Transactions of the American Entomological Society 115(4): 433-456, 1989

Systematics of *Pictonemobius* Ground Crickets (Orthoptera: Gryllidae)

SCOTT W. GROSS[1]
DAVID L. MAYS
and
THOMAS J. WALKER
Department of Entomology and Nematology
University of Florida, Gainesville, Florida 32611

ABSTRACT

The cricket genus *Pictonemobius* previously contained one named species, *ambitiosus*. Studies of calling songs, morphology, and habitat preferences demonstrated that the genus contains at least four sibling species. *P. ambitiosus* occurs in a variety of habitats in peninsular Florida, and probably extends to eastern Mississippi and North Carolina. It has a wingstroke rate of 44 - 54 per second at 25°C. *P. hubbelli* n. sp. has a similar range but generally prefers drier, more disturbed habitats and has a wingstroke rate of 30 - 42 per second. *P. arenicola* n. sp. is confined to scrub and sandhill communities characteristic of deep, coarse sand in peninsular Florida; its wingstroke rate is somewhat faster than *ambitiosus*, and the two species are easily distinguished morphologically. *P. uliginosus* n. sp. has the smallest range, limited to pine flatwood habitats in northern Florida and southern Georgia. It has the fastest wingstroke rate, 56 - 63 per second at 25°C.

Reproductive isolation among the species was demonstrated by populations coexisting in sympatry, by laboratory crosses, and by electrophoretic analysis. *P. arenicola* and *P. uliginosus* can be identified from specimens, but no morphological features were found that consistently separate *ambitiosus* from *hubbelli*.

A phylogeny of the genus was constructed based on electromorph frequencies, and populations from peninsular Florida clustered into species as predicted by song type. Populations from Georgia and northwest Florida, however, did not cluster as predicted by song type. These populations may represent additional species of *Pictonemobius*.

INTRODUCTION

The genus *Pictonemobius* contains small, flightless, ground-dwelling crickets endemic to the southeastern coastal plain of the United States, including peninsular Florida, and extending into the piedmont. The genus is easily recognized by the transverse pale stripe on the frons between the eyes. As in most other crickets, males produce a calling song that attracts potential mates. Singing is primarily diurnal, and in some habitats *Pictonemobius* is the most acoustically obvious, and probably the most abundant, diurnal orthopteran.

Examination of collections at the Philadelphia Academy of Natural Sciences, University of Michigan Museum of Zoology, United States National Museum, and Florida State Collection of Arthropods showed that the genus as a whole ranges from southern Florida to eastern Mississippi and North Carolina (Fig 1A). A literature record extends the range into the southern Blue Ridge Mountains (Rabun Co., Ga.; Rehn and Hebard 1916).

[1]Present mailing address: 48 Flints Grove Drive, Gaithersburg, MD 20878

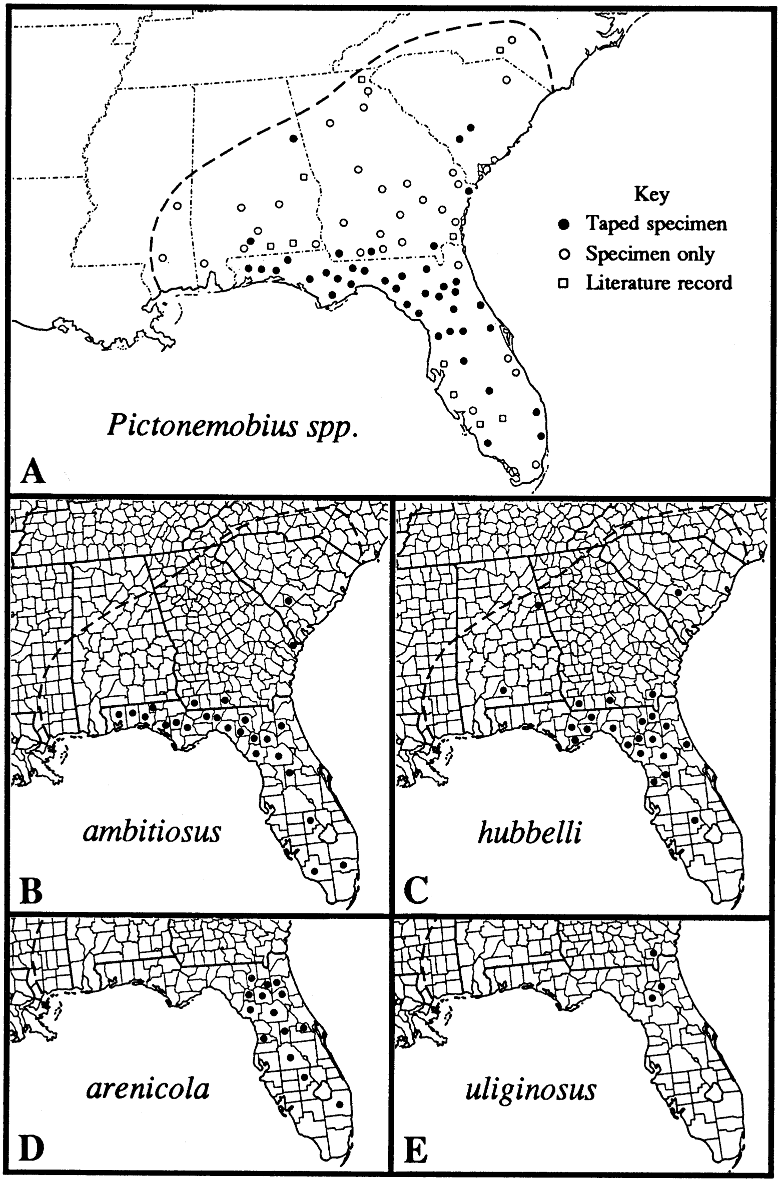

FIGURE 1. Distribution of *Pictonemobius* spp. A. County records, all species. B-E. Assignment of tape-recorded specimens to the four nominal species.

Previously only one species of *Pictonemobius* was recognized, *ambitiosus* (Scudder 1877), described from central Florida. This specific name has also been used in combination with the genera *Nemobius, Allonemobius,* and *Pteronemobius* (see Vickery and Johnstone 1970 for discussion). Fulton (1931) credited T.H. Hubbell for noting color differences between *ambitiosus* collected in scrub and mesophytic habitats. Fulton showed that the differences were heritable and speculated on the possibility of "physiological differentiation" within the species.

This paper summarizes what its three authors have learned about *Pictonemobius*. We begin by outlining the history of our study and the principal evidence that four species of *Pictonemobius* occur in the vicinity of Gainesville. We then assign names to the four species and describe our attempts to characterize them further and to detect other species — should they exist.

History of Present Study

Because our contributions to this study were diverse and largely sequential rather than concurrent, the following account is presented to clarify our roles.

In 1961, from a site near the Gainesville airport, J.D. Spooner brought TJW a *Pictonemobius* male that produced a song of much slower pulse rate (ca. 37 pulses per second at 25°C) than the *Pictonemobius* that TJW had previously studied (ca. 49 p/s at 25°C; see Walker 1962). Subsequently, TJW, JDS, and R.E. Love collected series of "slow *ambitiosus*" from both the original locality and from Gold Head Branch State Park, 34 km to the northeast. By 1965, TJW and REL had tape recorded and analyzed the songs of 32 slow *ambitiosus* males from these two localities, as well as a corresponding number of "fast *ambitiosus*" from the same and adjacent sites. The slow singers preferred drier, turkey oak habitats, whereas the fast singers occurred mostly in more mesic woods. Subtle differences in coloration were recognized, and in laboratory colonies, slow *ambitiosus* females produced only slow singers and fast *ambitiosus* females produced only fast ones. TJW concluded that two species of *Pictonemobius* occurred in north peninsular Florida.

