Synonymies of Wasp-Mimicking Species within the Katydid Genus Aganacris (Orthoptera: Tettigoniidae: Phaneropterinae)

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Synonymies of wasp-mimicking species within the katydid genus Aganacris (Orthoptera: Tettigoniidae: Phaneropterinae)

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Abstract

Five neotropical wasp-mimicking species of the genus Aganacris—two known only from females and three from males—are reviewed. Based on observation of interspecific interactions and morphological comparison, it is shown that sexual dimorphism occurs within species, and that female species are conspecific with sympatric male species. This is reinforced by field observations in northern Peru of a pairing between A. pseudosphex and A. nittida, wherein the male was in the process of secreting a spermatophore. Aganacris sphex and A. pseudosphex are morphologically nearly identical and probably represent variants of a single species. Since those species known from females only are both senior to sympatric male species, the number of species is reduced from five to two – A. nittida (A. pseudosphex and A. sphex designated herein as junior synonyms) and A. velutina (A. insectivora designated herein as a junior synonym).

Key words

katydid, Sphecidae, Pompilidae, mimicry

Introduction

Grant (1958) resurrected the genus name Aganacris Walker, 1871, to separate a group of three closely related neotropical species of wasp-mimicking katydids [Scaphura nittida Perty (1832), S. sphex Rehn, 1918, and S. velutina Kirby, 1906] from the other nine species of Scaphura Kirby, 1825. W. E. Kirby (1906) had designated Aganacris micans Walker, 1871, to be a junior synonym of S. nittida Perty. Grant (1958) designated S. nittida as the type species of the genus, using Walker’s (1871) genus name Aganacris and listing nine morphological differences to justify the separation of these species from Scaphura. He also described two new species, A. insectivora from Panama, and A. pseudosphex from Peru. Descriptions of three of the Aganacris species (A. insectivora, A. sphex, and A. pseudosphex) were based on specimens of males only, while the other two species (A. velutina and A. nittida) were based on specimens of females only. This circumstance of not knowing the opposite sex of any of these species is suspect and has led to a re-evaluation of Grant’s (1958) revision.

The present study is based on the original specimens from Grant’s (1958) study, along with additional specimens from other museums and those collected by me (Earthwatch project, 1986-1999) in northern Peru. Field observations of Aganacris species made in Peru lead me to propose several synonymies.

Material and Methods

Specimens examined.—The study is based on 24 males and 21 females from the following museums: Academy of Natural Sciences of Philadelphia [ANSP], American Museum of Natural History, New York, NY [AMNH], California Academy of Sciences [CALAC], The Natural History Museum, London, UK [NHM], United States National Museum of Natural History, Washington, DC [NMNH], and University of Michigan Museum of Zoology, Ann Arbor, MI [UMMZ].

Aganacris nittida: 2♀♂. HOLOTYPE: Panama: Ciudad de Panamá. 1♀ [ANSP].—The study is based on 24 males and 21 females from the following museums: Academy of Natural Sciences of Philadelphia [ANSP], American Museum of Natural History, New York, NY [AMNH], California Academy of Sciences [CALAC], The Natural History Museum, London, UK [NHM], United States National Museum of Natural History, Washington, DC [NMNH], and University of Michigan Museum of Zoology, Ann Arbor, MI [UMMZ].

Aganacris insectivora: 6♀♂. HOLOTYPE: Panama: Pedregal. 1♀ [ANSP].—Several synonymies. Grant designated A. sphex (1♀) [ANSP] and A. nittida (2♀♂) as the type species of the genus, using Walker’s (1871) genus name Aganacris and listing nine morphological differences to justify the separation of these species from Scaphura. He also described two new species, A. insectivora from Panama, and A. pseudosphex from Peru. Descriptions of three of the Aganacris species (A. insectivora, A. sphex, and A. pseudosphex) were based on specimens of males only, while the other two species (A. velutina and A. nittida) were based on specimens of females only. This circumstance of not knowing the opposite sex of any of these species is suspect and has led to a re-evaluation of Grant’s (1958) revision.

