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Original Article

Variation in some characters of the genus *Sceliphron* (Hymenoptera: Sphecidae) in the Philippines

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ABSTRACT

The observed morphological and color variations for *Sceliphron* species in the Philippines are hereby reported. *Sceliphron madraspatanum conspicillatum* and *Sceliphron rufopictum laticinctum* have several variations in propodeal maculation pattern and in pronotal collar and petiole of the former. Postmortem color changes were also observed in *S. r. laticinctum*. A single yellow band on the third tergite of *S. r. laticinctum* is distinct when it is alive, and an additional yellow band develops on the posterior part of abdominal tergites 2-5 after death. Mandibles may either be sharp or blunt, and clypeus may be lobed or flat for *S. r. laticinctum* and *Sceliphron javanum aemulum*. However, newly emerged adults of these species have sharper mandibles and lobed clypeus. DNA barcoding was used to address intraspecific color and morphological variation of the Philippine Sceliphrini, but not all specimens were successfully barcoded because most of the specimens were very old and contaminated by fungi. However, this study came up with a new primer that has successfully barcoded 3% of the specimens.

Introduction

Variation, whether genetic or nongenetic, is regarded as an important material for microevolution (Futuyma 2005; McKinnon 2010). Genetic changes can be caused by mutation or as a consequence of an organism's adaptation to its environment. Genes, which are expressed phenotypically, usually readily observed morphologically, are heritable and, therefore, affects the constancy of the allelic frequencies in a population (Futuyma 2005). However, there are many other types of nongenetic variation occurring in animals such as the age, season, sociality, and ecological variation, which taxonomists must be familiar with to avoid using or relying on them as diagnostic characters (Mayr and Ashlock 1991). In the genus *Sceliphron* (Hymenoptera: Sphecidae), structural and color variations were observed, but some of these characters are being used in diagnoses and even in keys to subspecies (van der Vecht and van Breugel 1968).

In this article, the extent of the variability of some characters among members of the *Sceliphron* in the Philippines is discussed. This study also attempted to analyze the intraspecific genetic diversity of *Sceliphron madraspatanum conspicillatum* and resolve whether the yellow patterns reflect different species or groups of populations or merely phenotypic plasticity using molecular analysis.

Material and methods

Specimens of *Sceliphron* deposited in University of the Philippines Los Baños Museum of Natural History (UPLB-MNH) and Philippine National Museum were loaned for examination coupled with nest collections from Mt. Makiling, Los Baños, Laguna, and University of the Philippines Land Grant, Real, Quezon, that allowed observations on characters of mouthparts of newly emerged individuals.

DNA sequencing of *Sceliphron* species and outgroups from the Sceliphrinae, Ammophilinae, and Sphecinae of the Philippines was conducted at the Korea Research Institute of Bioscience and Biotechnology. Mitochondrial cytochrome oxidase subunit I sequences for each species and morphospecies were extracted from five male and five female specimens. Tissues were sampled

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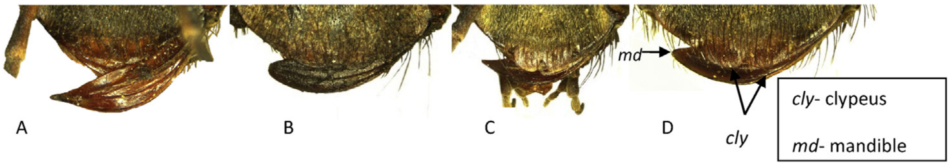

Figure 1. Structural variation in clypeus and mandibles of *Sceliphron javanum aemulum* Kohl: A, mandibular apex sharp, clypeus flat; B, mandibular apex round, clypeus flat; C, mandibular apex sharp, clypeus with emargination; D, mandibular apex round, clypeus with emargination.