In 1967, DLM began a study of *Pictonemobius*. He soon recognized a third taxon from xeric sites west of Gainesville. Females had distinct yellow longitudinal stripes on the tegmina, and both sexes lacked the heavy femoral striping characteristic of other *ambitiosus*. Males sang with a wingstroke rate of ca. 55 per second, and both song and color characteristics bred true. In 1969, DLM discovered yet another *Pictonemobius*. This taxon lived in pine flatwoods and was nearly black, in contrast to the browns and grays of the other three taxa; males sang with a wingstroke rate of ca. 60 per second. It now seemed evident that four species occurred in north peninsular Florida. DLM's studies of *Pictonemobius* culminated in a dissertation that included sections on song analyses, ecological distributions, phonotaxis, and hybridization (Mays 1975).

In 1982, SWG began an electrophoretic study of *Pictonemobius* to determine (1) if the previously recognized *Pictonemobius* taxa were genetically distinct and reproductively isolated, and (2) if remote *Pictonemobius* populations showed genetic similarities that correlated with their resemblances in morphology and song to the four taxa in north peninsular Florida. To accomplish these ends, SWG had to characterize the populations from which he obtained his specimens for electrophoresis. In his thesis, he reported not only electrophoretic results but also additional data on song, morphology, hybridization, and geographic distribution (Gross 1984).

Co-occurrence of Song Types Near Gainesville

Early in our study we recognized four "song-types" in north peninsular Florida. The most compelling evidence that the populations we initially characterized on the basis of song were species was that two or more song types often occurred and called together in the field without intermediate songs or other evidence of hybridization.

The following paragraphs describe the most intensively studied sites where two song types were observed to occur together without intermediates. Exact locations are given in Table 1. Song types were assigned code numbers for filing recordings in the Department of Entomology Tape Library. These codes — 531-D, 528, 531-B, and 525 — correspond to species that we eventually called *ambitiosus, hubbelli, arenicola,* and *uliginosus*.

531-D and 528 (= *ambitiosus* and *hubbelli*)

Gainesville airport. This site, the first place where 528 was collected and studied, included a recently cleared area where only 528 occurred and an adjacent open woods, dominated by turkey oak, bluejack oak, and longleaf pine, where 528 and 531-D occurred intermixed. The area was extensively studied by DLM (1975), who mapped the vegetation, quantified the hourly frequency of calling of the two song types, and plotted the microdistribution of calling males.

Gainesville, Morningside Nature Center. This municipal park preserves a section of longleaf pine, turkey oak, and palmetto woods where 531-D was abundant. Song type 528 occurred adjacent to the park in a pasture with young turkey oaks. SWG used crickets of both song types from this site for electrophoretic analysis.

531-D and 531-B (= *ambitiosus* and *arenicola*)

Archer. This site was in an area of fossil dunes associated with a former coastline. In a large area dominated by turkey oak, 531-B was the sole song type. Adjacent to the stand of turkey oak was a xeric hammock dominated by live oaks and occupied mostly by 531-D. At the edge of the hammock, where it interfaced with the stand of turkey oak, both types occurred intermingled and without intermediates (Mays 1975).

528 and 531-B (= *hubbelli* and *arenicola*)

Archer. In an open white sandy spot in one corner of the turkey oak area, DLM located a small population of 528. They were completely surrounded by 531-B.

Bronson. Here 528 and 531-B occurred in pure populations (e.g., 528 in a pasture and 531-B in a stand of turkey oak) and intermingled (e.g., under a tree in the pasture and in turkey oak areas recently planted to pine) (Mays 1975).

Gold Head Branch State Park. This was the first site that 528 and 531-B were found intermingled, but TJW initially attributed the faster pulse rates of 531-B to geographical variation in 531-D rather than to a new song type. DLM revisited the site and found 528 and 531-B manifesting ecological distributions similar to those at Bronson.

525 and 531-D (= *uliginosus* and *ambitiosus*)

Starke Country Club. This site was mostly pine flatwoods and was chiefly inhabited by 525, which produces a pulse rate noticeably higher and a chirp duration noticeably longer than 531-D. Occasional 531-D males occurred here, and their songs contrasted with those of 525. SWG electrophoretically analyzed specimens of 525 from this site.

Other sites. Unlike the other song types, 525 was not intensively studied at a site where it intermingled with others. However, in the vicinity of Gainesville, it was generally in contact with 531-D, but not with the other two song types, which were restricted to xeric, well-drained habitats. Song types 525 and 531-D occurred together at the Univ. of Fla. Horticultural Unit Farm.

Species Accounts

Types of new species were deposited in the Florida State Collection of Arthropods. Terminology for habitat descriptions is from Laessle (1942).

Pictonemobius ambitiosus (Scudder)

Nemobius ambitiosus Scudder, 1877: 81. Type locality: Fort Reed, (now) Seminole Co., Florida. Type series in the Academy of Natural Sciences at Philadelphia. Lectotype male designated by T.J. Walker in 1970.

We feel comfortable in assigning the crickets with ca. 48 wingstrokes/sec at 25 °C (song type 531-D) to *ambitiosus* because these crickets resemble the type specimens, and we have found them near the type locality. We also found *P. arenicola* near the type locality, but *arenicola* does not resemble the type specimens.

Distribution. — Peripheral records for which we have song recordings include S. CAROLINA: Colleton Co., Colleton State Park campground;

GEORGIA: Brooks Co., Quitman; FLORIDA: Santa Rosa Co., 1 mile W. Okaloosa Co. line on US 90; Collier Co., jct. SR 840 and SR 29 (Fig 1B).

Habitat. — Various forest types, including longleaf pine/turkey oak associations and broadleaf forest ravines (Florida panhandle), river bottomlands (S. Carolina) and live oak hammocks (peninsular Florida).

Adults occur throughout the year in peninsular Florida. All our records from South Carolina are from the summer and fall, and no nymphs or adults were seen or heard in the spring. In the northern part of its range, *ambitiosus* may overwinter in the egg or nymph stage.

Pictonemobius hubbelli Walker and Mays, n. sp.

This is the species corresponding to song type 528 (wingstroke rate ca. 37 per second, chirp length ca. 1 sec). We name this species in honor of T.H. Hubbell, who has contributed greatly to the study of Orthoptera in Florida.

Holotype: Male, FLORIDA: Alachua Co., Gainesville Airport (Section 24, R20E, T9S), 12-V-1965, T.J. Walker and R.E. Love. Color dark gray-brown, femora with two distinct longitudinal stripes (Fig 2A). Femur length 5.80 mm, head width 2.23. Calling song 38 wingstrokes per second at 25 °C. Song recording UFT 528-18. *Allotype*: Female, FLORIDA, Alachua Co., Monteocha Road W. of Fairbanks (Section 11, T9S, R20E), 6-XI-1966, D.L. Mays. Color dark gray-brown, femora striped as in holotype. Tegmina lighter at anterior dorso-lateral margin, becoming darker posteriorly (Fig 2E). Femur length 6.11 mm, head width 2.28, ovipositor length 6.07. Male progeny of allotype called with wingstroke rates of 32-35 per second.

