</td>
<td>15.2</td>
</tr>
<tr>
<td>A. allardi</td>
<td>Noble, Ohio</td>
<td>24.0</td>
<td>7,300</td>
<td>9.1</td>
<td>±0.3</td>
<td>3.0 ± 0.5</td>
<td>14.3</td>
</tr>
<tr>
<td>A. allardi</td>
<td>Litchfield, Conn.</td>
<td>24.0</td>
<td>7,200</td>
<td>8.7</td>
<td>±0.8</td>
<td>0.4 ± 0.5</td>
<td>18.5</td>
</tr>
<tr>
<td>A. allardi</td>
<td>Litchfield, Conn.</td>
<td>24.0</td>
<td>7,400</td>
<td>9.3</td>
<td>±1.3</td>
<td>1.0 ± 0.16</td>
<td>16.0</td>
</tr>
<tr>
<td>A. ful</td>
<td>Salem, N.J.</td>
<td>24.0</td>
<td>6,640</td>
<td>7.6</td>
<td>0</td>
<td>3.3 ± 0.32</td>
<td>22.0</td>
</tr>
<tr>
<td>A. ful</td>
<td>Noble, Ohio</td>
<td>23.5</td>
<td>6,720</td>
<td>12.0</td>
<td>±5.5</td>
<td>3.0 ± 0.05</td>
<td>24.9</td>
</tr>
<tr>
<td>A. ful</td>
<td>Noble, Ohio</td>
<td>23.5</td>
<td>7,000</td>
<td>9.2</td>
<td>±0.7</td>
<td>0.5 ± 0.04</td>
<td>26.8</td>
</tr>
<tr>
<td>A. ful</td>
<td>Washington, Ohio</td>
<td>23.0</td>
<td>6,900</td>
<td>12.6</td>
<td>±1.2</td>
<td>0.4 ± 0.10</td>
<td>24.7</td>
</tr>
<tr>
<td>A. ful</td>
<td>Washington, Ohio</td>
<td>24.0</td>
<td>7,000</td>
<td>9.0</td>
<td>±0.2</td>
<td>0.0 ± 0.10</td>
<td>24.0</td>
</tr>
<tr>
<td>A. ful</td>
<td>Wood, W.Va.</td>
<td>24.0</td>
<td>7,120</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0 ± 0.01</td>
<td>24.0</td>
</tr>
<tr>
<td>A. ful</td>
<td>Mercer, N.J.</td>
<td>24.5</td>
<td>7,500</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0 ± 0.01</td>
<td>24.0</td>
</tr>
<tr>
<td>A. ful</td>
<td>Mercer, N.J.</td>
<td>24.5</td>
<td>8,000</td>
<td>0.1</td>
<td>0.0</td>
<td>0.0 ± 0.01</td>
<td>24.0</td>
</tr>
<tr>
<td>A. allardi</td>
<td>Washington, Ohio</td>
<td>25.0</td>
<td>7,800</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0 ± 0.01</td>
<td>24.0</td>
</tr>
<tr>
<td>A. allardi</td>
<td>Washington, Ohio</td>
<td>23.0</td>
<td>7,600</td>
<td>10.0</td>
<td>±2.2</td>
<td>0.0 ± 0.10</td>
<td>24.0</td>
</tr>
<tr>
<td>A. allardi</td>
<td>Washington, Ohio</td>
<td>23.0</td>
<td>7,600</td>
<td>10.0</td>
<td>±2.2</td>
<td>0.0 ± 0.10</td>
<td>24.0</td>
</tr>
<tr>
<td>A. allardi</td>
<td>Mercer, N.J.</td>
<td>24.5</td>
<td>7,040</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0 ± 0.01</td>
<td>24.0</td>
</tr>
<tr>
<td>A. allardi</td>
<td>Salem, N.J.</td>
<td>24.5</td>
<td>7,040</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0 ± 0.01</td>
<td>24.0</td>
</tr>
</tbody>
</table>

*a* All as. allardi, A. ful, A. fultoni, A. wall, A. fascatius, A. soc, A. rostr. 

*Collection site localities are identified by county and state.