from legs of individuals, and DNA were extracted using invertebrate lysis buffer (Ivanova et al 2006) and proteinase K mixture. The barcode region was amplified from most specimens using the new primer MSPCDF1-5′GCTTAYCCWCGAATAAATAA3′ and a standard reverse primer LepR1 (Hajibabaei et al 2006). Polymerase chain reactions (PCRs) were carried out using a Maxime® PCR PreMix (iNtRON Biotechnology, Seongnam, Korea) with 2.0 ρmol of each primer and 2-50 *ng* of template DNA in a 20 μl reaction. PCR thermocycling was done under the following conditions: 2 min at 95°C; five cycles of 40 s at 94°C; 40 s at 45°C, 60 s at 72°C; 40 cycles of 40 s at 94°C; 40 s at 51°C; 60 s at 72°C; 5 min at 72°C; held at 4°C. PCR products were visualized in a 2% agarose gel stained with ethidium bromide and bidirectionally sequenced using a BigDye Terminator ver. 3.1 Cycle Sequencing Kit (Applied Biosystems Inc., Foster, CA, USA) on an ABI 3730XL capillary sequencer. Contigs were assembled using CodonCode Aligner ver 7.0.1 (CodonCode Co., Dedham, MA, USA) and checked for match using Bold Systems (www. boldsystems.org) and GenBank.

Results and discussion

Variation in mouthparts

In general, mouthparts in Sceliphrini, specifically the shape of the clypeus and of the mandibles, are sexually dimorphic. In *Chalybion*, sexual dimorphism is shown in the number of clypeal lobes and in *Sceliphron*, in the shape of clypeus. Mandibles in Sceliphrini are usually sickle-shaped for males but unidentate for most females (Bohart and Menke 1976; Hensen 1987; Hensen 1988; van der Vecht and van Breugel 1968). In most species of Sceliphrini, sex can easily be determined by simply looking at their mouthparts.

Sceliphron javanum aemulum was described to have clypeus as follows: "Anterior margin of the clypeus with a deep, narrow, V-shaped median emargination, separating the broad rounded, depressed lobes" (Rohwer 1922). However, variation in clypeal structure of females was observed among several specimens. Some have their clypeus as described by Rohwer (1922), whereas others appear flat. Some specimens even have the clypeus as a pair of lobes which may be apically continuous with the lateral margin or separated by an angle or incision from the lateral margin. The mandibles of females were also said to be "simple, without tooth on the inner side" (van der Vecht and van Breugel 1968), but the general shape of the mandible observed in this study had mandibular apices that may be pointed or rounded (Figure 1). These were assumed to be polymorphic characters in *S. j. aemulum* based on the museum specimens examined until new nest collections were obtained. Newly emerged individuals of *S. j. aemulum* have pointed mandibles, forming an acute angle of 30°, and clypeus without lateral incisions (Figure 3). It can be assumed that the mandibles become rounded, and the clypeus becomes flattened through time as a wasp repeatedly carries mud sediments for nest construction (Figures 1 and 3). Thus, those caught in flight before or in the earlier period of nest construction had sharper mandibles and more distinct clypeus.

Just like in *S. j. aemulum*, the clypeus of *Sceliphron rufopictum laticinctum* is variable. Lobes may or may not be separated from the lateral margin with incision and individuals with less distinct clypeal lobes tend to have rounder mandibular apices as compared with those with more distinct clypeal lobes, which have sharper or more pointed ones. Newly emerged adults of *S. r. laticinctum* have sharper mandibular tips, forming an acute angle of 20° (Figure 3), and the clypeus has a lateral incision (Figure 2). It is therefore inferred that for these two species, *S. j. aemulum* and *S. r. laticinctum*, mandibles and clypeus become worn out during the process of nest construction.

Among other Sceliphrini, only these two were observed to have variable clypeal and mandibular shapes. Worn mandible edges are common among hymenopteran museum specimens that pupate in hard substrate like wood, and a study revealed that mandibles with zinc and manganese tend to withstand the wear upon escape from the substrate (Quicke et al 1998). It is possible that mandibles of *S. j. aemulum* and *S. r. laticinctum* do not contain zinc and manganese, or perhaps they do but only in insufficient amounts. However, this cannot be concluded until these metals or similar substances are detected.