Distribution. — Peripheral records include S. CAROLINA, Orangeburg Co., Santee State Park; ALABAMA, Cleburne Co.; Conecuh Co., Herbert; FLORIDA, Highlands Co., Archbold Biological Station (Fig 1C).

Habitat. — Variable, including open pine and turkey oak woods (S. Carolina and north Florida) and grass tussocks bordering ponds in open oak scrub (south Florida).

Pictonemobius arenicola Mays and Gross, n. sp.

This is the species that produces song type 531-B (wingstroke rate ca. 55 per sec at 25 °C, chirp duration less than 0.4 sec). The species is named for its habitat (*arena* = L. sand, *cola* = dweller).

Holotype: Male, FLORIDA, Putnam Co., 3 km E. Melrose (Section 17, T9S, R23E), 16-VIII-1967, D.L. Mays. Pronotum and femora brown, femora somewhat lighter and without stripes (Fig 2B), tegmina darker brown with distinct light border. Head width 2.29 mm, femur length 5.33. Calling song 54 wingstrokes per second at 25 °C. Song recording UFT 531-137. *Allotype*: Female, FLORIDA, Clay Co., Crystal Lake, N. of Keystone Heights (Section 6, T8S, R23E), 7-IV-1984, S.W. Gross. Color as in holotype, tegmina with light stripe extending entire length of tegmen along dorsolateral

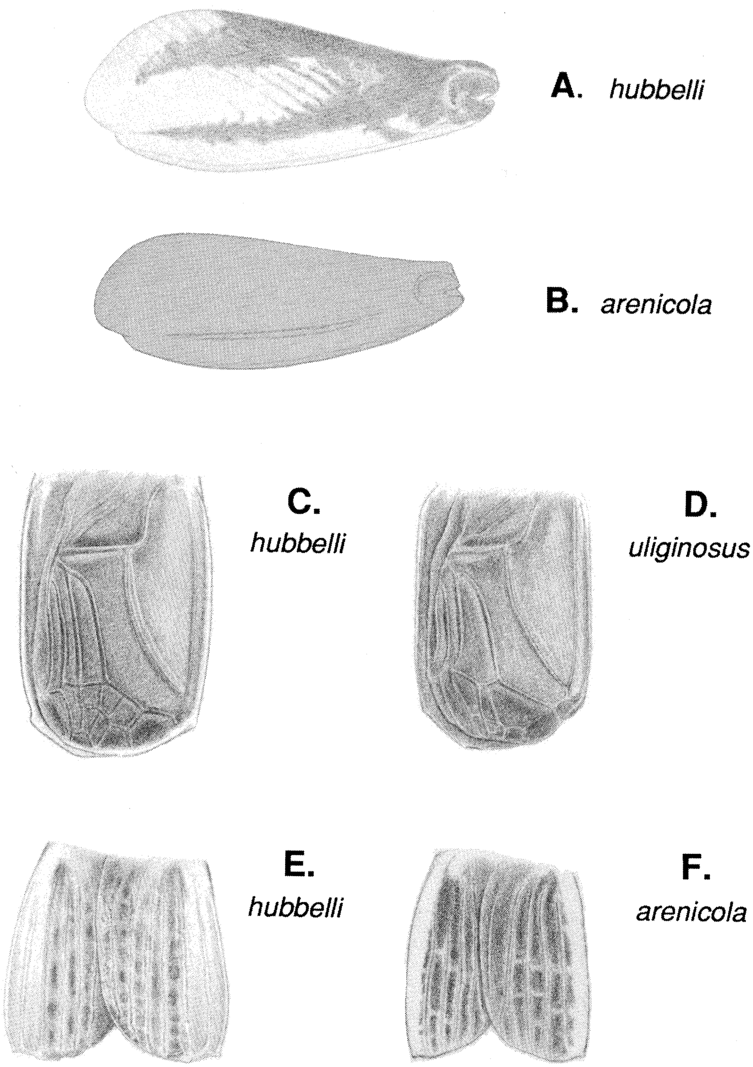

FIGURE 2. Morphological features of *Pictonemobius* spp. A-B. Lateral view of left femur. A. *hubbelli* (holotype). B. *arenicola* (holotype). C-D. Dorsal view of right tegmen. C. *hubbelli* (holotype). D. *uliginosus* (holotype). E-F. Dorsal view of female tegmina. E. *hubbelli* (allotype). F. *arenicola* (allotype).

margin (Fig 2F). Head width 2.29 mm, femur length 5.59, ovipositor length 5.85.

Distribution. — Peripheral records include FLORIDA: Columbia Co., 3 mile SE Suwannee Co. line on US 27; Palm Beach Co., Jupiter (Fig 1D).

Habitat. — Limited to habitats with well-drained, sandy soil, including sandhills (longleaf pine and turkey oak) and scrub (saw-palmetto, sand pine, and oaks) communities.

Pictonemobius uliginosus Mays and Gross, n. sp.

This species equates to song type 525 (wingstroke rate ca. 59 per sec at 25 °C and chirp length greater than 1 sec). The species name is derived from *uligo* (L. damp), referring to the low, wet habitat in which the species is found.

Holotype: Male, FLORIDA, Alachua Co., 6 km NW Gainesville, Univ. of Fla. Horticultural Unit Farm (Section 9, T9S, R19E), 4-II-1983, S.W. Gross. Color black, tegmina without distinct light edging (Fig 2D), femora dark gray with slightly darker longitudinal stripes. Head width 2.04 mm, femur length 5.10. Calling song 59 wingstrokes per second at 25 °C. Song recording UFT (525) SWG-49. *Allotype*: Female, FLORIDA, Alachua Co., 5 km N. Orange Heights (Section 30, T8S, R22E), 29–V-1969, D.L. Mays. Color dark brown-gray, tegmina uniformly colored without lighter areas, femora as in holotype. Head width 2.26 mm, femur length 5.59, ovipositor length 4.49.

Distribution. — The species is thus far known from FLORIDA: Alachua, Bradford, and Clay Cos.; GEORGIA: Charlton Co., Okefenokee Natl. Wildlife Ref., Billy's Lake (Fig 1E; Table 1).

Habitat. — Low, wet pine flatwoods.

Systematic Studies

Calling Song Analysis

In recent years, cricket systematists have concluded that sympatric populations manifesting different calling songs are almost certainly different species (Alexander 1962, Walker 1964). Supporting this conclusion is the fact that sexual pair formation in crickets generally begins with the female's attraction to the distinctive song of the conspecific male. Closely related species that are first recognized on the basis of calling songs can then generally be separated morphologically (e.g., Alexander 1957, Walker, 1963). In many instances the pulse rate, which corresponds to the wingstroke rate during stridulation, is the main feature of the song that differs between closely related species. Because pulse rate is temperature dependent, temperature must be specified when songs are compared.

Methods

We collected and tape recorded 450 males from 75 localities in four states. Crickets were brought to the lab, held in jars on moist sand, and given ground dog food and water (in a vial with a cotton wick). Calling songs were tape recorded and the ambient temperature was noted. Songs were analyzed using either a Kay Sona-Graph 7029A sound spectrograph or a Honeywell 1858 Visicorder. Wingstroke rates and chirp lengths were calculated from the audiospectrograms and oscillograms.

