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Source: Journal of Orthoptera Research, 21(2) : 245-250

Published By: Orthopterists' Society

URL: <https://doi.org/10.1665/034.021.0209>

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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. nitida*, 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. nitida* (*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 nitida* Perty (1832), *S. sphex* Rehn, 1918, and *S. velutina* Kirby, 1906] from the other nine species of *Scaphura* Kirby, 1825. W. F. Kirby (1906) had designated *Aganacris micans* Walker, 1871, to be a junior synonym of *S. nitida* Perty. Grant (1958) designated *S. nitida* 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. nitida*) 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

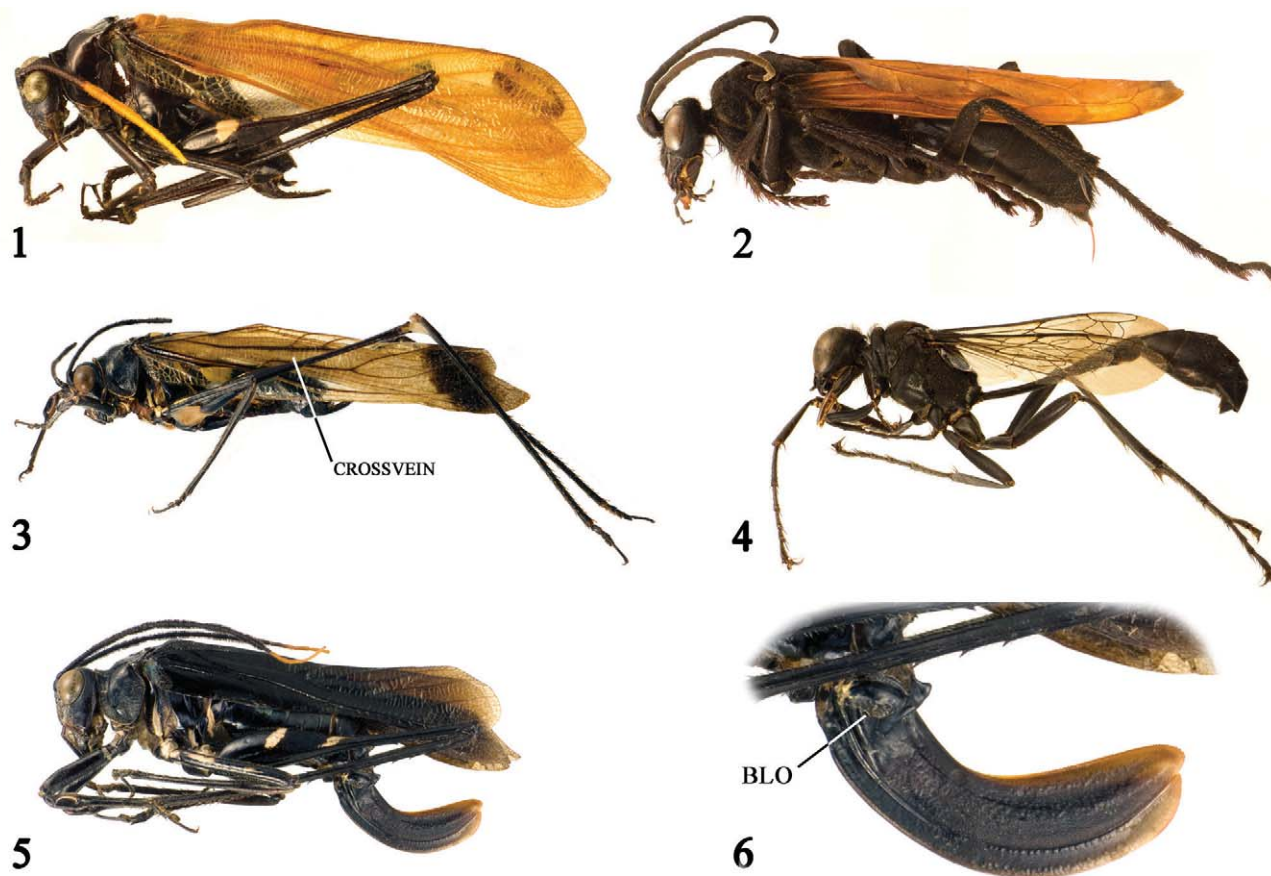
Specimens examined.—The study is based on 24 males and 21 females from the following museums: Academy of Natural Sciences

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 insectivora: 6 ♂♂. Holotype, ♂, PANAMA: Canal Zone. Barro Colorado Island, taken at light. V-19-1956 (C. and M. Rettenmeyer). [ANSP, type no. 5970]; [5 ♂♂ Paratypes] same locality as holotype, VI-4, 5, 14, 15-1956 [ANSP].