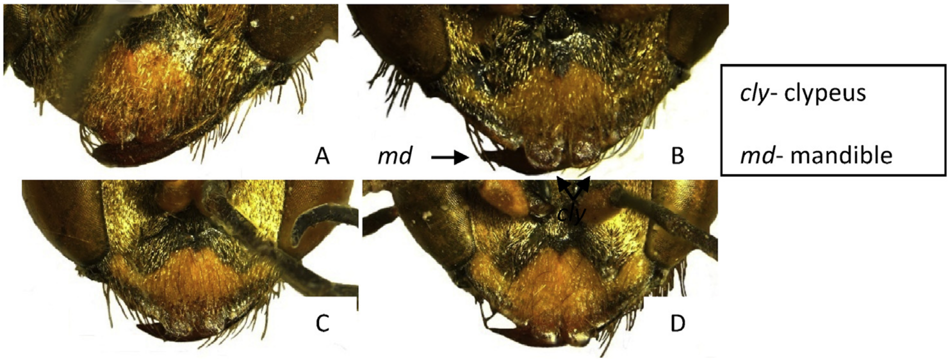

Figure 2. Structural variation in clypeus and mandibles of *Sceliphron rufopictum laticinctum* Hensen: A, mandibular apex rounded, clypeus without lateral incision; B, mandibular apex sharp, clypeus with lateral incision; C, mandibular apex sharp, clypeus without lateral incision; D, mandibular apex sharp, clypeus with lateral incision.

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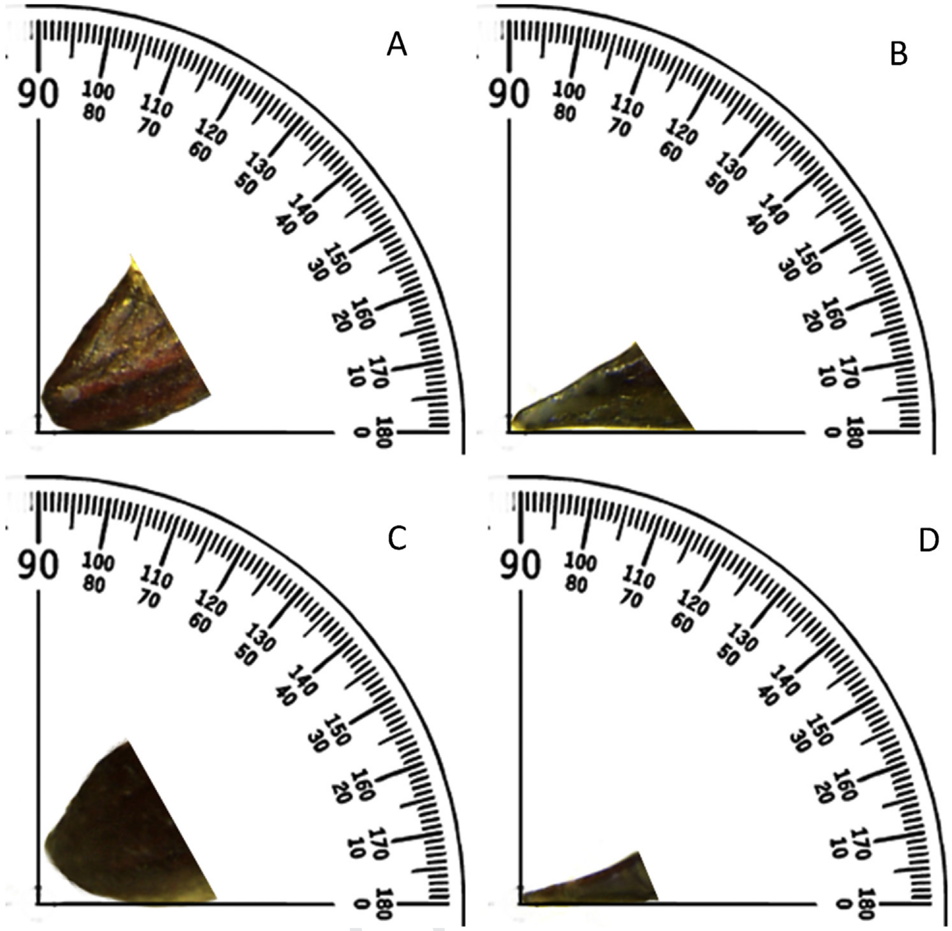