Since wingstroke rate varies linearly with ambient temperature, wingstroke rates were standardized to 25° using the equation:

$$\text{pulse rate at } 25\,^{\circ}\text{C} = \text{measured pulse rate} + 2.232(25 - T)$$

where T is the temperature at which the recording was made and 2.232 is the slope of the wingstroke rate vs. temperature graph for *P. ambitiosus* (Walker 1962).

Results

The species with the most variable calling song was *P. ambitiosus* with wingstroke rates ranging from 44 to 54 per second (Table 1). The variation was not clinal. For instance, faster wingstroke rates (>50) could be found in such distant localities as south Florida (Collier and Broward Cos.) and west Florida (Santa Rosa Co.). Similarly, wingstroke rates of less than 50 could be found throughout the range of *P. ambitiosus*. Chirp length, however, did appear to vary clinally. Populations in peninsular Florida had chirp lengths of 0.5-0.7 sec, while populations to the west in the Florida panhandle and to the north in Georgia and South Carolina had chirp lengths greater than one second.

The slowest wingstroke rates were found in *P. hubbelli,* varying from 29 to 42 per second. No geographic pattern to the variation was detected. Chirp lengths were generally ca. 1 sec, although several populations averaged 0.5 sec, and South Carolina *hubbelli* had chirps closer to 1.5 sec in duration.

P. uliginosus exhibited the fastest wingstroke rate, ca. 59 per sec, and chirp length was between 1 and 2 sec.

Wingstroke rates for *P. arenicola* varied from 43 to 57, a range similar to that of *ambitiosus*. However, in most areas of sympatry, *arenicola* wingstroke rates averaged 6-8 per second faster than *ambitiosus*. Chirp length was short, less than 0.4 sec, for all populations sampled.

Discussion

A male *Pictonemobius* from the vicinity of Gainesville should usually be assignable to one of the four species based on song alone, since wingstroke rates are nearly non-overlapping at 25 °C (Table 1). The species are separated by the closest series of species-specific wingstroke rates reported for any complex of sympatric cricket species. To a large extent females discriminate among the different songs and are attracted to songs of their own species (Mays 1975).

Because wingstroke rates change with temperature, microclimatic differences in temperature could result in confusing songs. For example, an individual *arenicola* singing in a cool, shady spot might have a wingstroke rate very similar to a nearby *ambitiosus* in a sunny spot. If this were a

TABLE 1. Wingstroke rates of *Pictonemobius* species. Land survey coordinates are given for Florida localities at first listing.

Species Locality: STATE, county — site no.: site (township, section)	n	Wingstroke rate (25 C) $\bar{x}$	range
ambitiosus			
FL-Alachua-1: Gainesville airport (T9S-R20E,24)	21	48	45-52
FL-Alachua-2: Morningside Nature Center (T9S-R20E, 35)	4	48	47-50
FL-Alachua-3: ¾ mi SW Archer (T11S-R18E, 19)	9	47	45-50
FL-Broward: jct. SR 810 & US 441 (T48S-R42E, 6)	2	51	50-51
FL-Calhoun: 4 mi W jct. SR 20 & 73 (T1N-R10W, 33)	4	53	51-55
FL-Clay-1: Gold Head Branch St. Park (T7S-R42E, 19)	3	47	46-49
FL-Collier: jct. SR 29 & 840 (T48S-R30E, 17)	9	51	50-53
FL-Gilchrist-1: Jenny Springs (T8S-R16E, 34)	9	44	42-47
FL-Holmes: 3 mi SW Westville on US 90 (T3N-R17W, 13)	7	53	49-56
FL-Lake-1: Leesburg (T19S-R24E, 35)	4	49	47-49
FL-Leon: Tall Timbers Res. Station (T3N-R1E, 14)	7	47	46-50
FL-Levy: Bronson (T12S-R17E, 8)	2	45	45
FL-Liberty-1: Torreya St. Park (T2N-R7W, 17)	11	44	44-48
FL-Okaloosa: 1 mi W Walton Co. line US 90 (T3N-R22W, 24)	6	53	51-54
FL-Santa Rosa: 3 mi W Holt US 90 (T2N-R26W, 12)	3	53	52-54
FL-Taylor: Perry (T4S-R8E, 32)	7	50	48-56
FL-Walton: DeFuniak Springs Country Club (T3N-R19W, 29)	3	50	48-51
GA-Brooks: Quitman	5	47	45-48
GA-Chatham: Ossabaw Is.	2	48	48-49
SC-Colleton St. Park campground	2	47	47
hubbelli			
AL-Cleburne: Shoal Creek Bridge campground, Taledega National Forest	1	41	41
AL-Conecuh: Herbert	2	40	39-40
FL-Alachua-1: [airport]	16	37	33-38
FL-Alachua-2: [Morningside]			
FL-Baker: 0.1 mi S Ga. state line SR 23 (T1S-R22E, 31)	2	37	37
FL-Clay-1: [Gold Head Branch]	10	41	39-43
FL-Dixie: Jena (T10S-R10E, 7)	6	40	38-42
FL-Flagler: 2 mi S Marineland (T10S-R31E, 30)	2	39	38-39
FL-Franklin: Carrabelle (T7S-R4W, 9)	4	41	39-42
FL-Highlands: Archbold Biol. Station (T38S-R30E, 7)	9	37	35-39
FL-Leon: [Tall Timbers]	3	35	33-36
FL-Levy: [Bronson]	27	38	36-40

TABLE 1. (continued)

Species Locality: STATE, county — site no.: site (township, section)	n	Wingstroke rate (25 C) $\bar{x}$	range
FL-Liberty-2: 5 mi E Bristol on SR 20 (T1S-R7W, 3)	3	33	29-36
GA-Brooks: 5.5 mi E Pavo on SR 122	1	38	38
SC-Orangeburg: Santee St. Park	2	37	37-38
arenicola			
FL-Alachua-3: [Archer]	9	54	51-57
FL-Clay-1: [Gold Head Branch]	6	53	52-54
FL-Columbia: 3 mi S Suwannee Co. line on US 27 (T6S-R16E, 29)	3	55	55-56
FL-Gilchrist-2: 5 mi W Newberry (T10S-R16E, 11)	4	53	52-54
FL-Hernando: 2 mi S Croom (T22S-R21E, 29)	5	48	46-49
FL-Highlands: [Archbold]	2	51	50-52
FL-Lake-2: 5 mi S Clermont on US 27 (T23S-R26E, 16)	5	45	43-47
FL-Levy: [Bronson]	4	55	54-57
FL-Palm Beach: Jupiter (T41S-R43E, 6)	1	51	51
FL-Polk: NE Haines City (T27S-R27E, 21)	1	54	54
FL-Putnam: 2 mi E Melrose (T9S-R23E, 17)	7	53	51-55
FL-Sumter: nr. Lake Co. line (T22S-R23E, 13)	6	53	52-55
uliginosus			
FL-Alachua-4: Univ. Fla. Horticultural Unit Farm (T9S-R19E, 9)	4	59	58-60
FL-Bradford: Starke Country Club (T6S-R22E, 24)	5	59	59-62
FL-Clay-2: 0.3 mi E Clay Co. line SR 16 (T6S-R23E, 16)	2	58	56-59
GA-Charlton: Okefenokee National Wildlife Ref., Billy's Lake	1	60	60

common occurrence in the field, calling song would be a weak barrier to interspecific mating (although courtship and post-mating barriers would still be in effect). However, Mays (1975) studied *Pictonemobius* spp. singing in the field and concluded that interspecific overlap in wingstroke rates was very rare.