Aganacris nitida: 22 ♀♀. BOLIVIA: La Paz, Corico 1908 (Fassl) 2 ♀♀ [VIENNA]; Sará. Santa Cruz, 450 m. 1922 (Steinbach) 1 ♀ [ANSP]. BRAZIL: Pará (Moss) 2 ♀♀ [NHM]; Amazonas. Teffé. II-1924 (Bassler) 1 ♀ [AMNH]; Amazonas. São Paulo de Olivença. [no date]. 1 ♀ [ANSP]. COLOMBIA: Meta. Villavicencio. 1924 (Maria) 1 ♀ [ANSP]. GUYANA: King William Frederick IV Falls, upper Courantyne River. XI-1935. 1 ♀ [NHM]. PERU: Loreto. Rio Ucayali. VII-19-1928 (Bassler) 1 ♀ [ANSP]; Loreto. Pucallpa. III-12-1947 (Schunke) 1 ♀ [NMNH]; Loreto. Explorama Lodge, Camp, ACEER, Inn 1988-1995 (Nickle and Castner, various Teams) 6 ♀♀ [NMNH]; Huanúco. Tingo Maria, 670 m, in jungle. VI-25-1937 (Woytkowski) 1 ♀ [ANSP]; Junín. Chanchamayo. I-25 (Schunke) 1 ♀ [NMNH]; Junín. La Merced. II-7-1949 (Schunke) 1 ♀ [NMNH]; Junín. 11°3'S lat., 75°17' W long. VIII-1908 (Schunke) 1 ♀ [NMNH]; Cuzco. Quiroz, Rio Paucartambo. X-24-1933 1 ♀ [ANSP].

Aganacris pseudosphex: 34 ♂♂: Holotype, ♂, PERU: Huanúco. Tingo Maria. X-1947 (Weyrauch) [ANSP, type no. 5969]; [13 ♂♂ Paratypes] Loreto. Napo River. VI-18-1920 (Parish) 1 ♂ [ANSP]; Loreto. Iquitos. III-25-?? (Bassler) 1 ♂ [AMNH]; Huanúco. Tingo Maria, 670 m. I-1947 (Weyrauch) XII-18-1954 4 ♂♂ [ANSP]; Tingo Maria (Schlinger and Ross) 1 ♂ [CALAC]; Huanúco. Leonpampa, 110 km east of Huanúco. XII-1937 (Woytkowski) 1 ♂ [ANSP]; Junín. Satipo. II-19-1948 (Paprzycki) 1 ♂ [ANSP]; Junín. Tarina, 1,600-3,000 m. II-19-1948 (Woytkowski) 2 ♂♂ [UMMZ]. BRAZIL: Amazonas. Hyutanahan, Rio Purús. I-1922, IV-1922 (Klages) 2 ♂♂ [ANSP]. PERU: Loreto. Explorama Lodge. Explorama Lodge, 80 km NE Iquitos, on Rio Yanamono, 1 km upstream from Rio Amazonas 03°30'S 73°05' W. XI.1-18.1986. (D.A. Nickle, Earthwatch Team I). 1 ♂ [UMMZ]; Exploraciones Amazonicas: Explorama Inn, 40 km downriver from Iquitos, on the Amazon River 03°26' S, 73°02' W. XI.1-18.1986. (D.A. Nickle, Earthwatch Team 1). 3 ♂♂ [UMMZ]; Explorama Inn. II.14-20.1987. (D.A. Nickle, Earthwatch Team 3). 1 ♂ [UMMZ]; Explorama Inn. VIII.22-IX.5.1992. (D.A. Nickle, Earthwatch Team 15). 1 ♂ [UMMZ]; Explorama Lodge. XI.1-18.1986. (D.A. Nickle, Earthwatch Team I). 1 ♂ [UMMZ].