Figure 3. Mandibular apices of A and B *Sceliphron javanum aemulum*: A, rounded tip from inferred older individual; B, sharp mandibular tip from newly emerged wasp; C–D, *Sceliphron rufopictum laticinctum*; C, rounded tip from inferred older individuals; C, sharp mandibular tip from newly emerged wasp. Q1

Variation in maculation

Variation in maculation which does not exhibit geographical patterns among Sphecidae *sensu lato* is quite common. This phenomenon had also been recorded in *Crossocerus walker* (Crabronidae) (Tsuneki 1970) and *Bembecinus bimaculatus* (Crabronidae) (Tsuneki 1971), but the probable cause for this variation has not been explained yet. In this study, variations in maculations were also observed in *S. r. laticinctum* and *S. m. conspicillatum*.

The typical propodeum of *S. r. laticinctum* bears a yellow spot on the anterior and a transverse yellow marking on the posterior part. There are only 52 specimens of *S. r. laticinctum* deposited in the UPLB-MNH, and only a few bear a pair of extra maculation in the middle part of the propodeum located near and inside the propodeal enclosure (Figure 4).

Variation in yellow marking in the propodeum of *S. m. conspicillatum* had been noted by van der Vecht and van Breugel (1968) (Figure 5). However, there is also variation in the maculations on

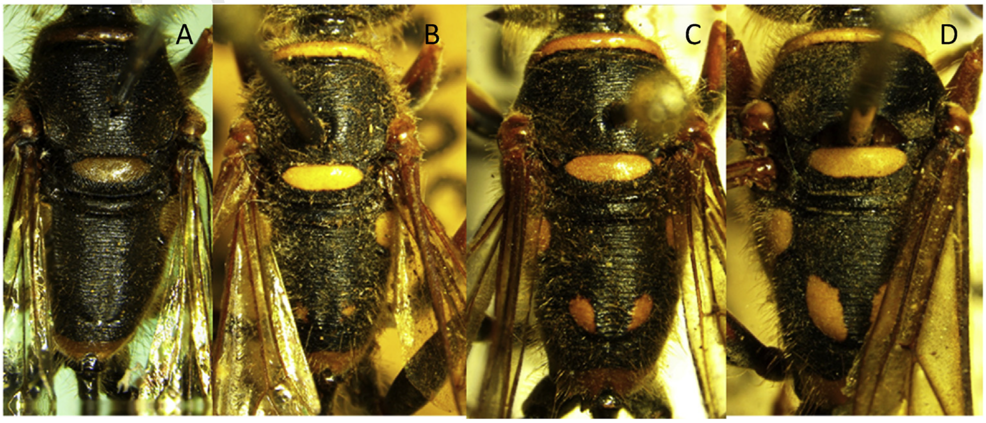

Figure 4. Variation in color in propodeal markings in *Sceliphron rufopictum laticinctum*: A, typical propodeal maculation (B-D) with extra pair of propodeal spots in the middle part of propodeum.

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the pronotal collar and petiole as observed among material examined in this study. Typical individuals of *S. m. conspicillatum* are known to have an entirely black propodeum, whereas the Philippine specimens may have one to three pairs of spots; first pair in the posterior part of the propodeum, second near and inside the propodeal enclosure, and the third anterior pair just below the metanotum outside the propodeal enclosure. It is constant that the spot on the posterior part is present whether there is one or three pairs of spots. On cases where there are one or two pairs of spots, the anterior pair of spots is usually the ones missing or lacking. Nevertheless, some specimens observed have spots only on the anterior and posterior portion. The posterior pair of spots was also observed to merge or contiguous in some specimens (Figure 5) (van der Vecht and van Breugel 1968).