Morphology

Color pattern and features of the stridulatory apparatus and male genitalia are often useful in distinguishing cricket species.

Methods

After individuals were identified to species by song type, a sample of males was selected from each species for examination of the stridulatory file and genitalia. The right tegmen was removed and mounted on a glass slide. The number of teeth on the file was counted and file length was measured along a straight line parallel to the central portion of the file. The genital complex was removed, mounted on a glass slide, and examined with a microscope.

The type specimens of *P. ambitiosus* were examined at the Philadelphia Academy of Natural Sciences. We also examined material from the University of Michigan Museum of Zoology, the United States National Museum, and the Florida State Collection of Arthropods.

Results

P. arenicola is unique in having reddish-brown hind femora that lack the longitudinal stripes characteristic of the other species (Fig 2B). In dried specimens the color changes to a tan hue. Occasional specimens appear to have faint hind femoral striping, but this is due to a shallow groove in the cuticle rather than true pigmentation. Female tegmina have light yellow or white longitudinal stripes running the full length of the tegmen (Fig 2F). In other species the stripes fade posteriorly. Some females of *hubbelli* from Leon Co., Florida, have tegminal stripes that run the entire length of the tegmina, but they are distinguished from *arenicola* by the hind femoral stripes typical of the species.

P. uliginosus is recognized by the lack of a light border surrounding the dorsal portion of the male tegmina (Fig 2D). General coloration is black.

The remaining two species, *ambitiosus* and *hubbelli,* resemble one another closely. Although an experienced observer can distinguish the two in the field in certain localities, it is difficult to characterize the species throughout their ranges, and subtle differences in live crickets are obscured in pinned material. Specimens of *ambitious* tend towards a brown hue while those of *hubbelli* are more of a gray or charcoal color. Beyond this generalization, no consistent differences in color or markings were recognized.

Analysis of measurements of male stridulatory apparatus revealed overlap of characters among the species when different localities were combined (Table 2). For example, a comparison of the range of measurements for file length showed overlap in every species-pair combination. However, differences were found when comparing sympatric populations. In Alachua Co., Florida, *P. uliginosus* and *arenicola* had fewer file teeth than either *ambitiosus* or *hubbelli.* There was also marked intraspecific variation. The number of file teeth in *hubbelli* from Alachua and Levy Cos. was greater than in that species from Clay Co.

No differences in male genitalia were found among the four species.

Discussion

The paucity of distinguishing morphological features suggests that *Pictonemobius* speciated relatively recently. Furthermore, one might expect fewer morphological differences in a group where species-specific calling songs are important barriers to hybridization. Natural selection should favor differences in calling song more than differences that play a role later in the mating sequence, such as genitalic structure.

TABLE 2. Characteristics of stridulatory files of *Pictonemobius* spp. in Florida.

Species		No. of teeth		Length of file (mm)		Teeth per mm	
County (FL)	n	$\bar{x}$ ± SD	Range	$\bar{x}$ ± SD	Range	$\bar{x}$ ± SD	Range
ambitiosus							
Seminole (lectotype)	1	115		0.98		117	
Alachua	14	106±9	93-125	0.94±0.07	0.83-1.07	113±9	94-127
Clay	10	99±6	91-109	0.84±0.07	0.80-0.99	113±6	103-122
Levy	4	94±1	92-95	0.89±0.05	0.82-0.91	106±4	103-112
hubbelli							
Alachua	13	118±6	108-127	1.02±0.07	0.92-1.16	116±6	106-127
Clay	10	92±4	84-100	1.07±0.05	1.01-1.14	86±5	82-96
Highlands	10	103±4	99-113	0.80±0.05	0.71-0.87	130±9	114-146
Levy	16	102±7	100-124	1.00±0.05	0.93-1.08	108±6	98-121
arenicola							
Alachua	15	85±5	79-94	0.84±0.04	0.76-0.92	101±5	94-108
Highlands	6	99±7	85-104	0.66±0.05	0.60-0.74	150±11	134-165
Levy	6	88±5	79-91	0.85±0.05	0.77-0.89	103±2	100-107
uliginosus							
Alachua	15	83±4	75-90	0.89±0.05	0.79-0.94	93±4	86-101

Hybridization

Laboratory crosses can yield important information about the relationships of field populations, but hybridization in the lab does not refute the hypothesis that two populations represent different species. In fact, congeneric species often hybridize under laboratory conditions. On the other hand, when populations suspected of being species do not hybridize in the lab and control crosses are successful, species status is supported.

Preliminary tests of compatibility showed that crosses between allopatric populations thought to be conspecific generally resulted in mating and progeny, while crosses between sympatric or allopatric populations of *ambitiosus* and *hubbelli* and of *ambitiosus* and *arenicola* produced no progeny (Mays 1975, Gross 1984).

Methods

Replicated crosses among the four species were made using *P. ambitiosus* and *arenicola* from FL-Alachua-3, *hubbelli* from FL-Levy, and *uliginosus* from FL-Bradford (Table 1). Females collected in association with singing males were maintained in jars as described above. Most females had mated in the field and readily oviposited in the damp sand. Offspring were reared and daughters were isolated prior to adulthood to obtain virgins for the crosses. To ensure that females were ready to mate, they were tested with conspecific males. When courtship had progressed to the point where the male produced a spermatophore, the female was considered receptive and was removed and set aside for use in a test cross.

The four species were crossed with each other in all 16 possible combinations, with each combination replicated four times. Each pair was observed for four hours, and the degree to which courtship proceeded was recorded (Mays 1971). The male was then removed and the female left in the jar to oviposit. Jars were tended for three months and periodically inspected for hatchlings.

Results

The results of the 64 crosses are shown in Table 3. Of 16 intraspecific crosses, only one failed to produce progeny. On the other hand, only one of the 48 interspecific crosses produced viable young, a cross between *ambitiosus* and *uliginosus.* In several of the interspecific crosses, mating proceeded to the point where the female accepted the spermatophore and left it attached for at least five minutes.

TABLE 3. Results of crosses of *Pictonemobius.* The four numbers for each cross are the results for the four replicates.[1]

	Male			
Female	*arenicola*	*ambitiosus*	*hubbelli*	*uliginosus*
arenicola	7 7 7 7	1 5 3 5	2 4 0 0	3 5 0 6
ambitiosus	5 5 0 0	7 7 7 7	1 1 1 1	1 7 1 1
hubbelli	0 1 0 1	0 1 1 1	7 7 7 7	0 0 6 1
uliginosus	2 1 1 0	1 0 1 6	1 0 0 0	7 5 7 7

[1]Results are coded as follows:
0 = no calling song, courtship, or mating
1 = calling song only
2 = calling and courtship songs
3 = mounting by female prior to male's forming spermatophore
4 = mounting by female after spermatophore formation
5 = spermatophore transferred to female
6 = spermatophore retained by female at least 5 minutes
7 = progeny

Discussion

Most interspecific courtships did not proceed to the point where the females mounted the male for spermatophore transfer. In only four such courtships did apparently normal spermatophore transfer and retention occur, and in three of these no progeny were produced. When courtship interactions did not prevent interspecific mating, physiological incompatibilities seem usually to have prevented normal fertilization or development of progeny.