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Methods. — This study is based on morphological characters reviewed by Emsley et al. (1967) and includes: shape of the vertexal and frontal fastigia; shapes of the pronotal disc, carinae, and lobes; structure of the periphery of the tympanum; spinulation of the legs and femoral genae; shape and venation of the tegmen; degree of exposure of hind wing beyond distal edge of tegmen in repose; shape of the meso- and metasternal lobes, respectively; development in the male of various components of external and internal genital armature, including tergite X, cerci, epiphallus and subgenital plate; and in the female, specializations of the posterior abdominal tergites, shape of the ovipositor and subgenital plate, and development of basal plates of the ovipositor. Stridulatory files of all male species were examined under a microscope and then imaged with a scanning electron microscope. Linear file tooth distribution (i.e., the shortest distance between successive teeth, disregarding the overall curvature of the file) is a character which often exhibits acute interspecific differences but which is intraspecifically relatively constant (Emsley et al. 1967). Measurements of characters and distances between consecutive file teeth were made with the apparatus described by Grant (1965). Tegminal vein nomenclature follows that used by Ragge (1955).

Specimens were examined under a Wilde W2 microscope. Photographs (Figs 1-6) were rendered using an EntoVision™ Imaging Suite consisting of a firewire JVC KY-75 3CCD digital camera connected to a Leica M16 zoom lens via a Leica z-step microscope stand. Multiple focal planes were merged using Cartograph 5.6.0™ software (Microvision Instruments, FR). Images were edited on Adobe Photoshop CS4™ for MacIntosh. Specimens used in scanning electron micrograph (SEM) imagery were softened for 10 sec in hot water (110°F) and dissected. The left tegmen of one specimen from each of the three male species was removed and the area surrounding the stridulatory file dried overnight. Once dried, structures were glued directly to SEM stubs. Stubs were sputter-sprayed with gold and photomicrographed with an Amray 1810™ scanning electron microscope. Images were digitally captured and edited with Adobe Photoshop CS4™ for MacIntosh for minor editing.

Results

Morphological comparisons

Aganacris nitida. — Nineteen specimens of this species were examined. This species has been reported in the literature from Bolivia, Brazil, Colombia, Guyana, and Peru (Kirby 1906, Grant 1958). Specimens from these countries were compared and found to be...
morphologically nearly identical across the species' range, with no differences in features usually used to distinguish females of different phaneropterine species (shape of subgenital plate, number of spines on genal lobes of femora, and shape of lateral lobe of pronotum). There were also no differences found in color patterns or in the yellow markings found on the hindfemur. *Aganacris nitida* extends throughout the Amazonian basin across a broad range from Brazil and the Guianas into Ecuador and Peru. There were no data to suggest that more than one species is represented within this widely dispersed sample.

Field observations of *A. nitida*.—*Aganacris nitida* (female of the ‘female species’) was observed paired with a male *Aganacris* species on XI.18.1986 (10:45 PM) at our Earthwatch research site (Explorama Inn, Loreto Prov., Peru). Specimens were on the dorsal surface of a broad leaf of a species of *Citrus*, in a grove near the edge of the rainforest. Observations were made with them in the copulation posture typical of phaneropterine katydids: male with head recessed under its body, tegmina raised vertically, abdomen acutely arched ventrally, female mounting his body from behind, with mouthparts