State Route 78, 17-X-1983, Howard (electrophoresis code MCO #24) (YPM). Paratypes: USA: 4 d&l, Ohio, Noble County, Macksburg, 22-VIII-1981, Howard (calling song #61, 62, 63, 65); 2 d&l, Ohio, Washington County, North Marietta, 23-VIII-1981, Howard (calling song #66, 67); 7 d&l, 12 yr, same data as holotype (electrophoresis code MBO #1), 2, 4, 5, 6, 7, 9, 14, 18, 36, 45, 46, 47, 49, 52, 55, 54, 55, 56, 45, 44, 52, 53, 54, 55, 56); 4 d&l, 4 yr, same data as allozyme (electrophoresis code MCO #22, 23, 25, 26, 27, 28, 30).

Most paratypes are deposited at YPM; 3 and 2 yr are also deposited at both USNM and PAN.

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

\textit{A. walkeri} is a relatively rare cricket. Even though his calling song was heard in the laboratory, pulse 24-25 per second at 8 kHz.

Allozonemobius fultoni

Color/Pattern. Copper, abodon, and tibiae brownish yellow.

Stridulatory File. (mean: 157; n: 101; d: 74). All species have a single stridulatory file (see Fig. 1).

MALES

<table>
<thead>
<tr>
<th>A</th>
<th>F</th>
<th>S</th>
<th>W</th>
<th>Fw</th>
<th>Lb</th>
<th>Lp</th>
<th>Wo</th>
<th>Lt</th>
<th>Tg 1</th>
<th>Tg 2</th>
<th>Tg 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

FEMALES

<table>
<thead>
<tr>
<th>A</th>
<th>F</th>
<th>S</th>
<th>W</th>
<th>Fw</th>
<th>Lb</th>
<th>Lp</th>
<th>Wo</th>
<th>Lt</th>
<th>Le</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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

May 1986
Allonemobius wa/ken is the species Howard & Fu/TH (1986) recog-
nized as A. z. It is named for the late B. B. Fulton.

Biological Notes. A/lonemobius Jultoni corre-
sponds to the species that Howard (1986) design-
ated as A. z. It is named for the late B. B. Fulton.

We have collected it from only three sites, two in
southern New Jersey and one in North Carolina.

In Fig. 1. However, Fulton reported finding a species
in southeastern Ohio, where its range over-
runs 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 collect-
ting 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 cat-
egorized as an irregularly broken trill (Table 1).
In the laboratory, pulses were delivered at the rate
of 24-25 per second at 23-25°C.

Allonemobius wa/ken Howard & Fu/TH, n. sp.

Color/PATTERN. Color, pattern of head, pronon-
turn, abdomen, and tegmen essentially as in A.
walkeri.

Stridulatory File Teeth Number. 140-174
(mean, 157, n, 10), differing significantly from A.
wakerci (159) and A. allardi (208).

Morphometries (nearest 0.1 mm).

Males Females

<table>
<thead>
<tr>
<th></th>
<th>12: localities</th>
<th>8: localities</th>
</tr>
</thead>
<tbody>
<tr>
<td>given below</td>
<td>(given below)</td>
<td></td>
</tr>
</tbody>
</table>

Morphometries nearest 0.1 mm.

Wp = 2.6-3.0 2.8
Lo = 7.9-9.6 8.6
Tg3 = 3.2-4.4 3.7

The males are significantly smaller in all mea-

sures 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 Lb (see Fig.
2).

Type Data. Holotype & USA: New Jersey, Salem
County, New Jersey Turnpike, Clara Barton Ser-
vice Area, 12-VIII-1981, Howard (deposited in
YPM). Allotype & USA: New Jersey, Salem Coun-
ty, New Jersey Turnpike, Clara Barton Service
Area, 12-VIII-1981, Howard (YP\M). Paratypes:
USA: 9 66, 3 29, same data as holotype; 2 66, 4 29,
New Jersey, Salem County, New Jersey Turnpike,
Clara Barton Service Area, 25-IX-1983, Furth
(ep9c USNM). SEM #60, 61, 67, 70, 75, YPM. Most
paratypes are deposited at YPM. At least 1 & 1 2 are
also deposited at both PANS and USNM.