Only one interspecific cross *(uliginosus* X *ambitiosus)* produced progeny. As noted above, this result does not warrant rejection of our hypothesis that *uliginosus* and *ambitiosus* are species. It is the lack of hybridization under natural conditions that is relevant to biological species status, and these two are sympatric.

Electrophoresis

The biological species concept presumes that no significant genetic exchange occurs between species under natural conditions. As species diverge from one another, a gradual acquisition of genetic differences accompanies their reproductive isolation (Ayala et al. 1974). The ability to detect genetic differences has been greatly enhanced over the past two decades by the technique of gel electrophoresis. A major assumption, repeatedly verified by progeny analysis, is that different rates of protein band migration in an electric field represent different alleles of a genetic locus. However, the converse is not true — not all alleles are detected by electrophoresis. Thus, bands on gels may represent classes of alleles of similar electrophoretic mobility *(electromorphs)* rather than single alleles. Sympatric populations may possess their own unique electromorphs, and often no individuals are found that possess both electromorphs (i.e., there are no hybrid genotypes). Reproductive isolation between the populations, and species status, is confirmed in these instances.

For allopatric populations, electrophoretic analysis can be used to estimate overall genetic similarity, but is insufficient to decide if the populations are specifically distinct. No particular degree of genetic divergence is equivalent to speciation. Electrophoretic data can also be used to construct hypothetical phylogenetic trees (Nei 1972, Rogers 1972, Farris 1972).

Harrison (1979) was first to use electrophoresis to determine genetic relationships among cricket species. The phylogeny of *Gryllus* that his data supported did not entirely agree with relationships suggested by morphology and song. Howard (1983) did a similar study of *Allonemobius,* and in this case, the electrophoresis-based phylogeny agreed well with that suggested by other evidence.

Methods

Eleven populations of *Pictonemobius* were sampled from nine localities in Florida and Georgia during September and October 1983 (Table 4). When possible, 30 to 40 crickets were collected from each population. Two to nine

TABLE 4. Calling song characters for *Pictonemobius* populations used for electrophoretic analysis. Localities are in Florida except Chatham Co., Georgia. Exact localities are given in Table 1.

Species and Locality[1]	n	Wingstroke rate[2] per second $\bar{x} \pm SD$	Chirp length (seconds) $\bar{x} \pm SD$
ambitiosus			
FL-Alachua-2	4	48 ± 0.7	0.4 ± 0.1
FL-Taylor	4	51 ± 0.3	0.9 ± 0.2
FL-Liberty	7	45 ± 0.8	1.0 ± 0.2
FL-Walton	3	50 ± 1.0	0.7 ± 0.1
GA-Chatham	2	48 ± 0.6	1.2 ± 0.1
hubbelli			
FL-Alachua-2	4	37 ± 0.8	1.1 ± 0.4
FL-Highlands	9	37 ± 0.4	0.6 ± 0.1
arenicola			
FL-Gilchrist-2	5	51 ± 0.6	0.3 ± 0.0
FL-Lake-2	3	47 ± 1.0	0.2 ± 0.1
FL-Highlands	2	51 ± 0.7	0.2 ± 0.1
uliginosus			
FL-Bradford	5	59 ± 0.6	1.3 ± 0.1

[1]See Table 1.
[2]Corrected to 25 °C

TABLE 5. Electromorph frequencies in eleven populations of *Pictonemobius*. For each nominal species, the population selected to represent the Gainesville area is listed first. Sample size for each population is given in parentheses. (See Table 1 for specifics of collection localities.)

Enzyme and electro-	morphs[1]	*ambitiosus*					*hubbelli*		*arenicola*			*uliginosus*
		F-Al-2 (30)	F-Tay (17)	FLib (30)	F-Wal (18)	G-Cht (20)	F-AL-2 (31)	F-Hgh (25)	F-Gil-2 (39)	F-Lak (30)	F-Hgh (25)	F-Brd (15)
ACP	80	—	—	1.00	—	—	—	—	—	—	—	—
	100	1.00	—	—	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	135	—	1.00	—	—	—	—	—	—	—	—	—
AO	85	—	1.00	1.00	1.00	1.00	1.00	1.00	—	—	—	1.00
	100	1.00	—	—	—	—	—	—	1.00	1.00	—	—
	115	—	—	—	—	—	—	—	—	—	1.00	—
EST	15	—	—	—	—	—	0.12	0.12	—	—	—	—
	45	—	0.09	—	—	—	—	0.58	—	—	0.03	—
	55	0.07	—	—	—	—	0.65	—	—	—	—	—
	70	—	0.09	0.03	—	—	—	—	—	—	—	—
	80	0.07	—	—	1.00	0.20	—	0.06	—	—	—	—
	90	—	—	—	—	—	—	—	—	0.36	—	—
	100	0.23	—	0.97	—	—	0.03	0.10	1.00	0.58	0.09	—
	110	—	0.70	—	—	0.80	—	—	—	—	—	1.00
	125	0.63	0.12	—	—	—	0.20	0.14	—	0.06	0.88	—
GPD	100	0.88	1.00	0.90	1.00	1.00	0.92	0.82	0.88	0.95	1.00	1.00
	120	0.12	—	0.10	—	—	0.08	0.18	0.12	0.05	—	—
GP	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
GOT	60	—	—	—	—	—	0.40	0.33	—	—	—	—
	75	0.04	0.07	—	1.00	—	0.50	0.59	—	—	—	—
	95	0.21	—	0.98	—	—	0.10	0.08	—	—	0.02	—
	100	—	0.61	—	—	—	—	—	1.00	1.00	0.98	0.89

	110	0.75	—	0.02	—	0.53	—	—	—	—	—	0.11
	120	—	0.32	—	—	0.47	—	—	—	—	—	—
MDH	67	0.56	—	—	1.00	—	0.03	—	—	—	—	—
	85	0.37	1.00	0.83	—	1.00	—	0.15	—	—	—	1.00
	90	—	—	0.17	—	—	—	—	—	—	—	—
	100	0.07	—	—	—	—	0.90	0.85	0.92	0.93	0.73	—
	110	—	—	—	—	—	0.07	—	0.08	0.07	0.27	—
ME	80	—	—	—	—	—	—	—	—	—	—	0.60
	85	0.07	—	—	—	0.60	0.97	1.00	0.01	—	0.03	0.40
	95	—	—	0.97	0.61	—	—	—	—	—	—	—
	100	0.55	1.00	0.03	0.39	0.40	0.03	—	0.99	1.00	0.97	—
	110	0.38	—	—	—	—	—	—	—	—	—	—
PEP	100	—	—	—	—	—	—	—	1.00	—	—	—
	200	0.10	—	—	—	—	0.96	—	—	—	—	—
	280	—	—	—	—	—	—	0.84	—	—	—	—
	330	0.90	1.00	1.00	1.00	1.00	0.04	0.16	—	1.00	1.00	1.00
PGI	55	0.04	0.03	0.03	—	—	0.02	0.23	0.19	0.26	0.17	—
	100	0.24	0.47	0.77	0.77	0.12	0.18	0.52	0.42	0.56	0.71	0.38
	142	0.63	0.35	0.20	0.23	0.79	0.73	0.20	0.39	0.16	0.12	0.36
	175	0.09	0.15	—	—	0.09	0.07	0.05	—	0.02	—	0.46
PGM	60	0.02	1.00	0.78	—	—	0.02	—	—	—	—	—
	65	—	—	—	0.75	—	—	—	—	—	—	—
	80	—	—	0.22	0.25	—	—	—	—	—	—	—
	87	0.08	—	—	—	—	0.73	1.00	0.06	—	—	—
	100	0.90	—	—	—	0.26	—	—	−0.94	0.95	0.98	0.79
	110	—	—	—	—	—	0.25	—	—	0.05	0.02	0.21
	125	—	—	—	—	0.74	—	—	—	—	—	—
XDH	100	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00

[1]See Methods for enzyme abbreviations.

males from each population were tape recorded and identified according to song type and appearance.