The variation in maculation on the propodeum, pronotal collar, and petiole of *S. m. conspicillatum* had been observed to occur among specimens from Los Baños, Laguna alone. This study attempted to check if there are correlations among maculations and sexes by encoding the number of individuals observed to have a particular pattern in a matrix. A total of 119 specimens from Los Baños, Laguna, of which 61 are females and 58 are males were examined (Table 1). The data revealed that 94% of specimens with three pairs of propodeal spots, regardless if petiole is ventrally lined with black or not (Figure 6) also have a yellow spot on the pronotal collar. Specimens from Palawan were remarked to have their petiole partly or entirely black (van der Vecht and van Breugel 1968), but recent examination revealed that petioles of specimens from mainland Luzon may have a black line ventrally (Figure 7).

Figure 5. Variation in color and pattern of propodeal markings in *Sceliphron madraspatanum conspicillatum*: A, no propodeal spot; B, one pair of propodeal spots; C, 2 pairs of propodeal spots; D–E, 3 pairs of propodeal spots; F, merged posterior propodeal spot (Palawan).

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Table 1. Number of individuals showing various combination of maculations in *Sceliphron madraspatanum conspicillatum*.

Propodeal maculations		Petiole lined with black maculation ventrally		Petiole entirely yellow		Total no. of individuals
		Yellow on pronotal collar (+)	Yellow on pronotal collar (-)	Yellow on pronotal collar (+)	Yellow on pronotal collar (-)	
No mesosomal spot	♂	0	0	3	14	17
	♀	0	0	0	5	5
Subtotal		0	0	3	19	22
1 Pair of mesosomal spot	♂	2	5	2	3	12
	♀	1	4	4	9	18
Subtotal		3	9	6	12	30
2 Pairs mesosomal spot	♂	1	1	3	4	9
	♀	3	1	3	10	17
Subtotal		4	2	6	14	26
3 Pairs mesosomal spot	♂	2	0	10	2	14
	♀	10	0	8	0	18
Subtotal		12	0	18	2	32
2 Pairs mesosomal spot	♂	0	1	3	2	6
(anterior and posterior spot)	♀	0	1	0	2	3
Subtotal		0	2	3	4	9
Total no. of individuals		19	13	36	51	119

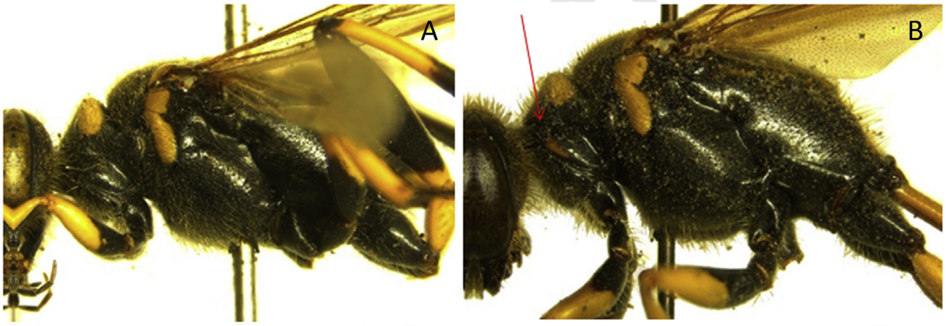

Figure 6. Maculation on the pronotal collar of *Sceliphron madraspatanum conspicillatum*: A, without yellow spot; B, with yellow spot.

As mentioned earlier, maculation patterns in propodeum are well observed in *S. m. conspicillatum* specimens from the Philippines. In Canada and Northern United States, yellow markings in *Sceliphron caementarium* increase in size southward suggesting that differences in pattern was because of climatic conditions (van der Vecht and van Breugel 1968). This thermoregulatory hypothesis, which suggests that increased yellow or lighter color patterns may be produced to reduce absorbance of heat because black or darker colors absorb more radiation (Cech 2011), is apparently not applicable for Philippine species as these spots or patterns occur in both males and females, in the same locality, and for both wet and dry seasons.