Aganacris pseudosphex and A. sphex.—Aganacris pseudosphex mimics species of the wasp Erinnophila (Sphecidae), commonly found throughout the Amazon region, while numerous species of glossy black predatory wasps such as Hemipepsis and related genera (Pompilidae) may act as multiple models for A. nitida throughout its range. Rehn (1918) described A. sphex from a single male from Brazil. Grant (1958) listed three additional males, one from Guyana and 2 from Brazil; he regarded A. pseudosphex and A. sphex as very similar, with minor differences in overall size and in configuration of the fastigium (which he described in A. pseudosphex to be narrower and less evenly trigonal in dorsal view). They differed in the W/L ratio of the pronotal disc (0.77 in A. pseudosphex, 0.86 in A. sphex), in the foretibia (with tympanum in A. pseudosphex more elongate relative to its width and often [but not always] with a small spine on dorsolateral margin at the distal face of the tympanal expansion). Grant also noted differences in the degree of elongation of the tenth tergite (in A. pseudosphex being more elongated and medially more margined), shapes of the cerci (in A. pseudosphex somewhat more curved with distal tooth less prominent), and shape of the subgenital plate (in A. pseudosphex being broader and apically more deeply margined).

The most significant difference highlighted by Grant (1958) involved coloration and venation of the tegmen: in A. pseudosphex the darkened distal area is smaller, covering only the distal fourth of veins M and Rs (in A. sphex Grant reported that it covers nearly half of these same veins). Furthermore, on the specimens in Grant’s type series of A. pseudosphex, a small dark colored crossvein connects veins Rs and M (Figs 10, 11). All of the specimens in Grant’s type and paratype series showing this venation difference were from higher elevations in central Peru. This character was reviewed again in this study: although all of the Peruvian specimens have this crossvein, specimens otherwise identifiable as A. pseudosphex from Loreto Province had wing coloration and venation more similar to A. sphex than to A. pseudosphex, while specimens listed from Brazil (Hyutanahan) also showed coloration patterns and venation that were intermediate within these two species.

Measurements and ratios made by me on all specimens of these two species overlapped, and no character could be used definitively to separate them (Table 1).

Aganacris pseudosphex was based on a single individual from Brazil, which falls within the levels of variation of A. pseudosphex, most specimens of which were collected in Peru. Comparing the stridulatory files of these two species, I found them to be similar [A. pseudosphex—with a tooth count of 98 teeth and a spatial distribution of teeth of 96 teeth/mm (Fig. 8); A. sphex with 100 teeth and 98 teeth/mm (Fig. 9)]. Comparing these two files with that of A. insectivora from Panama, the file of A. insectivora is longer, with a tooth count of 124 teeth and a spatial distribution of teeth of 128 teeth/mm (Fig. 7).

While it is not possible to rule out that these two species are distinct from one another, evidence has been presented herein that they are in fact very similar or the same. Reviewing evidence for supposing they are conspecific: (1) they both are found within the geographic range of A. nitida – A. sphex in the eastern area (Brazil and Guyana) and A. pseudosphex (Peru, Ecuador, Colombia, and western Brazil); (2) all measurements and morphometric ratios overlap (Table 1); and (3) the one character used by Grant (1958) to separate A. sphex from A. pseudosphex – the presence in A. sphex of a spine on the ventral anterior margin of the tympanal ridge – is also found in most specimens of A. pseudosphex. This evidence leads me to consider these two species to be variants of a single species. Aganacris pseudosphex and A. sphex also should be considered conspecific with A. nitida. Since the name “nitida” takes precedence, A. pseudosphex and A. sphex herein are both designated junior synonyms of A. nitida.

Table 1. Measurements of Aganacris species, given as means and ranges, in mm.