Figs 1-6. *Aganacris* species and probable hymenopteran Batesian models, left lateral aspect. 1. *A. insectivora*, 1.8 \times . 2. *Hemipepsis mexicana*, a tarantula predator of the family Pompilidae, probable model for *A. insectivora*, 1.4 \times . 3. *A. pseudosphex*, 1.4 \times . 4. *Erimnophila* species, 1.4 \times , a thread-waisted wasp of the family Sphecidae, probable model for both *A. pseudosphex* and *A. sphex*. 5. *A. nitida*, from Peru, 1.4 \times . 6. Ovipositor of *A. nitida*, same specimen as in Fig. 5, 4.5 \times [BLO, basal lobe of ovipositor]. For color version, see Plate X.

Aganacris sphex: 4♂♂. Holotype, ♂, BRAZIL: Pará, Igarape-assu [ANSP]; Pará, Pará (Moss) 2♂♂ [NHM]. GUYANA: Forest Reserve Survey Camp 3, Essequibo River, attracted by light. VIII-14-1930 (Brinsley and Martin). 1♂ [NHM].

Aganacris velutina: 2♀♀. COLOMBIA: Cundinamarca. Quetame. I-1913 (María) 1♀ [ANSP]. PANAMA: Chiriquí. Progreso IV-24-1923 (Gaije). 1♀ [UMMZ].

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; spination 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

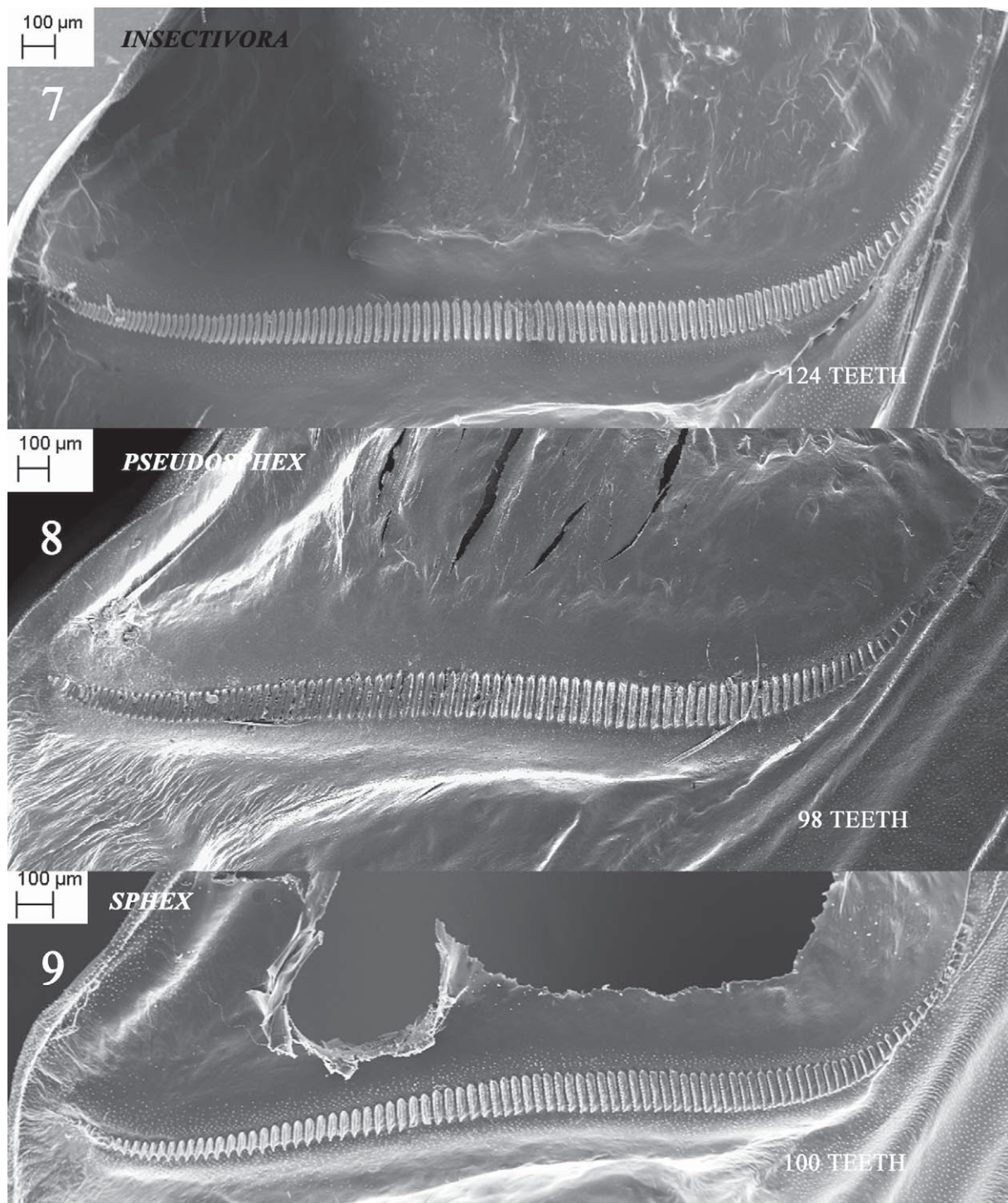
consecutive file teeth were made with the apparatus described by Grant (1965). Tegminal vein nomenclature follows that used by Ragge (1955).