Allonemobius fultoni Howard & Fu/TH, n. sp.

Color/PATTERN. Head pattern with longitudinal
stripes indistinct at base but distinct (variable) apic-
ally, on vertex between eyes.

Stridulatory File Teeth Number. 190-228
(mean, 206, n, 12) Alexander & Thomas (1959)
give a range of 165-200 for A. allardi.

Morphometries (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)
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 (Hilliard) = 3

Morphometrics. (All specimens are from FANS, and none were mentioned and measured by Fulton (1951) in his original description. To remain consistent with Fulton, cities are included in the locality description.)

Males: 1 paratype, New Hampshire Jackson; 1, Pennsylvania (Philadelphia) = 3
Females: 1 paratype, New Hampshire Jackson; 1, Pennsylvania (Philadelphia) = 3

Morphometrics (Fulton 1951):

- Tgl = 1.2±1.5
- Tg2 = 1.1±1.4
- Tg3 = 3.4±4.2

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

Biological Notes. The electrophoretic work of Howard (1982, 1983) did change the conception of A. tinnulus developed by Fulton (1925, 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. altardi (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) described 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. altardi 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. altardi, 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. altardi and A. tinnulus differ by 6-10 pulses per second.

Allonemobius fasciatus (De Geer)

Synonym. (For a as to 1913 see Hebard [11].

Nemobius socius Schub. Nemobius fasciatus so. 906); Hebard 1913: Nemobius fasciatus A. 592).

Pteronomobius fasciatus (75).

Allonemobius fasciatus 626-627.

Color/Pattern. Head stripes from base to olo Stridulatory File. (mean, 131; n, 10). At give a range of 101-14 Morphometrics (see

Males: 6, New Hampshire New Jersey = 12
Females: 5, New Hampshire Vermont = 12

Morphometrics:

- Tg2 = 1.0±1.2
- Tg3 = 3.3±4.0

Biological Notes. A granulated inhabitant, a population densities in the edge of ponds as Howard 1982. Howard Throughout its known range

A. fasciatus 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. fasciatus is a clear musical trill resembling that of A. altardi, but with the pulses delivered at a slower rate. We analyzed the vex. A. fasciatus males (Ta a fasciatus would be classt in 1982) and is ver socius. The only differ in the length of the int of A. fasciatus males b than those of A. socius.

Allonemobius socius

Synonym. (For a as to 1913 see Hebard [11].

Nemobius socius Schub. Nemobius fasciatus so. 906); Hebard 1913: Nemobius fasciatus A. 592).

Pteronomobius fasciatus (75).

Allonemobius fasciatus 626-627.

Color/Pattern. Head stripes from base to olo Stridulatory File. (mean, 131; n, 10). At give a range of 101-14 Morphometrics (see

Males: 4, Georgia, 5.
Color/Pattern. Head with dark longitudinal stripes from base onto vertex between eyes.

**Stridulatory File Teeth Number.** 112-144 (mean, 134; n, 11).

**Morphometrics (nearest 0.1 mm).**

<table>
<thead>
<tr>
<th></th>
<th>Males:</th>
<th>Females:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lb</td>
<td>8.8-10.4 (9.8)</td>
<td>9.9-11.9 (10.7)</td>
</tr>
<tr>
<td>Lp</td>
<td>1.7-2.0 (1.8)</td>
<td>1.6-2.5 (2.1)</td>
</tr>
<tr>
<td>Wp</td>
<td>2.4-3.0 (2.6)</td>
<td>2.5-3.1 (2.9)</td>
</tr>
<tr>
<td>Lf</td>
<td>5.7-7.1 (6.5)</td>
<td>6.4-7.8 (6.9)</td>
</tr>
<tr>
<td>Tg1</td>
<td>0.8-1.0 (0.9)</td>
<td>0.6-0.8 (0.7)</td>
</tr>
<tr>
<td>Tg2</td>
<td>1.0-1.2 (1.1)</td>
<td>0.8-1.0 (0.9)</td>
</tr>
<tr>
<td>Tg3</td>
<td>3.3-4.0 (3.5)</td>
<td>2.6-3.0 (3.0)</td>
</tr>
</tbody>
</table>