<table>
<thead>
<tr>
<th>Species:</th>
<th>pseudosphex</th>
<th>sphex</th>
<th>nitida</th>
<th>insectivora</th>
<th>velutina</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total length</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range</td>
<td>31.9-34.6</td>
<td>31.9-32.6</td>
<td>26.4-31.4</td>
<td>36.3-37.4</td>
<td>31.3-32.7</td>
</tr>
<tr>
<td>L pronotum</td>
<td>3.8</td>
<td>3.9</td>
<td>3.8</td>
<td>4.8</td>
<td>4.3</td>
</tr>
<tr>
<td>W pronotum</td>
<td>3.13</td>
<td>3.22</td>
<td>3.33</td>
<td>3.83</td>
<td>3.51</td>
</tr>
<tr>
<td>W posterior femur</td>
<td>1.9</td>
<td>2.0</td>
<td>2.2</td>
<td>2.4</td>
<td>2.6</td>
</tr>
<tr>
<td>L tegmen</td>
<td>25.0</td>
<td>24.2</td>
<td>22.5</td>
<td>28.6</td>
<td>24.1</td>
</tr>
<tr>
<td>W tegmen</td>
<td>23.6-27.0</td>
<td>23.5-25.1</td>
<td>21.6-24.3</td>
<td>28.3-28.9</td>
<td>24.0-24.1</td>
</tr>
<tr>
<td>Pars stridens</td>
<td>0.6-4.2</td>
<td>0.6-4.7</td>
<td>0.6-3.9</td>
<td>5.9-6.5</td>
<td>4.0-4.1</td>
</tr>
<tr>
<td>L Ovipositor</td>
<td>8.7</td>
<td></td>
<td></td>
<td>9.4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>8.2-9.1</td>
<td></td>
<td></td>
<td>9.3-9.4</td>
<td></td>
</tr>
</tbody>
</table>
Aganacris insectivora and A. velutina.—In Central America two other sympatric species – A. insectivora (known from males only) and A. velutina (known from females only) – are morphologically distinct from one another, reminiscent of the distinctions found in the South American species.

Aganacris insectivora (Fig. 1) mimics Hemipepsis mexicana (Lucas) (Pompilidae) (Fig. 2) (Belwood 1988), commonly found from Mexico to Colombia, while several species of glossy black predatory wasps including Hemipepsis and related genera (Pompilidae) may act as multiple models for A. velutina.

Belwood (1990) reported effects of predation on the singing behavior of A. insectivora on Barro Colorado Island, Panama. Leaf-gleaning bats often use echolocation for general orientation but tend to locate their katydid prey passively by listening for the sounds they make. Four of the six katydid species taken by Micronycteris hirsuta on Barro Colorado Island in Panama call in the 23-27 kHz range, suggesting which prey are taken depends on whether the bat can hear their call or not (Belwood 1990).

The selection pressure from bats has resulted in a number of adaptations in calling behavior. Some species avoid predation by calling when bats are least active. For example, Aganacris insectivora has two active periods, one during the day and one during the night. Their mimicry of wasps protects them from daytime predators such as birds, monkeys, and lizards, but not during the night. At night, they sing in a very narrow time band between 3 and 5 AM, coinciding with a lull in feeding behavior of leaf-gleaning bats. The strategy appears to be effective because gleaning bats do not appear to take these species (Robinson and Hall 2002). It has not been demonstrated whether this singing cycle also occurs in South American species, but in northern Peru leaf-gleaning bats are present in rainforests inhabited by A. pseudosphex and are most active in the early evening (9 PM-12 AM) (Belwood, pers. observ.).

Based on information that the two South American [male] species (A. pseudosphex and A. sphex) are conspecific with the sympatric species known only from females (A. nitida), it is expected that sexual dimorphism also occurs in the other species of Aganacris. Material at the Instituto Nacional de Bioversidad [INBIO] in Costa Rica and at the Smithsonian Tropical Research Institute [STRI] in Panama encompasses 35 specimens of A. insectivora and 27 specimens of A. velutina, with no specimens of the opposite sex found for either species, even though Costa Rica and Panama have been extensively collected for tettigoniids as part of ongoing biodiversity studies. It is unreasonable to expect that the opposite sex for both of these sympatric species should be so elusive as to avoid capture by trained collectors quantifying biodiversity at the several research sites in Costa Rica and Panama. It is therefore probable that these too represent a single dimorphic species. Since the name "velutina" takes precedence, A. insectivora is designated herein the junior synonym of A. velutina.