Electrophoresis was performed on a horizontal starch gel. Thirteen enzymes were examined; acid phosphatase (ACP), aldehyde oxidase (AO), esterase (EST), glutamate oxaloacetate transaminase (GOT), α-glycerophosphate dehydrogenase (GPD), malate dehydrogenase (MDH), malic enzyme (ME), peptidase (PEP), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), and xanthine dehydrogenase (XDH). A general protein (GP) was also examined. Gross (1984) listed the recipes for gel buffers and stains that were used.

Electromorph frequencies were calculated based on the banding patterns of the gels after staining. These frequencies were used to construct a matrix comparing the genetic relatedness of each population with every other population, using the methods of Rogers (1972) and Nei (1972). Finally, a hypothetical phylogenetic tree was constructed using the distance Wagner procedure of Farris (1972), with the assistance of the BIOSYS-1 computer program of Swofford and Selander, University of Illinois, Urbana.

Results

Frequencies of electromorphs for each enzyme are shown in Table 5. The banding patterns for the general protein and xanthine dehydrogenase were uniform for all species. The banding patterns for acid phosphatase and aldehyde oxidase were fixed within each population but varied among the populations. The remaining enzymes were polymorphic within one or more populations. Table 6 lists Rogers' and Nei's genetic distances among the populations. Fig 3 is a phylogeny based on Rogers' genetic distances.

Discussion

The Gainesville-area populations that were analyzed as representative of the four species were identifiable by unique combinations of electromorphs — for example, FL-Bradford *uliginosus* has AO 85 and EST 100 and FL-Gilchrist-2 *arenicola* had AO 100 and GOT 100. This supports their specific distinctness, because populations of the same species in a limited geographic area are unlikely to be fixed for different electromorphs.

However, with the exception of the two populations of *hubbelli,* all widely separated populations assigned to the same species also had unique combinations of fixed electromorphs — viz., the three populations assigned to *arenicola* and the five assigned to *ambitiosus* (Table 5). To illustrate, diagnostic combinations of fixed electromorphs for FL-Taylor *ambitiosus* were ACP 135 and AO 85; for FL-Walton *ambitiosus,* ACP 100, AO 85, and MDH 67.

While conspecific populations of *arenicola* and *hubbelli* clustered in the phylogeny based on Rogers' genetic distances, those of *ambitiosus* did not (Fig 3). West Florida and Georgia populations of *ambitiosus* were electrophoretically closer to *uliginosus* and *hubbelli* than to Alachua Co. *ambi-*

TABLE 6. Genetic distances among populations of *Pictonemobius*. Above diagonal are Nei's (1972) distances, and below diagonal are Rogers' (1972) distances. (See Table 1 for specifics of collection localities.)

Population	*ambitiosus*					*hubbelli*		*arenicola*			*uliginosus*
	F-Al-2	F-Tay	F-Lib	F-Wal	G-Cht	F-Al-2	F-Hgh	F-Gil-2	F-Lak	F-Hgh	F-Brd
amb F-Al-2	—	0.486	0.521	0.431	0.358	0.463	0.494	0.336	0.277	0.334	0.389
amb F-Tay	0.625	—	0.410	0.587	0.310	0.819	0.773	0.789	0.573	0.558	0.299
amb F-Lib	0.707	0.368	—	0.430	0.541	0.564	0.530	0.589	0.532	0.562	0.443
amb F-Wal	0.493	0.456	0.549	—	0.449	0.457	0.428	0.572	0.467	0.456	0.411
amb G-Cht	0.358	0.307	0.441	0.390	—	0.388	0.426	0.547	0.463	0.464	0.218
hub F-Al-2	0.636	0.545	0.858	0.563	0.464	—	0.216	0.686	0.689	0.695	0.450
hub F-Hgh	0.693	0.529	0.764	0.505	0.483	0.176	—	0.694	0.651	0.659	0.449
arn F-Gil-2	0.364	0.538	0.938	0.839	0.759	0.487	0.485	—	0.145	0.298	0.465
arn F-Lak	0.239	0.441	0.767	0.609	0.574	0.490	0.465	0.119	—	0.182	0.368
arn H-Hgh	0.325	0.440	0.846	0.596	0.577	0.512	0.489	0.315	0.160	—	0.369
ulg F-Brd	0.423	0.314	0.553	0.515	0.166	0.557	0.535	0.605	0.425	0.421	—

tiosus. Indeed no fixed electromorphs separated GA-Chatham *ambitiosus* and FL-Bradford *uliginosus,* and FL-Alachua-2 *ambitiosus* clustered with the *arenicola* populations. (The implications of this will be considered in the next section.)

Two pairs of sympatric populations were included in the electrophoretic analysis: *ambitiosus* and *hubbelli* from FL-Alachua-2, and *hubbelli* and *arenicola* from FL-Highlands. The populations of each pair had unique electromorphs, making hybrids electrophoretically recognizable. None occurred among the 61 crickets studied from Alachua County or the 58 crickets from Highlands County.

General Discussion

There is convincing evidence that four species of *Pictonemobius* occur in north central Florida — the previously named *ambitiosus* and three sibling species described in this paper. At all sites where more than one species occurred, we found differences in wingstroke rate, habitat preference, and coloration, and no evidence of hybridization. Our discussion will center on how populations outside of north peninsular Florida should be treated.