In *Bembecinus hungaricus* (Sphecidae) occurring in East Asia, variation in color was also observed, but the variation reflected geographic differences (Tsuneki 1965). In *Bombus* spp. (Apidae), a family closely related to Sphecidae, variations were also observed. Black color occurs in the tropics, whereas the light color patterns were observed on individuals from mid-latitude to temperate

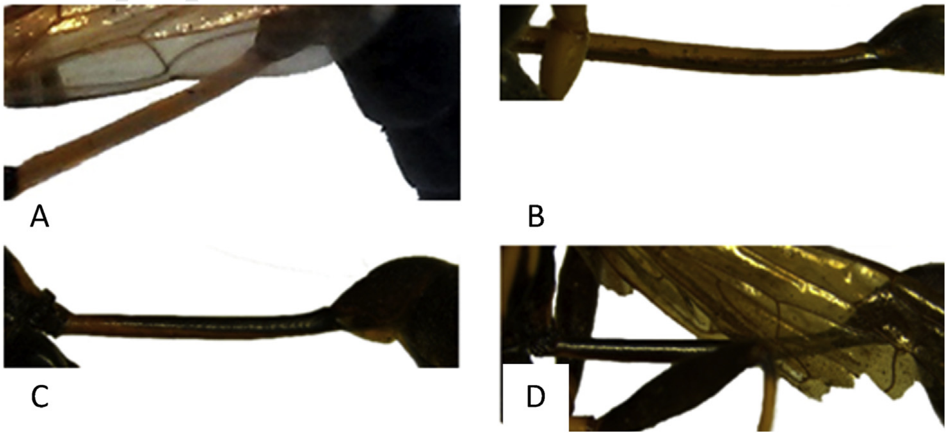

Figure 7. Maculation on the petiole of *Sceliphron madraspatanum conspicillatum*: A, entirely yellow; B, ventral side lined with black; C, posteriorly partly black dorsum (Palawan); D, entirely posteriorly black dorsum (Palawan).

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zones. Just like *Sceliphron, Bombus* species also have intraspecific variation in thoracic and abdominal coloration patterns as well as similar patterns for geographically isolated species. However, thermoregulatory hypothesis does not explain the observed variation as well (Williams 2007). In *Chauliognathus*, yellow-black complexes also exist, and molecular analysis of several species resulted into two clades. Machado et al (2004) proven that in their group, yellow-black complex is an example of Müllerian mimicry. Aside from thermoregulation, color is also important for intraspecific recognition in some groups especially for diurnal insects (Chapman 1998). In one study, *Sphex ingens* (Sphecidae) was observed to identify its mate by visual recognition before mounting (Souza et al 2015). The function of the mesosomal coloration patterns in *S. m. conspicillatum* in the Philippines whether it serve as signals for intraspecific recognition or as aposematic coloration is not yet known. It can be assumed that there could be separating populations, and the mesosomal patterns allow mate recognition, but the evidence is still insufficient to make conclusions because in terms of morphological structure and male genitalia (Figure 8), no distinct differences have been observed yet although possible differences may be behavioral.

Color polymorphism is thought to be a raw material for sympatric speciation as variations within species are needed in microevolution (Murayama et al 2011), which can also be correlated with other traits that can either be morphological or behavioral (Gray and McKinnon 2006; Mckinnon and Pieroti 2010).

Insect pigments are products of metabolic processes and may have evolved as a form of storage excretion. Aside from temperature, factors affecting color include humidity and crowding. Insects being poikilothermic, therefore, may have fluctuations in metabolic processes depending on the climatic conditions (Chapman 1998; Gullan and Cranston 2014). Color change may be thermoregulatory, but short-term color change is unusual in insects (Chapman 1998).