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.I.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 Alex-
Table 3. Mean allele frequencies in populations of A. fasciatus complex species

<table>
<thead>
<tr>
<th>Allele</th>
<th>All</th>
<th>tm</th>
<th>ful</th>
<th>sol</th>
<th>soc</th>
<th>wav</th>
</tr>
</thead>
<tbody>
<tr>
<td>Idh-1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>a</td>
<td>62</td>
<td>39</td>
<td>15</td>
<td>14</td>
<td>55</td>
<td>42</td>
</tr>
<tr>
<td>b</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>c</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hk</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>e</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>g</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>h</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Idh-2</td>
<td>54</td>
<td>36</td>
<td>15</td>
<td>51</td>
<td>49</td>
<td>0</td>
</tr>
<tr>
<td>a</td>
<td>0.02</td>
<td>0.21</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b</td>
<td>0.34</td>
<td>0.44</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>d</td>
<td>0.61</td>
<td>0.66</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>e</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>f</td>
<td>0.50</td>
<td>0.50</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>g</td>
<td>1.00</td>
<td>0.25</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>h</td>
<td></td>
<td>0.75</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>i</td>
<td></td>
<td>1.00</td>
<td>0.02</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* a, A. allardi; tm, A. tinnulus; ful, A. fultoni; soc, A. socius; wav, A. walkeri.

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. Briefly, the key 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 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. All species except to species having cross-reactive 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
2. Malate dehydrogenase mobility slower than standard ......................... 2
3. Hexokinase mobility same as standard or only slightly slower ... A. fasciatus (De Geer) Hexokinase mobility much slower than standard .................. A. socius (Scudder) 5
4. Hexokinase mobility faster than standard .................................. 4
5. Isocitrate dehydrogenase-1 mobility same as standard A. tinnulus (Fulton) Isocitrate dehydrogenase-1 mobility slower than standard .................. A. walkeri (Howard & Furth) 5
6. Hexokinase is an anodally migrating enzyme that appears as a three-banded pattern in most species, and this seems to represent the homologous phenotype (Howard 1982, 1986). Measuring relative to the standard S. Hexokinase mobility same as standard ........................................... A. fultoni (Howard & Furth)

Comments on Key

Couplet 3. There is a 4% difference between the two species in electrophoretic banding. The middle band of A. socius migrating ca. 1 mm faster and the outer bands ca. 5 mm faster than in A. allardi. This 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 distribution, four-banded phenotypes are also present. A. socius population sympatry has interspecific crossoptery (published data). Because hybridization between A. fasciatus and A. allardi is not identified in this key, these two species co-occur (Fig. 5). Banding patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Banding patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Banding patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Banding patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of several individuals were characterized for the purpose of identifying individuals of each of two species co-occurring in (Fig. 5). Baming patterns of s...
individual collected with A. he identification of the most
1 isocitrate dehydrogenase-1,
this key for which A. allardi
ic. Another requirement for
specimens killed equently stored at -60°C or
1 gel run crickets should be
part of buffer (0.1 M Tris/
omogenates are then used to
paper rectangles, which are
in a different starch gel.
re these three enzymes
be satisfactorily separated
ode buffer system. After the
und slices stained, used of the
e identification of most un-
and late instars, a single hind
gh) material for analysis and
body can be pinned or, in
mens, used in other studies.

**Allonemobius**

Nase mobility same as stan-
1 nase mobility slower than stan-
ity same as standard or only
A. fasciatus (De Geer)
ity much slower than stan-
A. socius (Scudder)
lity same as standard .... 5
ity faster than standard .... 4
ase-1 mobility same as
A. tinnulus (Fulton)
genase-1 mobility slower
1. walkeri (Howard & Firth)
genase-1 mobility same as
dardi (Alexander & Thomas)
genase-1 mobility slower
A. julioni (Howard & Firth)