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 *ca* 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



Figs 7-9. Stridulatory file on left tegmen of *Aganacris* species. 7. *A. insectivora* [Panama]. (n= 124 teeth on file). 100×. 8. *A. pseudosphex* [Peru]. (n= 98 teeth on file). 100×. 9. *A. sphex* [Brazil]. (n= 100 teeth on file). 100×.

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.1-18.1986 (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

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

Species:	<i>pseudosphex</i>	<i>sphex</i>	<i>nitida</i>	<i>insectivora</i>	<i>velutina</i>
Total length	\bar{x} 32.8	32.2	29.2	36.9	32.2
	Range 31.9-34.6	31.9-32.6	26.4-31.4	36.3-37.4	31.3-32.7
L pronotum	3.8	3.9	3.8	4.8	4.3
	3.5-4.1	3.7-4.3	3.5-4.0	4.7-4.8	4.1-4.3
W pronotum	3.13	3.22	3.33	3.83	3.51
	3.0-3.3	3.1-3.4	3.1-3.5	3.6-4.0	3.4-3.6
L posterior femur	15.9	15.8	16.1	16.7	16.8
	15.8-16.3	15.1-16.4	15.5-16.7	16.6-16.9	16.7-16.9
W posterior femur	1.9	2.0	2.2	2.4	2.6
	1.8-2.2	1.8-2.0	2.0-2.3	2.2-2.4	2.5-2.6
L tegmen	25.0	24.2	22.5	28.6	24.1
	23.6-27.0	23.5-25.1	21.6-24.3	28.3-28.9	24.0-24.1
W tegmen	5.7	5.0	3.5	6.2	4.0
	5.4-6.2	4.7-5.1	3.0-3.9	5.9-6.5	4.0-4.1
Pars stridens	2.3	2.2		2.8	
	2.2-2.5	2.1-2.3		2.6-3.0	
L Ovipositor			8.7		9.4
			8.2-9.1		9.3-9.4

lightly touching the base of his abdomen beneath the tegmina. The tip of the male abdomen continued to reach for the tip of her abdomen for nearly 40 min, during which time a spermatophore was partially formed at the base of the ovipositor. They disengaged when a heavy rain interrupted the pair-formation process. I collected both specimens: the male was *A. pseudosphex*, the female confirmed to be *A. nitida*. An attempt to keep these individuals alive in the laboratory for possible further mating ended 6 days later when the female died. Both specimens are retained in the NMNH collection.

Although a spermatophore was not passed successfully during this episode, it is highly unlikely that they were engaged in interspecific pair formation. Interspecific matings of crickets have been induced in laboratory environments, but no field observations of either crickets or tettigoniids ever have been made of interspecific matings. In those cases where interspecific matings did take place, eggs were not viable. The observation confirms that these two species, at least, are actually the same species displaying a high level of sexual dimorphism.

Aganacris pseudosphex and *A. sphex*.—*Aganacris pseudosphex* mimics species of the wasp *Erimnophila* (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 emarginated), 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 emarginate).