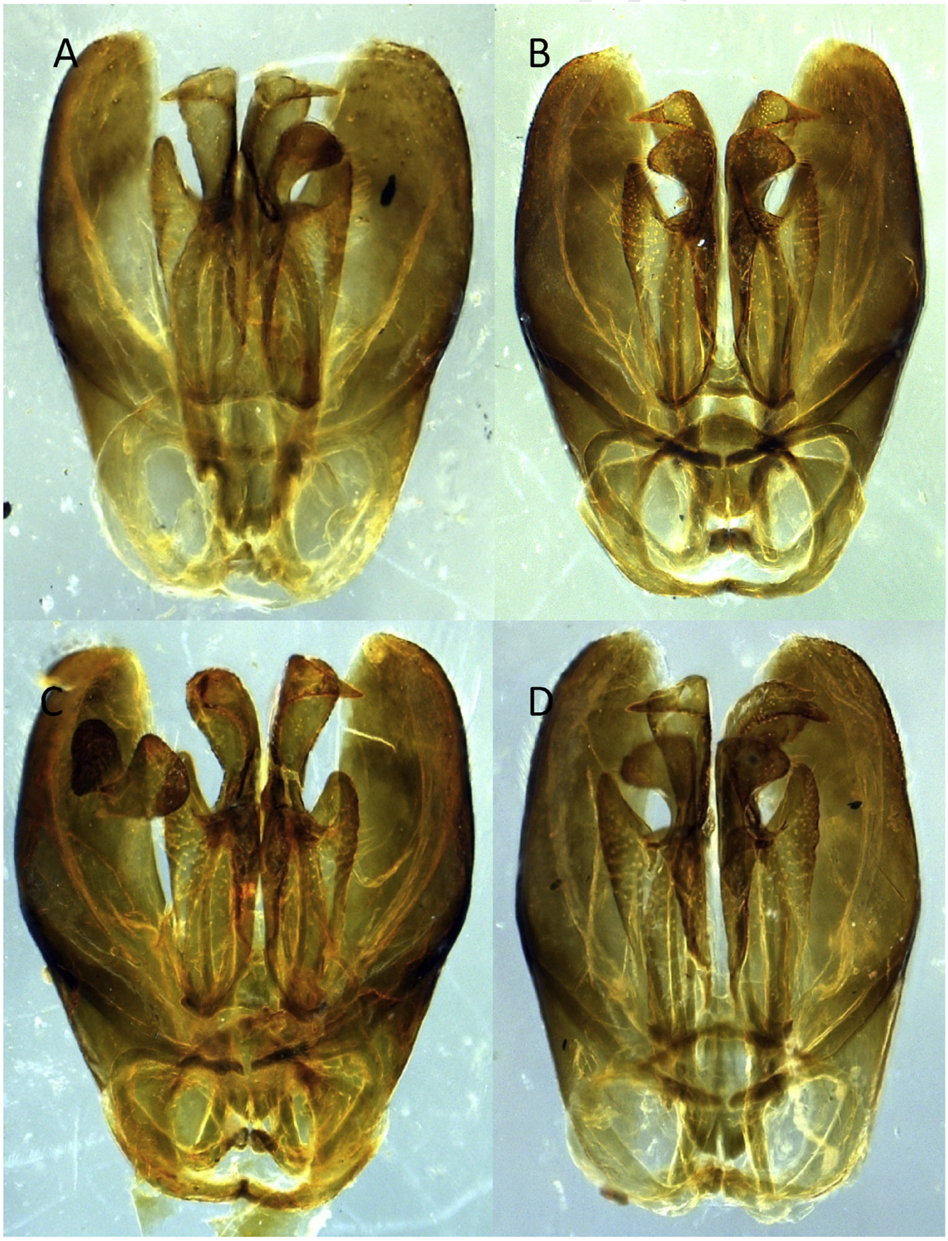

Figure 8. Genitalia of *Sceliphron madraspatanum conspicillatum*: A–B, with one pair of propodeal spots; C, with two pairs of propodeal spots; D, with three pairs of propodeal spots.

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Yellow color in Hymenoptera is produced by granules of pterins in the epidermis. Pterins are nitrogen-containing compounds derived from purines like uric acid (Chapman 1998). Bright color patterns especially those on the dorsal side are frequently associated with sexual signals in male-male and male-female interactions and intraspecific recognition. On the other hand, they may also function as aposematic coloration (Resh and Cardé 2009; Chapman 1998; Holloway et al 2002). The brightness of yellow color in Hymenoptera may fade, but it will never disappear nor change in size (Holloway et al 2002). It was observed, however, that the yellow color on the abdominal tergites of *S. r. laticinctum* becomes more defined after death than during its live adult stage.