A summary list follows:

**Aganacris nitida** (Perty), Scaphura nitida Perty, 1832: 121 [Type: ♂, Brazil, Minas Gerais] [Original description].

**Aganacris micans** Walker, 1871: 41 [Original description].

**Scaphura micans** (Walker: Kirby, 1906: 454 [Synonym].

**Scaphura nitida** Perty: Brunner von Wattenwyl, 1878: 478; Caudell, 1918: 57; Rehn, 1918: 209 [Diagnosis; distribution].

**Aganacris nitida** (Perty): Grant, 1958: 5 [New combination].

**Aganacris pseudosphex** Grant, 1958: 7 [Type: ♂, Peru, Huánuco, Tingo Maria] [Original description].

**Aganacris pseudosphex** Grant: = Scaphura nitida [New junior synonym].

**Scaphura sphex** Rehn, 1918: 192 [Type: ♂, Brazil, Para, Igarapé-assú] [Original description].

**Aganacris sphex** (Rehn): Grant, 1958: 6 [New combination].

**Aganacris sphex** (Rehn): = Scaphura nitida [New junior synonym].

**Aganacris velutina** (Kirby), Scaphura bicolor Brunner von Wattenwyl, 1891: 134-135 [♂, Panama, Chiriqui] [Original description].

**Scaphura velutina** Kirby, 1906: 454 [New name to replace bicolor Brunner].

**Aganacris velutina** Grant, 1958: 9 [New combination].

**Aganacris insectivora** Grant, 1958: 10-11 [Type: ♂, Panama, Canal Zone, Barro Colorado Island] [Original description].

**Aganacris insectivora** Grant: Otte, 1997: 37; Nickle, 1992: 144 Belwood, 1990: 44; Barranco, 2010: 511 [Diagnosis; behavior].

**Aganacris insectivora** Grant = Scaphura velutina [New junior synonym].
The advantage of this level of sexual dimorphism is that female Scaphura species are tropical rainforest species; Scaphura species tend to be found in open savanna, though one species (S. elegans Serville) is a rainforest species [interestingly, this is the only Scaphura species wherein the female is darker than the male, and tegmina of the male display a somewhat muted color pattern similar to A. sphex/A. pseudosphex].

Females of Aganacris are definitely larger than males and may require a larger model (e.g., pompilids vs sphexids) to be successful in their mimicry. Another possible factor favoring a trend to sexual dimorphism is that female Aganacris species have a large, robust ovipositor, very broadly upcurved and not easily hidden from visual appraisal by vertebrate predators such as monkeys or birds. To counterbalance this, they could have evolved glossy, black tegmina to completely conceal the profile revealing a phaneropterine ovipositor.

During the day, both males and females of Aganacris make rapid jerky movements similar to those of their respective wasp models. At night, rapid movement is curtailed, and activity on leaves becomes more cautious, no doubt in response to more common nocturnal predators such as night birds, leaf-gleaning bats, and various predatory arthropods (spiders, scorpions, centipedes, and predaceous katydids) (Belwood & Morris 1987, Belwood 1988, 1990, Nickle & Castner 1995).

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Discussion

It is interesting to try to understand Grant’s (1958) reasoning for naming two species of Aganacris based on males only. Since few specimens were then (and it remains so) available in world collections at the time of his study, the occurrence of a strikingly different morphospecies could easily have led Grant to believe these male forms were different taxa. Basing his study on the separation of these taxa as members of a new genus, different from other Scaphura, could have influenced him as well: Scaphura (sensu stricto) species display little sexual dimorphism, and females can easily be matched with conspecific males on the basis of similar coloration patterns (D.A. Nickle, pers. obs.).

What is the advantage of this level of sexual dimorphism? Aganacris species are tropical rainforest species; Scaphura species tend to be found in open savanna, though one species (S. elegans Serville) is a rainforest species [interestingly, this is the only Scaphura species wherein the female is darker than the male, and tegmina of the male display a somewhat muted color pattern similar to A. sphex/A. pseudosphex].

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