Binomial nomenclature may be inadequate to represent the true relationships of *Pictonemobius* populations. These crickets are flightless and small, and their populations are often restricted to island-like habitats. Their ap-

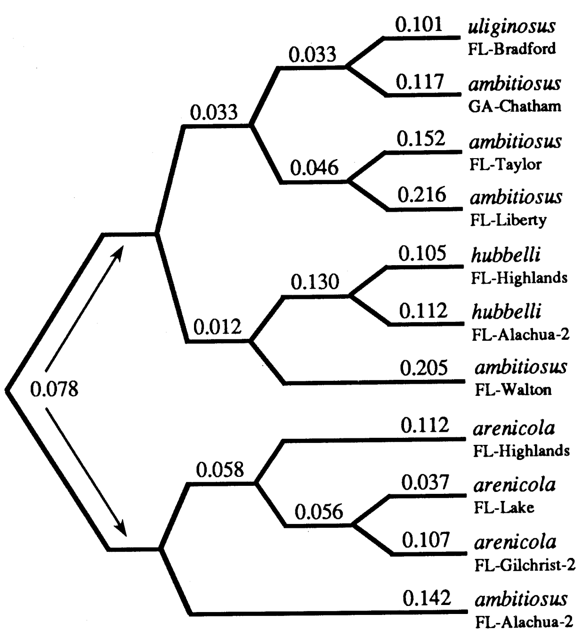

FIGURE 3. Hypothetical phylogeny of *Pictonemobius* populations based on Rogers' genetic distances (Table 6). Numbers on the tree represent branch lengths (branches not drawn to scale).

parent isolation is confirmed by our electrophoretic results. All but one pair of populations that we classed as conspecific had different fixed electromorphs. Genetic distances among conspecific populations of *Pictonemobius* were generally as large as those reported in *Gryllus* and *Allonemobius* for well-defined species (Table 6) (Harrison 1979, Howard 1983). This suggests that numerous undescribed species of *Pictonemobius* exist. The lack of sympatry of these candidate species means there are no natural experiments to verify or refute their distinctness. In analyses of the flightless Florida grasshopper complexes known as *Melanoplus puer* and *Aptenopedes sphenarioides,* Hubbell (1960) found a plethora of ''microspecies'' — i.e., ''morphologically distinct, non-overlapping populations that occupy adjoining and often very small territories separated by what appear to be trivial barriers.'' Although morphological differences among *ambitiosus* populations are not great, genetic differences are. Present day rivers, swamps, sandhills, and other geographic and ecological features evidently act to maintain isolated ''conspecific'' populations of *Pictonemobius* that have genetic differences as great as expected for cricket populations that are specifically distinct.

Having concluded that no division of *Pictonemobius* into a few species is likely to bring order to the mosaic of genetically distinct populations that evidently occupies Florida and adjacent states, we will explain our ad hoc treatment of populations occurring beyond the environs of Gainesville.

For *Pictonemobius* populations in Florida south of Gainesville it was relatively easy to assign species names by using Gainesville-area populations as standards. For example, *Pictonemobius* from FL-Highlands scrubby flatwoods were identified as *arenicola* because wingstroke rates and coloration were similar to *arenicola* from the Gainesville area. Progeny resulted from each of 3 crosses made between FL-Highlands and FL-Gilchrist populations, and the populations were also electrophoretically close (Fig 3).

Differences between sympatric populations of *Pictonemobius* were as striking in south Florida as in north Florida. Near the southern terminus of Florida's central ridge (FL-Highlands), in the scrubby flatwoods habitat, *arenicola* abounded (see above). In the wetter bayheads and grass tussocks bordering small ponds that dot the scrub, *hubbelli* was encountered, with its darker coloration and wingstroke rate of 37 per second. Electrophoresis revealed genetic differences with no hybrids; and the *hubbelli* population, like *arenicola,* was closely related to its north Florida counterpart (Fig 3). The southernmost record for *arenicola* was from scrub habitats at Jupiter, Florida. Crickets resembling Gainesville *ambitiosus* in song and coloration were encountered at sites as far south as Marco Island and Fort Lauderdale, and museum specimens from other south Florida sites were also assigned to this species.

Many of the *Pictonemobius* populations to the west and north of Gainesville were not easily assigned to any of the four available species categories. Populations in the Florida panhandle as far west as Leon and Liberty Counties generally fit, in wingstroke rate, habitat, and appearance, the characteristics of *ambitiosus* or *hubbelli* (Table 1). However, a population in Taylor County that we assigned to *ambitiosus* included individuals that were close to *uliginosus* in wingstroke rate (Table 1). Farther west, populations that looked like *ambitiosus* generally had faster mean wingstroke rates than Gainesville *ambitiosus,* although in most cases the ranges overlapped. Because they were found in sandhill habitats and the wingstroke rates resembled Gainesville-area *arenicola,* we could have assigned these panhandle crickets to *arenicola.* However, they lacked *arenicola*'s morphological hallmarks. Complicating the picture further, all genetically analyzed west Florida populations of *ambitiosus* were closer to Gainesville-area *uliginosus* than to either *arenicola* or *ambitiosus* (Table 6, Fig 3). Lacking a more attractive alternative, we left these populations with the specific name they had before — *ambitiosus.*

With one exception (*uliginosus,* GA-Charlton), populations north of Florida generally resembled *ambitiosus* or *hubbelli* in appearance, habitats, and wingstroke rates (Table 1, Fig 1). However, the only population genetically analyzed (from Ossabaw Island: GA-Chatham) was electrophoretically very close to *uliginosus* (Fig 3). In appearance and wingstroke rates the Ossabaw crickets were like Gainesville *ambitiosus,* but their chirps were long (>1 sec), like *uliginosus.*

The recognition of three new species of *Pictonemobius* gives needed names to Gainesville-area populations that maintain their integrity when they intermingle. Since these are species by all biological criteria, they should be recognized as such in all biological studies of *Pictonemobius.* We also use the names as labels for populations that likely represent additional allopatric species rather than being conspecific with Gainesville-area populations. So long as all species-level *Pictonemobius* populations in each locality are distinguished, even if the assigned specific names are ultimately changed, biologically important distinctions among *Pictonemobius* individuals have been facilitated. The present data suggest that no area is richer in *Pictonemobius* species than north peninsular Florida. To the south, north, and west the number of species drops. Which species drop out and which remain is less important than that the remaining species have distinguishing names. Otherwise, an investigator may be unaware that he is dealing with several species rather than one at a research locality.

As we have defined the names, *P. arenicola* and *uliginosus* are recognizable by appearance alone and have relatively limited distributions, but *ambitiosus* and *hubbelli* coexist over large areas of Alabama, Georgia, and Florida and can be separated only by song analysis. The museum worker will be faced with a subset of pinned *Pictonemobius* specimens that cannot be named with certainty. Except for north peninsular Florida, matters are actually worse, because the names we suggest will be assigned to populations that are unlikely to be truly conspecific with the Gainesville-area crickets that are the basis of the nomenclature. Like democracy, our nomenclature of *Pictonemobius* species is most attractive only when compared to available alternatives.

KEY TO THE SPECIES OF *PICTONEMOBIUS*

The following key should aid in assigning names to *Pictonemobius* specimens and populations.

1 Hind femora lacking lateral stripes, or at most possessing a pale line corresponding to femoral groove (Figure 2B). Females with tegminal stripe running entire length of tegmen . . . . *arenicola*

1′ Hind femora with lateral stripes present (Figure 2A). Females with tegminal stripe almost always fading posteriorly, not reaching posterior border of tegmen 2

2 Dorsum of male tegmen lacking light border (Figure 2D). Wingstroke rate at 25 C greater than 55 per second, usually greater than 58 per second. Habitat moist pine flatwoods . . . . *uliginosus*

2′ Dorsum of male tegmen with light-colored border (Figure 2C). Wingstroke rate at 25 C less than 57 per second. Habitat variable 3

3 Wingstroke rate at 25 C greater than 43 per second . . . . *ambitiosus*

3′ Wingstroke rate at 25 C less than 43 per second . . . . *hubbelli*

ACKNOWLEDGEMENTS

We thank Susan A. Wineriter for making the illustrations and J.E. Lloyd and M.C. Thomas for reviewing the manuscript. Portions of the research were supported by grants from NSF (DEB-8211975, most recently). Fla. Agric. Exp. Stn. Journal Series No. 9882.

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