In line with the variations described above, this article also attempted to analyze the intraspecific genetic diversity of *S. m. conspicillatum* and resolve whether the yellow patterns reflect different species or groups of populations or merely morphological variation (phenotypic plasticity) using molecular analysis. Bands were observed in gel electrophoresis images using primers LepF1/LepR1, MSPCDF4/LepR1, MSPCDF4/HCO, LSUF2/LSUR1, and ITS 5s/ITS 5.8s. However, amplified PCR products turned out to be all fungal.

Four primer sets were designed based on sequences of Sphecidae available at GenBank and Bold Systems to make the attachment more specific, and three individuals out of 89 samples (3%) were successfully barcoded using one of the new primers, MSPCDF1 (5' GCT TAY CCW CGA ATA AAT AA 3') paired with LepR1. These include *Sphex argentatus*, *Sphex sericeus*, and *Ammophila* sp. (GenBank accession numbers MN961665, MN967081, MN967082). Most of the specimens barcoded were very old (ca 10–66 years), and thus, the DNA contents were most probably already degraded by fungi. High temperature and humidity hastens DNA degradation and growth of fungi which also degrade DNA. The Philippines, being a tropical country, possesses these climatic characteristics. Fresher specimens are being collected for future DNA barcoding of Sceliphrinae.

The samples included *Chalybion* from the Philippines not only to serve as sister group but also to check male-female association especially because sexual dimorphism is common in Hymenoptera (Ayasse et al 2001). Several holotypes such as *Chalybion magnum* and *Chalybion gracile* among others are based mainly on the female as the males are not known. These cases make it difficult to associate respective sexual forms because of the number of sexually dimorphic characters. Differences in clypeus, mandibles, antennae, and abdominal sternites occur among males and females of the same species, whereas the mesosoma which is quite constant in males, and females of the same species may share the same characters with other species. Quantitative characters were used by some authors like Hensen (1988). However, the range of the indices is very variable and overlaps with other species. In some groups, wing morphometry is considered as an effective tool for discriminating species (Tüzün 2009; Oleksa and Tofilski, 2014); however, the wings of Sceliphrini are quite variable. This method did not work with *Bombus* as well (Aytekin et al 2007).

Arrhenotokous parthenogenesis or the production of female drones also occurs in some Hymenoptera (Chapman 1998, but in general, the order is haplodiploid (Grimaldi and Engel 2005). It was observed, however, that in some species particularly *S. j. aemulum* and *S. r. laticinctum*, the males are not common among collections. In fact, there were no males observed in the UPLB-MNH collection, and no new males were collected. The possibility of arrhenotokous parthenogenesis in sphecids is not yet known but based on observations such is possible. Another cause could be because of possible *Wolbachia* infection which is reported to be present in 54% of sphecid wasps (Gerth et al 2011).

It is, therefore, highly recommended that molecular barcoding be conducted for this group to address whether color polymorphism indicates separating populations, associate males and females of sexually dimorphic species, and know the genetic variation intraspecifically, interspecifically, and geographically.

Conclusion

Morphological and color variations for *S. j. aemulum*, *S. r. laticinctum*, and *S. m. conspicillatum* were discussed. *S. r. laticinctum* and *S. m. conspicillatum* exhibit several variations in propodeal maculation pattern as well as in pronotal collar. Additionally, *S. m. conspicillatum* shows variation in maculation in petiole. Postmortem color changes were also observed in *S. r. laticinctum*; a single yellow band on the third tergite is distinct when it is alive. After death, a yellow band develops on the posterior part of abdominal tergites 2-5. Mandibles may either be sharp or blunt, and clypeus may be lobed or flat for *S. r. laticinctum* and *S. j. aemulum*. However, newly emerged adults of these species have sharper mandibles and lobed clypeus. Thus, it is assumed that these parts are worn out in the process of nest construction.

DNA barcoding was used to address intraspecific color and morphological variation of the Sceliphrini, but not all specimens were successfully barcoded because most of the specimens were very old, and amplified products were mostly fungal. However, this study came up with a new primer that has successfully barcoded 3% of the specimens. Fresh specimens are being collected for future studies.

Conflicts of interest

The authors declare that there is no conflict of interest.

Acknowledgments

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