**Key**

1. nase is an anodally migrating
as a three-banded pattern in
1 this seems to represent the
he (Howard 1982, Tabach-
2). Measuring relative to the
contact individuals typically
wer than A. allardi individ-
ific difficulty to discern with-
middle band of A. socius mi-
er than the middle band of
ference is easily visualized.
of A. socius match the mo-
no bands of A. fasciatus and
no species overlap in distri-
ution, four-banded phenotypes occur. Four-
banded phenotypes are also found at low frequen-
cy in A. socius populations adjacent to areas of
sympathy. Interspecific crosses indicate that these
phenotypes represent heterozygotes (D.I.H., un-
published data). Because of variable levels of hy-
bridization 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 (How-

**Couplet 3.** There is a small chance of error at
this couplet. Usually, the phenotype of A. fasciatus
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 hetero-
yzogote. The Hardy-Weinberg law leads to the ex-
pectation 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 char-
acteristic of A. tinnulus.

**Couplet 4.** There are two zones of isocitrate de-
hydrogenase (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 mo-
vement than the Idh-1 allele. Because this is a
dimeric enzyme, heterozygotes have three bands.

**Discussion**

Fulton (1931), Alexander & Thomas (1959),
Vickery & Johnston (1975), and others have at-
ttempted to separate the species of Allonemobius
based on a variety of morphological characters such
as head and pronotum shape or pattern, hind fe-
mur 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 vari-
able 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, al-
though some show significant differences in two
species comparisons. The most reliable species in-
dicators 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. wak-
er, and A. fultoni were regarded as a single species
until recently. They are extremely similar in mor-
phology, overlap to some degree in distribution
(Fig. 1), and the two eastern central species (A. waf-
ken and A. fultoni) are comparatively rare
within 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. wa/ken and A. allardi. However, he
did not publish his results because of their prelimi-
nary 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 distin-
guish 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 diagno-
sic is restricted to males, namely number of strid-
ulatory file teeth. This character is quite distinc-
tive between A. allardi-A. tinnulus and A. fultoni,
and between A. wa/ken and A. walkeri, and some-
A. wa/ken is also polymorphic at this locus,
and both alleles code for enzymes with slower mo-
vement than the Idh-1 allele. Because this is a
dimeric enzyme, heterozygotes have three bands.
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 reproducting populations. Howard in nature. By this criterion there can be no doubt that A. allardi, A. tin- nulus, A. walkeri, and A. fultoni are distinct species. There is a measurable extent in areas of sympatry Howard 1982, 1983. Moreover, laboratory crosses between A. fasciatus and A. socius are the only species of A. fasciatus complex that hybridize to a measurable extent. Yet in areas of sympathy, electrophoretic analysis of diagnostic or close to diagnostic enzyme loci reveals no hybridization (Howard 1982, 1983).

**Alloinemobius 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 southeastern 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 and 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 1972) 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, 1983). 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, 1983). 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 detectable 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.

**Acknowledgment**

We thank Don Azuma and Daniel Otte (Acad. of Nat. Sci. of Philadelphia) and David Nickle (Natl. Mus. of Nat. Hist.) for hospitality and the loan of specimens. We are also grateful to Lawrence Gall (Yale Univ.) for assistance with the statistical analysis and to Kentwood Wells (Univ. of Connecticut) for helping us with the acoustic analysis. The research of D.J.H. was partially supported by a grant from the Theodore Roosevelt Memorial Fund of the Am. Mus. of Nat. Hist. and by NSF Grant DEB-8113479.

**Addendum**

T. J. Walker, of the University of Florida, has tape recordings and tape-recorded specimens that extend the known range of A. allardi as follows: ARKANSAS, Lee County, 19-VII-1972 (1 tape). ILLINOIS, Pope County, 7-VII-1967 (2 tapes, 1 specimen); LOUISIANA, Evangeline Parish, 13-VIII-1964 (2 tapes, 1 specimen); 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.

**References Cited**


Duncan, D. B. 1975. Tapes and other species supported by thp. 391.


Howard, D. J. 1982. Spe- 

Howard, D. J. & R. C. H. segregation in ground cr.

May 1986
Howard & Furti-

May 1986

REVIEW OF THE A. fasciatus COMPLEX


Received for publication 29 April 1985; accepted 14 January 1986.