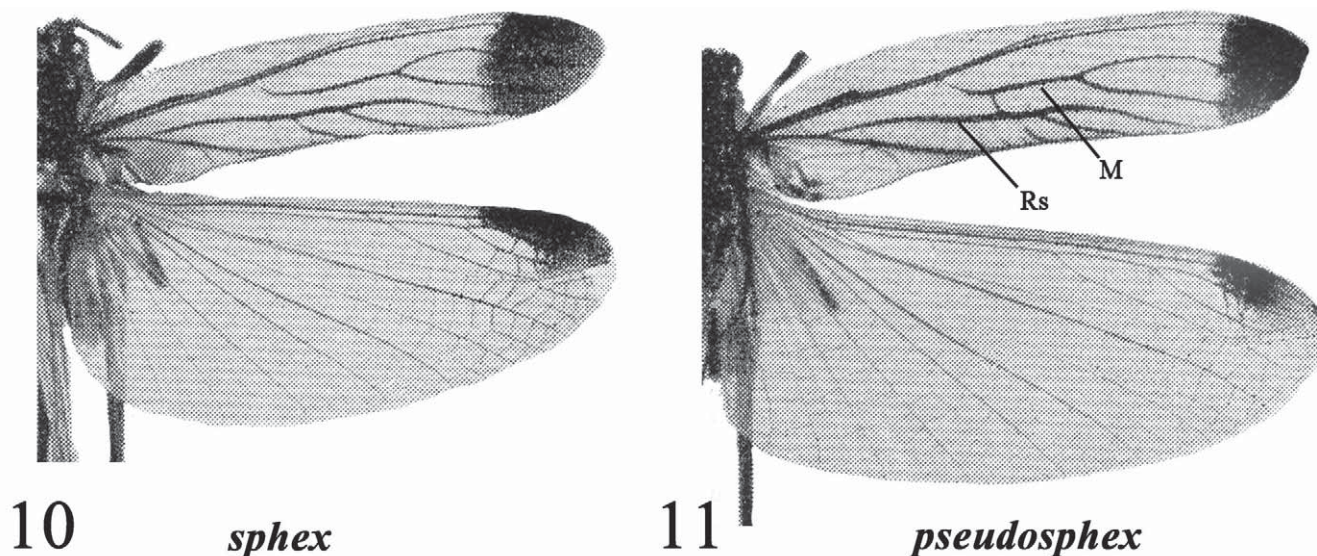
The most significant difference highlighted by Grant (1958) involved coloration and venation of the tegmen: in *A. pseudosphex*

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 sphex 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*.



Figs 10-11. Right tegmen and posterior wing of *Aganacris* species, showing pigmented cross-vein between M and Rs veins in *A. pseudosphex* (same vein present on *A. sphex* but not pigmented). 10. *A. sphex*, 2.0 \times . 11. *A. pseudosphex*, 2.0 \times . (Figures modified from Grant, 1958).

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 two 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, Chiriquí] [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].

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*].

Females of *Aganacris* are definitely larger than males and may require a larger model (*e.g.*, pompilids *vs* sphecids) 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).

Acknowledgments

I thank Theodore C. Cohn, University of Michigan Museum of Zoology, Ann Arbor, MI, Daniel Otte, Academy of Natural Sciences of Philadelphia, PA, Michael Engel, American Museum of Natural History, New York, NY, and Judith Marshall, The Natural History Museum, London, UK, for facilitating the loan of specimens. Thanks are extended also to Taina Litwak, SEL, Washington, DC, for photographing the specimens, and to Scott Whitaker, Scanning Electron Microscopy Laboratory, U.S. National Museum of Natural History, Washington, DC, for providing assistance with the SEM procedures. Thanks are also expressed to Piotr Naskrecki, Conservation International, Harvard University, Cambridge, MA, and Annette Aiello, Smithsonian Tropical Research Institute, Balboa, Ancon, Republic of Panama, for providing assistance on tropical collections. Finally, I am grateful to the following individuals for helpful comments made in their reviews of the manuscript: Gary Miller, SEL, Beltsville, MD, Matt Buffington, SEL, Washington, DC, and James L. Castner, Pittsburg State University, Pittsburg, KS.

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